Simulated impacts of black bear predation on neonatal loss in boreal caribou

by

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Abstract

Boreal caribou (*Rangifer tarandus caribou*) populations are declining across their range and the direct cause is predation. Black bears (*Ursus americanus*) can be significant predators of caribou neonates, but at high black bear densities in the boreal forest only a small proportion of bears could kill neonates without extirpating them. Bear predation is likely driven by bear density and spatial overlap with caribou neonates, but the interactive effect of density and overlap on predation rates is poorly understood. Using a simulation parameterized by empirical black bear and caribou data, we assessed i) how bear movement, habitat use, and density interact to influence predation on caribou neonates, and ii) whether caribou spatially separate from bears during calving to reduce predation risk (spatial separation hypothesis). We placed simulated neonates (≤2 weeks old) in either high-quality calving habitat or throughout caribou range. Neonates remained immobile and were killed when the movement paths of GPS-collared bears came within a specified detection distance. Simulations indicated that individual bears rarely kill neonates, but high-density bear populations can cause high neonatal mortality. However, reducing bear density did not result in a proportional reduction in predation. Bears were less likely to kill neonates in high-quality calving habitat than neonates with no habitat preference, supporting the spatial separation hypothesis. We emphasize the importance of predator density estimates to understand and effectively manage predation in systems with low-density, secondary prey such as boreal caribou. Removing bears is likely not an effective strategy to reduce bear predation on boreal caribou neonates. Future studies should aim to improve our understanding of how landscape alteration may affect bear demography.

Preface

This thesis is an original work by Liam G. Horne. The caribou data used in this research were provided by the Government of Alberta as part of their ongoing caribou monitoring program. The caribou calving analyses were conducted by Dr. Craig DeMars on behalf of the Government of Alberta; I provide an overview of these analyses for this thesis. Black bear density estimates were calculated and provided by Marcus Becker on behalf of the Alberta Biodiversity Monitoring Institute. Black bear movement data from 2013-2015 were provided by Melanie Dickie.

The research project, of which this thesis is a part, received research ethics approval from the University of Regina President's Committee on Animal Care, Animal Use Protocol 13-06, 2013-2015, and the University of Alberta Research Ethics Board, Project Name "Estimating kill rates of boreal caribou calves by black bears using camera collars", No. AUP00003099, 2019-2021.

To date, no manuscripts have been submitted for publication.

Dedication

I dedicate this thesis to the statistician George Box, whose quote, “All models are wrong, but some are useful” became something of a mantra for an ecology grad student thrust into the world of computer simulations.

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Every step of this thesis has been the product of the people around me. Thank you!

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Finally, I would like to extend my sincerest gratitude to the First Nations people who have been stewards of these lands since time immemorial. Treaty 7 is the traditional territory of the Blackfoot Confederacy (Siksika, Kainai, Piikani), the Tsuut’ina, the Iyarhe Nakoda Nations, and the Métis Nation of Alberta. It is also where I call home; thank you for being caretakers of the lands that inspired my passion for ecology.

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1. Introduction

The boreal ecotype of woodland caribou (*Rangifer tarandus caribou*) is federally listed as threatened due to widespread population declines (COSEWIC 2014). The proximate cause of decline is predation, which is ultimately facilitated by human-caused landscape alteration (Sorensen et al. 2008, Johnson et al. 2020, Serrouya et al. 2021) and climate change (Dawe and Boutin 2016, Laurent et al. 2021, Morineau et al. 2023). Boreal caribou avoid predation by living in low-productivity habitat that is spatially separated from predators and their primary prey (James et al. 2004, McLoughlin et al. 2005, Latham et al. 2011a, Leblond et al. 2016, Kittle et al. 2017), and are therefore secondary prey for most predators (Latham et al. 2011b, 2013, Found et al. 2017). Landscape alteration can compromise this spatial separation in two general ways. First, altered landscapes adjacent to caribou range can sustain higher numbers of prey (e.g., moose (*Alces alces*) and white tailed deer (*Odocoileus virginianus*)) because of high availability of ungulate forage (Rempel et al. 1997, Latham et al. 2011b, Serrouya et al. 2011), which can in turn support increased abundance of predators, such as wolves (*Canis lupus*; Latham et al. 2011b, Serrouya et al. 2021) and black bears (*Ursus americanus*; Schwartz and Franzmann 1991), which can "spill-over" into caribou range (DeCesare et al. 2010). Disturbed habitats can thereby increase caribou predation rates via bycatch without reciprocal influence on predator abundance (Boisjoly et al. 2010, Frenette et al. 2020, Serrouya et al. 2021). Second, industrial linear disturbances can increase predator use of caribou habitat (DeMars and Boutin 2018) and increase movement efficiency (Dickie et al. 2017, 2020), both of which may increase encounter rates with caribou (Whittington et al. 2011, McKenzie et al. 2012). Developing strategies that reduce predation rates are necessary to conserve threatened caribou populations (Spangenberg et al. 2019, Serrouya et al. 2019, Keim et al. 2021, McNay et al. 2022, Dickie et al. 2023).

