TWS et al.
Exhibit to Comments
December 16, 2020

EXHIBIT 1

Alaska News

Alaska reports a record 18 deaths and 533 new COVID-19 cases Saturday

Author: Anchorage Daily News Updated: 1 day ago Published 2 days ago

Alaska on Saturday reported a record 18 deaths and 533 new coronavirus infections, according to the state Department of Health and Social Services.

The 18 deaths announced Saturday mark the highest number of deaths reported in a single day. Of the deaths announced Saturday, five occurred recently while 13 were identified through reviews of death certificates.

The five recent deaths involved a Kenai woman in her 90s; a Kenai man in his 70s; an Anchorage woman in her 70s; an Anchorage man in his 70s; and an Utqiagvik man in his 60s.

The 13 COVID-19 deaths that occurred in the past months involved an Anchorage woman in her 90s; two Anchorage women in their 80s; an Anchorage man in his 80s; an Anchorage woman in her 70s; an Anchorage man in his 70s; an Anchorage man in his 50s; a man from the Bethel Census Area in his 80s; a man from the Yukon-Koyukuk Census Area in his 80s; a Wasilla woman in her 80s; a man from the Southeast Fairbanks Census Area in his 60s; and a woman from the Kusilvak Census Area in her 20s.

The previous record was 13 deaths reported Nov. 24, followed closely by the 12 deaths reported Dec. 4.

In total, 175 Alaskans and one nonresident with COVID-19 have died since the pandemic began here in March, according to the Department of Health and Social Services. Alaska's overall death rate per capita is one of the lowest in the country, but officials say it's difficult to compare Alaska to other states because of its vast geography and vulnerable health care system.

After weeks of surging daily case counts, Alaska as of Saturday ranked ninth in the country for average daily cases per capita over the past week, according to the Centers for Disease Control and Prevention. Rising case numbers have translated into increasing hospitalizations and deaths.

[First doses of COVID-19 vaccine are expected to arrive in Alaska in the next couple days]

Between the end of November and the first few days of December, COVID-19 cases continued to increase statewide, but the growth rate did slow over the past three weeks, state health officials wrote in a weekly report. They cautioned that new cases have overwhelmed the health department's ability to report them and that recent case counts underestimate the true number of new COVID-19 infections statewide.

Community transmission statewide is still high, both in urban and rural communities, with almost every region in the state seeing a recent increase. The Matanuska-Susitna Borough saw cases more than double between Nov. 20 and Dec. 5 while the Kenai Peninsula Borough had "extremely high rates of transmission" in that timeframe as well, health officials wrote.

In Anchorage, case counts started to plateau this week but remained much higher than health officials would like, Janet Johnston, epidemiologist with the Anchorage Health Department, told reporters during a Friday briefing. Using a modeling tool, Johnston demonstrated that a 10-person gathering in Anchorage has a 37% chance of one person being infected with COVID-19.

"One of the reasons we're so worried about case counts is that each case is a person who may experience both short- and long-term effects of COVID, and a person who may need care from the Anchorage health care system," Johnston said.

COVID-19 hospitalizations at the city's three hospitals have remained high in recent weeks, Johnston said, and as of Thursday there were only five intensive care unit beds available in Anchorage. Even if cases level

Most-Read

1 Alaska's first shipment of COVID-19 vaccine has arrived in Anchorage

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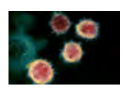
Alaska-News

Tracking COVID-19 in Alaska: 649 new cases reported Sunday, no new deaths



Alaska-News

Coronavirus Q&A: Can I get the vaccine if I've already had COVID-19?

Alaska-News

Alaska's first round of coronavirus vaccinations will occur this week

off, Johnston said she expects to continue seeing more deaths from the virus, given that they can occur weeks after someone initially tests positive.

State health officials continue to ask Alaskans to avoid indoor gatherings with non-household members, and have said that most Alaskans who contract the virus get it from a friend, family member or co-worker.

As infections continue to rise, so does concern from officials about the potential for the state's hospitals becoming overwhelmed as they continue to see major staffing issues.

By Saturday, 127 people with COVID-19 were hospitalized in Alaska and another 10 people in hospitals were suspected to be infected with the virus, according to preliminary data. Seventeen people with COVID-19 were on ventilators. There were 32 ICU beds available statewide out of 133 staffed beds, and about 15.6% of the adult patients hospitalized around the state had tested positive for COVID-19.

Of the 527 new cases reported by the state Saturday among Alaska residents, there were 200 in Anchorage, plus 17 in Eagle River and seven in Chugiak; 56 in Bethel; 54 in Fairbanks and 13 in North Pole; 50 in Wasilla, nine in Palmer and one in Willow; 25 in Kodiak; 11 in Utqiagvik; 10 in Kenai, nine in Homer, seven in Soldotna, three in Sterling and one in Seward; four in Juneau; three in Sitka; two in Nome; two in Kotzebue; two in Unalaska; two in Chevak; two in Hooper Bay; one in Cordova; one in Healy; one in Delta Junction; one in Ketchikan; and one in Craig.

Among communities smaller than 1,000 people not named to protect privacy, there were 13 resident cases in the Kusilvak Census Area; five in the Bethel Census Area; three in the southern Kenai Peninsula Borough; two in the Fairbanks North Star Borough; two in the Matanuska-Susitna Borough; two in the North Slope Borough; two in the Yakutat plus Hoonah-Angoon region; one in the northern Kenai Peninsula Borough; one in the Valdez-Cordova Census Area; and one in the Bristol Bay plus Lake and Peninsula boroughs.

Six cases were reported among nonresidents: one in Anchorage, one in Fairbanks, one in Juneau and three identified as unknown.

The statewide test positivity rate was 6% based on a seven-day rolling average. Rates over 5% can indicate inadequate broad testing, as well as increased community transmission.

While people might get tested more than once, each case reported by the state health department represents only one person.

It is not clear how many of the people who tested positive in Saturday's results were showing symptoms. The CDC estimates about a third of people with coronavirus infections are asymptomatic.

— Morgan Krakow

Help us report on the coronavirus. What do you want to know about COVID-19 in Alaska?

0/500

Your contact info

We'll be in touch if we look into your question.

Name | Email address | Where do you live?

☐ Yes, I want to sign up for the ADN's Morning Newsletter to get the latest updates on local news, politics, and COVID-19 in Alaska.

☐ Please don't publish my name

☐ I am over 16 years old

☐ I accept the Terms of Service

Submit

Novel Coronavirus

TWS et al.
Exhibit to Comments
December 16, 2020

EXHIBIT 2

RELATED TOPICS

Alaska

Coronavirus pandemic

Alaska Native Medical Center exceeds coronavirus capacity

November 26, 2020

BETHEL, Alaska (AP) — The Alaska Native Medical Center, which specializes in health care for Alaska Native and American Indian people in the state, said it is now over capacity with coronavirus patients and had to open an alternate care site to handle overflow.

The hospital's Acting Administrator Dr. Robert Onders said during a virtual town hall on Monday that the critical care unit is so flooded that it cannot hold all the Anchorage hospital's most seriously ill patients.

"So we're extremely tenuous right now," Onders said.

There are now multiple critical patients who require individual nursing and who are lying on their stomachs in a prone position to help them breath, KYUK-AM reported in Bethel Tuesday.

The Yukon-Kuskokwim Delta region in southwestern Alaska had the highest coronavirus case rate in the state as of Tuesday with about 273 cases per 100,000 people across the region on Tuesday.

The Yukon-Kuskokwim Health Corporation in Bethel had urged earlier this month for every community in the region to shelter-in-place for a month in response to a spike in virus cases.

The state reported a record-high 13 deaths in a single day on Tuesday, though only five of the deaths were classified as "recent." Alaska reported a record-high number of new confirmed cases on a single day on Nov. 14 with 745.

The number of infections is thought to be far higher because many people have not been tested, and studies suggest people can be infected with the virus without feeling sick.

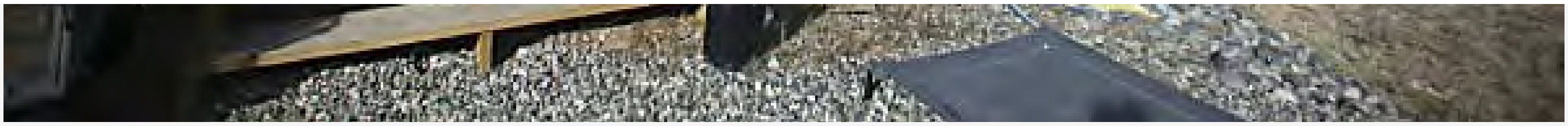
About 20% of coronavirus patients at the ANMC require critical care. Onders said he expects the hospital's situation to worsen.

"Now is the time to act to reduce our case loads and try to prevent us from completely overwhelming the entire health care system," said Dr. Ellen Hodges, chief of staff for the

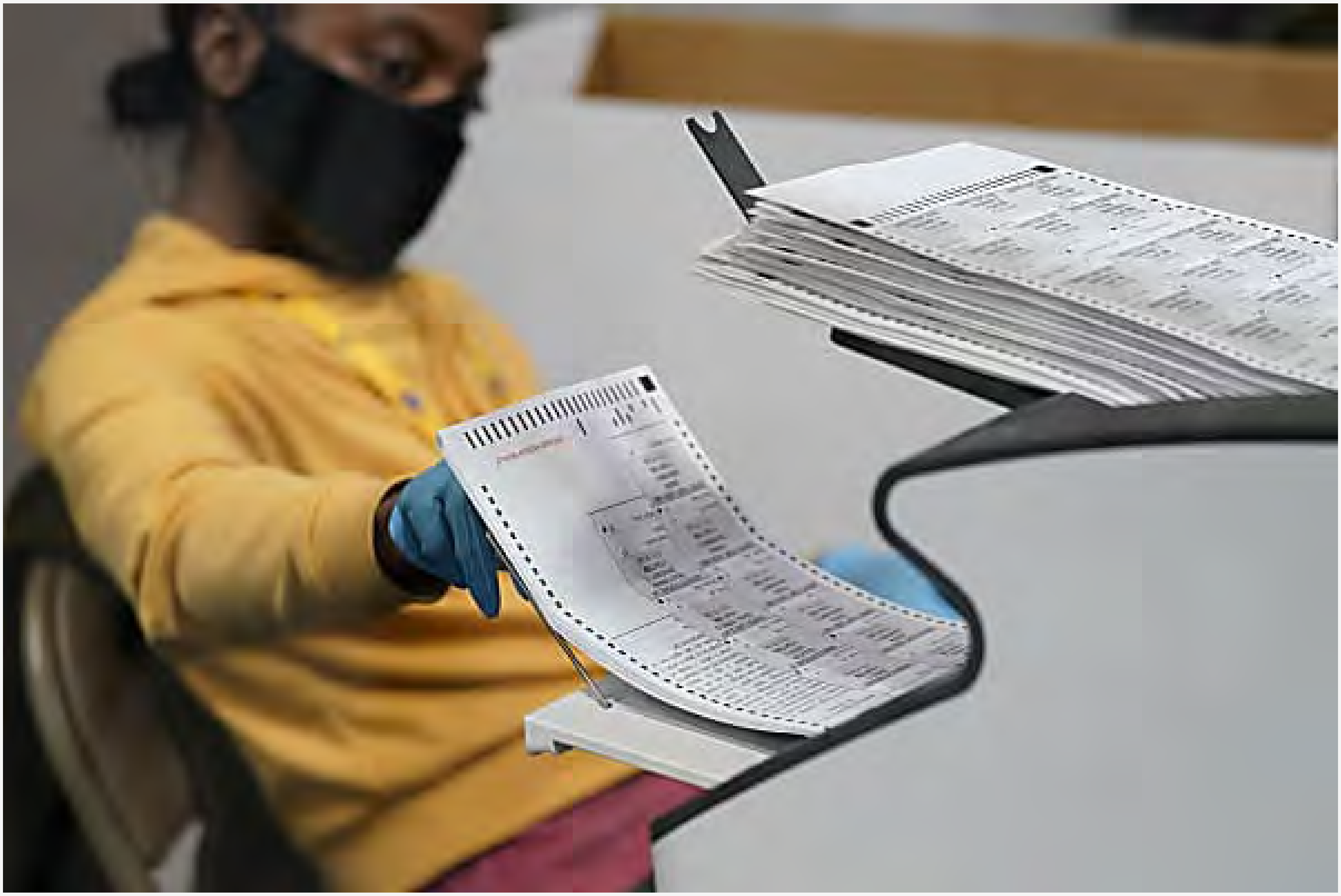
Yukon-Kuskokwim Health Corporation.

For most people, the new coronavirus causes mild or moderate symptoms, such as fever and cough that clear up in two to three weeks. For some — especially older adults and people with existing health problems — it can cause more severe illness, including pneumonia, and death.

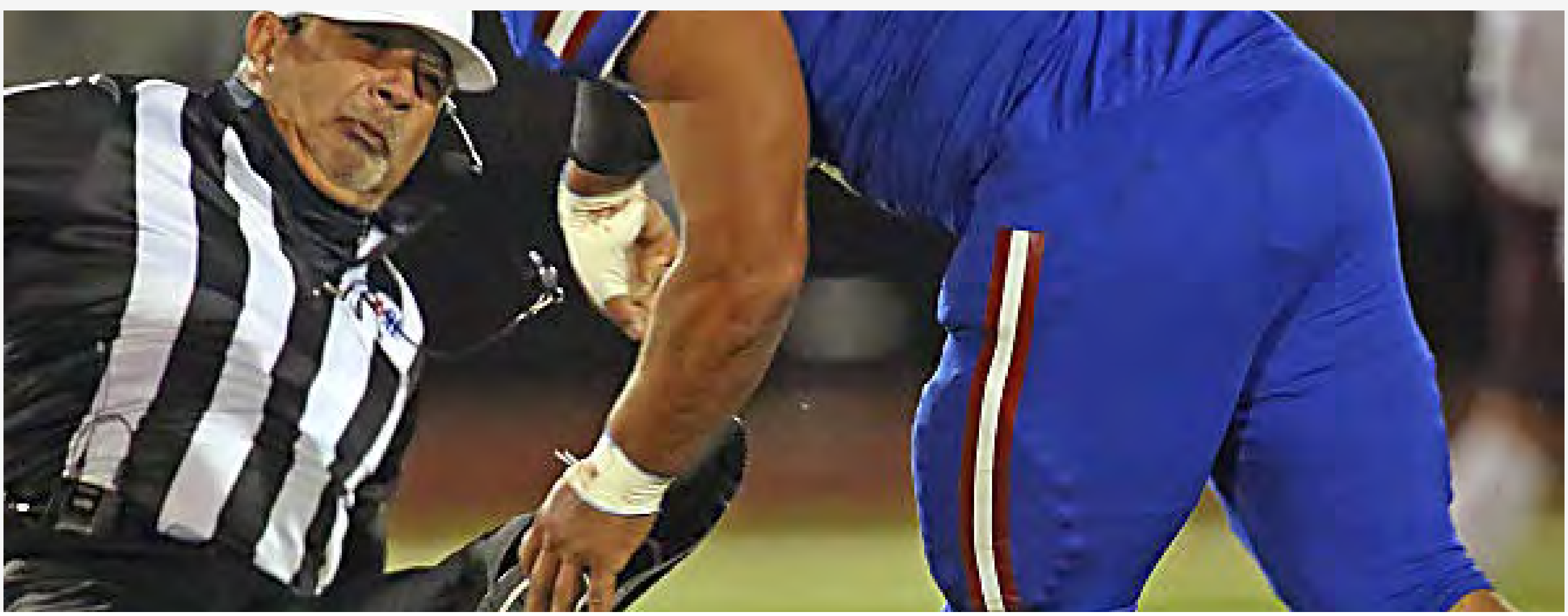
Trending on AP News



Homophobic confrontation ignites strong feelings in Wyoming



Nevada judge mulls bid to nullify Biden win, stop 6 electors



Texas prep football player attacks referee

Homophobic confrontation ignites strong feelings in Wyoming

WAPITI, Wyo. (AP) — When she heard a knock on the door, Colin Monahan figured it had to be ...

December 5, 2020

Nevada judge mulls bid to nullify Biden win, stop 6 electors

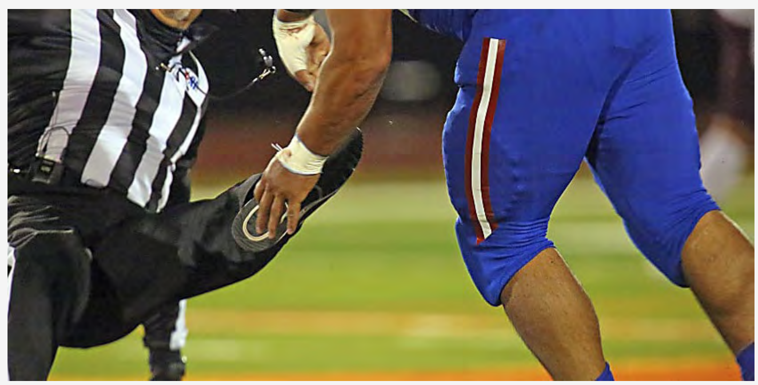
LAS VEGAS (AP) — A state judge heard arguments but made no immediate decision ...

AP December 3, 2020

Texas prep football player attacks referee

EDINBURG, Texas (AP) — A Texas high school football player charged onto the field and bowle...

AP December 4, 2020



Judge calls Trump request in Wisconsin lawsuit 'bizarre'

MADISON, Wis. (AP) — A judge hearing President Donald Trump's federal lawsuit seeki...

AP December 4, 2020

California attorney withdraws from Rittenhouse criminal case

KENOSHA, Wis. (AP) — A California attorney for an Illinois 17-year-old accused of fatally shootin...

AP December 4, 2020

Texas prep player faces assault charge, team out of playoffs

EDINBURG, Texas (AP) — A Texas high school football player who ran onto the field and ...

AP December 4, 2020

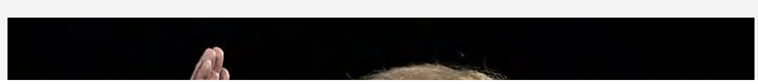
Sheriff: Defiant NYC bar owner struck deputy with his car

NEW YORK (AP) — The co-owner of a New York City bar that authorities said has been defying ...

AP yesterday

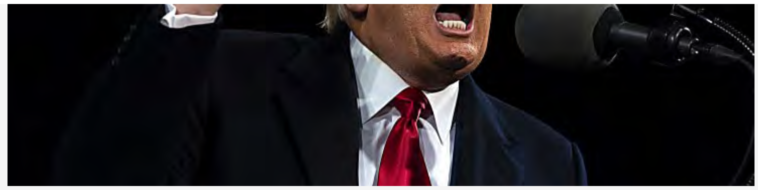
Georgia governor again rejects lawmakers replacing electors

ATLANTA (AP) — Georgia's governor is again



telling lawmakers that he won't call a special ...

33minutes ago



Former state Sen. Sandoval dies of COVID-19 complications

CHICAGO (AP) — Former state Sen. Martin Sandoval, who was facing prison after pleading ...

December 5, 2020

Trump lawyer Rudy Giuliani tests positive for COVID

WASHINGTON (AP) — President Donald Trump said Sunday his personal attorney Rudy Giuliani...

AP yesterday

Trump tactics to overturn election could have staying power

ATLANTA (AP) — Even after he exits the White House, President Donald Trump's efforts to ...

AP yesterday

Netflix rejects calls to add disclaimer to The Crown

LONDON (AP) — Netflix has "no plans" to add a disclaimer to "The Crown" stating that its lavish ...

AP yesterday

Former legislative aide accuses California lawmaker of rape

SANTA ANA, Calif. (AP) — A former legislative aide has filed a criminal complaint against ...

AP December 4, 2020

Nevada GOP to appeal judge's refusal to nullify Biden win

LAS VEGAS (AP) — The Nevada state Republican Party promised Friday to appeal a judge's refusa...

AP December 4, 2020

EXPLAINER: How does AP choose which lawsuits to cover?

The Associated Press has tallied roughly 50 cases ...

brought by the campaign of President Donald ...

AP yesterday

Religious right eyes Biden warily after Trump's good favor

WASHINGTON (AP) — Conservative evangelical Christians have proven some of Donald Trump's...

AP December 5, 2020

House votes to decriminalize marijuana at federal level

WASHINGTON (AP) — The Democratic-controlled House on Friday approved a bill to ...

AP December 4, 2020

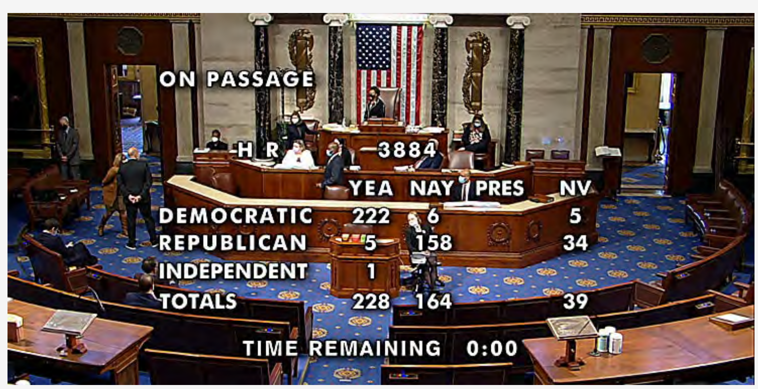


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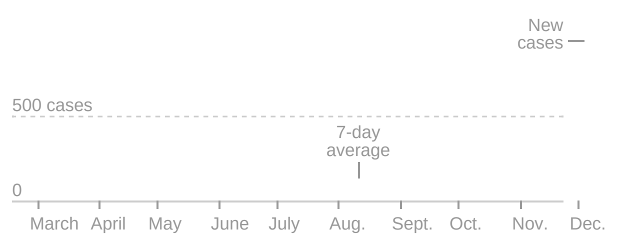
EXHIBIT 3

Alaska Coronavirus Map and Case Count

By The New York Times Updated December 6, 2020, 8:28 P.M. E.T.



	TOTAL REPORTED	ON DEC. 5	14-DAY CHANGE
Cases	36,847	945	+19%
Deaths	136	1	+600%
Hospitalized		166	+16%

Day with data reporting anomaly.
Hospitalization data from the Covid Tracking Project; 14-day change trends use 7-day averages.

Map
By county
New cases
Clusters

At least 1 new coronavirus death and 945 new cases were reported in Alaska on Dec. 5. Over the past week, there has been an average of 686 cases per day, an increase of 19 percent from the average two weeks earlier.

Limited testing and uneven reporting may disrupt the counts in many locations this week. Some states and counties may show artificial spikes in their numbers when data reporting resumes after the holiday.

Hot spots | Total cases | Deaths | Per capita

Average daily cases per 100,000 people in past week

10
30
50
70
100
250
Few or no cases

Sources: State and local health agencies. Population and demographic data from Census Bureau.

About this data

As of Sunday evening, there have been at least 36,800 cases and 136 deaths in Alaska since the beginning of the pandemic, according to a New York Times database.

The table below was recently changed to show the average number of cases per day in the last seven days instead of the total number of cases over the last seven days.

Reported cases and deaths by county

This table is sorted by places with the most cases per 100,000 residents in the last seven days. Charts are colored to reveal when outbreaks emerged.

Cases | Deaths

Search counties

	TOTAL CASES	PER 100,000	DAILY AVG. IN LAST 7 DAYS	▼ PER 100,000	WEEKLY CASES PER CAPITA (FEWER MORE)
Alaska	36,847	5,037	686.3	93.8	March 1 – Dec. 5
Bethel Census Area	1,708	9,290	36.1	196.6	
Matanuska-Susitna Borough	4,909	4,532	209.1	193.1	
Kodiak Island Borough	461	3,547	23.3	179.1	
North Slope Borough	561	5,706	13.1	133.7	
Kenai Peninsula Borough	2,982	5,079	58	98.8	
Southeast Fairbanks Census Area	327	4,744	6.7	97.4	
Anchorage Municipality	18,478	6,416	249.9	86.8	
Kusilvak Census Area	461	5,545	6.4	77.3	
Sitka City and Borough	223	2,626	5.7	67.3	
Fairbanks North Star Borough	3,739	3,861	46.6	48.1	

Show all

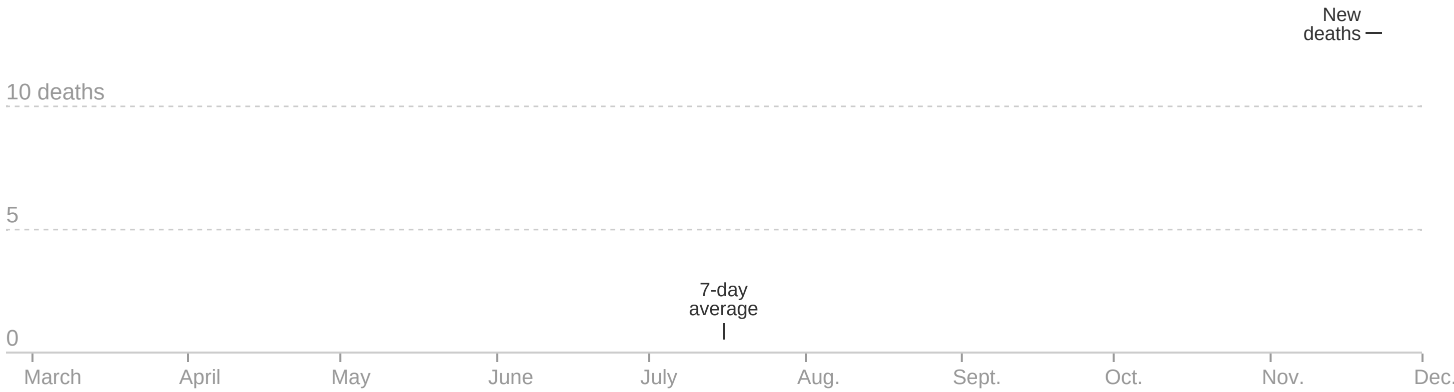
About this data

The New York Times is engaged in a comprehensive effort to track details about every reported case in the United States, collecting information from federal, state and local officials around the clock. The numbers in this article are being updated several times a day based on the latest information our journalists are gathering from around the country.

The New York Times has found that official tallies in the United States and in more than a dozen other countries have undercounted deaths during the coronavirus outbreak because of limited testing availability.

Daily reported new cases

Daily reported deaths

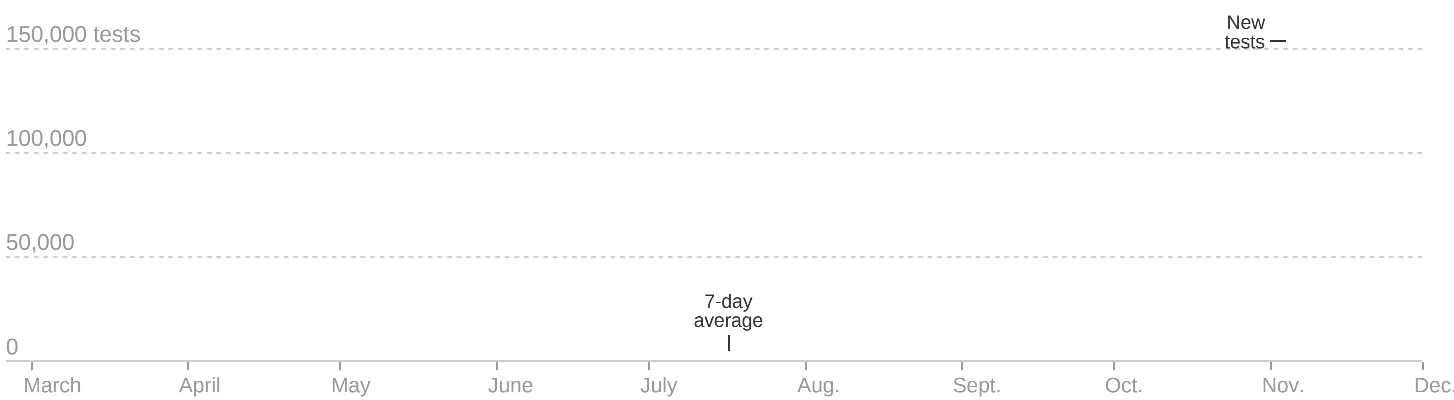


These are days with a data reporting anomaly. Read more here.

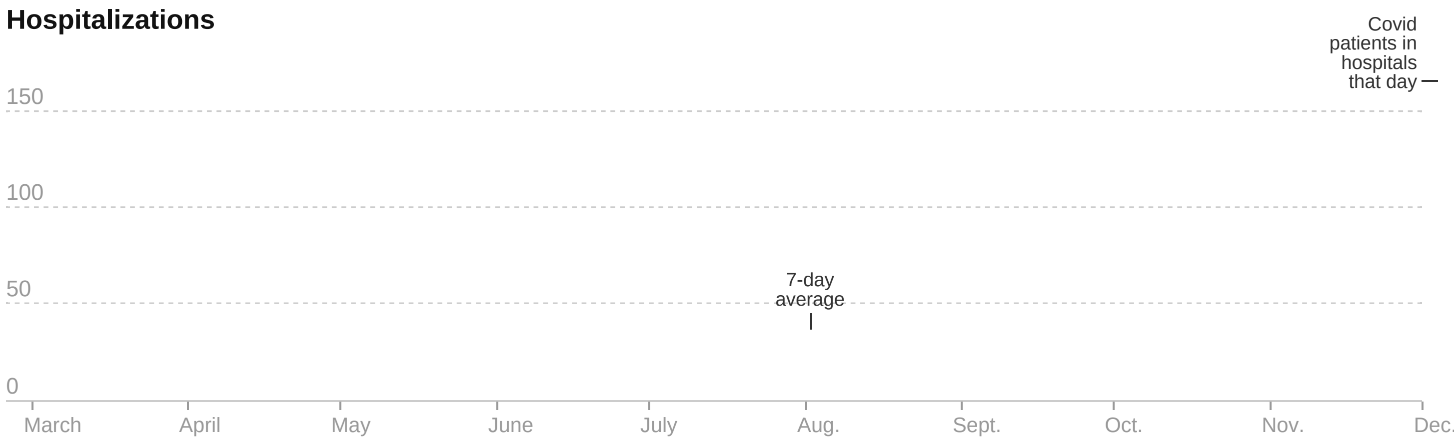
Note: The seven-day average is the average of a day and the previous six days of data.

Daily case and death reports show the severity of the pandemic over time. The picture can be put into further context by considering the number of tests performed and people hospitalized.

Daily reported specimens tested



Hospitalizations



Source: Testing and hospitalization data from the Covid Tracking Project.

About this data

If the previous level of testing was low, and hospitalizations are not increasing, a rise in daily cases could be explained as a result of increased testing. If daily tests have been increased and cases and hospitalizations have fallen or stayed low, that is a sign that the situation is improving or under control. Hospitalizations and deaths usually lag behind new cases, as it takes time for symptoms to develop and worsen.

Because the definitions used for testing and hospitalization data vary between states, it is not always possible to compare that data in one state to the figures reported in another.

We're tracking restrictions in Alaska »

Since March, The Times has paid special attention to cases in nursing homes, food processing plants, correctional facilities and now at colleges and universities. Information on cases linked to these places comes from official releases by governments, companies and institutions directly. The Times is publishing lists of groupings of 50 or more cases related to a specific site, workplace, school or event.

Search clusters

CASES CONNECTED TO	CASES	LOCATION
+ Other	1,013 cases at 7 clusters	
+ Colleges and universities	116 cases at 3 schools	

About the data

In data for Alaska, the Times primarily relies on reports from the state. Alaska typically releases new data each day. Weekend counts may be lower because fewer sources report to the state. The state includes residents by county of residence and separately counts nonresidents in the county of diagnosis. As of June 5, the Times includes cases and deaths from nonresidents that occurred in the state since many are seasonal workers living there for an extended time. Cases and deaths of Alaska residents who died out of state are excluded.

The Times has identified the following reporting anomalies or methodology changes in the data:

- The state reports nonresidents in the location where they were diagnosed. The Times includes these nonresidents, many of whom are seasonal workers temporarily living in Alaska.

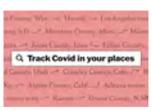
The tallies on this page include cases that have been identified by public health officials as probable coronavirus patients through antigen testing. **Confirmed cases and deaths**, which are widely considered to be an undercount of the true toll, are counts of individuals whose coronavirus infections were confirmed by a molecular laboratory test. **Probable cases and deaths** count individuals who meet criteria for other types of testing, symptoms and exposure, as developed by national and local governments. Governments often revise data or report a single-day large increase in cases or deaths from unspecified days without historical revisions, which can cause an irregular pattern in the daily reported figures. The Times is excluding these anomalies from seven-day averages when possible.

Read more about the methodology and download county-level data for coronavirus cases in the United States from The New York Times on GitHub.

Tracking the Coronavirus

United States

Latest Maps and Data
Cases and deaths for every county



Your Places
Build your own dashboard to track cases

Deaths Above Normal
The true toll of the pandemic in the U.S.

Cities and Metro Areas
Where it is getting better and worse

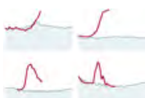
Restrictions
What is open and closed in each state

Nursing Homes
The hardest-hit states and facilities

Colleges and Universities
Cases at more than 1,700 schools

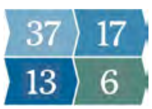
World

Latest Maps and Data
Cases and deaths for every country

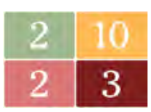


Deaths Above Normal
The true toll of coronavirus around the world

Health



Vaccines
Track their development



Treatments
Rated by effectiveness and safety

Countries

Brazil

Canada

France

Germany

India

Italy

Mexico

Spain

U.K.

United States

States, Territories and Cities

Alabama
Alaska
Arizona
Arkansas
California
Colorado
Connecticut
Delaware
Florida
Georgia
Hawaii
Idaho
Illinois
Indiana
Iowa
Kansas
Kentucky
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New Hampshire
New Jersey
New Mexico
New York
New York City
North Carolina
North Dakota
Ohio
Oklahoma
Oregon
Pennsylvania
Puerto Rico
Rhode Island
South Carolina
South Dakota

Data

What you can do

Experts' understanding of how the Covid-19 works is growing. It seems that there are four factors that most likely play a role: how close you get to an infected person; how long you are near that person; whether that person expels viral droplets on or near you; and how much you touch your face afterwards. Here is a guide to the symptoms of Covid-19.

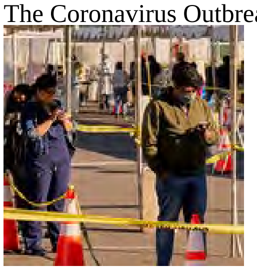
You can help reduce your risk and do your part to protect others by following some basic steps:

- Keep your distance from others. Stay at least six feet away from people outside your household as much as possible.
- Wear a mask outside your home. A mask protects others from your germs, and it protects you from infection as well. The more people who wear masks, the more we all stay safer.
- Wash your hands often. Anytime you come in contact with a surface outside your home, scrub with soap for at least 20 seconds, rinse and then dry your hands with a clean towel.
- Avoid touching your face. The virus can spread when our hands come into contact with the virus, and we touch our nose, mouth or eyes. Try to keep your hands away from your face unless you have just recently washed them.

Here's a complete guide on how you can prepare for the coronavirus outbreak.

By Sarah Almukhtar, Aliza Aufrichtig, Anne Barnard, Matthew Bloch, Weiyi Cai, Julia Calderone, Keith Collins, Matthew Conlen, Lindsey Cook, Gabriel Gianordoli, Amy Harmon, Rich Harris, Adeel Hassan, Jon Huang, Danya Issawi, Danielle Ivory, K.K. Rebecca Lai, Alex Lemonides, Allison McCann, Richard A. Oppel Jr., Jugal K. Patel, Kirk Semple, Julie Walton Shaver, Anjali Singhvi, Charlie Smart, Mitch Smith, Albert Sun, Derek Watkins, Timothy Williams, Jin Wu and Karen Yourish. · Reporting was contributed by Jordan Allen, Jeff Arnold, Ian Austen, Mike Baker, Ellen Barry, Samone Blair, Nicholas Bogel-Burroughs, Aurelien Breeden, Elisha Brown, Emma Bubola, Maddie Burakoff, Alyssa Burr, Christopher Calabrese, Sarah Cahalan, Zak Cassel, Robert Chiarito, Izzy Colón, Matt Craig, Yves De Jesus, Brendon Derr, Brandon Dupré, Melissa Eddy, John Eligon, Timmy Facciola, Bianca Fortis, Matt Furber, Robert Gebeloff, Matthew Goldstein, Grace Gorenflo, Rebecca Griesbach, Benjamin Guggenheim, Barbara Harvey, Lauryn Higgins, Josh Holder, Jake Holland, Jon Huang, Anna Joyce, Ann Hinga Klein, Jacob LaGesse, Alex Lim, Alex Matthews, Patricia Mazzei, Jesse McKinley, Miles McKinley, K.B. Mensah, Sarah Mervosh, Jacob Meschke, Lauren Messman, Andrea Michelson, Jaylynn Moffat-Mowatt, Steven Moity, Paul Moon, Thomas Gibbons-Neff, Anahad O'Connor, Ashlyn O'Hara, Azi Paybarah, Elian Peltier, Sean Plambeck, Laney Pope, Elisabetta Povoledo, Cierra S. Queen, Savannah Redl, Scott Reinhard, Thomas Rivas, Frances Robles, Natasha Rodriguez, Jess Ruderman, Alison Saldanha, Kai Schultz, Alex Schwartz, Emily Schwing, Libby Seline, Sarena Snider, Brandon Thorp, Alex Traub, Maura Turcotte, Tracey Tully, Lisa Waananen Jones, Amy Schoenfeld Walker, Jeremy White, Kristine White, Bonnie G. Wong, Tiffany Wong, Sameer Yasir and John Yoon. · Data acquisition and additional work contributed by Will Houp, Andrew Chavez, Michael Strickland, Tiff Fehr, Miles Watkins, Josh Williams, Shelly Seroussi, Rumsey Taylor, Nina Pavlich, Carmen Cincotti, Ben Smithgall, Andrew Fischer, Rachel Shorey, Blacki Migliozzi, Alastair Coote, Steven Speicher, Hugh Mandeville, Robin Berjon, Thu Trinh, Carolyn Price, James G. Robinson, Phil Wells, Yanxing Yang, Michael Beswetherick, Michael Robles, Nikhil Baradwaj, Ariana Giorgi, Bella Virgilio, Dylan Momplaisir, Avery Dews, Bea Malsky and Ilana Marcus.

The Coronavirus Outbreak



Philip Cheung for The New York Times

Trump Officials Push Ambitious Vaccine Timeline as California Locks Down

2h ago

Scott Schauer

Anti-Vaccine Doctor Has Been Invited to Testify Before Senate Committee

2h ago

Steve White, via Associated Press
After Defying Virus Rules, Bar Manager Drives Car Into Sheriff’s Deputy
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More in U.S. News

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Suzanne DeChillo/The New York Times
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Dec. 5

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Two Retiring Senators, Two Divergent Views on How to Save the Senate
Dec. 5

Bill Sikes/Associated Press
video
Winter Storm Blankets New England
12h ago

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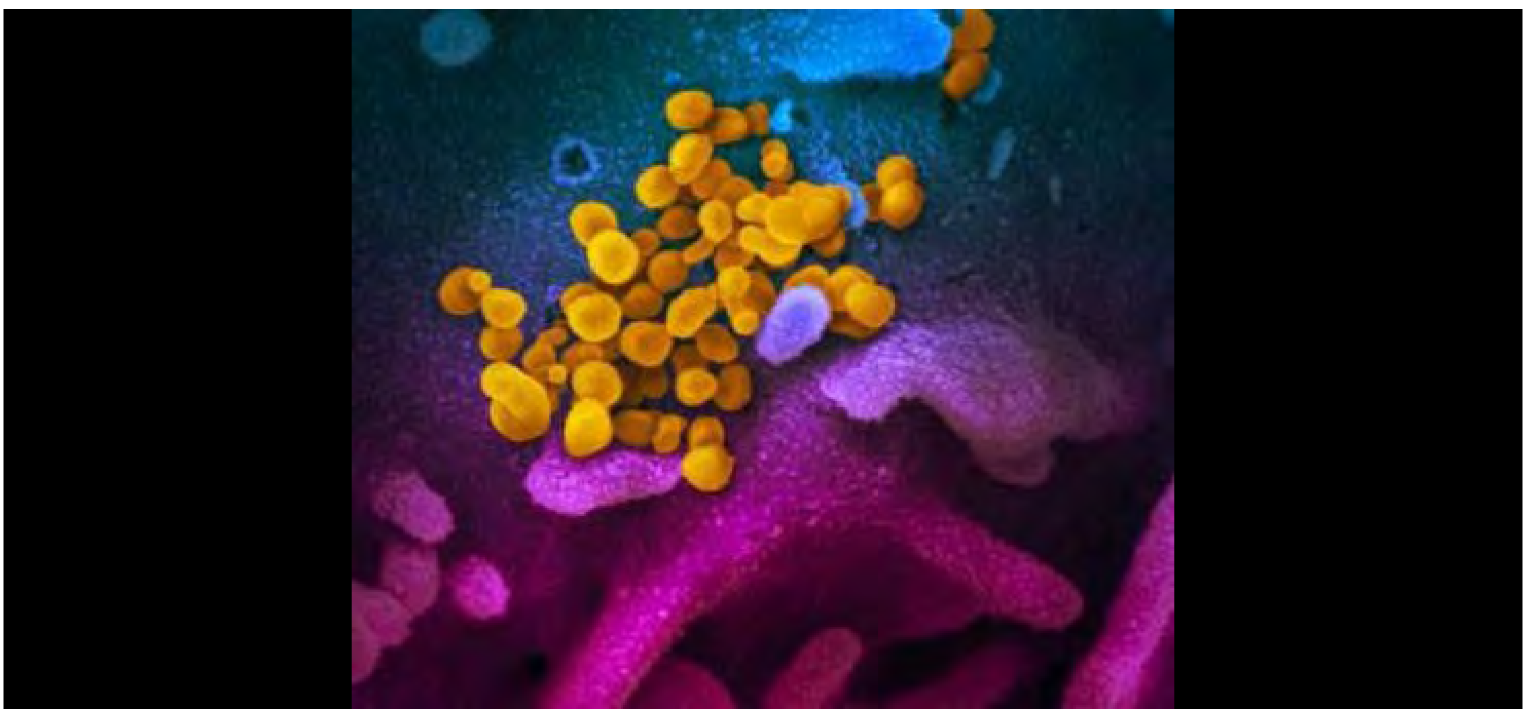
TOP STORY

COVID cases soar in Alaska, Fairbanks borough

Amanda Bohman, abohman@newsminer.com Dec 5, 2020 Updated Dec 5, 2020



This scanning electron microscope image shows SARS-CoV-2 (yellow)—also known as 2019-nCoV, the virus that causes COVID-19—isolated from a patient in the U.S., emerging from the surface of cells (blue/pink) cultured in the lab.
Credit: NIAID-RML

MORE INFORMATION

Fairbanks' top hospital official seeks

mask mandate to slow virus spread

Updated 4:31 p.m.: The state of Alaska reported 933 new COVID-19 cases on Saturday, a big spike from the previous state high of 760.

The uptick extended to the Fairbanks North Star Borough, which logged 143 new cases after a week in which new case rates were trending down. On Monday, the borough logged 14 new cases.

Clint Brooks, co-commander of the Interior COVID-19 response team, attributed the spike to people gathering for Thanksgiving. Brooks is also an administrator at Fairbanks Memorial Hospital.

“We haven’t seen a dramatic spike in in-patient positive patients, but it is impacting our staffing,” Brooks said. “We seem to be a little bit better off than some of the hospitals in Anchorage right now, but that can change fairly quickly.”

Five people, including two COVID-19 patients, were in the Intensive Care Unit at Fairbanks Memorial Hospital on Saturday, according to hospital spokeswoman Kelly Atlee. The ICU has 13 beds, she said.

One new virus death was reported, a woman in her 70s of Anchorage, in Alaska on Saturday, according to the COVID-19 case count summary by the Department of Health and Social Services.

“Our thoughts are with her family and loved ones,” the state report reads.

That brings the number of virus fatalities in the state to 142 with 40% of them reported in the last four weeks, according to state data.

Alaska’s COVID-19 numbers are updated daily to reflect the previous 24-hour period through midnight.

The total number of resident and nonresident cases reported in Alaska is now 36,271, with 3,721 cases in the Fairbanks borough, since the start of the pandemic.

Saturday’s case count report reflected the highest number of new daily cases in the Interior and in the Fairbanks borough since Nov. 20 when 108 and 93 new cases were reported respectively.

New case numbers in the Fairbanks borough had tempered last week with the highest day showing 41 new cases.

Hospitalizations in Alaska have grown to 164 people diagnosed or suspected to have COVID-19 as of Saturday with 24 of them on ventilators.

Atlee said Fairbanks Memorial Hospital had 10 virus patients and 54 non-virus patients on Saturday.

“We have 67 employees out today who are unable to work due to situations related to COVID,” Atlee added.

That includes employees who are sick, tested positive or were exposed to the virus.

Brooks said face masks are working to control the spread of COVID-19 at the hospital. Masks have been required there since March 29 and ever since there have been no reports of someone contracting COVID-19 from exposure at the hospital, he said.

“Even though we’ve had employees test positive, we have still been able to control that because they're wearing a mask,” Brooks said.

“It is kind of surprising the number of people who are asymptomatic but do test positive,” he said. “We know that from our own employees. They are actually shocked that they are positive because they have no symptoms whatsoever.”

Brooks said he is anticipating more spikes in numbers in the coming weeks until after the holidays.

“We knew this was going to be a dangerous time of year,” he said.

Last week, Jeff Cook, president of the foundation that owns Fairbanks Memorial Hospital, called for Gov. Mike Dunleavy to mandate face masks as a way to slow virus spread.

Cook is concerned the health care system is going to be overwhelmed by COVID-19 patients in the coming weeks and months.

Over 1 million COVID-19 tests have been conducted in Alaska, according to the latest case count report.

Contact staff writer Amanda Bohman at 459-7545. Follow her on Twitter: @FDNMborough.

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EXHIBIT 5

From: Ellis-Wouters, Lesli J <lellis@blm.gov>
Sent: Thursday, December 3, 2020 4:21 PM
To: Lois Epstein <lois_epstein@tws.org>; Svejnoha, Wayne <wsvejnoh@blm.gov>
Subject: Re: [EXTERNAL] FW: Question about the Call for Nominations for the Arctic Refuge

It's my understanding that we won't be able make a determination on that until the comment period closes.

Lesli J. Ellis-Wouters
Communications Director
Bureau of Land Management, Alaska
Interior Region 11
(907) 271-4418
cell (907) 331-8763

From: Lois Epstein <lois_epstein@tws.org>
Sent: Thursday, December 3, 2020 4:13 PM
To: Ellis-Wouters, Lesli J <lellis@blm.gov>; Svejnoha, Wayne <wsvejnoh@blm.gov>
Subject: Re: [EXTERNAL] FW: Question about the Call for Nominations for the Arctic Refuge

Hi Lesli. Thanks for this note. I don't think it answers my question, however - I apologize if I was unclear. I'm wondering if bids will be taken on areas smaller than the full tracts? Thanks.

Lois Epstein, P.E.
Engineer & Arctic Program Director
The Wilderness Society
(p) 907.205.4449, (c) 907.748.0448

From: Ellis-Wouters, Lesli J <lellis@blm.gov>
Sent: Thursday, December 3, 2020 4:07:20 PM
To: Lois Epstein <lois_epstein@tws.org>; Svejnoha, Wayne <wsvejnoh@blm.gov>
Subject: Re: [EXTERNAL] FW: Question about the Call for Nominations for the Arctic Refuge

Lois,
Sorry for the delay. Although, the Notice of Sale will publish in the Federal Register on December 7, comments on tract submissions will continue until Dec. 17. BLM may amend or withdraw tracts from leasing prior to the issuance of leases and may announce such changes after the Call for Nominations and comments period closes.

Please feel free to send future questions my way.

Lesli J. Ellis-Wouters
Communications Director
Bureau of Land Management, Alaska
Interior Region 11

(907) 271-4418
cell (907) 331-8763

From: Lois Epstein <lois_epstein@tws.org>
Sent: Thursday, December 3, 2020 11:34 AM
To: Svejnoha, Wayne <wsvejnoh@blm.gov>
Cc: Ellis-Wouters, Lesli J <lellis@blm.gov>
Subject: [EXTERNAL] FW: Question about the Call for Nominations for the Arctic Refuge

This email has been received from outside of DOI - Use caution before clicking on links, opening attachments, or responding.

Hi Wayne. Can you please help? Thank you.

Lois

P.S. Copying Lesli in case you're out and this should be redirected to someone else. Thanks, Lesli.

Lois Epstein, P.E.
Engineer & Arctic Program Director
Anchorage, Alaska
The Wilderness Society | The Wilderness Society Action Fund
ph. 907 205-4449 | cell 907 748-0448

From: Lois Epstein
Sent: Tuesday, December 1, 2020 3:52 PM
To: wsvejnoh@blm.gov
Subject: Question about the Call for Nominations for the Arctic Refuge

Hi Wayne. I hope you are well.

I'm writing with a question about the lease tracts available in the Call for Nominations. Since they are fairly large, will BLM be asking for bids on smaller portions of those tracts when the lease sale is announced? Feel free to call me on my cell if the answer is complicated.

Thanks for your help with this question.

Best,
Lois

Lois Epstein, P.E.
Engineer & Arctic Program Director

Anchorage, Alaska
The Wilderness Society | The Wilderness Society Action Fund
ph. 907 205-4449 | cell 907 748-0448

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EXHIBIT 6

GREENWIRE THE LEADER IN ENERGY AND ENVIRONMENT NEWS

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ARCTIC

Democrats question legality of ANWR lease sale

Heather Richards, E&E News reporter

Published: Monday, December 7, 2020

House Natural Resources Chairman Raúl Grijalva (D-Ariz.) and other top committee lawmakers are pressing the Interior Department on Arctic lease sales. Francis Chung/E&E News

RESIZE TEXT SHARE PRINT

House Natural Resources Democrats say the Trump administration is thumbing its nose at existing regulations so it can conduct the first-ever oil and gas lease sale in the Arctic National Wildlife Refuge before President-elect Joe Biden takes office.

The Trump administration today published official notice of a Jan. 6 oil and gas lease sale in the 1.6-million-acre ANWR coastal plain. Sealed bids are due by Dec. 31 (***Energywire***, Dec. 4).

In a letter today to Interior Secretary David Bernhardt, Chairman Raúl Grijalva (D-Ariz.) and California Democratic Reps. Jared Huffman and Alan Lowenthal argued that the sale schedule "almost certainly violates" regulations.

Huffman leads the Water, Oceans and Wildlife Subcommittee, and Lowenthal chairs the Energy and Mineral Resources panel.

The lawmakers cited Bureau of Land Management requirements for a 30-day notice of sale in the National Petroleum Reserve-Alaska — a large block of federal land that lies west of ANWR where Interior has carried out an oil and gas program for many years.

The oil and gas program in ANWR, mandated by the Republican-led Congress as part of the 2017 tax overhaul, is supposed to mirror regulations for the NPR-A.

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Trump admin to hold first ANWR oil lease

"Tricks like these may allow DOI to issue its desired press release announcing lease sales in the Arctic Refuge before President-Elect Joseph Biden takes over, but it increases the chances that any issued leases will be legally indefensible," the Democrats wrote.

They asked Bernhardt to provide a legal argument for why the sale notice would not be a full 30 days before bids were due.

Alaska BLM spokesperson Lesli Ellis-Wouters pushed back on the allegations of a rushed process.

"This process started in 2017," she said. "We spent more than two years developing the [environmental review], then almost another year on the [record of decision]."

Ellis-Wouters noted that the call for nominations on tracks continues until Dec. 17 and that bids will be accepted between Dec. 21 and Dec. 31. The agency can also withdraw tracts at any time, before or after the sale, up until the leases are issued to bidders, she said.

Experts say the January sale date would give the administration just two weeks to transmit leases to oil and gas bidders before the Biden administration takes office.

Biden has made restoration of ANWR protections a "day one" priority, while the Trump administration has often pointed to ANWR as one of the president's chief triumphs in office.

The announcement of a January sale kicked off a firestorm of criticism from those who oppose oil and gas development in the refuge and follows months of uncertainty as to whether the administration would hold a sale before leaving office.

Bernadette Demientieff, affiliated with the Gwich'in Steering Committee, said in a statement today that the Gwich'in people, who hold the ANWR coastal plain sacred, will continue to fight the oil and gas sale. The Gwich'in are among several groups that have sued the Trump administration over the oil and gas program.

"The Trump administration continuously disrespects the Indigenous people in this country especially in their push to sell off our lands to fossil fuel companies, but we will not allow them to get away with this rushed, sloppy, and corrupt process," she wrote.

In their letter today, the House Democrats echoed environmentalists' argument that the administration has carried out a "reckless method" for developing the oil and gas program in the refuge.

Twitter: **@hroxaner** | Email: **hrichards@eenews.net**

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December 16, 2020

EXHIBIT 7

The Journal of Wildlife Management 84(3):401–412; 2020; DOI: 10.1002/jwmg.21809

Featured Article

Caribou Use of Habitat Near Energy Development in Arctic Alaska

HEATHER E. JOHNSON,[1] *U.S. Geological Survey, Alaska Science Center, 4210 University Drive, Anchorage, AK 99508, USA*
TREVOR S. GOLDEN,[2] *U.S. Geological Survey, Alaska Science Center, 4210 University Drive, Anchorage, AK 99508, USA*
LAYNE G. ADAMS, *U.S. Geological Survey, Alaska Science Center, 4210 University Drive, Anchorage, AK 99508, USA*
DAVID D. GUSTINE, *Grand Teton National Park, P.O. Box 170, Moose, WY 83012, USA*
ELIZABETH A. LENART, *Alaska Department of Fish and Game, 1300 College Road, Fairbanks, AK 99701, USA*

ABSTRACT Increasing demands for energy have generated interest in expanding oil and gas production on the North Slope of Alaska, USA, raising questions about the resilience of barren-ground caribou (*Rangifer tarandus*) populations to new development. Although the amount of habitat lost directly to energy development in the Arctic will likely be relatively small, there are significant concerns about habitat that may be indirectly affected because of caribou avoidance behaviors. Behavioral responses to energy development for wildlife have been documented, but such responses are often assumed to dissipate over time, despite scant information on the ability of animals to habituate. To understand the long-term effects of energy development on barren-ground caribou, we investigated the behavior of the Central Arctic Herd in northern Alaska, which has been exposed to oil development on its summer range for approximately 40 years. Using recent (2015–2017) location data from global positioning system (GPS)-collared females, we conducted a zone of influence analysis to assess whether caribou reduced their use of habitat near energy development, and if so, the distance the effects attenuated. We conducted this analysis for the calving, post-calving, and mosquito harassment periods when caribou exhibit distinct resource selection patterns, and contrasted our results to past research that investigated the responses of the Central Arctic Herd immediately following the construction of the oil fields. Despite the long-term presence of energy development within the Central Arctic Herd summer range, we found that female caribou exhibited avoidance responses to infrastructure during all time periods, although the effects waned across the summer. Caribou reduced their use of habitat within 5 km of development during the calving period, within 2 km during the post-calving period, and within 1 km during the mosquito harassment period; these areas were predicted to overlap 12%, 15%, and 17% of important calving, post-calving, and mosquito period habitat, respectively. During the calving period, the indirect effects we observed were similar to those observed in past research, whereas during the post-calving and mosquito periods, we detected avoidance responses that had not been previously reported. These findings corroborate a growing body of evidence suggesting that habituation to industrial development in caribou in the Arctic is likely to be weak or absent, and emphasizes the value of minimizing the footprint of infrastructure within important seasonal habitat to reduce behavioral effects to barren-ground caribou.

KEY WORDS barren-ground caribou, Central Arctic Herd, coastal plain, energy infrastructure, human disturbance, *Rangifer tarandus*, resource selection, zone of influence.

As the global demand for energy increases, infrastructure and activities related to oil and gas production are expanding (International Energy Agency 2015), with subsequent effects on some wildlife populations (Northrup and Wittemyer 2013). The composition of energy development infrastructure is variable in different locations but often includes the construction of roads, wells, well pads, pipelines, and various support facilities, and associated activities (i.e., drilling, vehicle traffic). Although new infrastructure causes habitat loss and fragmentation, the area directly affected is often small relative to habitat that can be indirectly affected because of animal avoidance of development and related activities. Indeed, animals exhibit a variety of behaviors in response to development including large-scale displacement (Sawyer et al. 2006), altered patterns of movement (Dyer et al. 2002, Sawyer et al. 2013), and changes in habitat use

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and selection (Holloran et al. 2010, Beckmann et al. 2012, Northrup et al. 2015).

Although there is a growing body of literature on the behavioral responses of wildlife to energy development, little is known about how such behaviors may change over time. Often, there is an assumption that animals display the strongest response to development right after construction, gradually minimizing their reaction over time with subsequent exposure (Sawyer et al. 2017). Although such patterns of habituation have been observed for some species and development types (Thompson and Henderson 1998, Madsen and Boertmann 2008), investigators have also reported that habituation responses can be species-specific, weak, or even absent (Conomy et al. 1998, Côté et al. 2013). For example, Sawyer et al. (2017) reported that mule deer (*Odocoileus hemionus*) avoided energy infrastructure even after 17 years of exposure, exhibiting a stronger response to development at the end of the study period than they did during the initial construction phase. With energy infrastructure and activities continuing to expand into undeveloped landscapes, it is becoming increasingly important to quantify their effects on wildlife populations, and how such effects may vary across time.