In many caribou populations, predation can be high on neonates (e.g., < 6 weeks old; Adams et al. 1995, Valkenburg et al. 2004, Gustine et al. 2006, Pinard et al. 2012, Leclerc et al. 2014), resulting in low rates of juvenile recruitment which can reduce caribou population growth rates (DeCesare et al. 2012). In multi-predator systems, bears (black and/or grizzly (*U. arctos*)) are often dominant predators of neonate ungulates, including caribou, during the first few weeks post-parturition when they are less mobile (Zager and Beecham 2006, Barber-Meyer et al. 2008, Leclerc et al. 2014, Rayl et al. 2018, Berg et al. 2022). For caribou ecotypes that congregate at calving (e.g., barren-ground caribou), individual bears can kill many calves (Brockman et al. 2017, Rayl et al. 2018, Bonin et al. 2023), but kill rates are unknown, though presumably lower, in systems like the boreal forest where caribou are lower density and disperse at calving. Despite likely lower kill rates and the rarity of caribou in black bears' spring diet in the eastern boreal forest (Mosnier et al. 2008b, Lesmerises et al. 2015, McLaren et al. 2021, Rioux et al. 2022), black bears can be dominant predators of neonates (Dussault et al. 2012, Pinard et al. 2012, Leclerc et al. 2014). This suggests that bear predation of neonates may be the result of high bear densities (Bastille-Rousseau et al. 2011, Pinard et al. 2012, Leblond et al. 2016). Understanding the effects of bear predation on boreal caribou could be improved by expanding studies to western boreal ranges where bear-caribou predation dynamics are largely unknown.

Studies of bear predation on caribou neonates have largely focused on either the bear or the neonate perspective rather than how the predation process connects bear kill rates with neonate predation rates. The predation process is primarily governed by the encounter rate and the probability of a successful kill upon encounter (Lima and Dill 1990). For immobile prey, the encounter rate will be influenced by predator movement (Benhamou 1992, Mitchell and Lima 2002, Bastille-Rousseau et al. 2011), predator-prey spatial overlap (Sih 1984, Sims et al. 2006, Rayl et al. 2015, 2018), and the densities of predator and prey (Holling 1959, Rogers 1972, Beddington 1975, Charnov et al. 1976, Sih 1979). In the context of boreal caribou, if the density of caribou neonates is held constant, then the encounter and predation rate (given a constant kill success rate) will be dictated by bear movement, how much bear space-use overlaps with calving habitat, and bear density. These three parameters have not been explicitly addressed when evaluating bear predation on boreal caribou neonates (but see Mosnier et al. 2008a).

In this paper, we used a simulation to investigate how black bear movement, habitat-use, and density interact to influence predation on boreal caribou neonates. We tracked bear predation of neonates ≤ 2 weeks old, a period during which neonate mobility is limited (typically < 1 km of movement away from the parturition site; Walker et al. 2021) and vulnerability to predation from bears can be high (Leclerc et al. 2014). We parameterized our simulation using location data from a sample of GPS-collared bears occurring within and adjacent to caribou range, remote camera-based estimates of bear density, estimates of caribou density and parturition rates, and caribou habitat selection during calving. Given the rarity of caribou neonates in the spring diet of black bears in the eastern boreal forest, we hypothesized that bear-neonate predation dynamics in the western boreal forest will be driven primarily by high bear density rather than high kill rates by individual bears. Specifically, we predicted that individual bear movement and habitat-use will result in low individual kill rates of neonates; however, these kill rates scaled to the population density of bears will result in a relatively high rate of predation on neonates. We also predicted that decreasing bear density will result in a proportional decrease in the rate of predation on neonates, assuming (as in our simulation) that bear behaviour does not change in response to bear density (James et al. 2004).