As energy production increases in the United States, there is great interest in expanding oil and gas development on the North Slope of Alaska (Meier et al. 2014), raising significant concerns about the potential effects on barren-ground caribou (*Rangifer tarandus*). Caribou have high ecological, recreational, and economic value, and are a particularly important subsistence resource for Alaskans (Fall 2016). On the North Slope, caribou use coastal areas in the summer for calving, foraging, and as refuge from insects (White et al. 1975, Griffith et al. 2002, Wilson et al. 2012), the same areas targeted by industry for energy production (National Academy of Sciences 2003). Although caribou populations widely fluctuate in size, recent declines in 3 of 4 Alaska Arctic herds (Central Arctic, Teshekpuk, and Western Arctic herds have declined; Porcupine Herd has increased) have heightened interest in factors influencing their trends, and renewed questions about the resilience of caribou to expanding human disturbance. Currently, substantial development exists only within the summer range of the Central Arctic Herd (CAH), but new projects are currently being initiated and proposed within the summer ranges of the adjacent Teshekpuk and Porcupine caribou herds (Bureau of Land Management 2018*a*, *b*). Although habitat lost directly to energy infrastructure has been, and will likely continue to be, relatively small, wildlife managers and conservation practitioners are concerned about indirect habitat loss, displacement of caribou from important areas (e.g., calving grounds), the reduced ability of caribou to move between foraging areas and insect-relief habitat, and ultimately, their cumulative effects on caribou populations (Nellemann and Cameron 1998, Griffith et al. 2002, Cameron et al. 2005).

Within the CAH summer range, the above-ground footprint of oil development rapidly expanded in the 1970s and 1980s, with only modest increases during more recent years as a result of advances in directional drilling. Data collected in the late 1970s to early 1990s indicated that densities of calving caribou declined near infrastructure and as a function of road density, calving grounds shifted away from infrastructure, and movements between foraging and insect-relief areas were inhibited by roads and pipelines (Smith and Cameron 1985; Dau and Cameron 1986; Cameron et al. 1992, 2005; Nellemann and Cameron 1998). Subsequent studies concluded, however, that caribou used elevated roads and well pads for insect relief (Pollard et al. 1996), and that summer caribou distributions were not strongly affected by energy infrastructure (Cronin et al. 1998, Noel et al. 2004). These conflicting reports have generated uncertainty about the long-term effects of energy development on caribou behavior and the ability of caribou to habituate to infrastructure in the Arctic, key issues for federal agencies analyzing the potential effects of new development projects (Bureau of Land Management 2018*a*, *b*).

To understand the long-term behavioral responses of barren-ground caribou to energy development, we examined summer habitat use patterns of caribou in the CAH relative to energy infrastructure after approximately 40 years of exposure. Our specific research objective was to determine whether caribou reduce their use of habitat near energy development, and if so, by what distance. Earlier studies of CAH behavior were largely based on aerial or road surveys, limiting the frequency (for aerial surveys) and spatial distribution (for road surveys) of data collection, and potentially inducing bias (Joly et al. 2006). To address these shortcomings, we conducted a zone of influence (ZOI) analysis (White and Gregovich 2017, Plante et al. 2018) using recent (2015–2017), fine-scale location data from global positioning system (GPS)-collared animals. Our analysis provides a contemporary snapshot of caribou responses to development and enabled us to evaluate those responses relative to past CAH research.

STUDY AREA

The CAH early summer range occurs on the Arctic coastal plain, on the North Slope of Alaska (Fig. 1; 15,973 km^2). The plain gradually rises from sea level along the coast to approximately 250 m at the edge of the foothills of the Brooks Range. The coastal plain is largely covered by thaw lakes and wetlands interspersed with ice-wedge polygons. The primary vegetation communities are wet and moist graminoid tundra, dominated by water sedge (*Carex aquatilis*) and cottongrass (*Eriophorum* ssp.) with mosses and dwarf shrubs typically on hummocks. Summers are generally characterized as short, cool and moist, whereas winters are long, cold and dry, with annual precipitation averaging approximately 103 mm (http://climate.gi.alaska.edu/Climate/Normals, accessed 25 Oct 2019). Between 2010 and 2017, the average temperature in July (the warmest month) was 9.1°C and in February (the coolest month) was −24.2°C (Deadhorse weather station; http://climate.gi.alaska.edu/acis_data, accessed 25 Oct 2019). The area is generally snow-free from June through September. Caribou are the dominant large herbivore on the coastal plain, although moose (*Alces alces*) and muskox (*Ovibos moschatus*) also occur in low densities. The primary predators of caribou are brown bears (*Ursus arctos*), wolves (*Canis lupus*), and golden eagles (*Aquila chrysaetos*). Lands used by

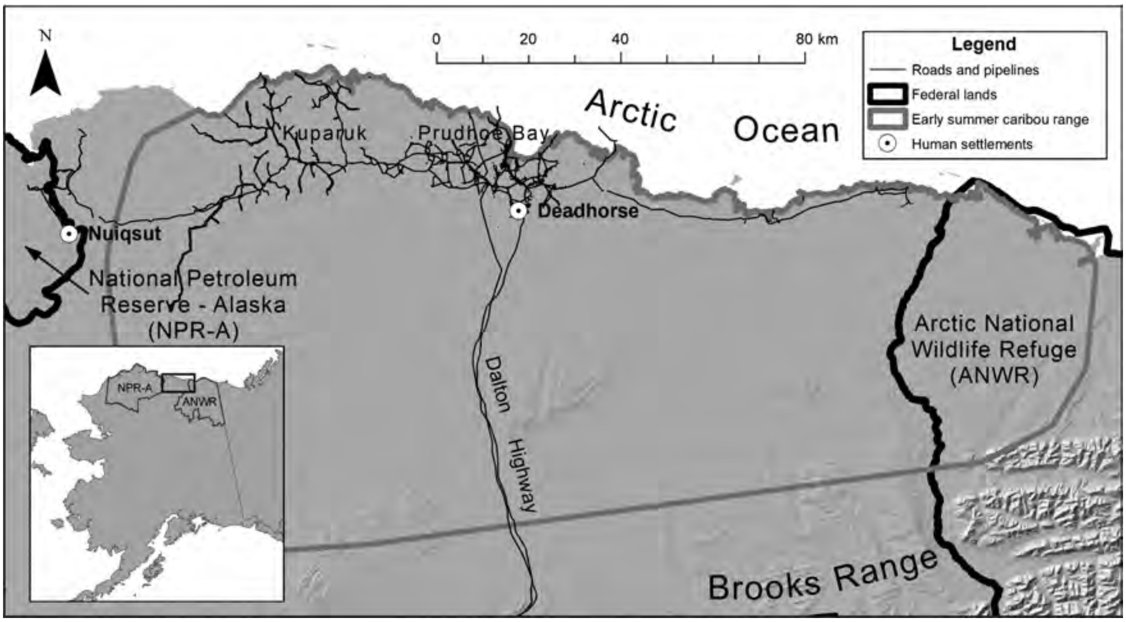

Figure 1. Central Arctic Caribou Herd early summer (1 Jun–15 Jul) range in northern Alaska, USA, based on a 100% minimum convex polygon of caribou collar locations, 2015–2017. Outside the federal land parcels, land is owned and managed by the State of Alaska.

CAH during early summer are primarily owned and managed by the State of Alaska and the United States Fish and Wildlife Service Arctic National Wildlife Refuge (Fig. 1).

In May, female caribou in the CAH typically migrate north from the Brooks Range to their calving grounds on the Arctic coastal plain. After calving in early June, they continue to move north towards the coast during the midsummer period of mosquito (Family Culicidae) harassment, and then shift south towards the foothills of the Brooks Range later in the summer (White et al. 1975, Arthur and Del Vecchio 2009, Nicholson et al. 2016). In mid-September, caribou in the CAH migrate to winter ranges on the south side of the Brooks Range or remain on the coastal plain (Nicholson et al. 2016). Regular monitoring of caribou abundance in the CAH began in 1978 when the herd was estimated to be 5,000 animals. Abundance gradually increased until it was about 68,000 in 2010, and subsequently declined to about 28,000 in 2017 (Alaska Department of Fish and Game [ADFG] 2017, 2018).

Oil infrastructure within the CAH summer range is concentrated within approximately 25 km of the Arctic Ocean (Fig. 1) and consists of a network of roads, pipelines, well pads, processing stations and support facilities primarily operated by BP and ConocoPhillips. In addition to the oil fields, the CAH summer range is bisected by the Trans-Alaska Pipeline and Dalton highway (Fig. 1).

METHODS

Caribou Data

During 2015–2017, we captured adult female caribou in the CAH (≥2 yr old) via net gun (Barrett et al. 1982) following protocols approved by ADFG's institutional animal care and use committee (protocols 2015-06, 2016-30, and 0019-2017-19). We conducted captures in April in 2015 and 2017, and late June in 2016, and attempted to mark a representative sample of female caribou in the herd. We fit caribou with GPS-satellite collars (Telonics, Mesa, AZ, USA) programmed to collect a location every 2 hours during summer (ADFG managed GPS-collar data).

For our analyses, we opted to use collar locations collected between 1 June and 15 July because this was when caribou in the CAH were commonly located within 20 km of development (Fig. S1, available online in Supporting Information), well within the distance they would be expected to exhibit any responses to development based on past research (Dau and Cameron 1986; Cameron et al. 1992, 2005). Additionally, this time frame encapsulated 3 different periods recognized by management agencies where caribou exhibit distinct behavioral patterns: calving (1–15 Jun), post-calving (16–24 Jun), and mosquito harassment (25 Jun–15 Jul; Person et al. 2007, Wilson et al. 2012). All collared individuals in our analysis appeared to be exposed to energy infrastructure during early summer; the 100% minimum convex polygons (MCP) for each collared female each year (1 Jun–15 Jul) overlapped infrastructure.

We screened all locations to remove gross errors (i.e., outside Alaska) and faulty timestamps, which comprised <0.2% of the data. We excluded data from a collared caribou in 2015 and another in 2017 that left the CAH and joined adjacent herds. In 2016, we collared 16 caribou at the start of the mosquito period; we excluded locations from the first week those animals were collared to reduce any capture-related effects.

Characterizing Caribou Habitat and Energy Development

We assessed caribou responses in the CAH to different habitat variables irrespective of energy development, quantifying their selection for distance to the coast, topography (i.e., elevation, aspect, slope), vegetation, and water. These factors have been associated with caribou resource use in previous studies (Walsh et al. 1992, Parrett 2007, Wilson et al. 2012) and depict general patterns in habitat conditions on the Arctic coastal plain. We characterized use and availability of different habitat covariates within 1-km^2 circular buffers of locations to account for landscape-scale selection, the high movement rates of caribou during summer (Person et al. 2007), and the large extent of the study area (Fig. 1; 15,973 km^2).

Caribou often move towards the coast during periods of intense mosquito harassment because cooler, windier weather along the Arctic Ocean provides insect relief (White et al. 1975). We calculated the Euclidean distance (km) between the coast and the center of each buffer (corresponding to the location; Alaska State Geo-Spatial Data Clearinghouse; http://www.asgdc.state.ak.us/?#2974; 1:63,360 scale, accessed 1 Sep 2017). To characterize topography, we acquired elevation data from the United States Geological Survey (USGS) National Elevation Dataset (http://www.usgs.gov, accessed 23 Aug 2017; 25-m resolution), and derived slope and aspect (aspect was categorical: north, east, south, west, flat). We calculated the average elevation and slope within each buffer, and the dominant aspect class. To quantify spatial variation in the proportion of different vegetation communities, which represent forage opportunities in the vicinity, we used the coarse landcover classification developed by the Alaska Center for Conservation Science (Boggs et al. 2016; 30-m resolution). Within our study area there were 14 different classes; we combined bare ground and sparse vegetation into a single sparse category, and dwarf shrub and dwarf shrub-lichen into a single dwarf shrub category. For vegetation types that comprised ≥4% of the study area (dwarf shrub, herbaceous marsh, herbaceous mesic, herbaceous wet, low shrub, sparse, and tussock tundra; Table S1, available online in Supporting Information), we calculated the proportion of each type within the buffer around each location. Additionally, we used the Alaska Center for Conservation Science landcover classification to delineate pixels (100-m resolution) categorized as water (binary; 1 = water) because lakes are abundant along the coast and not generally used by caribou (Wilson et al. 2012).

To depict the footprint of energy development within the CAH summer range, we compiled digital spatial data from oil companies (BP, ConocoPhillips) and the Alaska government (Alaska State Geospatial Data Clearinghouse) detailing the locations of roads, pipelines, well pads, processing stations, and support facilities. We used the World Imagery base map from ArcMap 10.5 (Esri, Redlands, CA, USA) to manually digitize infrastructure around Point Thomson because digital spatial data were unavailable for that area. We excluded pads that had no recent activity (considered inactive; identified as being overgrown with vegetation and devoid of any equipment) from further consideration. These abandoned pads (10% of all pads) were primarily related to exploratory activities when the oil fields were initially developed in the 1970s and 1980s. Around all active infrastructure (~48.8 km^2, comprising 0.3% of the study area), we created nested concentric 1-km buffers ranging from 1 km to 20 km, to be employed in our ZOI analysis.

Resource Selection Modeling

To conduct our analysis, we first developed and validated resource selection function (RSF) models (Manly et al. 2002, Koper and Manseau 2012) to predict caribou use based solely on ecological covariates not related to energy development. Habitat selection of Arctic caribou during the early summer (1 Jun–15 Jul) is dynamic (Fig. S1), shifting in response to calving, mosquito harassment, and forage conditions (Griffith et al. 2002, Parrett 2007, Wilson et al. 2012). To account for this variation, we modeled caribou selection separately for the calving, post-calving, and mosquito periods. For each period, we quantified population-level patterns of resource selection (second order; individual selection within the population range; Meyer and Thuiller 2006) using a use-availability design (Manly et al. 2002). We delineated available habitat for all periods as the 100% MCP around caribou locations collected from 1 June to 15 July (Fig. 1). We used a consistent area of availability to enable comparisons in resource selection across periods and because caribou are highly mobile and can easily travel within this area during early summer (Arthur and Del Vecchio 2009, Nicholson et al. 2016). We removed areas within the MCP that overlapped with the Arctic Ocean (bounding the north end of the study area). Within the population-level MCP, we randomly selected locations using a 1:10 ratio of those that were used to those considered available (Koper and Manseau 2012). We attributed habitat covariates to all used and available locations.

We developed RSF models (Manly et al. 2002) for each period using covariates representing distance to coast, topography, proportions of different vegetation types, and the presence of water. We used generalized linear mixed models (GLMMs; Bolker et al. 2009) with a logit-link function to accommodate our use-availability design. All models included a random effect for each animal-year data set (Gillies et al. 2006). Although the variance for the random effects in some post-calving and mosquito period models were estimated to be zero (indicating that they did not explain additional variation beyond that estimated by the residual variation), we retained the random effects structure in all models to facilitate model comparisons and reflect our study design. Prior to running models, we tested for multicollinearity among covariates using correlation coefficients ($|r| \leq 0.6$) and variance inflation factors (VIFs; VIFs ≤ 3; Zuur et al. 2010). In all periods, elevation was correlated with slope and the proportion of tussock tundra ($r \geq 0.63$), so we removed elevation from further analyses. The proportion of tussock tundra continued to have a high VIF (>10), so we also removed that variable from further consideration. After these removals, correlation coefficients were ≤0.39 and VIFs were ≤2.24.

For each period, we tested all possible combinations of variables to determine the set of habitat factors that exhibited the best model fit. Our habitat covariates included distance to coast, slope, aspect, the proportion of different vegetation types (models included either all vegetation types or none of them), and whether a pixel was classified as water. Our reference class for aspect (categorical variable) was north. For models with distance to coast or slope, we also tested models with quadratic terms for these variables to allow for nonlinear responses. We scaled continuous variables (all variables except aspect and water) to facilitate model convergence and the interpretation of relative effects (Schielzeth 2010). We used Akaike's Information Criterion (AIC) to score models, and identified the best performing model as having the lowest AIC score and highest model weight (Burnham and Anderson 2002). Because the top model for each period had an AIC value at least 6 units below the second-best model (and ≥95% of the model weight), we did not conduct model averaging. For modeling, we used the lme4 (Bates et al. 2015) and MuMIn (Barton 2016) packages in R version 3.5.2 (R Core Team 2018).

We validated the top model for each period using k-fold cross validation (Boyce et al. 2002), including all locations from each animal-year data set in either the model training or testing set (Koper and Manseau 2012). We used 5 folds and 10 bins, repeating the process 10 times to generate a mean Spearman correlation. For models with high predictive power (mean $r_s \geq 0.70$), we calculated predicted probabilities of caribou resource selection across the study area (scaled between 0 to 1). We then used the contrast validation index (CVI; Hirzel et al. 2006, Fedy et al. 2014) to objectively determine an RSF probability threshold (in increments of 0.05, ranging between 0 and 1) for identifying habitats with high probabilities of use. This approach distinguishes an RSF threshold of the highest predicted probabilities of use that contain the maximum proportion of observed locations, while minimizing the proportion of the landscape that is included. We considered areas identified by the CVI during each period to be particularly important caribou habitat.

Assessing the Influence of Energy Development on Caribou Behavior

We used coefficients from our top habitat selection models to generate spatial predictions of the relative probability of female caribou use during the calving, post-calving, and mosquito periods. For robust habitat models with high predictive power (i.e., mean $r_s \geq 0.70$), these RSF predictions should be strongly correlated with patterns of observed caribou use in the absence of any development effects. Thus, we assessed patterns of observed and expected caribou use to determine whether the presence of development altered this expectation (White and Gregovich 2017, Plante et al. 2018). This approach is considered a quasi-treatment-control experiment given that caribou use in the absence of development can be estimated from patterns of habitat selection. We compared the proportion of observed caribou locations to those that would be expected from predictions of our habitat models within nested, concentric 1-km buffers that ranged from 0 to 20 km from infrastructure. We conducted calculations within 20 km of energy infrastructure because past research found that CAH responses to energy development occurred well within this distance (caribou densities declined within 4 km from development; Cameron et al. 1992, 2005).

For each 1-km buffer for each period, we calculated observed use as the number of used caribou locations within the buffer divided by the total number of used locations across all buffers (for that period). We calculated expected use as the summed relative probability of use (RSF volume) within each buffer divided by the total across all buffers (total RSF volume; period-specific), and then weighted by the animals' starting locations following White and Gregovich (2017). The weighting accounted for caribou exposure to development being dependent upon their general location and movement patterns within the study area (as development was patchily distributed). Within each period, for each animal-year data set, we determined the distance between an animal's starting location (their first location within the period) and all their other GPS locations. We then randomly simulated locations using those same distances from their starting location, but with random azimuths (i.e., radiating in random directions from the starting location), emulating animal-year-specific movement patterns. If a random point was generated outside the study area (i.e., in the Arctic Ocean), we regenerated the point. We calculated the distance to the nearest infrastructure for each random location and pooled those distances across individuals to estimate the proportion of locations within each 1-km buffer (0–20 km from infrastructure). We used the proportion of simulated locations within each buffer to weight the expected use value, such that expected use became a function of both habitat conditions and the likely distribution of caribou within the study area.

We then determined buffer-specific selection ratios (observed/expected use) for each period, where values <1 indicated that observed caribou use was less than expected, and values ≥1 indicated that use was equal or greater than expected. We used a non-parametric bootstrap approach to determine 95% confidence intervals for each selection ratio (Efron and Tibshirani 1993) based on randomly drawing (with replacement) used locations for each period. Bootstrapped selection ratios ($n = 10{,}000$/period) were based on different samples of observed use, given the expected use. We considered the ZOI to be the distance from development where the selection ratios and 95% confidence intervals were consistently <1. This approach is useful for quantifying specific thresholds in animal behavioral responses to habitat conditions, which can be difficult to identify directly from generalized linear models (Ficetola and Denoël 2009, Boulanger et al. 2012), even when disturbance covariates are incorporated (e.g., including a term for distance to disturbance in a GLMM). This approach also yielded results that could be evaluated in the context of earlier investigations of CAH densities within different 1-km distance intervals to development (Cameron et al. 1992, 2005; Cronin et al. 1998; Noel et al. 2004).

RESULTS

Across the 3 years of the study, we fit 56 adult female caribou with GPS-collars, collecting 87 animal-year data sets: 16 in 2015, 27 in 2016, and 44 in 2017. During the calving and post-calving periods, we collected 71 animal-year data sets, and during the mosquito period, we collected 87 (because 2016 captures occurred in late Jun). Between 1 June and 15 July, we obtained 34,041 caribou locations: 11,390 during calving, 6,472 during post-calving, and 16,179 during the mosquito period. Across all periods, collars had a median fix rate of 84%. When fix rates are <90% there is a concern that locations may be missed as a function of specific habitat features (i.e., dense overstory vegetation) and introduce bias in resource selection studies (Frair et al. 2010). We obtained 100% of our programmed fixes (between 1 Jun and 15 Jul) from collars that were recovered from the field, indicating that our missing fixes were a function of errors in the Argos uplink transmission, not due to specific habitat features. Indeed, the Arctic coastal plain is relatively flat, with limited topographic relief, and low-growing tundra vegetation. As a result, we considered missing fixes to be random with respect to habitat attributes.

Resource Selection Modeling

The best performing models for all periods included all habitat variables, with quadratic terms for distance to coast and slope (ΔAIC $\geq$ 6.1 for second-best models; Table 1; see Tables S2–S5, available online in Supporting Information, for coefficients of top models and all modeling results). During the calving period, caribou most strongly selected for areas that were at intermediate distances to the coast (~50 km; Fig. 2A), had low slopes (<5 degrees; Fig. 2B), and had southern and eastern aspects (Fig. 3). Female caribou also strongly selected for areas with higher proportions of herbaceous mesic vegetation, and avoided areas with low shrubs, sparse vegetation, and water (Fig. 3). During the post-calving period, areas selected by caribou shifted towards the coast (with areas ~30 km from the coast having the highest probabilities; Fig. 2A). They similarly selected areas that had low slopes (<5 degrees; Fig. 2B), southern and eastern aspects, and higher proportions of herbaceous mesic vegetation, and avoided water (Fig. 3). Although caribou avoided sparse vegetation (i.e., sand and gravel bars) during the calving period, they selected sparse vegetation during the post-calving period, probably in response to some early mosquito harassment (Fig. 3). During the mosquito period, caribou selected areas directly adjacent to the coast, with minimal slopes (<1 degree; Fig. 2A,B). Although they still selected areas with higher proportions of herbaceous mesic vegetation, their selection for distinct vegetation types generally dampened (Fig. 3). Similar to the post-calving period, caribou selected for areas with sparse vegetation and avoided water. Whereas caribou selected most strongly for southern aspects during the calving and post-calving periods, they selected most strongly for eastern aspects during the mosquito period.

The top model for each summer period (Fig. 4) validated well with mean Spearman's rank correlations $\geq$0.91 (Table 1). The CVI analysis identified threshold RSF values of 0.15 for the calving period and 0.10 for the post-calving and mosquito periods. For each period, these threshold values delineated large portions of the study area (3,859–7,475 km^2) that were required to encompass a majority of the observed caribou locations (68–93%; Table 2; Fig. S2, available online in Supporting Information).

Caribou Behavioral Responses to Energy Development

Based on buffer-specific selection ratios, the ZOI (where the selection ratios and their 95% CIs were consistently <1) was estimated to be 5 km during the calving period, 2 km during the post-calving period, and 1 km during the mosquito period (Table 2; Fig. 5; Table S6, available online in Supporting Information). Selection ratios for the mosquito period were high for distance intervals >12 km (Fig. 5C) where proportions of expected use were very small (<0.01). Based on the CVI analysis (Fig. S2), the ZOI during the calving period overlapped 12% of important calving habitat, the ZOI for the post-calving period overlapped 15% of important post-calving habitat, and the ZOI for the mosquito period overlapped 17% of important mosquito period habitat (Table 2).

Table 1. Model selection criteria for female caribou resource selection during the calving (1–15 Jun), post-calving (16–24 Jun), and mosquito periods (25 Jun–15 Jul) in the Central Arctic Herd, Alaska, USA, 2015–2017. Model covariates included distance to coast (coast), slope, aspect, water, and proportions of different vegetation types (veg; dwarf shrub, herbaceous marsh, herbaceous mesic, herbaceous wet, low shrub and sparse). We present the log-likelihood (LL), Akaike's Information Criterion (AIC), and weight for each model. We provide the top 2 models for each period; no other models had ΔAIC values <10. We also include the mean cross validation correlation (r_s) for each top model.

Model	n	Groups[a]	df	LL	AIC	ΔAIC	Weight	$\bar{x}\ r_s$
Calving								
Coast+coast^2+slope+slope^2+aspect+water+veg	125,290	71	17	−27,880.0	55,794.0	0.0	1.00	0.91
Coast+coast^2+slope+aspect+water+veg	125,290	71	16	−27,951.3	55,934.5	140.5	0.00	
Post-calving								
Coast+coast^2+slope+slope^2+aspect+water+veg	71,192	71	17	−18,228.4	36,490.8	0.0	1.00	0.98
Coast+coast^2+slope+slope^2+aspect+veg	71,192	71	16	−18,292.6	36,617.2	126.4	0.00	
Mosquito								
Coast+coast^2+slope+slope^2+aspect+water+veg	177,969	87	17	−44,957.8	89,949.6	0.0	0.95	0.97
Coast+coast^2+slope+aspect+water+veg	177,969	87	16	−44,961.8	89,955.7	6.1	0.05	

[a] The number of animal-year data sets included in the modeling.

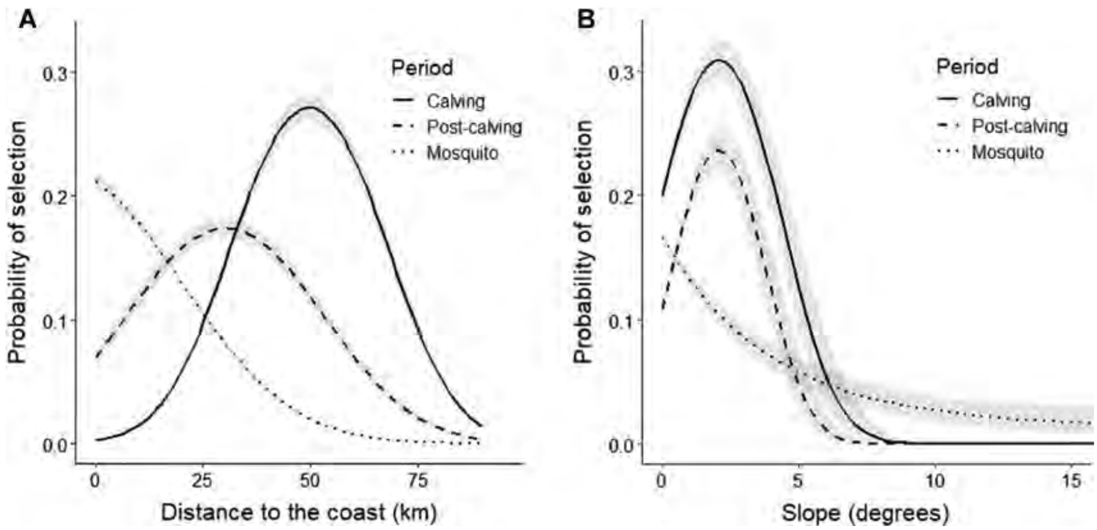

Figure 2. Female caribou relative probability of selection (and 95% CIs) for distance to the coast (A) and slope (B) during the calving (1–15 Jun), post-calving (16–24 Jun), and mosquito harassment (25 Jun–15 Jul) periods, Central Arctic Herd, Alaska, USA, 2015–2017. We held all other covariates from the top models at their mean values for used locations.

DISCUSSION

Despite the long-term presence of energy development within the CAH summer range, female caribou reduced their use of habitat near infrastructure during all the time periods we examined, although the effects waned across the summer. Caribou avoidance of infrastructure was strongest during the calving period, and similar to results from past studies conducted immediately post-construction. For example, in the years following the initial development of the Kuparuk oil field (1982–1987), helicopter transect surveys were conducted during the calving season to assess caribou densities within different 1-km intervals from infrastructure. Investigators reported that densities were less than expected within 4 km of infrastructure (Cameron et al. 1992, 2005). Approximately 30 years later, calving females reduced their use of habitat within 5 km of infrastructure, with observed use being, on average, about half of what was expected (Fig. 5A; Table S6).

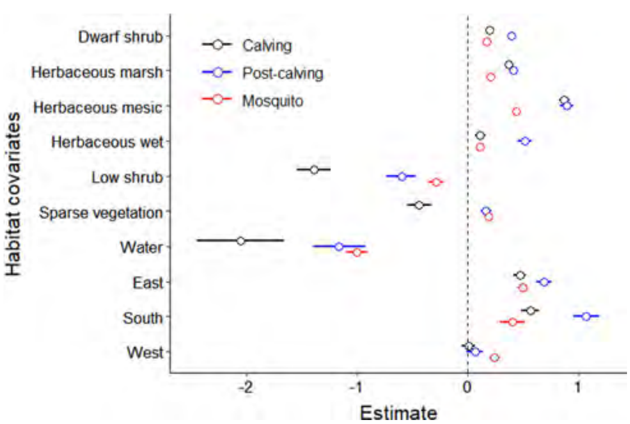

Figure 3. Coefficients and 95% confidence intervals (where visible) for female caribou selection of different proportions of vegetation types, water (binary), and aspects (categorical, with north as the reference class) during the calving (1–15 Jun), post-calving (16–24 Jun), and mosquito harassment (25 Jun–15 Jul) periods, Central Arctic Herd, Alaska, USA, 2015–2017. We standardized values for proportions of vegetation types.

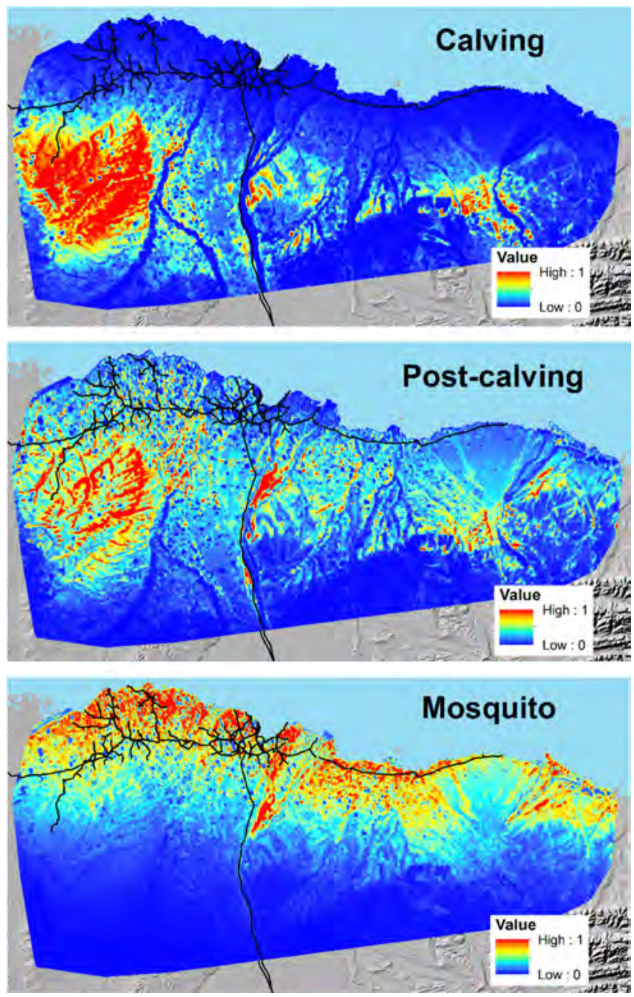

Figure 4. Predicted resource selection probabilities (based on habitat attributes not related to energy development) for female caribou during the calving (1–15 Jun), post-calving (16–24 Jun), and mosquito harassment (25 Jun–15 Jul) periods, Central Arctic Herd, Alaska, USA, 2015–2017. Black lines depict infrastructure associated with energy development (e.g., roads, pipelines, pads).

Table 2. Summary statistics for each caribou period including the zone of influence (ZOI) of energy development estimated for female caribou, the number of observed locations used to calculate the ZOI, the resource selection function (RSF) threshold value used to identify important seasonal caribou habitat, the area encompassed by the threshold value, the proportion of caribou locations contained by the threshold, and the proportion of important seasonal habitat within the ZOI. We provide statistics for the calving (1–15 Jun), post-calving (16–24 Jun), and mosquito periods (25 Jun–15 Jul) in the Central Arctic Herd, Alaska, USA, based on collar data collected during 2015–2017.

Season	ZOI (km)	Number of observed locations[a]	RSF threshold value	Area within threshold (km^2)	Proportion of locations contained	Proportion of important habitat within ZOI
Calving	5	6,474	0.15	3,859	0.82	0.12
Post-calving	2	4,810	0.10	4,627	0.68	0.15
Mosquito	1	14,825	0.10	7,475	0.93	0.17

[a] Number of observed locations within 20 km of energy development.

Habituation occurs when there is a waning of a behavioral response over time as a result of repeated stimulation (Thorpe 1963), a process that does not appear to have occurred for caribou in the CAH during the calving period. These results are consistent with findings from other Arctic caribou herds, where habituation to anthropogenic development has been weak or absent (Boulanger et al. 2012, Johnson and Russell 2014). Although some ungulate populations have exhibited stronger avoidance responses to energy development over time (Sawyer et al. 2017), we suspect that the slight increase we observed from past studies partially reflects a shift in the calving distribution (Cameron et al. 1992). In the early 1980s, caribou largely calved in areas close to the coast that were subsequently developed (Cameron et al. 2005). As development expanded, the distribution of calving females shifted inland, reducing the number of calving caribou close to infrastructure (Noel et al. 2004). Such abandonment of habitat close to energy development has been similarly observed for pronghorn (*Antilocapra americana*; Beckmann et al. 2012) and mule deer (Sawyer et al. 2006) on their winter ranges.

Although caribou also reduced their use of habitat near infrastructure during post-calving and mosquito periods, their responses were weaker (2 km and 1 km, respectively) than during the calving period, likely because of increasing mosquito harassment. Mosquito harassment largely drives caribou behavior during mid-summer when caribou increase their movement rates and travel to cooler, windier areas along the coast for relief (White et al. 1975, Cameron et al. 1995, Pollard et al. 1996), areas that also happen to be close to energy development (Fig. 4). In the past, mosquito harassment typically began during late June, although earlier spring phenology in the Arctic is causing mosquitos to hatch earlier (Culler et al. 2015) such that harassment now begins during the post-calving period in some years. As the severity of mosquito harassment increases across the summer, we suspect that caribou cannot afford to be strongly risk averse (Frid and Dill 2002); they must traverse the oil fields to access insect-relief habitat near the ocean (Fig. 4). As our findings demonstrate, however, caribou use of developed landscapes does not imply that infrastructure has no influence on their behavior, just that the distance it appears to alter their behavior is reduced. Similar patterns have been observed in bison (*Bison bison*) and mule deer, where avoidance of human activity or infrastructure declines during late winter or severe winters, when animals are presumed to be experiencing additional stress (Hayward et al. 2015, Sawyer et al. 2017). Responses of female caribou to development may also have waned across the summer as a function of their calves getting older. Stankowich (2008) reported that female ungulates with more vulnerable offspring were most sensitive to disturbance.

Although our work corroborates research on caribou responses to development during the calving period, it

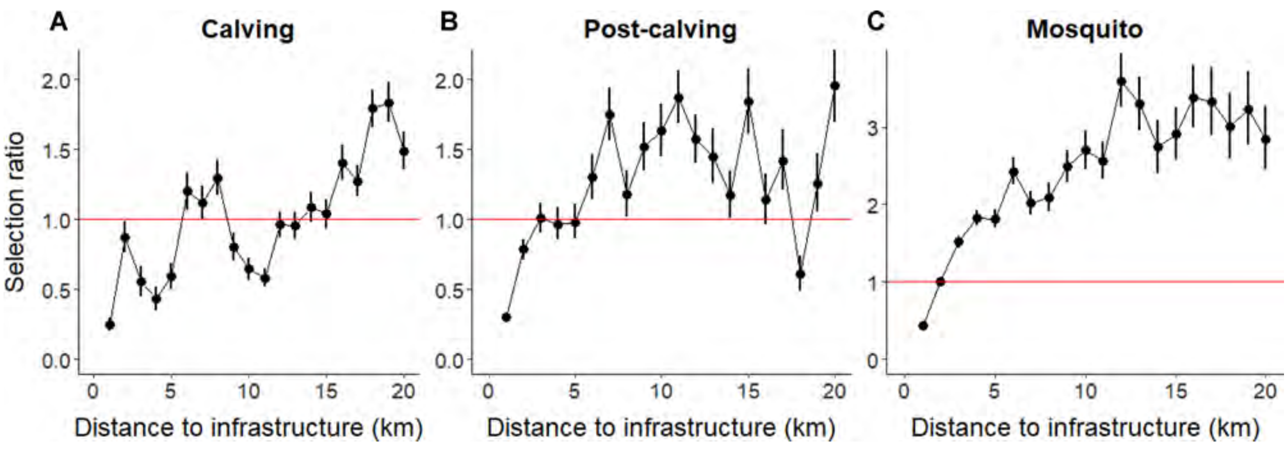

Figure 5. Selection ratios (and 95% CIs where visible) of female caribou (observed/expected use) within 1-km distance intervals from energy infrastructure during the calving (1–15 Jun), post-calving (16–24 Jun), and mosquito harassment (25 Jun–15 Jul) periods, Central Arctic Herd, Alaska, USA, 2015–2017. The red lines indicate the value where observed caribou use equals expected use. Note that during the mosquito harassment period, intervals ≥8 km from development had very low proportions of expected use (<0.02).

contradicts past studies conducted during the post-calving and mosquito periods. For example, Cronin et al. (1998) modeled summer (mid-Jun to mid-Aug) caribou numbers as a function of distance to infrastructure and other covariates and concluded that caribou distributions were not influenced by the presence of development. They failed to detect significant relationships between caribou distributions and any covariate, even distance to coast, despite its known importance in predicting summer habitat use (White et al. 1975, Pollard et al. 1996). Similarly, Noel et al. (2004) reported no influence of roads on caribou densities during late June through mid-August (although they failed to account for new development within their study area; Joly et al. 2006). We suggest that the results of these studies were likely confounded by their analysis periods. Both studies evaluated caribou locations collected across a 6–8-week period when their use of different areas is highly dynamic, as caribou move between coastal insect-relief areas and inland foraging areas (Figs. 2–4, S1; White et al. 1975, Parrett 2007, Wilson et al. 2012). Furthermore, both studies failed to account for spatial heterogeneity in habitat conditions relative to energy development, and how it shifts across the summer (Fig. 4). We suspect that these shortcomings diminished the ability of these studies to accurately estimate caribou responses to infrastructure, emphasizing the importance of quantifying caribou responses within periods when behavior is relatively consistent and after accounting for spatial variation in habitat quality.

Caribou selection for different habitat covariates (i.e., distance to coast, topography, vegetation, and water) was dynamic across the 3 periods we evaluated (Figs. 2–4). Some of the patterns we observed were similar to past research on caribou herds in Arctic Alaska, and some patterns were unique. Comparable to past research on the CAH and the neighboring Teshekpuk Herd, caribou moved towards the coast during mid-summer when insect harassment was high (Fig. 2; White et al. 1975, Pollard et al. 1996, Wilson et al. 2012). This behavior is different from caribou in the nearby Porcupine Herd, which typically move up into the foothills and mountains of the Brooks Range for insect relief (Walsh et al. 1992, Russell et al. 1993), likely because of their proximity to higher elevations relative to other herds. Whereas monitoring data collected on the CAH in the early 1980s reported that calving grounds were located adjacent to the coast (Cameron et al. 2005), our results mirrored patterns in more recent studies where calving grounds were located inland, south of the oil fields (Fig. 4; Arthur and Del Vecchio 2009, Nicholson et al. 2016). Similar to the Teshekpuk and Porcupine caribou herds, caribou in the CAH selected for herbaceous mesic vegetation during the calving period (Fancy and Whitten 1991, Wilson et al. 2012), and reduced their selection for wetter vegetation types during the mosquito harassment period (Walsh et al. 1992, Parrett 2007, Wilson et al. 2012). Caribou in the CAH also increased their selection for sparse vegetation during the post-calving and mosquito periods, presumably in response to greater insect harassment, whereas caribou in the Teshekpuk Herd avoided that land cover type until later in the summer (Wilson et al. 2012). Disparities between the CAH and other caribou herds may be partly due to different compositions and juxtapositions of land cover types within their respective ranges.

Investigators have raised concerns that indirect losses of habitat could reduce access to key foraging areas, and ultimately, have demographic consequences for the CAH (Nellemann and Cameron 1998, Cameron et al. 2005). During the short Arctic summer, caribou must regain and amass body stores that can be used for the subsequent winter and reproductive season (Barboza and Parker 2008, Taillon et al. 2013). As a result, White (1983) suggested that even minor declines in nutrients could have multiplier effects on body condition, survival and reproductive success. Recent research reported that nitrogen, which is likely limiting for caribou (Barboza et al. 2018), is highest early in the summer on the coastal plain, emphasizing the importance of this area for early summer foraging (Barboza et al. 2018, Johnson et al. 2018). Depending on the period, we found that caribou use was reduced in significant portions of important habitat areas; the ZOI overlapped with 12% of important calving habitat (based on our CVI analysis), 15% of post-calving habitat, and 17% of mosquito habitat, respectively. Despite these potential reductions in forage accessibility, major changes in the population size of CAH appear unrelated to changes in development. For example, when energy development expanded around Prudhoe Bay during the 1980s and 1990s, the CAH population increased from about 5,000 to approximately 28,000 individuals (Cameron et al. 2005). Recently, the CAH population declined from approximately 68,000 in 2010 to about 28,000 in 2017 (ADFG 2018), years when energy infrastructure and activities were relatively consistent. These patterns suggest that non-development factors (e.g., forage quality, weather, emigration) have been the primary drivers of major population trends, even though other studies have demonstrated that development appears to have some measurable effects. For example, Cameron et al. (2005) reported that between 1988 and 1994 parturition rates were lower and reproductive pauses higher for females in the western portion of the CAH summer range where development was concentrated, compared to the eastern portion of the range where development was minimal. Lenart (2015), however, reported no significant differences in parturition rates between the 2 areas using data collected between 1997 and 2014. Arthur and Del Vecchio (2009) also compared caribou calving parameters between western and eastern portions of the CAH range and reported that calves in the west (with increased development) were smaller and lighter than those born in the east but that survival rates did not significantly differ. These studies indicate that additional fitness investigations of the CAH may be warranted, particularly given that the influence of energy development may be dependent on variation in environmental conditions or herd density (e.g., reduced forage accessibility may be important only when herd abundance is high). Indeed, anthropogenic effects on wildlife populations can be weak or variable (Hansen et al. 2005, Harju et al. 2010) and an increasing number of studies have linked expanding energy infrastructure to reduced vital rates and abundance in ungulate populations (Christie et al. 2015, Johnson et al. 2017, Sawyer et al. 2017, Peterson et al. 2018).

Our study quantified broad-scale avoidance responses of female caribou to energy development, but there were key limitations of our analyses that are important to recognize. For example, we combined all types of infrastructure (e.g., roads, pads, pipelines) into a single footprint of development, and thus were unable to discriminate fine-scale responses of caribou within the oil fields. Murphy and Curatolo (1987) reported that caribou were more likely to cross a single structure (pipeline or road) than multiple adjacent structures (e.g., pipelines situated adjacent to roads), and Cameron et al. (1995) noted that pipelines constructed <1.0 m above the ground were largely barriers to caribou movement, whereas those elevated to a height of >1.5 m could allow movement. Given these observations, different infrastructure designs likely elicit distinct behavioral responses from caribou, which may be mediated by the surrounding habitat conditions. Because the spatial extent of our analysis was so large (encompassing all of the early summer range; Fig. 1) and distances to different development types were highly correlated within this area, our analytical approach was not appropriate for estimating infrastructure-specific responses. This is an important need for future work. Furthermore, our inferences are based on a recent snapshot of 3 years of caribou GPS-collar data, when the size of the herd had substantially declined (~28,000). It will be useful to investigate this issue for different herd sizes and foraging conditions in the future with additional years of data.

MANAGEMENT IMPLICATIONS

Our work suggests that habituation to industrial development by Arctic caribou is likely to be weak or absent. Minimizing the influence of energy development on caribou behavior may be accomplished by reducing the overall footprint of development within key seasonal habitat areas and movement corridors. The long-term indirect effects of energy infrastructure are poorly understood but deserve additional study because they could reduce the carrying capacity of important seasonal ranges and potentially have demographic effects. Finally, given the dynamic nature of caribou resource selection across summer, our work highlights the importance of assessing behavioral patterns for distinct life-history periods, as animal responses could otherwise be masked.

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SUPPORTING INFORMATION

Additional Supporting Information may be found in the online version of this article at the publisher's website.

TWS et al.
Exhibit to Comments
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EXHIBIT 8

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Research Article

Caribou Distribution and Movements in a Northern Alaska Oilfield

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ABSTRACT As industrial development increases in the range of barren-ground caribou (*Rangifer tarandus granti*) across the warming Arctic, the need to understand the responses of caribou to development and to assess the effectiveness of mitigation measures increase accordingly. The Central Arctic Herd (CAH) of caribou ranges across northern Alaska, USA, and the herd's summer range includes the Prudhoe Bay and Kuparuk oilfields, where the herd has been exposed to oil development for >4 decades. We used location data from global positioning system (GPS) radio-collars deployed on female CAH caribou for 106 collar-years, recording locations every 2 hours during 2008–2019, to examine caribou distribution and movements during 7 different seasons of the year in relation to infrastructure in the Kuparuk oilfield, which is characterized by more design improvements and mitigation measures than the older Prudhoe Bay oilfield. We examined movement metrics in terms of distance to gravel infrastructure (roads and pads) and time before and after movements across infrastructure (crossings). We also employed integrated step-selection analysis to compare caribou movements with random movements. Caribou distribution was influenced by insect activity, distance to coast, landcover, and terrain ruggedness, and we found large seasonal differences in caribou responses to infrastructure. Consistent with previous research findings, avoidance of areas near roads and pads was strongest during the calving season and some caribou used roads and pads as insect-relief habitat when oestrid flies (warble fly [*Hypoderma tarandi*] and nose bot fly [*Cephenemyia trompe*]) were active. Caribou moved through the Kuparuk oilfield repeatedly during summer, averaging >2 road or pad crossings a day when harassment by mosquitoes (*Aedes* [*Ochlerotatus*] spp.) and oestrid flies were the predominant factors influencing caribou movements. Caribou moved faster while crossing roads and pads but showed little pattern in speed or turn angle with distance to roads and pads. These results demonstrate that the effects of petroleum development on a caribou herd with long-term exposure to industrial activity vary widely by season. Maternal caribou avoid active roads and pads during calving, but the incorporation of appropriate mitigation measures in oilfield design allows caribou to move through the Kuparuk oilfield during other snow-free seasons.

KEY WORDS Central Arctic Herd, crossing rates, development, GPS collars, mitigation, movement analysis, *Rangifer tarandus*, step-selection analysis.

The combined effects of a rapidly warming Arctic and expanding industrial development are likely to affect arctic ecosystems in diverse ways and impose multiple, sometimes interacting, stressors on wildlife populations (Weladji and Forbes 2002, Arctic Climate Impact Assessment 2005, McRae et al. 2008, Fauchald et al. 2017, Mallory and Boyce 2018). Potential activity changes, displacement, or nutritional stress resulting from human activities could be exacerbated by effects on animal distribution or body condition caused by a changing climate. The additional uncertainty regarding the effects of future climate change makes assessing effects on wildlife from development, which is already challenging, even more difficult. Accordingly, the need to understand the effects of current development on wildlife is important for predicting the potential effects of planned development across the changing Arctic.

As the most-abundant large mammals in northern Alaska, USA, barren-ground caribou (*Rangifer tarandus granti*) are a vital cultural and subsistence resource (Titus et al. 2009, Stephen R. Braund & Associates 2010). Because caribou herds range over large areas (Skoog 1968, Fancy et al. 1989, Joly et al. 2019) and rely on the use of seasonally important areas for calving, insect-relief, and winter range (Russell et al. 1993, Murphy and Lawhead 2000, Person et al. 2007), negative effects could result if development limits herd movements or use of specific areas of seasonally important range. Globally, numerous caribou herds have experienced declines across much of their ranges, possibly as a result of

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climate change (Vors and Boyce 2009, Russell et al. 2019), and the effects of industrial activity on this species have been of particular concern for current and proposed development in Arctic Alaska (Cameron 1983, Cronin et al. 1994, Murphy and Lawhead 2000, National Research Council 2003).

Oil and gas production on the central Arctic Coastal Plain of northern Alaska has recently been expanding to the west and east of the established oilfields with potential effects on wildlife and subsistence harvesters in the region. Prior to lease sales and permit approvals for new projects, a range of different alternative development scenarios and stipulations are considered during the environmental impact assessment process under the National Environmental Policy Act (Bureau of Land Management 2019*a*, *b*). This process requires the best available data to predict effects on wildlife and to apply effective mitigation strategies. Caribou are a principal focus of such analyses.

Petroleum development in the range of the Central Arctic Herd (CAH) of caribou began with construction of the Prudhoe Bay oilfield and the Trans-Alaska Pipeline System (TAPS) in the 1970s, followed by construction of the Kuparuk and Milne Point oilfields between the Kuparuk and Colville rivers west of Prudhoe Bay in the 1980s. The Kuparuk–Milne Point area is 1 of 2 areas that consistently supported concentrations of calving caribou in the CAH since the late 1970s (Whitten and Cameron 1985, Lawhead and Cameron 1988, Cameron et al. 2005, Lenart 2015); the other area is east of the Prudhoe Bay oilfield, between the Sagavanirktok and Canning rivers, in an area where limited development currently occurs.

Concerns about the effects of petroleum development on the CAH resulted in numerous basic and applied studies of the herd (Shideler 1986, Cronin et al. 1994, National Research Council 2003, Lawhead et al. 2006). These studies focused on several major issues (Cameron 1983, Murphy and Lawhead 2000, National Research Council 2003): the potential displacement of maternal caribou during calving, the ability of caribou to cross oilfield infrastructure while moving between inland foraging areas and coastal mosquito (*Aedes* [*Ochlerotatus*] spp.) relief habitat, potential changes in behavior and energetics due to disturbance, and potential changes in caribou distribution and movements that could influence harvest effort or success by local subsistence hunters.

Previous researchers reported evidence of behavioral effects, including displacement of maternal caribou during calving (Dau and Cameron 1986, Cameron et al. 1992, Lawhead et al. 2004, Johnson et al. 2020), lower densities of calving caribou in areas of high road density (Nellemann and Cameron 1998), delayed and deflected movements when crossing roads and elevated pipelines (Fancy 1983, Smith and Cameron 1985, Curatolo and Murphy 1986, Johnson and Lawhead 1989, Lawhead et al. 1993), and changes in activity budgets of caribou near active infrastructure (Murphy and Curatolo 1987, Johnson and Lawhead 1989). Some potential demographic effects, such as lower parturition rates during 1988–1994 for caribou calving near development, have also been reported (Cameron et al. 2005), although a difference in parturition rate was not apparent in data from 1997–2014 (Lenart 2015, Johnson et al. 2020). Arthur and Del Vecchio (2009) reported lower body mass in June, September, and March for calves born west of the Sagavanirktok River (near development) than for those born east of it, but changes in body mass did not differ consistently and calf survival did not differ significantly between the 2 areas during most years and seasons. Despite these potential effects, the population of the CAH grew steadily from the 1970s to 2010 (with a short-term dip in the early to mid-1990s; Lenart 2015) as oil development increased, although the potential growth rate in the absence of development remains unknown.

Oilfield design and mitigation measures for caribou have been developed and improved through extensive research over the last 4 decades (Cronin et al. 1994, Murphy and Lawhead 2000, Lawhead et al. 2006). After recognizing the impediments posed by low-elevation pipelines in the Prudhoe Bay oilfield, natural resource managers for the State of Alaska required that pipelines in the Kuparuk oilfield be elevated to a minimum height of 1.5 m (Lawhead et al. 2006). Newer construction (since 2000) has required a minimum pipeline height of 2.1 m and a minimum separation distance of 150 m between roads and pipelines, whenever possible (Lawhead et al. 2006).

In the 1970s and 1980s, caribou studies in the region of the North Slope oilfields relied primarily on ground-based behavioral observations and aerial methods (systematic transect surveys and tracking of very high frequency [VHF] radio-collars). Examining fine-scale global positioning system (GPS)-collar locations collected year-round provided a new opportunity to study seasonal caribou distribution and movements after decades of annual exposure to petroleum development infrastructure and activities.

The effect of infrastructure could result in changes in movement metrics (speed and turn angle) near roads or during road crossings, or in changes in movement toward or away from roads if caribou are displaced or attracted to roads or pads. For example, if roads create a temporary barrier to caribou movements, this effect could be manifested in changes in speed and turn angle before crossings and near roads. Caribou also respond to roads and pads in different ways during different seasons (White et al. 1975, Murphy and Lawhead 2000, Johnson et al. 2020).

Most development in our study area occurred prior to our study; therefore, our objective was to describe how female caribou in the CAH seasonally used the Kuparuk oilfield by examining patterns of distribution and movements in relation to environmental characteristics and oilfield infrastructure. We examined 4 questions regarding caribou distribution and movements within the Kuparuk oilfield area: did patterns of caribou distribution change relative to distance to roads or pads; did caribou movement metrics (speed and turn angle) change at different distances to road or pads and before and after road or pad crossings; did caribou movements differ from random movements at different distances to roads or pads, after adjusting for other potentially important factors influencing areas used or movement characteristics; and did these relationships change during different seasons? Based on previous studies, we expected female caribou to occur at lower densities near roads or pads during calving, to use roads and pads for oestrid fly (warble fly [*Hypoderma tarandi*] and nose bot fly [*Cephenemyia trompe*]) relief habitat, and to cross roads frequently when mosquitoes were active, with some alterations of movement parameters during road crossings.

STUDY AREA

We conducted the study during 2008–2019 in a 4,800-km^2 study area extending east from the Colville River to the Kuparuk River and north from latitude ~69.9°N to the Beaufort Sea coast in northcentral Alaska (Fig. 1). This area encompassed the entire Kuparuk oilfield, the Milne Point oilfield, the Alpine pipelines corridor east of the Colville River, and the westernmost portion of the Prudhoe Bay oilfield (west of the Kuparuk River). The study area extended 20 km south of the southernmost oilfield road to include areas well beyond previously reported displacement distances for caribou calving in the area (Dau and Cameron 1986, Cameron et al. 1992, Lawhead et al. 2004). We excluded the oilfield area east of the Kuparuk River from our analyses, including most of the Prudhoe Bay oilfield, because that older development did not incorporate the same mitigation standards for facilitating caribou movements as in the Kuparuk oilfield and because the Prudhoe Bay area is not used consistently by the CAH outside of the mosquito and oestrid fly seasons.

The area is primarily owned by the State of Alaska, which leases much of it for oil development. The oilfields consist of a network of gravel pads for drill pads, housing, and processing facilities connected by gravel roads and elevated pipelines. Gravel roads and pads typically are 2 m thick to maintain thermal stability of the underlying ground. The volume of vehicle traffic varies by location in the oilfields, with higher levels occurring on major roads and closer to the main Kuparuk camp and airstrip than on operating drill sites farther away.

The landscape in the Kuparuk–Colville region gently slopes to the Beaufort Sea from upland, moist tussock tundra inland to moist and wet tundra with numerous small lakes and ponds near the coast. The elevation rises from sea level along the Beaufort Sea coast to elevations of approximately 150 m in the southern hills. The terrain is characterized by permafrost-related features, such as oriented thaw-lakes, drained-lake basins, beaded streams, high- and low-centered polygons, and pingos. The physiography, vegetation, and climate of the central Arctic Coastal Plain were described by Walker et al. (1980). The area has short, cool summers (Jun–Aug) and cold winters (Nov–Apr). Snow typically melts in late May or early June. Between 1981 and 2010, the mean temperature in July (the warmest month) was 9.3°C, the mean temperature in February (the coldest month) was –26.7°C, and the annual precipitation was 96.5 mm (Kuparuk weather station;

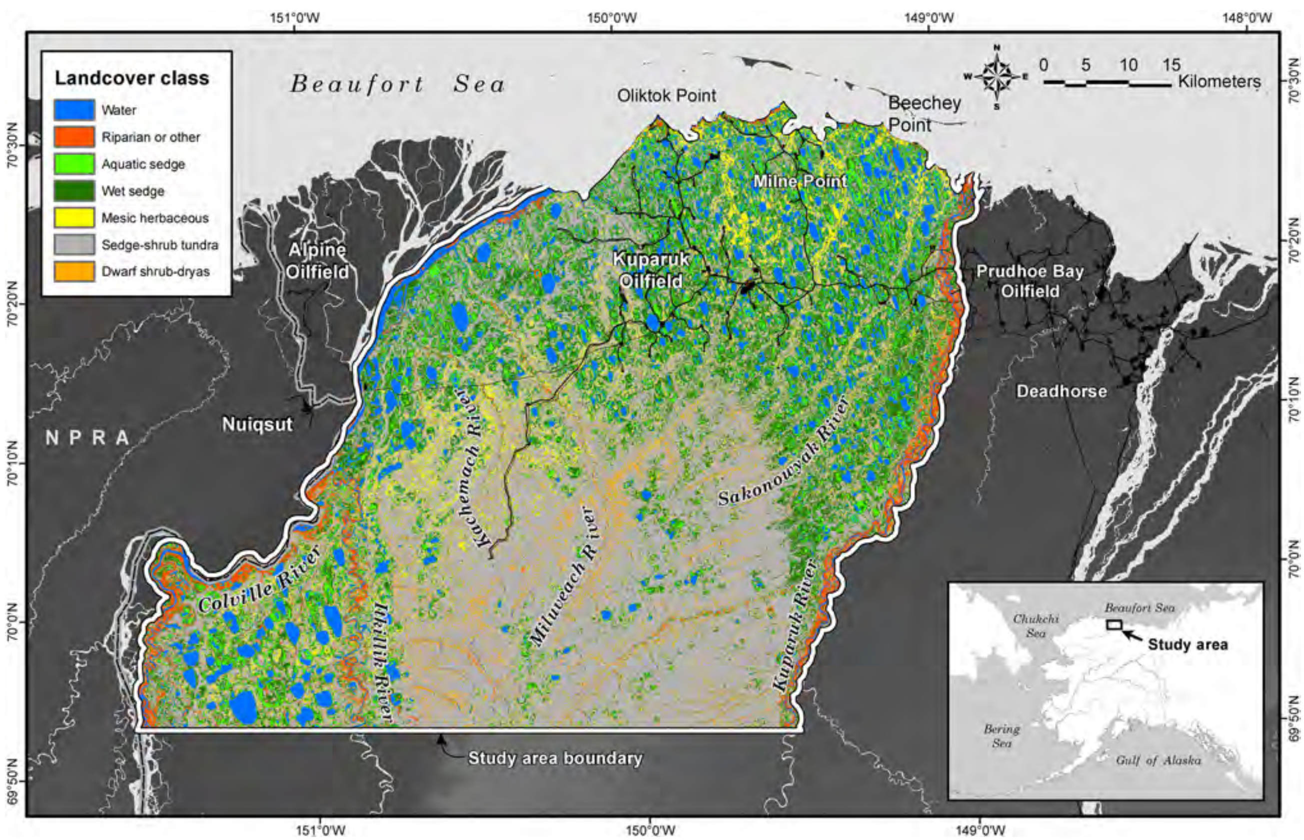

Figure 1. Study area boundary and landcover classes in the Greater Kuparuk Area, northern Alaska, USA, 2008–2019.

http://climate.gi.alaska.edu/acis_data, accessed 6 Mar 2020). The onset of autumn snow accumulation typically occurs by late September, although the onset date has been getting later in recent decades (Cox et al. 2017).