We also used our simulation to test whether caribou selection of habitat during calving reduced the risk of neonates being killed by bears. Boreal caribou spatially separate year-round to reduce predation risk, but during calving parturient females are hypothesized to further reduce risk for their vulnerable offspring by dispersing from conspecifics (Bergerud et al. 1990, DeMars et al. 2016) and increasing spatial separation from predators (Bergerud et al. 1990, Leblond et al. 2016). The spatial separation hypothesis, however, has not been directly evaluated with respect to bear predation of boreal caribou neonates. Here, we test the spatial separation hypothesis. If parturient caribou select calving habitat to reduce spatial overlap between bears and neonates and thus reduce neonate predation risk from bears, then we would expect bear predation rates to be lower when caribou calve in high-quality calving habitat compared to if they calved throughout caribou range.

2. Materials and Methods

2.1 Study Area

Our study area straddles the Alberta-Saskatchewan border in Canada and comprises parts of the Cold Lake (CL) and East Side Athabasca River (ESAR) boreal caribou population ranges in northeastern Alberta (Fig. 1). These ranges are situated within the Boreal Plains ecozone and are comprised of a mosaic of deciduous and conifer upland forests interspersed with low-lying bog and fen peatland complexes (See Appendix E for details on land cover classes). There is minimal elevational difference between lowland and upland habitats (450 to 750 m above sea level). Petroleum extraction and timber harvest are common in the region. Disturbances associated with petroleum extraction include well pads and linear disturbances (e.g., seismic lines and pipelines). Cut blocks from timber harvest are present in upland deciduous and conifer stands (James et al. 2004, Dickie et al. 2020). Fire is a common source of natural disturbance, and the CL and ESAR ranges have comparable 40-year fire histories (Konkolics et al. 2021). Moose and white-tailed deer are the most abundant ungulates in the region, with white-tailed deer density increasing over the past three decades (Latham et al. 2011b, Dawe and Boutin 2016, Laurent et al. 2021). Potential ungulate predators in our study area besides black bears are wolves, coyotes (*Canis latrans*), and Canada lynx (*Lynx canadensis*). Caribou calves can also be killed by golden eagles (*Aquila chrysaetos*) and wolverines (*Gulo gulo*) (Adams et al. 1995, Gustine et al. 2006), but these species are rare in our study area.

We defined the study area by fitting a 100% minimum convex polygon (MCP) around all GPS-collared black bear locations used in this study (see 2.2 below). This 10,537 km^2 area overlaps 4,646 km^2 of the CL and 1,506 km^2 of the ESAR ranges (as defined by the Government of Alberta; Fig. 1). Both ranges have a high degree of anthropogenic landscape disturbance (CL: 76%, ESAR: 78%) based on the Environment Canada definition of disturbance (Environment Canada 2019). Within the study area, the CL range overlaps 2,395 km^2 of the Cold Lake Air Weapons Range (CLAWR), where civilian access is restricted and there is no timber harvest (Czetwertynski et al. 2007). Black bears are hunted in the spring and fall, except in the CLAWR where bear hunting is minimal (Czetwertynski et al. 2007).

2.2 Bear Movement Data

We deployed 69 GPS collars on black bears in northeastern Alberta from 2013-2015 (2013: n=2, 2014: n=22, 2015: n=20; see Dickie et al. 2020, 2021 for more details) and 2019-2021 (2019: n=5, model Vertex Plus, Vectronic Aerospace, Berlin, Germany; 2021: n=20, model LiteTrack Iridium, Lotek Wireless, Newmarket, Ontario, Canada). During captures, we targeted bears in and adjacent to the CL and ESAR ranges. Bears were captured using either helicopter darting or culvert traps. Capture and handling procedures followed approved animal care protocols (2013-2015: University of Regina Animal Use Protocol 13-06; 2019-2021: University of Alberta Animal Use Protocol AUP00003099).

We were unable to retrieve five collars from 2019-2021 due to collar failures (Vectronic: n=1, Lotek: n=4). For the remaining collars, we used GPS data collected within the caribou calving season (15 April – 15 July; DeMars and Boutin 2018). Collars recorded GPS locations (‘fixes’) every 5, 10, 15, or 60 minutes, but we used the *AMT* package (Signer et al. 2019) to resample fixes to every 60 (± 2.5) minutes to standardize the maximum number of fixes possible per bear per calving season. We screened the GPS data before analysis to remove potential erroneous fixes (Appendix A) and remove fixes recorded before spring den departure (Appendix B), after which we excluded collar deployments with <85% fix success (Frair et al. 2004). Additionally, we excluded one bear (2019) from the analysis because it dispersed far out of caribou range in early spring, and one bear (2021) because it was harvested two days after collar deployment.