The CAH was first identified as a distinct herd in the 1970s (Shideler 1986). Herd size grew from a few thousand in the mid-1970s to a peak of 68,442 animals by 2010 (Lenart 2015), before declining to an estimated 22,630 animals by 2016 (McFarland and Taras 2016). The most recent CAH size estimate was 30,000 caribou in 2019 (Lenart 2019).

After calving, caribou in the CAH typically use coastal areas for relief from mosquito harassment, and winter in or near the central Brooks Range (Murphy and Lawhead 2000, Arthur and Del Vecchio 2009, Lenart 2015, Nicholson et al. 2016), with most wintering north of the Brooks Range since 2016. Predators of adults or calves include grizzly bears (*Ursus arctos*), wolves (*Canis lupus*), wolverines (*Gulo gulo*), and golden eagles (*Aquila chrysaetos*), although predator densities are low on the Arctic Coastal Plain (Shideler and Hechtel 2000, Young et al. 2002) and caribou survival generally is high during the summer (Lenart 2015). Caribou in the CAH are harvested by subsistence hunters from local communities and by non-local resident and nonresident (out-of-state) hunters, primarily along the Dalton Highway (Lenart 2015).

Caribou in the CAH are mostly absent from the North Slope oilfields during winter (Arthur and Del Vecchio 2009, Nicholson et al. 2016) but may come into contact with oilfield infrastructure during the rest of the year. The general pattern of the CAH seasonal response to oilfield infrastructure has been established by decades of research and changes dramatically with seasonal weather and caribou life-history events. Before calving in spring, snowmelt is accelerated adjacent to gravel roads because of fallout of dust (i.e., the dust-shadow effect), which attracts some female caribou arriving before calving (Lawhead and Cameron 1988, Murphy and Lawhead 2000, Lawhead et al. 2004). During and immediately after calving, females with young calves avoid areas within 2–5 km of oilfield facilities and human activity in the Kuparuk–Milne area (Dau and Cameron 1986, Lawhead 1988, Cameron et al. 1992, Lawhead et al. 2004, Johnson et al. 2020).

Mosquitoes typically emerge by late June and become the predominant factor influencing caribou movements on the Arctic Coastal Plain until approximately mid-July (White et al. 1975, Dau 1986). During mid-July caribou move more rapidly than at any other time of the year (Fancy et al. 1989, Person et al. 2007, Prichard et al. 2014). Caribou in the CAH aggregate in large groups and move north to the Beaufort Sea coast during periods of mosquito harassment, then return inland when lower temperatures or higher wind speeds reduce mosquito activity (Murphy and Lawhead 2000). Thus, caribou in the CAH often move back and forth through the Kuparuk oilfield multiple times during late June to mid-July (Smith et al. 1994, Murphy and Lawhead 2000).

From mid-July to early August, oestrid flies become dominant factors influencing caribou behavior, resulting in marked differences in behavior compared to the mosquito season. During the oestrid fly season, large aggregations of caribou break up, disperse inland, and use unvegetated areas (sand dunes, mudflats, river bars), areas with tall shrubs, and elevated locations (pingos, bluffs) as fly-relief areas (White et al. 1975, Roby 1978, Murphy and Lawhead 2000). During this period, caribou often occur on or near gravel roads and pads and in shaded locations under pipelines and buildings seeking relief from fly harassment because these structures are similarly unvegetated, elevated, or shaded (Curatolo and Murphy 1986, Johnson and Lawhead 1989, Pollard et al. 1996, Noel et al. 1998). Caribou in the CAH disperse widely during late summer before moving south during fall migration (Nicholson et al. 2016).

METHODS

Alaska Department of Fish and Game (ADFG) biologists deployed GPS collars (TGW-3680 GEN-III and TGW-4680 GEN-IV collars, Telonics, Mesa, AZ, and Iridium TrackM 3D collars, LotekWireless, Newmarket, Ontario, Canada) on yearling or adult female caribou in the CAH. Biologists captured caribou using a handheld net-gun fired from a low-flying helicopter. Procedures for handling live animals conformed to guidelines of the American Society of Mammologists (Sikes and Gannon 2011) and were approved by the ADFG Animal Care and Use Committee (approval number ADFG-0019).

We analyzed data only from female caribou. Previous researchers reported that female–calf groups reacted to human disturbance more than did male groups (Roby 1978, Murphy and Curatolo 1987, Stankowich 2008). In addition, male ungulates are difficult to outfit with GPS collars due to changes in neck size during the rut (Dick et al. 2013); therefore, no GPS data was available from males. The CAH is segregated sexually during calving, with males not typically arriving in the study area until postcalving. During periods of mosquito harassment, the CAH forms large mixed-sex aggregations, which tend to segregate sexually when mosquitoes are not active (White et al. 1975, Murphy and Lawhead 2000). Our data includes parturient and non-parturient females, but most females in the CAH calve in most years. Most collared females ≥4 years old (89.3%) and 3-year-old females (77.4%) were parturient during 1997–2014 (Lenart et al. 2015).

Biologists deployed GPS collars in April (2012–2015), late June (2009–2010, 2014, 2016–2017, 2019), and July (2008). All collars used in this study were programmed to record locations at 2-hour intervals during spring, summer, and fall. We selected all locations within the study area during 2008–2019 (Fig. 1). We deleted locations within 7 days of collar deployment to avoid potential effects of capture activities on caribou distribution or movements. We removed animals with <10 locations within the study area during a given season in a given year from analysis for that season. We collected 51,124 GPS-collar locations in the study area at 2-hour intervals from 2008 through 2019; most data were from 2014–2019 (Table 1). The number of

Table 1. Number of locations and number of collars (in parentheses) of global positioning system-collared female caribou within the study area in the Central Arctic Herd, Alaska, USA, used in the step-selection function analysis, by season and year, 2008–2019. We obtained location data at 2-hour fix intervals.

Year	Spring migration	Calving	Postcalving	Mosquito	Oestrid fly	Late summer	Fall migration
2008				0 (0)	0 (0)	193 (1)	129 (1)
2009	226 (2)	248 (2)	122 (2)	22 (1)	0 (0)	0 (0)	0 (0)
2010	0 (0)	0 (0)	0 (0)	211 (3)	670 (5)	321 (1)	31 (1)
2011	76 (3)	607 (3)	371 (4)	168 (3)	96 (2)	58 (2)	186 (3)
2012	0 (0)	182 (1)	117 (2)	149 (2)	0 (0)	0 (0)	0 (0)
2013	0 (0)	342 (2)	188 (4)	930 (4)	222 (3)	224 (2)	116 (3)
2014	157 (4)	1,390 (9)	938 (9)	1,346 (12)	790 (10)	271 (3)	770 (4)
2015	526 (6)	1,482 (8)	32 (8)	2,381 (8)	420 (7)	378 (4)	994 (7)
2016	532 (4)	1,034 (6)	436 (7)	2,023 (12)	692 (13)	1,147 (6)	2,190 (5)
2017	495 (5)	1,231 (7)	795 (8)	1,560 (13)	976 (13)	1,152 (5)	2,491 (10)
2018	167 (1)	684 (6)	679 (8)	2,279 (12)	1,047 (6)	1,067 (6)	1,225 (6)
2019	255 (3)	814 (6)	194 (4)	2,369 (14)	812 (13)	748 (9)	3,950 (10)
Total	2,434 (28)	8,014 (50)	3,872 (56)	13,438 (84)	5,725 (72)	5,559 (39)	12,082 (50)

collar-years used in the analyses was 28–84 per season for all years combined (Table 1).

We divided the year into 8 seasons based on mean movement rates and observed timing of caribou life-history events adapted from studies of other adjacent herds (Russell et al. 1993, Person et al. 2007): winter (1 Dec–30 Apr), spring migration (1–29 May), calving (30 May–15 Jun), postcalving (16–24 Jun), mosquito (25 Jun–15 Jul), oestrid fly (16 Jul–7 Aug, which also includes some periods of mosquito harassment), late summer (8 Aug–15 Sep), and fall migration and rut (16 Sep–30 Nov). These seasons are based on fixed dates and do not account for annual variability in the timing of these life-history events, with 1 exception. In several years with warm springs, mosquito emergence occurred during the postcalving season, so we started the mosquito season on the first date of moderate or severe mosquito harassment based on field observations by biologists working in the area. Years of earlier mosquito emergence were 2012 (22 Jun), 2013 (20 Jun), 2015 (16 Jun), and 2016 (23 Jun). Caribou in the CAH typically occur in small numbers in the study area during winter (Arthur and Del Vecchio 2009, Lenart 2015, Nicholson et al. 2016), so we omitted that season from analysis.

We used National Weather Service meteorological data to estimate the probability of insect harassment during summer. We calculated hourly estimates of mosquito and oestrid fly activity based on hourly temperatures and wind speed at Nuiqsut (west of the Kuparuk oilfield) using predictive equations developed by Russell et al. (1993). If the temperature at Nuiqsut or wind speed data were missing, we used weather data from Deadhorse (east of the Kuparuk oilfield). For some analyses, we defined periods of expected mosquito and oestrid fly harassment as occurring when their respective probabilities were >0.4. Some level of insect harassment was likely to occur below this level, but severe harassment was likely to occur for all values >0.4.

We adapted a landcover map (30-m pixel size) created by Ducks Unlimited (North Slope Science Initiative 2013). We combined similar cover classes and those that were rare in the study area and we added areas covered by gravel roads and pads as a new cover class (Fig. 1). We merged the tussock tundra, tussock shrub tundra, and mesic sedge (*Carex* spp.)–dwarf shrub tundra classes into a single landcover type: sedge–shrub tundra. We grouped the open water, ice and snow, and pendant grass (*Arctophila fulva*) classes together as water. Water covered 10.7% of the study area, with the proportion of lakes and ponds increasing near the coast. In addition, we lumped bare ground, sparsely vegetated, birch (*Betula* spp.)–ericaceous low shrub, low–tall willow, and coastal willow, which together composed 4.8% of the study area, as riparian and other because most of those cover classes occurred along streams, rivers, and coastal mudflats. The final map had 7 landcover classes (excluding water). Most of the landcover area was sedge–shrub tundra (53.2%), wet sedge tundra (21.6%), or aquatic sedge (i.e., water sedge [*Carex aquatilis*]; 10.1%). The only tall shrubs in the area occur near large rivers in the southern portion of the study area. We removed 0.7% of caribou locations from the analyses involving landcover because they occurred in the water class.

In most of the Kuparuk oilfield, elevated pipelines are associated with gravel roads and pads, and the 2 tend to parallel each other. Because of the association of roads, pads, and pipelines, we analyzed caribou crossing behavior relative to roads and pads only, rather than trying to analyze pipelines crossings separately. When interpreting the results, however, it is understood that most road or pad crossings also required caribou to cross under adjacent pipelines, with the exception of a small number of locations where gravel ramps were constructed over pipelines as a mitigation measure to facilitate caribou crossings. Pipelines that are not adjacent to roads only occur between the west end of the Kuparuk oilfield and the Alpine oilfield on the Colville River delta and in short sections to reach offshore developments. Because these pipelines had no associated vehicle traffic or human activity and were not common enough to analyze as a separate class, we removed the pixels under pipelines from the analysis.

To visualize caribou seasonal distribution patterns, we used dynamic Brownian bridge movement models (dBBMM) to create maps of caribou movements from the locations of GPS-collared individuals (Kranstauber et al. 2012). We included all locations to map caribou movements, including locations outside the Kuparuk study area.

These dBBMMs, which are a modification of earlier Brownian bridge models (Horne et al. 2007), use an animal's speed and trajectory calculated from GPS locations to create a probability map describing relative use of the area traversed. We computed the 95% isopleth of movements for each individual collared caribou in the area and then overlaid each caribou's isopleth layer for each season to calculate the proportion of collared caribou in the area that used each 100-m pixel. This visualization displayed the seasonal use of the area by caribou as a function of caribou distribution and movements. We computed dBBMMs using the move package in R (Kranstauber et al. 2017, R Core Team 2019) with a window size of 20 steps.

We calculated movement metrics from the GPS-collar data, including step speed (step length divided by duration [2 hr]) and turn angle (the angle between each set of 3 successive locations). We graphed these movement metrics in relation to distance to roads or pads and time before and after crossings of roads or pads occurred. We defined crossings as any movements that crossed ≥1 road or pad based on straight-line distance between successive locations 2 hours apart.

We also plotted the proportion of caribou locations among distance-to-road-or-pad categories for each season. For ease of interpretation, we divided density in each distance category by the maximum density in a distance category to produce values proportional to the maximum value. We used bootstrap resampling of individual caribou-years (1,000 simulations) to calculate 95% confidence intervals for each season.

We used integrated step-selection analysis (iSSA) to test for differences in space use and movement characteristics of caribou by season. This method allowed us to model caribou movement patterns in relation to variables thought to be important to caribou distribution during different seasons (landcover, terrain ruggedness, distance to coast) and then to examine the pattern of movements in relation to distance to roads or pads while accounting for the effect of other important covariates. Step-selection analysis uses random locations generated at each step in an animal's path to compare where an animal goes to other choices available along the movement path (Fortin et al. 2005, Thurfjell et al. 2014). The iSSA modification extends typical step-selection models by selecting random points from analytical distributions, which allows movement-related covariates (step length and turn angle) to be included in the model (Avgar et al. 2016). This procedure makes it possible to simultaneously examine which factors influence locations selected by caribou and how movement metrics change. In iSSA models, space-use parameters can be analyzed based on the end location of the movement and movement parameters can be analyzed as an interaction between the condition at the starting location and turn angle or step length (Avgar et al. 2016, Signer et al. 2018).

We used the R package amt (Signer et al. 2018) to run the iSSA models. For each caribou location, we generated 15 new random locations inside the study area and not in the water class. Package amt selects random locations from a gamma distribution for step length and a von Mises distribution for turn angle (Signer et al. 2018). Random locations were selected separately for each animal in each season and therefore were sampled from distributions estimated from movement characteristics specific to each individual and season. We compared used and random locations using a conditional logistic regression model that treated each movement step as a stratum.

For each starting location and the 16 ending locations (1 used and 15 random), we calculated the landcover class, distance to the nearest road or pad, distance to the coast, terrain ruggedness (calculated over a 150-m transect using methods of Sappington et al. [2007]; log-transformed), and the probability of mosquito activity and oestrid fly activity based on air temperature and wind speed at Nuiqsut or Deadhorse. We calculated road or pad distances based on the infrastructure that existed during each year, to incorporate the addition of several new facilities during the study period. Landcover type influences caribou distribution through various factors such as ease of walking, forage quality or quantity, or amount of snow or water. Terrain ruggedness was related to caribou distribution during calving in the Milne Point oilfield (Nellemann and Cameron 1996) and could be associated with insect relief habitat, predation risk, or forage quality. Distance to coast is an important factor because caribou move north during spring and calving, use coastal areas for insect relief, and move inland during late summer and fall.

We used iSSA models to evaluate the importance of the explanatory variables on caribou movements and then examine the effect of roads or pads after adjusting for these other potential factors influencing caribou distribution. We scaled continuous variables by subtracting the mean and dividing by the standard deviation before running the model to aid in interpretation. We first found the best model using all combinations of 3 variables: landcover class, terrain ruggedness, and distance to coast. We did not include interaction terms in the model selection. We included individual caribou identification (ID) as a cluster variable and adjusted standard errors for autocorrelation by calculating a robust standard error using a Huber sandwich estimator (Therneau 2015). We included the step-length (log-transformed) and turn-angle (cosine of turn angle) variables in all models (Forester et al. 2009). Because caribou movement is generally rapid following the onset of mosquito harassment (Yokel et al. 2011), we modeled step length as varying with the probability of mosquito harassment (e.g., step length was linearly related to the probability of mosquito harassment) during the mosquito season models. We also modeled step length as varying with the probability of oestrid fly harassment for oestrid fly season models, but we modeled this relationship as a quadratic term because caribou may move less during periods of severe oestrid fly harassment.

We selected the model with the lowest Akaike's Information Criterion (AIC) score as the best model (Burnham and Anderson 2002), using a 2-stage model selection process for each season. In the first stage, we found the best model using the initial variables. In the second stage, we added a distance-to-roads-or-pads variable to the best first stage model. We used the natural cubic spline of distance to roads or pads to allow for a more flexible model. Cubic splines fit a series of cubic equations to sections of the data but constrain the different lines to meet at pre-defined locations (knots) on the x-axis. Adding more knots adds additional flexibility to the model. We ran the best model from the first stage of model selection with the addition of the distance-to-road-or-pads variable with 3 different series of knot locations (2 and 6 km; 2, 6, and 10 km; or 2, 6, 10, and 14 km) and chose the final model with the lowest AIC score as the best model.

We used bootstrap resampling of individual caribou to calculate 95% confidence intervals of the model coefficients from the best model. We ran the model once, then took a random sample of individual caribou-years (with replacement) equal to the original number of caribou-years in the data set for that season, and reran the model. We ran each model with 999 resampled data sets to produce 1,000 model runs. We then calculated the 95% confidence intervals as the 25th and 975th highest values of each model coefficient.

To examine changes in caribou movements during periods of insect harassment, we ran the iSSA models separately for movements during active (probability of activity > 0.4) and inactive periods (probability of activity < 0.4) of mosquitoes and oestrid flies. Because we conducted these comparisons separately for periods with and without insect harassment, we did not include the effect of insect probability as a continuous variable in these models.

RESULTS

The percentage of collared caribou in the study area varied seasonally and among years (Table S1, available online in Supporting Information), with the highest use occurring from the calving season through the oestrid fly season (36.8–47.8% of collars; 13.5–34.6% of locations) and lower use (20.7–31.9% of collars; 5.4–12.3% of locations) during the spring, late summer, and fall seasons. During some seasons (spring, oestrid fly, late summer, and fall), the proportion of collars using the study area was much higher than the proportion of locations because many caribou were present only for a portion of the season.

Collared caribou began to arrive in the southern portion of the study area during spring migration and generally remained south of the oilfield during the calving season (Fig. 2). During the postcalving season, caribou moved farther north but largely remained in the same area used for calving until

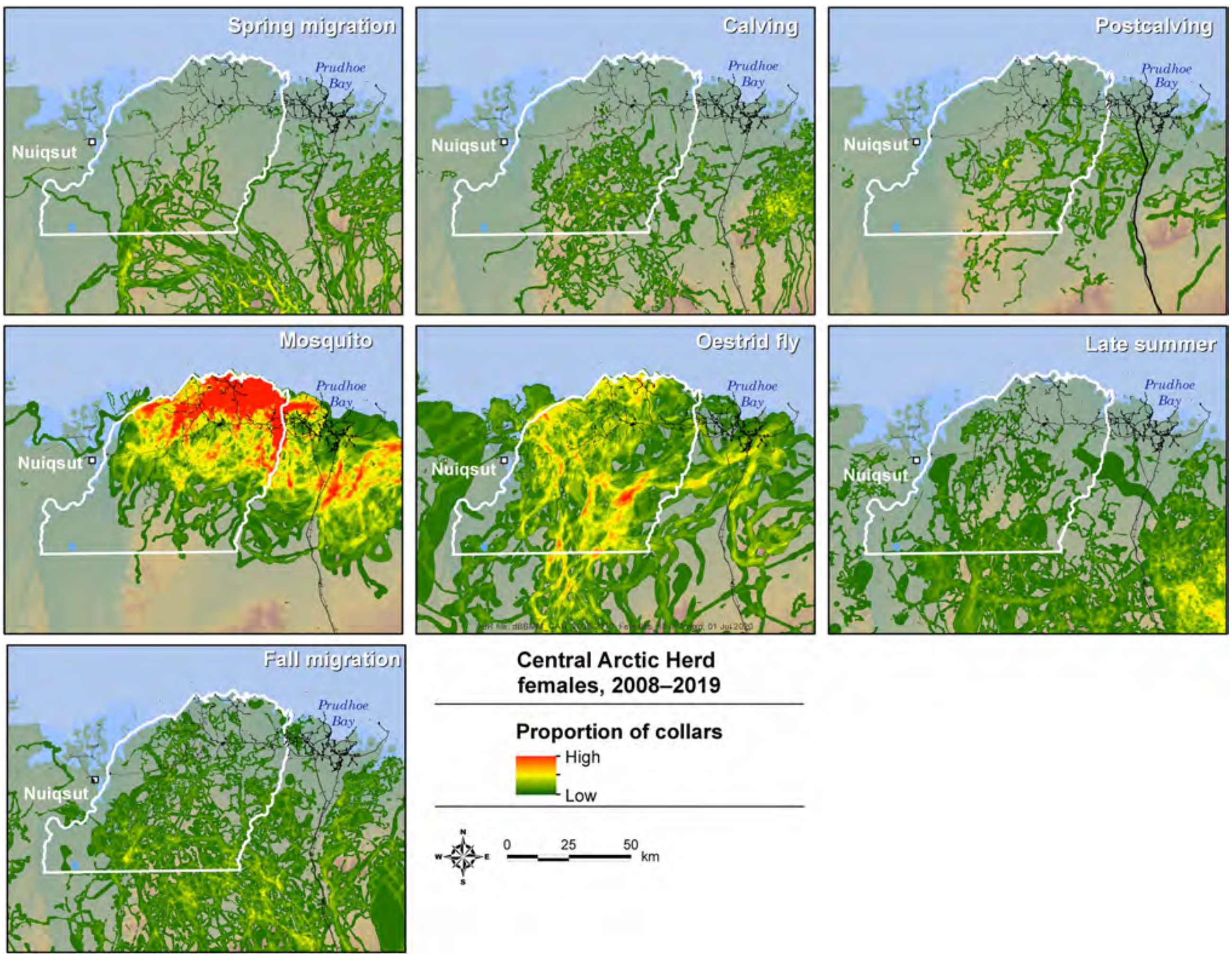

Figure 2. Movements (based on dynamic Brownian bridge models) of global positioning system-collared female caribou in the Central Arctic Herd during 7 seasons in northern Alaska, USA, 2008–2019.

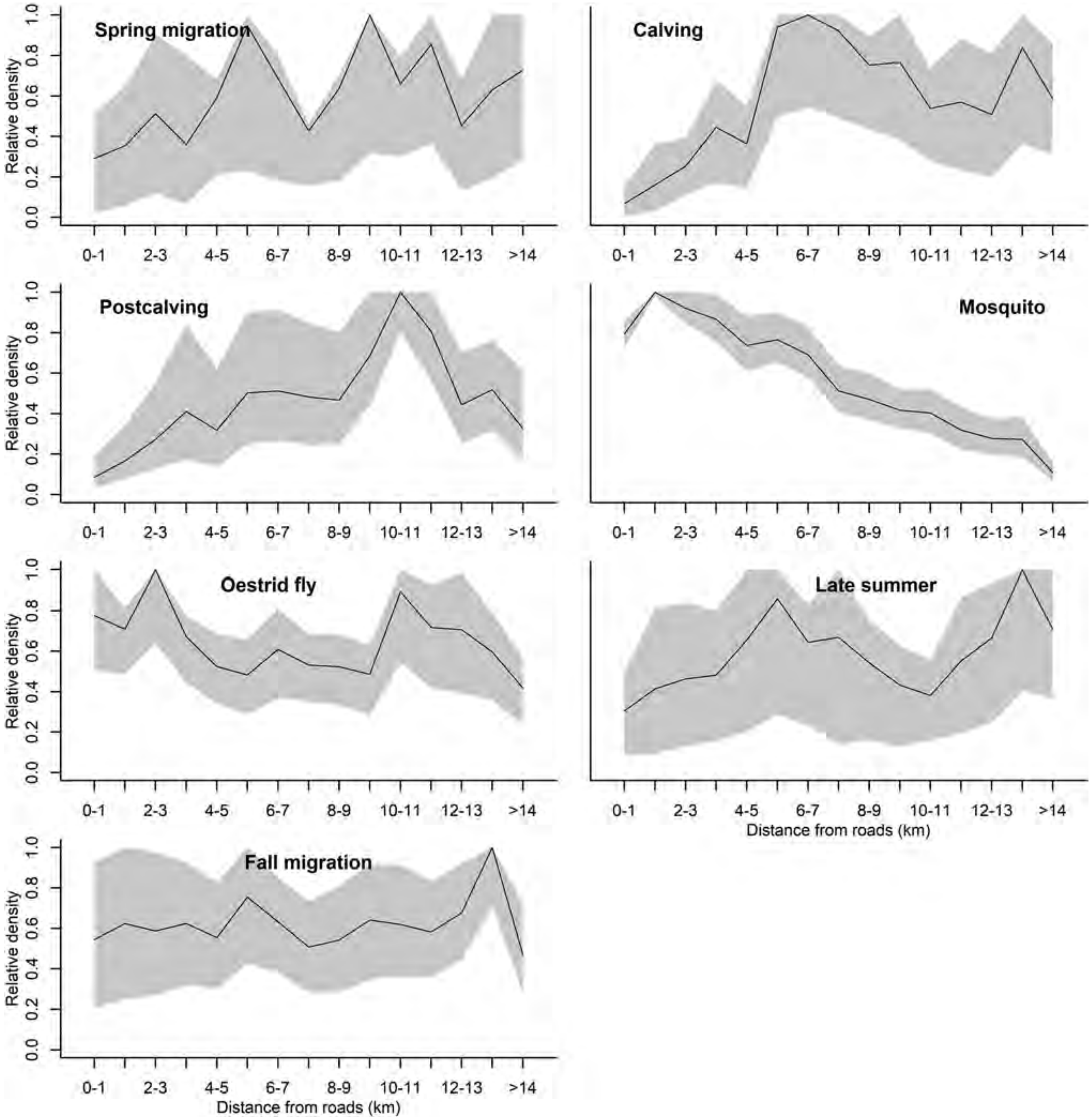

Figure 3. Density of caribou locations (relative to maximal distance category) among seasons by distance to roads and pads in and near the Kuparuk oilfield for global positioning system-collared female caribou in the Central Arctic Herd in northern Alaska, USA, 2008–2019. Black lines represent the mean and gray shading represents the 95% confidence interval calculated by bootstrapping individual caribou.

mosquitoes emerged. During the mosquito season, the areas of highest use were located between the main east–west road (i.e., Spine Road from Prudhoe Bay to the Kuparuk oilfield) and the Beaufort Sea coast, extending across the Oliktok Point and Milne Point roads, and along the Kuparuk River. Virtually the entire study area received some use during the oestrid fly season and the areas of highest use shifted inland to the southernmost portions of the study area during late summer and fall migration (Fig. 2).

These patterns are reflected in the seasonal distribution of caribou density in relation to distance from roads or pads (Fig. 3). The relative density of caribou locations during spring migration was low within 0–4 km; beyond 4 km, density was higher but more variable. A similar, albeit stronger, pattern occurred during calving, when density was lowest near roads or pads and reached the highest levels at 5–8 km from roads or pads. Caribou density during postcalving also increased farther from roads and pads, with the highest densities 10–11 km away from roads or pads, possibly as a result of new caribou moving in from south of the study area, likely including a disproportionate number of non-parturient females. In contrast, density peaked 1–2 km

Table 2. Mean number of movement tracks per 24 hours and per 10 km of movements in the study area by global positioning system-collared female caribou in the Central Arctic Herd, northern Alaska, USA, that crossed roads or pads, by season, 2008–2019.

Season	Crossings/ day	SE	Crossings/ 10 km	SE
Spring migration	0.143	0.027	0.207	0.038
Calving	0.028	0.007	0.043	0.010
Postcalving	0.102	0.018	0.132	0.023
Mosquito	1.234	0.033	0.610	0.016
Mosquitoes active	2.115	0.168	0.728	0.058
Mosquitoes inactive	1.171	0.033	0.597	0.017
Oestrid fly	1.136	0.049	0.476	0.020
Oestrid flies active	3.407	0.367	0.974	0.105
Oestrid flies inactive	1.009	0.047	0.434	0.020
Late summer	0.205	0.021	0.250	0.026
Fall migration	0.165	0.013	0.276	0.021

from roads or pads during the mosquito season and 2–3 km away from roads or pads during the oestrid fly season. Caribou density during the late summer and fall migration seasons was highly variable and showed only weak patterns in distribution with respect to distance from roads or pads.

The number of caribou movements across roads or pads also varied by season (Table 2), with the lowest rates occurring during calving (0.028/day, 0.043/10 km) and the highest rates during the mosquito season (1.234/day, 0.610/10 km). Crossing rates during the mosquito season were higher when mosquitoes were predicted to be active (2.115/day, 0.728/10 km) than when they were inactive (1.171/day, 0.597/10 km). Similarly, crossing rates during the oestrid fly season were higher when oestrid flies were predicted to be active (3.407/day, 0.974/10 km) than when they were not (1.009/day, 0.434/10 km).

Movement metrics (speed and turn angle) showed a few patterns in terms of time to crossing and distance to roads or pads (Fig. 4). Step speeds were consistently higher during crossing events in all seasons and increased near roads or pads during the mosquito season. Step speed also showed strong differences among seasons; the highest step speeds occurred during the mosquito and oestrid fly seasons. The mean turn angle tended to decrease around crossings during most seasons, indicating a weak tendency for more directional movements to occur during and after crossings.

The first-stage iSSA model selection results were generally consistent among seasons, with landcover type, distance to coast, and terrain ruggedness being selected in the top model for most seasons. The exceptions were that only landcover and distance to coast were in the best first-stage models when mosquitoes and oestrid flies were active (Table 3). Some model uncertainty (ΔAIC between top first-stage models < 2) was indicated for some seasons. During the second stage of model selection, adding the distance-to-roads-or-pads variable improved the model (lowered the AIC estimate) in all cases except during the postcalving season (AIC increased by 1.96). Some model uncertainty ($\Delta \text{AIC} = 1.12$) was apparent between the model with distance to roads or pads and the next-best

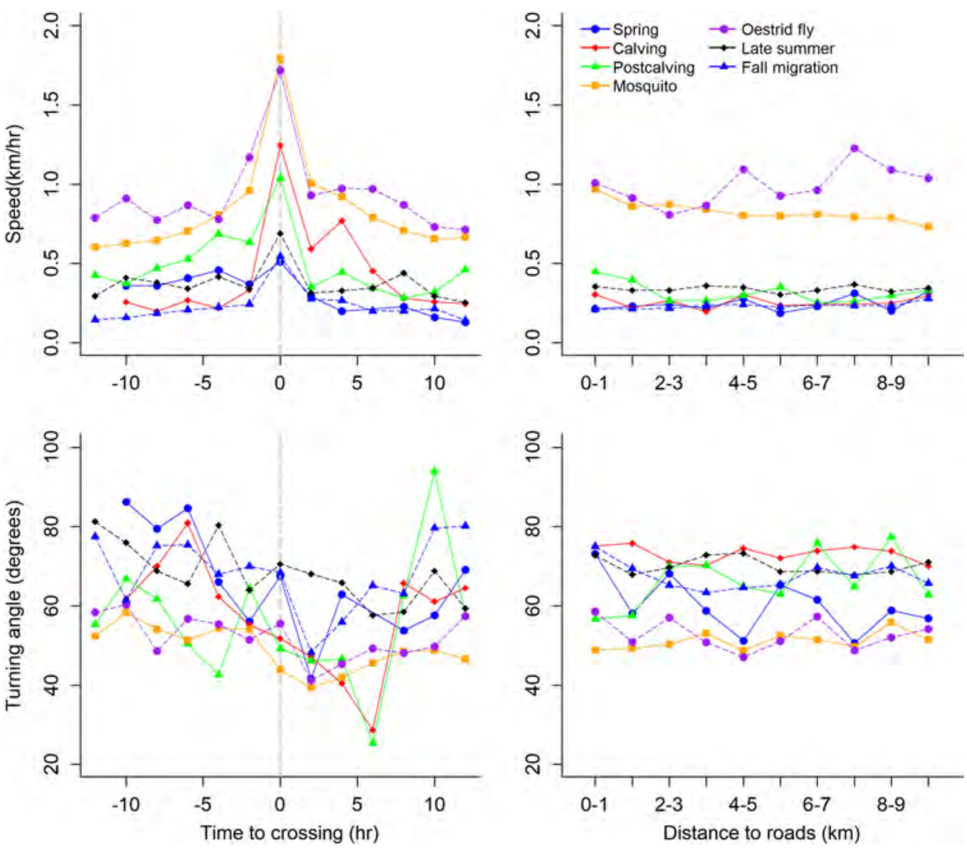

Figure 4. Movement metrics of global positioning system-collared female caribou in the Central Arctic Herd by time to crossing and distance from roads or pads in and near the Kuparuk oilfield in northern Alaska, USA, 2008–2019.

Table 3. Model selection results (top 3 models) for movement of female caribou in the Central Arctic Herd in northern Alaska, USA, by season, 2008–2019. The first stage model selection was conducted without distance to road, the second-stage model selection added distance to road to the best first-stage model. The number of knots reflects the amount of flexibility in the natural cubic spline curves.

Season	Model	AIC[a]	First stage ΔAIC[b]	Second stage ΔAIC[b]
Spring migration	Best plus distance from roads (4 knots)	13,000.90		0.00
	Landcover, coast, ruggedness	13,039.34	0.00	38.44
	Landcover, coast	13,043.42	4.08	42.52
Calving	Best plus distance from roads (3 knots)	43,022.18		0.00
	Landcover, coast, ruggedness	43,052.89	0.00	30.71
	Landcover, coast	43,055.03	2.13	32.85
Postcalving	Best plus distance from roads (2 knots)	20,683.74		1.96
	Landcover, coast, ruggedness	20,681.78	0.00	0.00
	Landcover, coast	20,686.71	4.93	4.93
Mosquito	Best plus distance from roads (2 knots)	73,300.30		0.00
	Landcover, coast, ruggedness	73,381.20	0.00	80.90
	Landcover, ruggedness	73,426.98	45.78	126.68
Mosquito (inactive)	Best plus distance from roads (4 knots)	67,969.17		0.00
	Landcover, coast, ruggedness	68,038.57	0.00	69.40
	Landcover, ruggedness	68,087.33	48.76	118.16
Mosquito (active)	Best plus distance from roads (2 knots)	4,417.35		0.00
	Landcover, coast	4,433.60	0.00	16.25
	Landcover, coast, ruggedness	4,435.57	1.97	18.22
Oestrid fly	Best plus distance from roads (3 knots)	30,226.25		0.00
	Landcover, coast, ruggedness	30,239.40	0.00	13.16
	Landcover, ruggedness	30,241.03	1.63	14.79
Oestrid fly (inactive)	Best plus distance from roads (3 knots)	28,768.10		0.00
	Landcover, coast, ruggedness	28,787.38	0.00	19.28
	Landcover, ruggedness	28,793.12	5.73	25.02
Oestrid fly (active)	Best plus distance from roads (2 knots)	1,481.00		0.00
	Landcover, coast	1,487.59	0.00	6.59
	Landcover, coast, ruggedness	1,489.52	1.93	8.52
Late summer	Best plus distance from roads (2 knots)	29,916.84		0.00
	Landcover, coast, ruggedness	29,917.96	0.00	1.12
	Landcover, ruggedness	29,920.12	2.15	3.28
Fall migration	Best plus distance from roads (2 knots)	64,962.25		0.00
	Landcover, coast, ruggedness	64,966.01	0.00	3.76
	Landcover, coast	64,968.60	2.59	6.34

[a] Akaike's Information Criterion.
[b] Change in Akaike's Information Criterion.

model during the late summer season. The number of knots selected for the best model varied by season (Table 3).

Clear patterns in landcover selection were evident in the iSSA results (Fig. 5). Based on the 95% confidence intervals of the model coefficients, relative to sedge–shrub tundra, the reference class, caribou avoided aquatic sedge during all seasons and selected dwarf shrub tundra and avoided wet sedge tundra during most seasons. Avoidance of wet sedge tundra was strong from spring through the mosquito season. Riparian areas were avoided during spring, calving, postcalving, and fall but were selected during the oestrid fly season. The coefficients for road or pads (as a landcover class) had large confidence intervals because of the relatively small area covered by gravel, but that class was avoided during the spring, fall, and mosquito seasons and selected during the oestrid fly season (Fig. 5). When oestrid flies were predicted to be active, caribou selected for roads or pads and riparian areas but showed no significant selection or avoidance of other landcover classes (Fig. 5).

During the mosquito season, caribou speeds increased with increasing mosquito harassment probability. The relationship between predicted oestrid fly harassment and caribou speed was modeled with a quadratic term. During the oestrid fly season, caribou speeds increased at low levels of oestrid fly harassment probability but then decreased as predicted harassment became more severe (Fig. S1, available online in Supporting Information). Strong patterns of caribou movements were evident in terms of distance to the coast. Caribou tended to move toward the coast from spring to mosquito season and moved inland during fall migration (Fig. S2, available online in Supporting Information). Caribou selected areas with relatively high terrain ruggedness during the postcalving, mosquito, oestrid, and late summer seasons but did not select high terrain ruggedness during calving (Fig. S2).

After accounting for the other variables in the models, plots of relative selection versus distance to roads or pads indicated general movement toward roads or pads during spring and late summer (Fig. 6), likely as a result of general herd movement north. Avoidance of the area within 5 km of roads or pads was evident during calving, but this pattern was largely gone during postcalving and distance to roads was not included in the best model during that season. During the mosquito season, there was an indication of weak avoidance of areas close to roads when mosquitoes were not active. When mosquitoes were active,

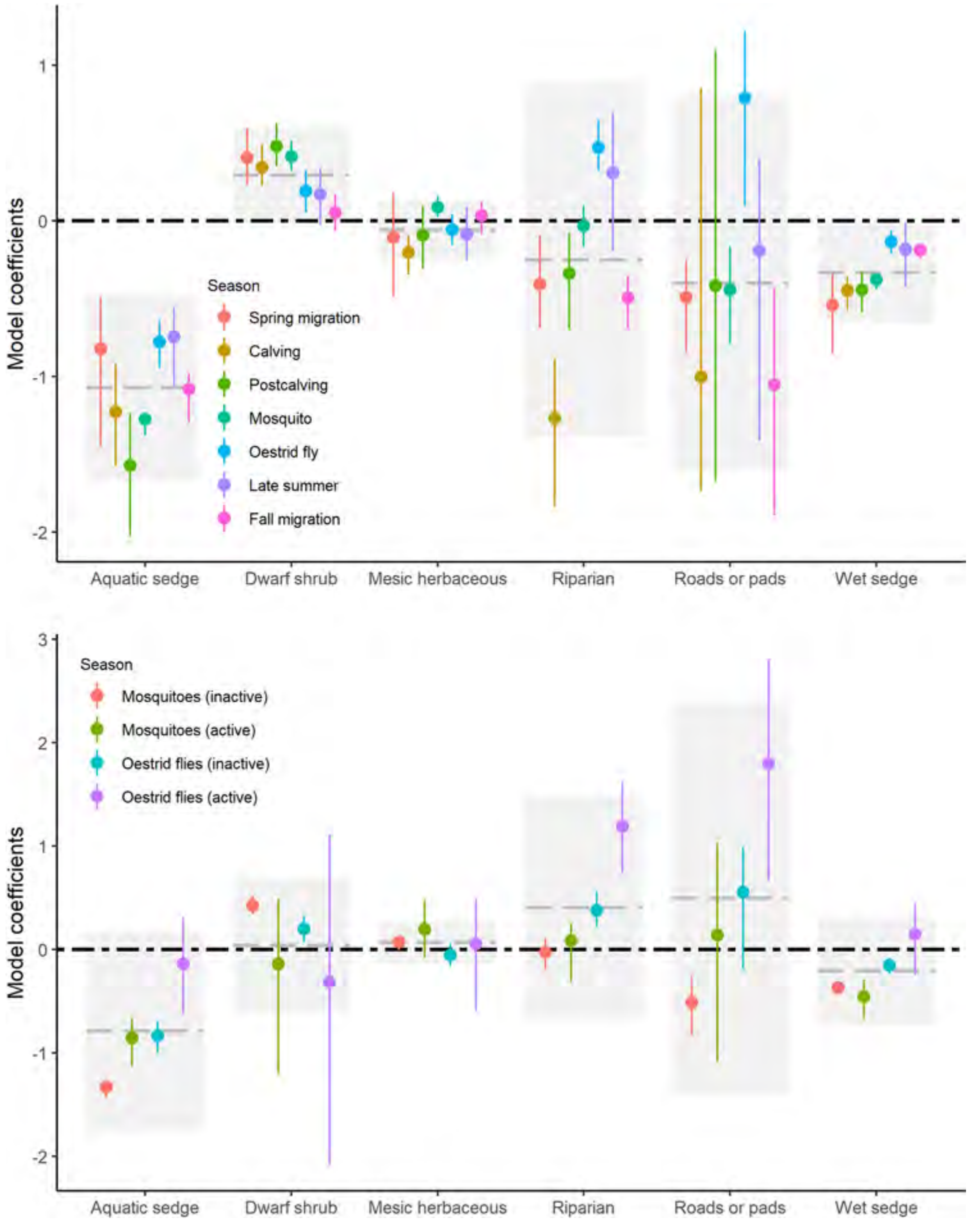

Figure 5. Landcover selection results from integrated step-selection analysis of global positioning system-collared female caribou movements in and near the Kuparuk oilfield in northern Alaska, USA, 2008–2019. Landcover classes are compared with the reference category of sedge–shrub tundra. Gray dashed lines and shading represent mean and 95% confidence intervals of all seasons for individual variables.

caribou far from roads or pads moved toward them (relative to random movements, as shown by the negative slope), likely a result of caribou leaving inland areas of higher mosquito harassment. In contrast, caribou already near roads or pads moved away from roads or pads (as shown by the positive slope near zero), resulting in weak selection for areas approximately 5–10 km from roads or pads when mosquitoes were active. When oestrid flies were active, caribou within 10 km of roads or pads moved toward roads or pads. Examination of caribou locations during these periods of predicted oestrid fly harassment indicated that caribou were widespread, but many caribou were on or near roads or pads, whereas others were along the coast or far inland, suggesting that caribou used roads, pads, and other oestrid fly relief areas (Fig. S3, available online in Supporting Information).

DISCUSSION

By using high-resolution GPS-collar data over 12 years, we provide new information on caribou distribution, movements, and responses to infrastructure in and near a northern Alaska oilfield. Our results add support for previous research showing that female caribou responses to infrastructure vary widely among life-history seasons (Russell et al. 1993, Smith et al. 1994, Murphy and Lawhead 2000, Person et al. 2007, Johnson et al. 2020), ranging from avoidance of areas of active infrastructure during calving to selection of gravel roads and pads during

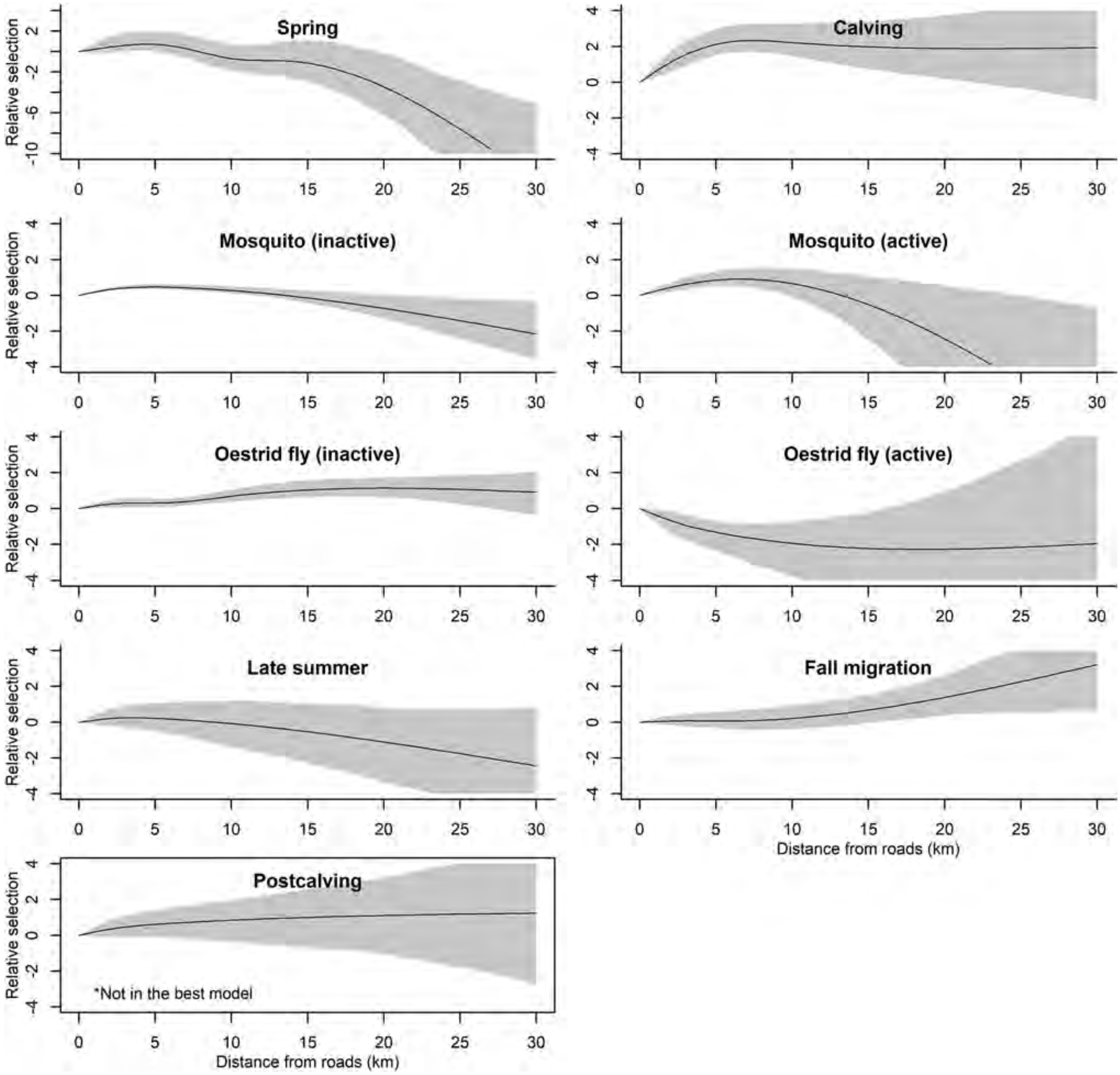

Figure 6. Effect of distance to roads or pads on caribou distribution during 7 seasons based on integrated step-selection analysis of global positioning system-collared female caribou movements in and near the Kuparuk oilfield in northern Alaska, USA, during 2008–2019. Black lines represent the mean and gray shading represents the 95% confidence intervals from bootstrapping of individual caribou. Positive slopes indicate movement away from roads and negative slopes indicate movement towards roads.

oestrid fly harassment. These responses are also likely to vary with infrastructure design, type and level of associated human activity, availability of alternative areas of seasonal ranges, extent of previous exposure to infrastructure, and caribou motivation. Although quantifying demographic effects of development was outside the scope of our study, having a better understanding of the behavioral and distributional effects of infrastructure provides useful insights into potential demographic effects of development for the CAH and other herds that may be exposed to industrial development.

By including landcover, distance to the coast, and terrain ruggedness in the iSSA models, we were able to account for some of the factors, other than infrastructure, that affect seasonal distribution of caribou. Selection of landcover type was largely consistent among seasons and was consistent with results from the nearby Teshekpuk Caribou Herd, where wetter landcover types were avoided during all seasons at 2 scales of selection and the riverine class was avoided during most seasons except the oestrid fly season (Wilson et al. 2012). Distance to coast was a strong predictor of caribou movements during most seasons as caribou moved north in the spring, responded to insect activity during summer, and left the study area in the fall. Caribou tended to use locations with higher terrain ruggedness during all seasons except calving.

The optimal response of wildlife to anthropogenic development will depend on animals accurately differentiating between real versus perceived risk and then balancing the risk of being near development with the cost of abandoning areas of preferred habitat. If no real risks are associated with roads, then avoidance behavior could be maladaptive (Frid and Dill 2002), and if predator densities are lower in areas of human development, selection of these areas may result in increased survival (Berger 2007, Dussault et al. 2012). During calving, a heightened vulnerability to predation results in strong selection pressure for strategies to lower predation risk (Bergerud and Page 1987). In the CAH, this anti-predator behavior evidently results in avoidance of areas near active roads and pads during calving despite decades of exposure to oilfields and a lack of hunting from oilfield roads (Dau and Cameron 1986, Cameron et al. 1992, Lawhead et al. 2004, Johnson et al. 2020, this study). Calving reindeer have also been reported to avoid areas near wind turbines, with higher levels of displacement occurring in areas where the movement of turbines was visible, suggesting that displacement behavior was associated with movement of infrastructure (Skarin et al. 2018).

Our results indicated that high-density calving occurred in the southern portion of our study area (south of the Kuparuk and Milne Point oilfields). The distribution of the portion of the CAH calving near the Kuparuk oilfield gradually shifted south of the oilfields in the decades following oilfield construction (Murphy and Lawhead 2000, Wolfe 2000, Noel et al. 2004, Joly et al. 2006), a period of herd growth. Approximately 300–2,100 caribou were estimated to be in the Kuparuk–Milne Point area (north of the main Spine Road and east of the road to Oliktok Point) annually during 1979–1987 (Cameron et al. 1992). Based on aerial surveys conducted in 1995–2017, the number of caribou in this area during calving continued to fluctuate annually with occasional years of high use; in 1996, 1,820 caribou (~9.9% of the herd) were estimated to be in the area and in 2008, 782 caribou (~1.2% of the herd) were estimated to be in the area, but <100 caribou were estimated to be in the area annually during 2010–2017 (B. E. Lawhead, ABR Inc., unpublished data). Thus, it appears that the change in calving distribution occurred incrementally, with an initial avoidance of areas within 4 km of roads (Dau and Cameron 1986, Cameron et al. 1992), followed by a gradual shift of high-density calving to areas south of the Kuparuk oilfield over a period of approximately 30 years after initial construction.

Although maternal caribou have not habituated to active roads and pads during the calving period, the evidence for habituation is mixed during other seasons. The distance from roads or pads was not included in the best model during the postcalving period, caribou crossed roads and pads frequently during the mosquito and oestrid fly seasons, and caribou selected roads and pads when oestrid flies were active. During the insect seasons, when calves are mobile and the predation risk is lower, avoidance of mosquito and oestrid fly harassment is a dominant factor influencing caribou behavior, leading them to be more tolerant of areas near human activity (Skarin et al. 2004).

Our iSSA models indicated a tendency for caribou to select areas 5–10 km from roads and pads when mosquitoes were active (Fig. 6), but examination of caribou locations during this period shows that this result likely reflects selection for the area near Beechey Point, east of the Milne Point Road and west of the Kuparuk River delta (Fig. S3). Mosquito-harassed caribou moving east along the coast into the prevailing easterly wind direction (White et al. 1975, Yokel et al. 2011) resulted in heavy use of this area, which is the eastern extent of the coastline within the Kuparuk study area. The orientation of the coastline perpendicular to prevailing winds in this area and the presence of large lakes provide better mosquito-relief habitat than other coastal locations farther west in the study area.

Johnson et al. (2020) also examined the distribution of the CAH in relation to infrastructure using a different data set from the years 2015–2017. They used resource selection functions combined with zone-of-influence analysis (White and Gregovich 2017, Plante et al. 2018) to examine caribou distribution across the CAH summer range, but their analysis was limited to the calving, postcalving, and mosquito seasons and their study area also included the Prudhoe Bay oilfield, which was constructed before effective mitigation measures for caribou were developed. Nevertheless, their results are broadly similar to ours. They reported lower-than-expected use of areas within 5 km, 2 km, and 1 km of roads during the calving, postcalving, and mosquito seasons, respectively, which represented 12–17% of seasonally important habitats.

We found a similar tendency to avoid areas near roads and pads as Johnson et al. (2020) during the calving season, but had different results during the postcalving period, likely because of the different methods of analysis. Caribou in the CAH generally remain near the calving area during the postcalving period but move closer to the coast before the emergence of mosquitoes (Murphy and Lawhead 2000, Lawhead et al. 2004), which could result in different conclusions for analyses of distribution versus analyses of movements. Johnson et al. (2020) reported that caribou were at lower-than-expected densities within 5 km of infrastructure during calving, but this zone of influence declined to 2 km during the postcalving period. This decline suggests that, although caribou may still be at a lower density within 2 km of roads, they make a net movement towards roads and pads during the short postcalving period. Other studies have also reported more use of areas near roads during mid- to late June (Smith et al. 1994, Lawhead et al. 2004, Haskell et al. 2006).

Although Johnson et al. (2020) reported that caribou densities were lower than expected within 1 km of infrastructure during the mosquito season, we found that caribou frequently crossed roads or pads during this season. Caribou movements during road crossings did tend to be faster and more directional (Fig. 4), indicating that caribou crossed roads rapidly and then departed the immediate area near roads. This conclusion is also supported by caribou densities being the highest during the mosquito season 1–2 km from roads and pads (Fig. 3). Hence, caribou crossed roads and pads and moved through the Kuparuk oilfield frequently during the mosquito season but did not remain near roads after crossing.

We did not include the characteristics of specific road and pipeline sections in our analysis, but it is likely that caribou select movement routes that avoid areas of high traffic, pipelines with low ground clearance, or other potential impediments to crossing. Previous researchers reported that caribou have difficulty crossing linear corridors where elevated pipelines are closely adjacent to roads with high traffic rates (Curatolo and Murphy 1986, Murphy and Curatolo 1987). Smith et al. (1994:iv) studied caribou movements in the Kuparuk area during 1978–1990 and concluded that "Although there is evidence of some habituation to the road system, caribou avoid areas of intensive activity, especially before and during calving." Traffic volume has been reported to be one of the most important factors affecting the responses of caribou to roads (Curatolo and Murphy 1986; Lawhead et al. 1993, 2006; Leblond et al. 2013) and traffic volumes tend to be low on access roads to individual pads. Our movement maps suggest that several movement routes, including the Kuparuk River floodplain, may be used preferentially, as previously reported by Smith et al. (1994). The use of these preferred routes could be an important component of habituation to oilfields.

Changes in activity budgets have been observed previously near roads and pads (Fancy 1983, Murphy and Curatolo 1987, Johnson and Lawhead 1989, Murphy et al. 2000). Murphy and Curatolo (1987) reported that caribou spent less time lying down when within 300 m of roads without traffic and within 600 m of roads with traffic, although the time spent feeding did not change. That finding is consistent with our results showing that caribou moved faster when crossing roads or pads during all seasons. Plante et al. (2018) also reported that caribou increased speeds during road crossings and Prokopenko et al. (2017) reported that elk (*Cervus canadensis*) moved faster in the vicinity of roads. Measuring the speed of movement during road crossings introduces a degree of bias to comparisons. To cross roads, caribou have to be moving, so the distribution of movements during crossing events excludes resting animals, resulting in higher mean speeds; in addition, even if movements are random, rapid movements are more likely to cross roads just by chance.

All caribou in this study were born long after oil development began in northern Alaska and most caribou in the CAH encounter some development infrastructure and associated activities every year. Because of differences in methodology, it is not possible to compare our results directly with those from research conducted soon after the construction of the Kuparuk oilfield to assess the degree of habituation that has occurred in the CAH with regard to crossing behavior. Small changes in speed or turn angle may have occurred at a finer temporal resolution than our data (2-hour fix intervals), but we did not find evidence of frequent long delays or large-scale changes in behavior that were reported during research conducted soon after construction of the Kuparuk oilfield (Smith and Cameron 1985, Johnson and Lawhead 1989, Smith et al. 1994).

The nature of interactions with infrastructure and levels and types of associated human activities influence the levels of disturbance that animals experience, and the rate and degree of habituation. Ungulates have shown an ability to tolerate development and use areas near human activity under certain conditions, including consistent and predictable human actions (Thompson and Henderson 1998, Garrett and Conway 1999, Burson et al. 2000). Humans on foot elicit the strongest behavioral reactions from caribou (Curatolo and Murphy 1986, Lawhead et al. 1993) and hunting may increase the degree of avoidance of infrastructure by ungulates (Ciuti et al. 2012, Paton et al. 2017, Plante et al. 2018). Human activity in the Kuparuk oilfield is controlled and predictable. Most potential disturbance stimuli stem from human activities on roads and pads; little off-road human activity occurs in the oilfield and the roads are not used for hunting (hunting by oilfield personnel is prohibited). Drivers are instructed to stop whenever caribou are observed trying to cross roads (Bureau of Land Management 2019*b*).