Following this processing, we used movement data from 54 bears and 61 bear-years for our simulation (28M:26F; 4M & 3F bears had data spanning 2 years). We considered bear-year to be our sampling unit because home range overlaps (100% MCPs) between years for the same bear were comparable to overlaps between bears in the same year, suggesting that bear-years could be considered independently (Appendix C). Monitoring times averaged 51 days per collar (range 6-92), with an average fix success of 94% per collar (range 86-100; Appendix D).

2.3 Bear Density

Bear density was derived from remote camera data, the size of the study area, and the timing of spring den departure. We derived 594 estimates of bear density (2016: n=20, 2017: n=24, 2018: n=62, 2019: n=240, 2020: n=202, 2021: n=46) at 288 camera locations that were operational for an average of 165 days per camera per year (range 27-365; Fig. 1). We calculated two density estimates for our study area using the time in front of camera (TIFC) method for each camera (Becker et al. 2022) and averaging all camera estimates. These two estimates (average and reduced) covered a range of plausible densities and tested the effect of changing bear density on predation rates. In brief, the TIFC approach treats the camera's field of view as a quadrat, deriving a density estimate for each camera by accounting for the time bears spent in the field of view while correcting for behavioural alterations due to the camera's presence. For the average density scenario (157 bears/1000 km^2), we corrected for only unambiguously altered behaviours. For the reduced density scenario (102 bears/1000 km^2), we corrected for all potentially altered behaviours and calculated the lower 90% confidence limit of the mean density estimate (see Becker et al. 2022 for details). We calculated population abundances of 1649 bears (average) and 1072 bears (reduced) by multiplying the density estimates by our study area size. We corrected bear abundance for the timing of den departure by multiplying the specified bear abundance by the cumulative proportion of bears that had departed their dens each day. Most bears (88%, n=26) had departed their dens by April 22 (Appendix B).

2.4 Neonate Density and Parturition Timing

For all scenarios in our simulation, a total of 177 neonates (CL: n=133; ESAR: n=44) were born during the calving season, as determined by multiplying female abundance (female density × caribou range size within our study area) by the parturition rate for boreal caribou. We used the most recent female caribou density estimates for the CL (36.7 females/1000 km^2) and ESAR (37.6 females/1000 km^2) ranges (McFarlane et al. 2020, Table S3.3). We used a 0.775 parturition rate based on the average of recent parturition rates reported for boreal caribou in northeastern British Columbia (0.79; DeMars 2015) and northern Ontario (0.76; Walker et al. 2021).

We inferred parturition dates based on decreases in the movement rates of 62 GPS-collared adult female caribou from 2009-2015 (CL: n=13 caribou-years; ESAR: n=82 caribou-years) following DeMars et al. (2013). The inferred parturition dates were binned into 7-day periods starting April 15, which resulted in a distribution of weekly parturition probabilities throughout the calving season. No neonates were born from April 15-21. Nearly 80% of parturition occurred from April 29-May 26, with the highest parturition rate from May 6-12 (Appendix D).

2.5 Neonate Spatial Distribution

Neonates were considered immobile and were randomly distributed within the spatial constraints dictated by a given scenario (see below). Neonate distribution was further constrained such that neonates were spaced ≥ 1 km apart to account for the dispersal behaviour of boreal caribou at calving (Bergerud et al. 1990, DeMars et al. 2016). To assess the influence of bear movement, habitat-use, and density on neonate predation rates (i.e., the proportion of neonates killed), neonates were distributed within habitat that was highly selected by parturient females during calving (“high-quality” calving habitat). To test the spatial separation hypothesis, we compared predation rates when neonates were distributed within high-quality calving habitat versus when neonates were distributed throughout caribou range regardless of habitat quality. We evaluated calving habitat selection using a use-available resource selection function (RSF) that compared GPS locations of females accompanied by a calf ≤ 4 weeks old (use) to random locations within each caribou range (available). We identified females that calved each year and whether the calf survived to 4 weeks of age (CL: n = 8, 2013-2015; ESAR: n = 42, 2009-2015) following DeMars et al. (2013). The resulting range-specific RSFs were 30 m × 30 m resolution maps of the relative habitat quality for female boreal caribou with a calf at-heel. The relative habitat quality values were divided into 10 bins, with the highest bin considered high-quality calving habitat for the simulation (Fig. 1). See Appendix E for more details on RSF development.