Our results suggest that, with the exception of the calving season, current best management practices, including design features with sufficiently elevated pipelines, adequate separation of roads and pipelines, restrictions on human activity, and traffic speed limits appear to facilitate some level of tolerance of infrastructure and ensure that caribou with long-term exposure to development can navigate infrastructure to reach essential foraging areas and insect-relief terrain. Some short-term changes in behavior, distribution, and movements may occur, and exposure to anthropogenic activities could also potentially result in increased physiological stress not apparent from movement behavior (Wasser et al. 2011). Additional research is needed to determine if these remaining changes result in substantial changes in demographic parameters such as survival, productivity, or body condition.

These results can help assess future development effects in other areas, but the predictions should account for potential differences among herds and seasonal range areas. These potential differences include the likelihood of greater effects in early years of exposure to development; the potential for different effects if hunting occurs from roads; the potential for larger herds to form much larger groups during the mosquito season, which may respond to infrastructure differently; and the likelihood that the effects of calving displacement may depend on the availability and quality of alternative calving habitat, which will need to be assessed individually for each herd and location.

MANAGEMENT IMPLICATIONS

These results from the CAH demonstrate the importance of understanding different caribou behavioral responses by season and levels of insect activity, and the necessity of tailoring mitigation measures and research efforts to these seasonal requirements. Some avoidance of active infrastructure during calving continues to occur after >4 decades of exposure to oilfields and future development should anticipate this effect; however, current mitigation measures are largely successful at allowing passage through newer oilfields outside of the calving season in a herd with previous exposure to development. Consistent, sustained monitoring of herd movements and population dynamics, and cooperation across agency, local government, and industry groups, as has been conducted for the CAH, is imperative for effective management of caribou as industrialization increases across the Arctic.

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SUPPORTING INFORMATION

Additional supporting information may be found in the online version of this article at the publisher's website.

EXHIBIT 9

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The Effects of Pipelines, Roads, and Traffic on the Movements of Caribou, *Rangifer tarandus*

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Curatolo, James A., and Stephen M. Murphy. 1986. The effects of pipelines, roads, and traffic on the movements of Caribou, *Rangifer tarandus*. Canadian Field-Naturalist 100(2): 218–224.

The frequency of Caribou, *Rangifer tarandus*, crossings of roads, pipelines, and pipelines along roads was studied in the Prudhoe Bay and Kuparuk oil fields on the Arctic Coastal Plain of Alaska. Caribou crossed an elevated pipeline or a road with a frequency similar to the control. It was only where a pipeline paralleled a road with traffic, that crossing frequencies were significantly less than expected (30% versus 66%). It is postulated that vehicles act in a synergistic fashion with a pipeline to produce a negative stimulus that results in decreased crossing frequency. Caribou crossing under elevated pipelines did not select for particular pipe heights within the range studied (152–432 cm). Caribou did select buried sections of pipeline as crossing sites more often than expected.

Key Words: Caribou, *Rangifer tarandus*, pipeline, road, oil development, Alaska.

The Central Arctic Caribou (*Rangifer tarandus*) Herd (CAH) ranges on the north slope of the Brooks Range between the Canning and Colville rivers (Cameron and Whitten 1979). The majority of the CAH remain on the Arctic Coastal Plain during summer, where they travel to the coast during periods of mosquito (*Aedes* spp.) harassment and move inland during mosquito-free periods (White et al. 1975). This movement pattern regularly brings the CAH into areas of oil development.

The most recent expansion of oil development on the North Slope of Alaska has been in the Kuparuk River Oilfield and western end of the Prudhoe Bay Oilfield, approximately 40 km west of Prudhoe Bay and within the summer range of the CAH. Development has been proceeding rapidly there since 1978 and has included construction of the Kuparuk Pipeline, a 40 km, east-west oriented, 40 cm diameter elevated pipeline. This pipeline and an expanding network of feeder pipelines intersect the summer movements of the CAH.

In 1980 the State of Alaska required that the minimum pipeline height be 1.5 m in the Kuparuk River Oilfield to allow for free passage of Caribou. At that time no quantitative data were available to substantiate the effectiveness of this stipulation. In 1981 studies were initiated by the oil industry to determine if this criterion was an effective mitigative measure and to gain insight into the reactions of Caribou to pipelines for future oilfield planning.

This report discusses the frequency that Caribou crossed pipelines and roads, whether pipeline height affected selection of crossing sites, and whether ramps (i.e. buried sections of pipeline) were preferentially used as crossing sites.

Study Area and Methods

This study was conducted near the Kuparuk and Ugnuravik rivers in Alaska, 10–20 km south of the Beaufort Sea coast (Figure 1). This region, dominated by wet sedge (*Carex* spp.) tundra and nearly flat except for pingos, river banks, and man-made structures, is typical of the Arctic Coastal Plain. Geobotanical aspects of the region are described by Walker et al. (1980).

Seven study sites ranging in size from 180 to 275 hectares (Figure 1) were used between 1981 and 1983, although not all study sites were used every year. Site 1 was used in 1981 and 1982; its northern border was an elevated pipeline (range 152–279 cm) adjacent to a road with traffic. Site 2 was used in 1983, and its northern border also consisted of an elevated pipeline (range 119–229 cm) adjacent to a road with traffic. Site 3 was used in 1981 through 1983; its northern border was an elevated pipeline (152–432 cm) adjacent to a construction pad with no traffic. Site 4 was used in 1983, and had as its northern border a high elevated pipeline (>650 cm) with no adjacent road. Site 5 was used in 1982 and was bounded on the north by a road with traffic. Sites 6 and 7 were used in 1981 and 1982; the northern borders of these sites were hypothetical pipelines consisting of a line of orange stakes placed at 50 m intervals. Three of the study sites (Sites 1–3) also had ramps (sections of buried pipe that were 50, 30, and 20 m wide, respectively).

Data were collected during the insect season: 2 July to 5 August 1981, 29 June to 1 August 1982, and 25 June to 29 July 1983. Variable-power spotting scopes and binoculars were used to observe Caribou from 3 m high towers. Observation times were not set; rather an effort was made to observe Caribou,

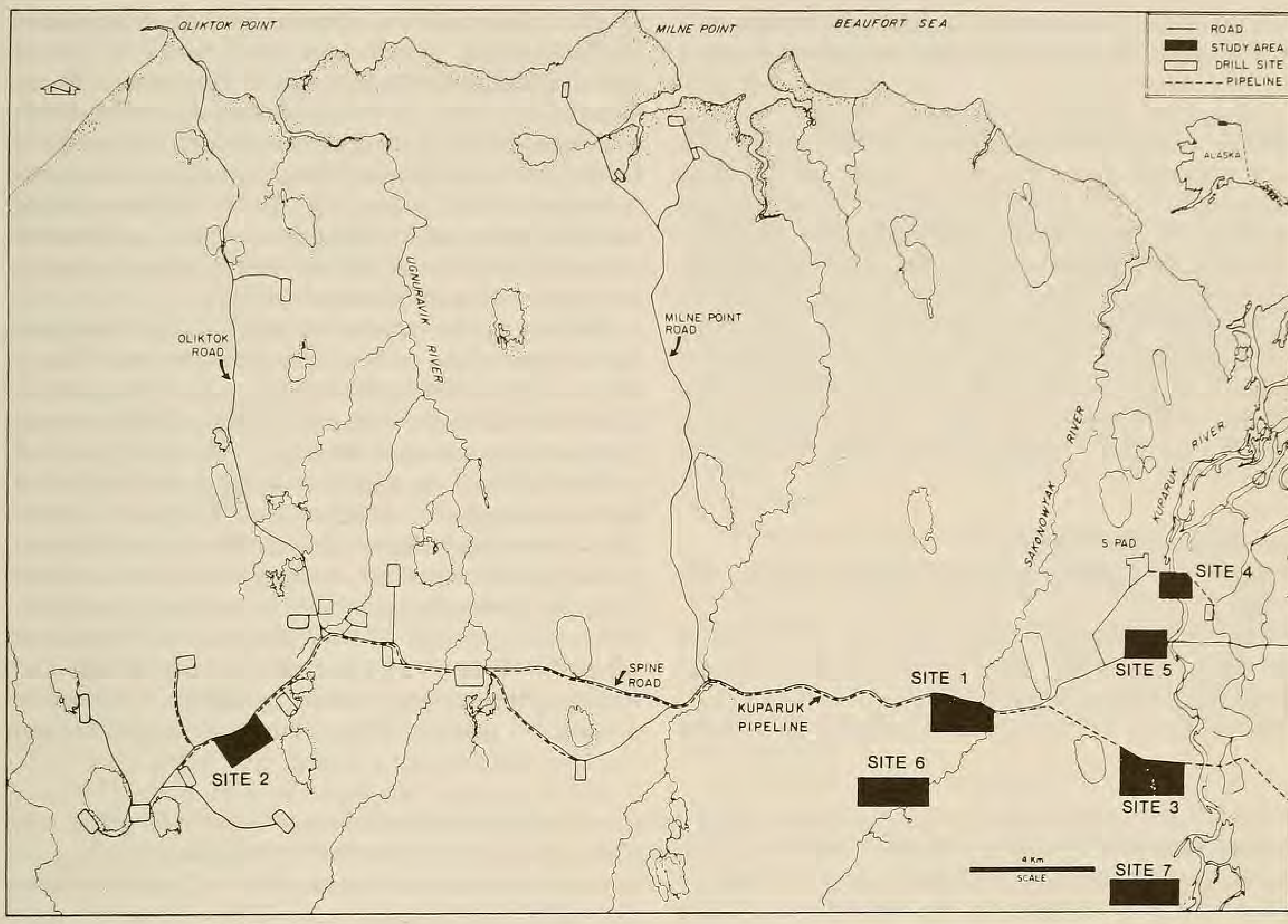

FIGURE 1. Location of study areas near the Kuparuk and Ugnuravik rivers in Alaska. Sites 1 and 2 are bounded by a pipeline adjacent to a haul road with traffic, site 3 is bounded by a pipeline adjacent to a construction pad with no traffic, site 4 is bounded by a pipeline, site 5 includes a haul road with traffic, and sites 6 and 7 are controls.

rather an effort was made to observe Caribou when they were in the vicinity and for as long as they were present. Data collected included group size, group composition (cow, calf, yearling, bull), route of travel through the study site, reactions of Caribou while crossing a road or pipeline, and number of vehicles in the study site. In addition, 10-minute point-in-time scans were taken of air temperature, wind speed, and insect presence. The presence (moderate/severe) or absence (none/light) of mosquitoes was determined using the relationship between mosquito activity and temperature and wind speed developed by White et al. (1975). The presence of oestrid flies was determined by observation of stereotyped behavioral responses to oestrids exhibited by Caribou, such as wild running (Curatolo 1975) and rigid standing (Espmark 1968) or by direct observations of flies. A severe reaction was recorded when caribou moved away from a disturbance at a trot or run. Severe reactions were distinguishable from ongoing activities, such as running induced by mosquitoes. Crossings of groups rather than individuals were selected for analyses because groups generally behaved as a cohesive unit. Crossing frequencies of individuals are also included for comparison.

Pipeline height was measured from the bottom of the pipe to the ground at each vertical support member (VSM). Caribou crossing between any two VSMs were recorded as having crossed under the pipeline at the mean height of those VSMs. All VSMs were numbered to locate crossing sites of Caribou. A Caribou group was arbitrarily considered to have crossed a pipeline successfully when $>50\%$ of the group crossed.

Observations of Caribou crossing pipelines and/or roads were classified according to the presence or absence of mosquitoes and oestrid flies to determine the effect these insects have on crossing frequency. Crossings by Caribou were also classified as either southbound or northbound because mosquitoes caused highly directional movements during most of the field season.

Chi-square analysis was used to test whether pipeline crossing frequencies at experimental sites were different from expected, based on crossing frequencies of northern borders (hypothetical pipelines) in the controls. Only complete data sets were used for analysis (e.g. caribou observed entering and exiting study sites). The log-likelihood ratio for contingency tables (Zar 1974) was used where expected values were small, such as the frequency of ramp crossings; and the Mann-Whitney Test was used to test differences in pipe height selection. Significance was evaluated at the 95% confidence level.

Results and Discussion

Frequency of Caribou Groups Crossing Pipelines and Roads

Caribou movement patterns and the relative number of Caribou groups traveling north or south across the northern border (e.g. pipeline) of the study sites appeared to be highly dependent on insects (Table 1). For example, when insects were not present, Caribou going south accounted for 77% of all crossings of the northern border of the controls. When mosquitoes were present, Caribou traveling north accounted for 80% of all crossings of the northern border of the controls. These patterns reflect the movements of Caribou during the summer, when Caribou, harassed by mosquitoes, travel north to the coast for relief and return south when mosquito activity declines (White et al. 1975).

Caribou groups tended to exhibit non-directional movements when oestrid flies were present. This is characteristic behavior during fly harassment (Curatolo 1975; Thomson 1971). Caribou near pipelines also had a propensity to seek relief from flies in the shade of the pipeline in a manner similar to reindeer using the shade of trees (Espmark 1968). Caribou tended to ignore the pipeline and traffic when standing in the shade or, at most, tended to run short distances when chased by flies or startled by vehicles. Repeated crossings of the pipeline were common when flies were present as Caribou weaved back and forth under the pipe, resulting in multiple crossings of at least 37 groups (39%). Therefore, the north and

TABLE 1. Per cent of Caribou groups that crossed the northern border of the study sites, which consisted of a pipeline, road, pipeline/road, or a hypothetical pipeline. More than 50 per cent of a group had to cross to be considered successful.

Insects Present	Structure					
	Pipeline/ Road Site 1	Pipeline/ Road Site 2	Pipeline Site 3	Pipeline Site 4	Road Site 5	Control Sites 6,7
None						
Total number groups	43	18	180	21	24	75
Southbound	16%*	11%*	61%	38%	42%	51%
Northbound	21%	22%	14%	14%	4%	16%
Total crossings	37%*	33%*	75%	52%	46%	66%
Mosquitoes						
Total number groups	45	9	118	23	27	61
Southbound	2%*	0	10%	0	0*	13%
Northbound	29%*	0*	58%	65%	100%*	51%
Total crossings	31%*	0*	68%	65%	100%*	64%
Oestrid Flies						
Total number groups	24	17	55	—	—	54
Southbound	54%	6%	9%	—	—	11%
Northbound	25%	35%	62%	—	—	56%
Total crossings	79%	41%	71%	—	—	67%
Overall						
Total number groups	112	44	353	44	51	190
Total crossings	44%*	30%*	72%	59%	75%	66%
Total number individuals	2014	1151	9846	2834	3325	2742
Total crossings	30%	5%	72%	57%	78%	61%
Traffic level (vehicles/hour)	moderate (15)	high (30)	very light (<0.1)	none (0)	moderate (15)	none (0)

*Indicates crossings significantly different from controls; only total crossings were tested for oestrid flies.

south crossing frequencies were not tested for the oestrid fly data because they did not adequately describe crossings during this period; most movements were non-directional.

Crossing frequencies similar to the controls were observed at the pipeline study sites (Sites 3 and 4) and the road study site (Site 5) when insects were not present and when mosquitoes were present. There were no significant differences between these sites and the controls, except that crossing frequency over the road was significantly greater than the control when mosquitoes were present. On the other hand, crossings at the pipeline/road study sites (Sites 1 and 2) were significantly lower than the controls during both of these periods, and the pattern of northbound and southbound movements were similar to the controls only when mosquitoes were present. The frequencies of total crossings at all of the pipeline and pipeline/road study sites were not significantly different from those of the controls during periods of oestrid fly harassment (Table 1).

Sixty-two per cent of the Caribou (n = 262) reacted severely (i.e. running) when crossing the pipeline/road at Site 1 compared to 47% crossing the road at Site 5 (n = 5106), 12% crossing the pipeline at Site 3 (n = 4371), and 10% crossing the pipeline at Site 4 (n = 4453). The high frequencies of severe reactions at the pipeline/road and at the road study areas provide evidence that Caribou respond to moving stimuli. A high frequency of severe responses to traffic (not associated with a pipeline) was also observed by Horesji (1981). However, because traffic usually is a transient stimulus, Caribou movements are not necessarily affected when no other structures are present.

We attribute the lower crossing frequency at the pipeline/road sites to the combination of vehicular traffic and a pipeline. Indeed, crossing frequency was lowest where traffic adjacent to an elevated pipeline was highest (1 vehicle every 1.9 minutes at Site 2 versus 1 vehicle every 3.9 minutes at Site 1). These observations may be best interpreted in terms of inherent behavioral traits of Caribou. Caribou evolved in open habitats with wolves as their major predator (Bergerud 1974). Thus, Caribou tend to avoid or be more alert in habitats that can conceal a predator (Curatolo 1975).

It seems that the frequency of traffic along a pipeline is important because Caribou must have sufficient time between vehicle encounters to successfully cross both the pipeline and the road. As Caribou approach an elevated pipeline, they usually hesitate up to 10 minutes before crossing, whether or not vehicles are present. A passing vehicle usually causes Caribou to retreat from the pipeline or, at least interrupts their attempt to cross. Thus, as traffic levels increase, opportunities for Caribou to cross the pipeline decrease.

Influence of Group Type and Group Size on Crossing Frequencies

Within each study site there was no significant difference between the percentage of cow-calf groups and bull groups that crossed the pipeline (Table 2). Other studies have identified cow-calf groups as the most sensitive segment of the herd (Bergerud 1974; Curatolo 1975; Roby 1978). The Kuparuk Pipeline traverses important routes to mosquito relief habitat. The similarity of crossing frequencies between bull and cow-calf groups in our study may be a result of the intensity of the drive to reach mosquito relief habitat on the coast.

There was a tendency for large groups ($>$ 100) to be less successful than small groups ($<$ 100) when crossing the pipeline/road within Site 1 or Site 2, although no significant differences were found (Table 2). Crossing frequencies for individuals were also lower than for groups at these sites (Table 1), suggesting that large groups were less successful than small groups.

In summer, Caribou usually form large groups during periods of mosquito harassment (Curatolo 1975); indeed the largest groups form during times of the most severe harassment. These large groups have a greater probability of containing some individuals that are more easily disturbed than others; this may, in turn, affect the behavior of the entire group. Large groups take more time to cross a pipeline than small groups, and this delay increases the potential for encounters with traffic. Thus, traffic along a pipeline may contribute to the lower crossing success of large groups that we observed.

There were no differences in crossing frequencies between large and small groups within sites with only a pipeline. In contrast, Child (1974) concluded that small groups crossed his simulated pipeline (no vehicular traffic) more often than large groups. It may be that Child's simulation was more disturbing to large groups (already under mosquito harassment) than the Kuparuk Pipeline or that sufficient habituation has occurred so that the pipeline we observed was no longer a disturbing factor.

Pipe Height Selection

Clearance of the elevated pipeline ranged from 152–432 cm at the three study areas where data on crossing site selection by Caribou groups were collected (Table 3). The mean pipeline height of crossing sites selected by Caribou at both pipeline/road study sites (Sites 1 and 2) did not differ significantly from the mean pipe height available. In

TABLE 2. Pipeline and pipeline/road crossing frequencies by group size and group type.

Study Area	Year	Group type[1] cow-calf	n	bull	n	Group size < 100	n	≥ 100	n
Pipeline/road (Site 1)	1981-1982	49%	58	38%	47	45%	107	20%	5
Pipeline/road (Site 2)	1983	24%	33	36%	11	30%	43	0%	1
Pipeline (Site 3)	1981-1983	71%	112	75%	202	72%	325	75%	28
Pipeline (Site 4)	1983	57%	21	67%	21	56%	36	75%	8
Control (Sites 6 and 7)	1981-1982	59%	81	71%	94	66%	185	60%	5

[1]More than 50 per cent of the Caribou in the group were either bulls or cows and calves; excludes individuals and cow-yearling groups.

1981, but not in 1982 or 1983, the mean pipeline height of crossing sites selected by Caribou at the pipeline study site (Site 3) was significantly higher than the mean pipe height available (Table 3).

There are no other quantitative studies for comparison with these data. The fact that Caribou selected for higher pipe heights only one year out of three suggests that pipe height is not an important factor in crossing site selection within the range of pipe heights we studied. Pipeline heights above 1.5 m are largely determined by topographic variations and it appears that normal movement patterns along certain topographic features (e.g., river drainages) probably account for the crossings observed under

TABLE 3. Mean heights of elevated pipeline available for crossing compared with mean heights of pipeline selected by Caribou for crossing.

Location	Type of Data	Year	Mean (cm)	SD	Range (cm)	n[1]
Pipeline/road (Site 1)	actual pipeline	—	186	27	152-279	168
	Caribou crossings	1981	188	29	152-279	92
	Caribou crossings	1982	183	23	152-279	78
Pipeline/road (Site 2)	actual pipeline	—	182	16	119-229	92
	Caribou crossings	1983	184	20	149-227	36
Pipeline (Site 3)	actual pipeline	—	261	65	152-432	139
	Caribou crossings	1981	301	70	152-432	138
	Caribou crossings	1982	274	66	152-432	345
	Caribou crossings	1983	278	68	152-432	184

[1]This number represents the number of VSMs in the actual pipeline in the study site or the number of crossings made by Caribou in the study site. A "crossing" consisted of one or more Caribou crossing under a pipeline between two adjacent VSMs in a more or less cohesive manner. Thus, one Caribou group can account for one or more crossings.

higher pipe heights. It is also possible that habituation may account for the lack of selection of high pipeline in the last two years of the study. A pipeline is a stationary structure, and is a relatively low level stimulus compared with a pipeline adjacent to a road with moving vehicles. Perhaps Caribou crossed under the high pipeline in 1981 (the first year the pipeline was in place) because it was less frightening than crossing under low pipeline sections. If this is so, it appears Caribou readily habituated, as there was no apparent selection for high pipeline in the following two years. On the other hand, the lack of selection of high pipeline in the pipeline/road site during any year (Table 3) may be explained by the additional disturbances caused by traffic at that site and by the lack of prominent topographic features for Caribou to follow.

Use of Ramps as Crossing Sites

Pipeline crossings were classified as either crossings under an elevated pipeline or crossings over a ramp (buried pipeline) to determine whether Caribou preferred specific pipeline configurations for crossing sites (Table 4). Six per cent, twelve per cent and nine per cent of the crossings at Sites 1, 2, and 3, respectively, were over ramps. These crossings were significantly more frequent than expected because the buried pipe constituted less than 2% of the pipeline at these sites. A preference for ramps was also observed in Prudhoe Bay in 1972 (Child 1974). Child found that 76% of the Caribou crossing a simulated pipeline crossed over ramps that represented 22% of the total length of the simulation.

The preference for ramps as crossing sites by Caribou appears to reflect the effect of elevated pipelines on Caribou behavior. Caribou tend to follow linear structures for some distance before crossing (LeResche and Linderman 1975). When Caribou encounter an elevated pipeline they may parallel it even though that may entail a change in the direction of travel. Upon reaching a ramp, the visual stimulus of the elevated pipeline is gone; this may provide a "path of least resistance" for Caribou to follow.

Summary and Conclusions

The frequency of crossings by Caribou of a pipeline adjacent to a road with traffic during both insect-free periods and periods of mosquito harassment was significantly less than expected. There was no significant difference when oestrid flies harassed Caribou. Our studies suggest that Caribou react to two types of stimuli in an oilfield: structures possibly resembling concealing habitat (e.g. raised pipeline) and moving objects possibly resembling predators (e.g. vehicles). It was only when Caribou observed these stimuli together (i.e. a pipeline adjacent to a road with traffic) that there was a significant decrease in the percentage of Caribou crossings.

Caribou readily crossed under an elevated pipeline or over a road. The ability of Caribou to cross a single structure (e.g. pipeline) compared to multiple structures (e.g pipeline and road) suggests that separation of roads and pipelines would facilitate Caribou movements in areas of oil development.

There did not appear to be selection for particular pipeline heights within the range we studied (152–432 cm), regardless of the traffic level. Therefore, it appears that the 150 cm minimum pipeline height that was required by the State of Alaska is adequate for Caribou passage.

There was a preference for ramps as crossing sites, although the crossing frequency was low. We doubt that any type of special crossing structure would be able to lessen the impact on Caribou when traffic levels are very high (i.e. one vehicle every two minutes). It may be that ramps do not function effectively under heavy traffic conditions during oilfield construction. Rather, ramps may be more applicable once the oilfield is in production and traffic levels decrease.

TABLE 4. A comparison between the number of ramp crossings[1] and the number of elevated pipeline crossings by Caribou groups, observed in three different locations along the Kuparuk Pipeline, Alaska.

		Ramp crossings		Elevated pipeline crossings	
Structure	Year	Observed	Expected	Observed	Expected
Pipeline/Road Site 1	1981-1982	10	1.07	170	178.93
Pipeline/Road Site 2	1983	5	0.85	36	40.15
Pipeline Site 3	1981-1983	65	5.27	667	726.73

[1]A "crossing" consisted of one or more Caribou crossing under a pipeline between two adjacent VSMs or over a ramp in a more or less cohesive manner. Thus, one Caribou group can account for one or more crossings.

Acknowledgments

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Avoidance of roads by large herbivores and its relation to disturbance intensity

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Keywords
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Abstract

Avoidance of roads has been demonstrated for many animal species, but little is known about the relationship between anthropogenic disturbance levels and the degree of avoidance by animals. We investigated the hypothesis that the strength of road-avoidance behaviour increases with the intensity of the disturbance for a large, disturbance-sensitive herbivore: the forest-dwelling caribou *Rangifer tarandus caribou*. We assessed the behaviour of 53 global positioning system-collared caribou monitored during the gradual modification of a highway over a 7-year period, while controlling for potentially confounding factors. We studied caribou movements, resource selection and distribution before, during and after road modifications at multiple scales. We expected that the degree of avoidance would be positively related to road width, traffic density and the presence of active construction sites. The proportion of individuals that excluded the highway from their home range increased as highway modifications progressed. A lower proportion of caribou locations was found in a 5000 m road-effect zone during and after highway modifications compared with before. Within that zone, caribou avoided habitat types that were selected at the home range scale. Caribou displayed higher movement rates in the vicinity of the highway, especially when traffic density was high. Our data support the hypothesis that avoidance of roads by large herbivores is positively related to disturbance intensity. Our results shed light on the behavioural mechanisms determining avoidance of human infrastructure by large herbivores, and suggest that increased human activity may affect behaviour at multiple scales. Conservation efforts in areas where roads are constructed or modified should be directed towards maintaining access to critical habitat resources, while also restoring habitat quantity and quality.

Introduction

Many human infrastructures influence the survival (Gibbs & Shriver, 2002), reproduction (Gerlach & Musolf, 2000), dispersal (Shepard *et al*., 2008), predator–prey interactions (Rogala *et al*., 2011) and behaviour (May *et al*., 2006) of animals. The North American road network, for example, covers more than 8 million km, and its development shows no sign of slowing (Forman *et al*., 2002). Each year, roads are improved worldwide to allow for greater traffic densities, and new roads are created in previously pristine wildlife habitats. Roads may be complete barriers to small animals (Shepard *et al*., 2008), and certain road widths (Smith-Patten & Patten, 2008) or traffic densities (Gagnon *et al*., 2007) may partially disrupt movements for larger species. Large animals are more likely to be negatively affected by roads, because their vagility and use of large home ranges increase their probability of interacting with roads (Gibbs & Shriver, 2002). Long-lived species with low reproductive rates are also the most vulnerable to road effects (Rytwinski & Fahrig, 2011), because their populations are less able to recover from high mortality rates caused by roads, both directly (e.g. road collisions) and indirectly (e.g. increased predation risk).

Many studies have highlighted negative impacts of human infrastructure on the behaviour of large herbivores. Caribou *Rangifer tarandus* consistently avoid paved and forestry roads (Leblond *et al*., 2011), seismic lines (Dyer *et al*., 2001) and tourist resorts (Vistnes & Nellemann, 2008) by several kilometres. Mountain goats *Oreamnos americanus* were unable to cross a highway in Montana at high traffic densities, and showed behaviours indicative of fear (e.g. running, erected tail and hair) even in the absence of vehicles (Singer, 1978). Moose *Alces alces* in Québec had higher movement rates in the vicinity of a highway, up to 3 h before and after crossing (Dussault *et al*., 2007). The level of disturbance associated with human infrastructure, however, is difficult to assess and their frequent association with other features (e.g. buildings are found near access roads) may confound our ability to disentangle their individual impacts on animal behaviour. Although the avoidance of human infrastructure by large herbivores has been demonstrated in many systems, we know little about the relationship between disturbance levels associated with these infrastructures and their relative degree of avoidance by animals. Such knowledge would be of paramount importance to implement suitable mitigation and conservation measures of human activities for large herbivore populations.

We investigated the hypothesis that the strength of road-avoidance behaviour by animals increases with disturbance intensity associated with the road. We studied a species that repeatedly demonstrates strong reactions to anthropogenic disturbances, the forest-dwelling caribou *R. t. caribou*. Throughout its range, forest-dwelling caribou are subject to several sources of disturbance, of which roads have among the strongest adverse impacts on their distribution and behaviour (Dyer *et al*., 2002; Leblond *et al*., 2011). Caribou may avoid the road surface, but also a road-effect zone (*sensu* Forman *et al*., 2002) of at least 1250 m around paved roads (Leblond *et al*., 2011), possibly because of avoidance of traffic noises (Jaeger *et al*., 2005). Near roads, caribou reduce their food acquisition and increase their energy expenditure, and they tend to have higher movement rates and increased vigilance (Murphy & Curatolo, 1987). Although caribou react strongly to humans and human infrastructure, they were also found to be sensitive to low-disturbance human footprints in the landscape, such as abandoned seismic lines in Alberta (Dyer *et al*., 2001).

To relate the strength of avoidance of caribou to various levels of a disturbance, we studied a long span of spatio-temporally changing highway, therefore controlling for potentially confounding factors such as the surrounding habitat. Highway 175 in Québec, Canada, has undergone significant changes between 2006 and 2010, changing from a two-lane to a four-lane highway, more than three times wider than before. This highway intersects the Charlevoix caribou range, a threatened forest-dwelling caribou population of less than 85 individuals. We used a long-term telemetry programme performed throughout the gradual modification of the highway to assess caribou behaviour before, during and after highway modifications. We thus considered the highway as a dynamic disturbance of varying intensity. We used highway width, human activity on construction sites and traffic density as surrogates of disturbance intensity, expecting that a larger highway, higher traffic densities and the presence of active construction sites (with workers, large trucks and blasting) would result in stronger avoidance (or a wider road-effect zone) by caribou.

We predicted that the highway would have specific effects on caribou behaviour; caribou would cross the highway less than expected when compared with random movements across the landscape (Dyer *et al*., 2002), and caribou would travel through the road-effect zone at a higher movement rate (Dussault *et al*., 2007) because they would perceive this area as a risky environment (Frid & Dill, 2002). We also predicted that as the intensity of highway disturbance increased, the number of caribou crossings would decrease, and that the width of the road-effect zone for caribou would increase in the vicinity of active construction sites (Mahoney & Schaefer, 2002), after the enlargement of the highway, and when traffic densities were high (Gagnon *et al*., 2007).

Materials and methods

Study area

Our study area (approximately 7250 km^2) was located north of Québec City in the Laurentides Wildlife Reserve (between 47°10' and 48°00' N, and 70°30' and 71°50' W), Québec, Canada (Fig. 1). It received a heavy annual snowfall (average >350 cm) and was characterized by a mixture of coniferous and mixed forest stands, typical of the boreal region. Balsam fir *Abies balsamea* and black spruce *Picea mariana* dominated at higher altitudes, whereas valleys and low-lying sectors were covered with mixed and deciduous stands. The study area was approximately 56% forested, and 37% was covered by disturbed habitats, mostly clearcuts of different ages and roads.

Sampling design

The study area was intersected by Highway 175, of which 95.5 km crossed the caribou range. Modifications of the highway began as early as May 2006 and as late as June 2009, and lasted between 100 and 900 days (depending on local terrain conditions, Table 1). Within this period, the highway was widened from approximately 25 to 90 m. Construction sites within the caribou range averaged 7 km in length. There was activity on construction sites during both day and night, and throughout most of the year, with short stops during holidays or because of adverse weather conditions. All highway modifications were completed by the end of 2010. Hence, within a given year, caribou could interact with the highway before, during, and/or after its modification.

Caribou capture and telemetry

Between April 2004 and March 2010, we captured 53 adult caribou (37 F and 16 M) by net-gunning from a helicopter, and fitted them with global positioning system telemetry collars (models TGW 3600 and 4600, Telonics Inc., Mesa, AZ, USA) programmed to collect locations every 3 or 7 h depending upon the collar model. Capture and handling procedures were approved by Animal Welfare Committees (Ministère des Ressources naturelles et de la Faune du Québec and Université du Québec à Rimouski). We recaptured caribou at 1- or 2-year intervals to download location data and replace battery packs. Collars were equipped with a timer release mechanism and were programmed to drop at the end of the study.

Spatio-temporal data

We used digital forest maps (minimum mapping unit size = 4 ha for forest stands, 2 ha for non-forested areas) to determine land-cover types using ArcGIS 9.3 (ESRI Inc., Redlands, CA, USA). These vector maps were derived from aerial photographs taken in 1998 at the scale of 1: 20 000. We updated maps

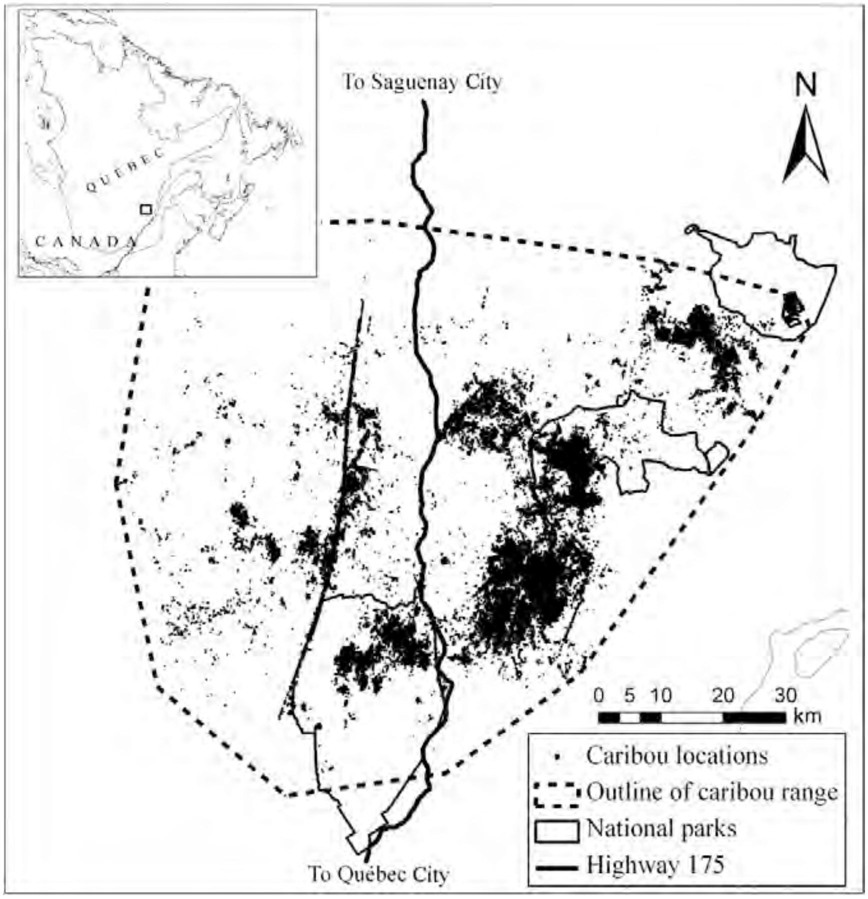

Figure 1 Map of the study area showing Highway 175 crossing the forest-dwelling caribou range in the Charlevoix region, Québec, Canada. Québec National park boundaries and caribou locations ($n = 364\,100$) obtained with the global positioning system telemetry programme between 2004 and 2010 are shown.

Table 1 Length of Highway 175 segments crossing the forest-dwelling caribou range in the Charlevoix region, Québec, Canada, by highway status and year

	Highway status length (km)		
Year	Before highway modifications	During highway modifications	After highway modifications
2004	95.5	0.0	0.0
2005	95.5	0.0	0.0
2006	80.4	15.1	0.0
2007	80.4	15.1	0.0
2008	23.2	61.7	10.6
2009	0.0	80.4	15.1
2010	0.0	36.6	58.9

Highway modifications began in 2006.

each year to include new clearcuts, and combined available habitat types into 10 vegetation classes, including old mature conifer-dominated forests (conifer and mixed stands ≥90 years old; availability = 11.5% of the landscape), young mature conifer-dominated forests (conifer and mixed stands 50–90 years old; 31.0%), mature deciduous forests (>50 years old; 2.8%), recent clearcuts or natural disturbances (≤5 years old; 10.7%), old clearcuts or natural disturbances (6–20 years old; 10.5%), regenerating stands (generally 20–30 years after disturbance; 25.6%), open lichen woodlands (1.0%), wetlands (2.3%), powerlines (0.4%), and others (e.g. lakes, unproductive open lands; 4.2%). We used a digital elevation model with a 50-m resolution to measure local elevation and slope. We updated the map of the highway fortnightly to account for the spatio-temporal evolution of highway modifications and assigned a status to each 1-km road segment, that is either before, during or after road modifications.

We developed a mean hourly traffic index based on summary reports provided by the Ministère des Transports du Québec, which collected data using an electromagnetic traffic counter placed on the highway near the centre of our study area. We used a composite index based on the mean hourly traffic for the whole year, *i* (i.e. 24 different values of $\bar{\chi}_{\mathrm{hour}}$, 1 for each hour), which we modified to consider relative variations in traffic density between months, *j* (12 different average values), and weekdays, *k* (7 different average values). We calculated the index using the equation:

$$\text{Traffic density} = \bar{\chi}_{\mathrm{hour}_i} \times \frac{\chi_{\mathrm{month}_j}}{\bar{\chi}_{\mathrm{month}}} \times \frac{\chi_{\mathrm{weekday}_k}}{\bar{\chi}_{\mathrm{weekday}}}$$

The resulting index, varying between 18 and 786 vehicles per·hour, was assigned to every caribou location based on date and time. Because our index was collected on a single highway, it was independent from road width. This allowed us to overcome a bias often found in other disturbance studies comparing roads of different traffic densities (i.e. large roads are likely to have high traffic and vice versa).

Data analysis

Impacts of the highway on caribou behaviour

To determine if caribou crossed the highway less frequently than expected by chance, we simulated 1000 random highways by translating and rotating the actual highway in our study area to a new location within the caribou range (highway sections that fell outside of the range were deleted). *A posteriori* analyses revealed that the environment next to the real highway was not different from the environment around random roads. We counted the number of crossings of the random highway made by caribou along their movement paths, and performed one-sample *t*-tests comparing the mean annual number of random highway crossings per km to the observed annual number of crossings per km.

To determine if caribou increased their movement rate in the vicinity of the highway, we compared the movement rate ($m\ h^{-1}$) of caribou while crossing the highway (T0) to their movement rate a few hours before (five time-steps preceding T0, T-1 to T-5) and after (five time-steps following T0, T+1 to T+5) crossing (Dussault *et al*., 2007). We also created a continuous time variable increasing from 1 to 11 for each time-step, to take the non-independance of time series into consideration. We used a mixed effects linear regression model with movement rate as the dependent variable, time-step as the fixed effect independent variable, and crossing event (n = 93), individual (n = 12), time, and time^2 (i.e. based on our prediction that movement rate would increase near the highway) as random factors. We computed the least squares means of fixed effects and we performed multiple *post hoc* comparisons between the different time-steps using the Tukey's adjustment.

Impacts of increasing highway disturbance intensity on caribou behaviour

To determine if caribou avoided the highway, we assessed habitat selection by caribou at different spatial scales (i.e. landscape, home range and road vicinity). Our first step was to assess if caribou changed the location of their home range in the landscape according to the intensity of disturbance. To do so, we assessed the correlation between year (used as an approximation of increasing highway disturbance intensity) and highway density ($km{\cdot}km^{-2}$) in annual home ranges (determined using the 100% minimum convex polygon) of individuals that included the highway at least 1 year. Similarly, we performed a Spearman correlation between the number of crossings per km per·individual of the highway and year to determine whether the number of caribou crossings decreased as highway modifications progressed.

To determine if caribou avoided the highway within their home range, we measured the minimal distance between each caribou location and the highway. We included this distance, along with 10 vegetation classes, elevation and slope, in a mixed-effect resource selection function (RSF) model (Manly *et al*., 2002). RSFs contrasted habitat features at observed locations with those found at a similar number of random locations drawn within the annual home range of caribou. We performed collinearity diagnostics and found that collinearity was low in our dataset (variance inflation value < 2). We set individual (year) as a random intercept to account for differences in sample size among caribou and for variation in selection among years. We included a second-order polynomial term for elevation, which was also centred on the mean to improve model fit. We used the predominant vegetation class, young mature conifer forests, as the reference category. We employed k-fold cross-validation to evaluate the robustness of our RSF (Boyce *et al*., 2002), and reported the average $\overline{r_S}$ resulting from 10 iterations. We included vegetation classes and topography as covariates because previous studies have outlined their importance to forest-dwelling caribou (see Leblond *et al*., 2011 for more details).

Although we predicted that the reaction of caribou would gradually increase with the intensity of highway disturbance, we also expected that this gradual response would be more easily observed within a given distance from the highway, likely determined by the perception range of caribou (Olden *et al*., 2004). Consequently, we assessed the impacts of disturbance level on caribou behaviour by constraining our analyses to a small fraction of caribou home ranges located in the vicinity of the highway. To do so, we used different road-buffer zones potentially representative of the perception range of caribou: 1250, 2500 and 5000 m. We explored larger road-buffer zones during preliminary analyses and obtained similar results with widths >5000 m and the global analysis using all caribou locations. By narrowing some of our analyses to the area close to the highway (our finest scale of analysis), we focused on the behaviour of individuals that did not exclude the highway from their home range. To determine if avoidance by caribou was higher near active construction sites and the larger highway compared with the unmodified highway, we evaluated RSF models of the same form as the global model using only the locations (observed and random) within the 1250-, 2500- or 5000-m road-buffer zones, and included interaction terms between minimum distance to the highway and highway status (before, during or after road modifications). In this analysis, we could not consider individual and year as random effects because of small sample sizes.

Although our RSF assessed the relative probability of caribou occurrence in relation to the highway, we wanted to evaluate the impact of disturbance intensity on the proportion of caribou locations within different road-buffer zones. We performed log-linear regressions to determine if the proportion of caribou locations within the 1250-, 2500- and 5000-m road-buffer zones was influenced by traffic density (with low and high values set below or above the median of 186 vehicles per·hour, respectively) or highway status (before, during or after highway modifications). We also performed a linear

Table 2 Annual number of crossings per km and crossings of Highway 175 by forest-dwelling caribou in the Charlevoix region, Québec, Canada, for each highway status

Year	Number of crossings per km (and crossings) of the highway				Mean number of crossings per km of the 1000 random highways ± standard deviation	*t*-value
	Before highway modifications	During highway modifications	After highway modifications	Total		
2004	0.14 (13)	–[a]	–	0.14 (13)	1.00 ± 2.13	12.83**
2005	0.21 (20)	–	–	0.21 (20)	1.19 ± 2.68	11.61**
2006	0.06 (5)	0.07 (1)	–	0.06 (6)	1.50 ± 2.93	15.47**
2007	0.16 (13)	0.07 (1)	–	0.15 (14)	1.87 ± 2.26	24.09**
2008	0.04 (1)	0.26 (16)	0.38 (4)	0.22 (21)	2.98 ± 3.89	22.44**
2009	–	0.01 (1)	0.07 (1)	0.02 (2)	2.16 ± 3.38	19.99**
2010	–	0	0.29 (17)	0.18 (17)	2.84 ± 3.91	21.53**
Total	(52)	(19)	(22)	0.97 (93)	14.17 ± 16.99	24.57**

The observed number of crossings per km was compared with the number of crossings of 1000 simulated (random) highways using *t*-tests.
[a]Highway status unavailable.
$^{**}P < 0.001$.

regression with movement rate as the dependent variable, traffic density as the independent variable and individual caribou ($n = 12$ caribou that crossed the highway) as a random factor, to assess if the movement rate was influenced by increased traffic density. We performed all statistical analyses using SAS 9.2 (SAS Institute Inc., Cary, NC, USA).

Results

Impacts of the highway on caribou behaviour

Only 12 (8 F and 4 M) of the 53 (23%) caribou crossed the highway at least once between 2004 and 2010, and only 93 of the 364 100 (<0.03 %) caribou locations were the end point of a movement step that crossed the highway. The annual rate of caribou crossings was much lower on the real highway than on random roads (Table 2). We observed a negative trend between the number of crossings per km per individual and year ($n = 7$ years; $r = -0.68$; $P = 0.09$).

The movement rate of caribou was higher during crossings of the highway (1011 m h^{-1} on average) than during time-steps just preceding or following crossing (≤683 m h^{-1}, Fig. 2). The movement rate of caribou was also higher during the two time-steps preceding (T-1 and T-2, 7.5 h before crossing on average) and the time-step immediately following the crossing (T+1, 3.5 h after crossing on average) compared with movement rates recorded at every other preceding and succeeding time-steps.

Impacts of increasing highway disturbance intensity on caribou behaviour

The correlation between highway density in caribou home ranges and year was negative ($r = -0.17$, $P = 0.03$). Eight out of nine individuals whose home range included the highway at least once during the study and that we monitored for ≥ 2 years changed the location of their home range to avoid the highway at a large scale during (n = 3) or after (n = 5) its modification.

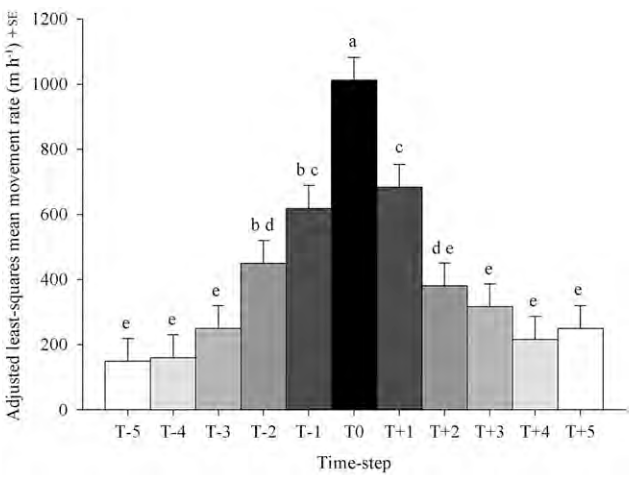

Figure 2 Adjusted least-squares mean movement rate [m h^{-1} + standard error (SE)] of forest-dwelling caribou during crossing of Highway 175 (T0), as well as five time-steps before (T-1 to T-5) and five time-steps after (T+1 to T+5), in the Charlevoix region, Québec, Canada, from 2004 to 2010. Bars sharing the same letter did not differ significantly.

The RSF model using all caribou locations (Table 3) revealed that caribou avoided the highway at the home-range scale. Only 1713 (0.47%), 6974 (1.92%), and 16 067 (4.41%) locations were within the 1250-, 2500- and 5000-m road-buffer zones, respectively, which was 1.3–2.3 times less than random locations. Results from the RSF models focusing on the road-buffer zones showed that caribou generally avoided the highway even when they were in its vicinity (Table 3). Within these zones, they avoided all vegetation classes except power-lines and wetlands within 5000 m.

Caribou crossed the highway at a significantly higher movement rate when traffic density was high [1.60 ± 0.77 (standard

Table 3 Selection coefficients (β) and associated 95% CL of models of resource selection by forest-dwelling caribou in the Charlevoix region, Québec, Canada, from 2004 to 2010

	Within 1250 m of the highway (n = 1713) β (95% CL)	Within 2500 m of the highway (n = 6974) β (95% CL)	Within 5000 m of the highway (n = 16 067) β (95% CL)	All caribou locations (n = 364 100) β (95% CL)
Vegetation class[a]				
Old mature conifer	−1.11 (−1.37:−0.85)	−1.15 (−1.27:−1.03)	−0.48 (−0.55:−0.42)	0.31 (0.15:0.47)
Open lichen woodland			−1.04 (−1.80:−0.28)	1.90 (1.68:2.12)
Wetland	−0.23 (−0.57:0.12)	−0.25 (−0.49:−0.01)	1.01 (0.91:1.12)	0.90 (0.77:1.04)
Deciduous		−1.29 (−1.62:−0.96)	−0.77 (−0.94:−0.59)	0.43 (−0.07:0.93)
Young disturbance (<5 years)	−0.56 (−0.81:−0.31)	−0.55 (−0.69:−0.40)	−0.16 (−0.23:−0.08)	1.37 (1.18:1.56)
Old disturbance (6–20 years)	−1.28 (−1.82:−0.74)	−0.40 (−0.59:−0.22)	−0.41 (−0.52:−0.30)	0.34 (0.17:0.51)
Regenerating (>20 years)	−2.38 (−2.77:−1.99)	−2.10 (−2.28:−1.92)	−1.90 (−2.02:−1.78)	−0.87 (−1.04:−0.71)
Other	−3.27 (−3.82:−2.72)	−2.89 (−3.34:−2.44)	−0.80 (−0.95:−0.65)	−0.61 (−0.76:−0.46)
Powerline	2.29 (1.98:2.60)	2.46 (2.21:2.72)	2.23 (2.01:2.44)	4.28 (3.89:4.67)
Topography				
Elevation (km)	−5.86 (−7.51:−4.20)	−1.43 (−2.57:−0.30)	2.86 (2.42:3.31)	2.12 (0.69:3.56)
Elevation^2	130.05 (108.46:151.63)	75.95 (63.06:88.85)	17.11 (12.24:21.98)	5.80 (−0.61:12.22)
Slope (°)	−0.02 (−0.04: < 0.01)	0.05 (0.04:0.06)	0.04 (0.03:0.04)	−0.03 (−0.04:−0.02)
Distance to the highway				
Minimum distance to the highway (km)	0.57 (0.29:0.85)	0.82 (0.73:0.91)	0.04 (0.01:0.06)	0.03 (0.01:0.05)
Interaction between the minimum distance to the highway (km) and highway status[b]				
During highway modifications	−0.81 (−1.35:−0.28)	−0.14 (−0.27:−0.01)	0.05 (0.01:0.09)	
After highway modifications	−2.07 (−2.59:−1.54)	−2.95 (−3.30:−2.60)	−0.18 (−0.24:−0.12)	
Random effect [individual (year)]				0.11 (−0.08:0.31)
Validation (Spearman $\bar{r}_S$)	0.854	0.955	0.935	0.961

Models were first ran using all caribou locations (n = 364 100) and then using caribou locations within the road-buffer zones (1250, 2500 and 5000 m). Open lichen woodlands within 1250 and 2500 m, and deciduous stands within 1250 m were removed from the models because no caribou locations were observed in these classes. Results of model validation (Spearman's correlation $\bar{r}_S$ values) are provided.
[a]Reference category = young mature conifer-dominated stands.
[b]Reference category = before highway modifications.
CL, confidence limits.

Table 4 Parameter estimates (β) and associated 95% CL of the log-linear regression analyses assessing the influence of the interaction between traffic density or highway status and distance to the highway on the proportion of caribou locations within 1250-, 2500- and 5000-m road-buffer zones by forest-dwelling caribou in the Charlevoix region, Québec, Canada, from 2004 to 2010

	Within 1250 m of the highway		Within 2500 m of the highway		Within 5000 m of the highway	
	β	95% CL	β	95% CL	β	95% CL
Traffic density (reference category = low)						
High	0.25	0.16:0.35	−0.03	−0.08:0.01	<−0.01	−0.04:0.03
Highway status (reference category = before highway modifications)						
During highway modifications	−0.78	−0.91:−0.66	0.02	−0.03:0.07	−0.05	−0.08:−0.01
After highway modifications	−0.17	−0.29:−0.05	−1.48	−1.59:−1.37	−1.45	−1.55:−1.41

High and low traffic densities were set above and below the median value of 186 vehicles per hour of the traffic index, respectively.
CL, confidence limits.

error), P = 0.04]. Moreover, a higher proportion of caribou locations were found within 1250 m of the highway when traffic density was high, compared with when it was low (Table 4). We did not find a similar trend within 2500 and 5000 m of the highway. Caribou also used road-buffer zones less during and after highway modifications compared with before (although not significantly within 2500 m, Table 4).

Discussion

We investigated caribou reactions towards a single gradually modified highway, thereby controlling for potentially confounding factors, and our data support the hypothesis that avoidance of roads by large herbivores is positively related to disturbance intensity. The increased intensity of disturbance resulting from the wider highway, the presence of active construction sites, and higher traffic densities led to stronger behavioural reactions by caribou at several scales. The impacts of human activity on animal behaviour and distribution have been studied extensively in recent years (e.g. Hebblewhite & Merrill, 2008; Rogala *et al.*, 2011). However, to our knowledge, we are the first to relate the strength of avoidance shown by a mammal species towards a human infrastructure with the level of disturbance associated with that infrastructure.

At a broad scale, the few individuals that used the highway before road modifications gradually modified their space use to exclude it from their home range as the modifications progressed. The low number of annual highway crossings by caribou showed a decreasing trend ($P = 0.09$, low sample size) during the course of the study. At a finer scale, we found a lower proportion of caribou locations in the road-buffer zones during and after highway modifications as compared with before, showing that increased road disturbance resulted in stronger avoidance behaviour by caribou. Within these road-buffer zones, caribou avoided the habitat types that they selected elsewhere in their home range. The proportion of caribou locations in road-buffer zones did not decrease with increasing traffic density, as reported for other ungulate populations (e.g. Gagnon *et al.*, 2007), but rather translated into higher movement rates by caribou, which we also interpret as a reaction of caribou to increased disturbance. Although we considered the relative impacts of road width, human activity on construction sites, and traffic density separately, we underscore that these effects may occur simultaneously and act synergistically to influence the behaviour of large herbivores living in human-modified landscapes, thereby degrading habitat quality and landscape connectivity.

Caribou were already found to avoid infrastructure usually associated with little to no human activity, such as forestry roads, seismic lines, dams and pipeline corridors (e.g. Vistnes & Nellemann, 2008). Our results indicate that, even if caribou were reacting to increased disturbance levels, most individuals were using areas away from the highway before its modifications, suggesting that road disturbance had already shaped caribou distribution (May *et al.*, 2006). Individuals establishing their home range far from the highway likely showed the strongest road-avoidance. Therefore, the minimal disturbance intensity we measured (i.e. the unmodified two-lane highway with lowest traffic density) likely exceeded the threshold initiating a behavioural reaction for most caribou.

Animals face a conflicting trade-off when encountering a road: the strong incentive to access resources found on the other side of the road may be overcome by the perceived risks associated with vehicles and human activity. We found that 77% (41/53) of caribou did not cross the highway. It is likely that the individuals most sensitive to road disturbances were not able to access resources potentially available on the opposite side of the highway (including suitable areas protected by national parks). This represents a potential loss of 52–61% of the caribou range, for individuals west or east of the highway, respectively.

Animals generally mitigate the effects of the factors most detrimental to their fitness by avoiding them at broad scales (Rettie & Messier, 2000). As such, the highway was a determining feature for caribou when establishing their home range in the landscape (May *et al.*, 2006). For caribou, this may be a good strategy to increase survival: only three caribou–vehicle collisions occurred in our study area during our 7-year study. Our results suggest that the high disturbance levels found in the vicinity of the highway decreased habitat suitability up to at least 5000 m from it. As found with moose (Dussault *et al.*, 2007), caribou showed increased movement rates many hours before and after crossing, suggesting that a large disturbance zone around the road was perceived as risky, unsuitable habitat. This also suggests that, for most caribou, the perceived benefits of using resources up to 5 km away from the road were not strong enough to offset the perceived risks.

Despite the negative reactions we observed at the population level, some individuals may have benefited from living near the highway. For example, a few individuals may have selected sites to feed in the open terrain under powerlines adjacent to the highway, where abundant shrubs and herbaceous plants can be found. Proximity to the road may also result in lower predation risk for caribou (Muhly *et al.*, 2011). In the Greater Yellowstone Ecosystem (USA), Berger (2007) found that moose used the vicinity of roads to shelter from their traffic-averse predators. Given that individuals using the road-buffer zones reacted to increased disturbance, the perceived risks of living near roads for large herbivores could therefore surpass the former benefits following road enhancement projects or increased traffic levels.

Our study showed that the avoidance behaviour of a large, disturbance-sensitive herbivore is related to disturbance intensity. It may help to understand why sensitive species slowly disappear from fragmented, human-altered landscapes, adding to the global biodiversity decline. Conservation efforts in areas where roads are constructed or modified should be directed towards maintaining access to critical resources and restoring habitat quantity and quality. Although connectivity across the highway could be increased by constructing wildlife crossing structures (Olsson, Widen & Larkin, 2008), the strong avoidance behaviour shown by sensitive species like caribou could limit their effectiveness. In the case of a large or busy road, the wide road-effect zone might prevent individuals from finding and using the passages. To facilitate the adaptation of sensitive species to wildlife passages, we recommend to limit the intensity of human disturbances in their surroundings (e.g. by limiting human presence and vehicle noises; Clevenger & Waltho, 2005).

Our results suggest that the negative impacts of roads and increasing disturbance levels may affect animal behaviour over a wide range of scales. It may take several years after road modifications are completed to further evaluate their full impacts on animal behaviour. Time lags are common in studies assessing long-term impacts of human disturbances (Ewers & Didham, 2006), and forest-dwelling caribou were shown to display such delayed responses (Vors *et al.*, 2007). In the case of the Charlevoix caribou, if the wider four-lane highway eventually becomes a complete barrier to caribou movements, the population could be subdivided into two smaller groups, each having a greater risk of local extinction because of stochastic events (Hanski & Ovaskainen, 2003). We encourage further studies on road-avoidance behaviour to investigate whether behavioural impacts of human disturbances on wildlife may translate to impacts on population dynamics.

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