2.6 Simulation Methodology

We tracked bear-neonate encounters on an hourly basis throughout the calving season. To simplify tracking, we assigned each GPS fix for each bear to the nearest whole hour to advance hourly bear movements simultaneously during the simulation. There are no data on the distances at which bears encounter caribou neonates in a forested environment or how likely they are to kill a neonate upon encounter. As such, we ran simulations across a range of plausible detection distances (20, 50, 100, 300, 500 m) and kill success probabilities (0.2, 0.5, 0.8) to assess the sensitivity of our outputs to these parameters. In our simulation, these parameters simply varied the number of chances bears had to encounter neonates (detection distance) and the number of encounters that resulted in a kill (kill success).

At the start of each iteration of the simulation, we assigned a birth week to each neonate based on the distribution of estimated parturition dates and assigned a random birth hour within that week. One complete iteration involved repeating the following steps every hour from April

15 until the end of the calving season (July 15). Any neonates born in the given hour were randomly placed according to the scenario (high-quality habitat or caribou range), and ≥ 1 km away from existing neonate locations. Neonates remained on the landscape until they were killed by a bear or survived to 2 weeks of age. Next, bears with GPS fixes in the given and subsequent hour (i.e., 57.5-62.5 minutes later) were moved in a straight line from their current to their next location. An encounter was recorded if a bear came within the specified detection distance of a neonate. Upon encountering a neonate, the specified kill success parameter was used as the probability in a binomial draw to determine whether the bear killed the neonate. If a bear did not have a fix in the subsequent hour, only the bear's current location (i.e., no movement) was used. If multiple bears encountered the same neonate in the same hour, only the bear closest to the neonate would be used for the binomial draw. If a bear encountered a neonate but did not kill it, then the neonate remained in the same location.

We estimated kills by the bear population in the same hour that the kill(s) by the collared bears occurred, which allowed us to account for hourly variability in bear sample size (Appendix D) and for the depletion of neonates due to predation (Rogers 1972, Charnov et al. 1976). If bears killed neonates, these neonates were removed from the landscape, and an hourly kill rate was calculated as the number of neonates killed in the given hour divided by the number of bears with a GPS fix in the given hour. We estimated total number of neonates that would be killed by the population of bears by multiplying the hourly kill rate by the specified bear abundance for the given hour and scenario. After subtracting the number of neonates already killed in the given hour from the total, we randomly removed the remaining number of neonates killed by the bear population from the pool of neonates still on the landscape. Due to a limited sample of bears collared after July 15, any neonates that were still ≤ 2 weeks old at the end of the calving season were assumed to have avoided bear predation.

2.7 Simulation Analysis

We ran 30 iterations (calving seasons) for each of the 60 scenarios (2 bear densities and 2 neonate distributions, each with 15 sensitivity analysis scenarios). At the end of each iteration, we calculated the average kill rate per bear by summing the hourly kill rates for the bear population (number of neonates killed by the population/bear abundance in that hour) over the whole calving season, and we calculated the predation rate as 100 × (total neonates killed/177 neonates born). For each scenario, we calculated the mean kill and predation rates across the 30 iterations, then estimated bootstrapped 95% confidence intervals (95% CI) for each rate (n = 10,000 iterations).

To evaluate the effect of bear density, we compared predation rates in high-quality calving habitat scenarios when bear density was considered average (157 bears/1000 km^2; 1649 bears) versus reduced (102 bears/1000 km^2; 1072 bears), while controlling for detection distance and kill success. To evaluate the spatial separation hypothesis, we used the average bear density scenario to compare predation rates when neonates were distributed within high-quality calving habitat versus throughout caribou range (controlling for detection distance and kill success). Both comparisons were paired designs, where the effect size of the manipulated variable is measured as the mean of the difference in predation rate between paired replicates (not the difference between the means). Our replicates (iterations) were arbitrarily paired, so we randomized which iterations were paired, calculated the mean difference in predation rate among pairs, then bootstrapped this process (n = 10,000 iterations) to calculate an overall mean difference in predation rate (effect size) and estimate 95% confidence intervals. The differences were calculated to align with our predictions, such that a positive value indicates that the predation rate was lower at reduced versus average bear density, and the predation rate was lower when neonates were distributed within high-quality calving habitat versus throughout caribou range. All simulations and analyses were performed using R Statistical Software (R Core Team 2023; v4.2.3).

3. Results

3.1 Influence of Bear Movement, Habitat-Use, and Density on Neonate Predation Rates

Increasing detection distance and kill success probability increased the neonate predation rate (Fig. 2), but we focused on the scenarios with a 0.8 kill success probability because varying kill success did not fundamentally change the simulation inferences (see Appendix F for other scenarios). Scaling to a population of 1649 bears (average density scenario), the average kill rate was consistently low (range: 0.02 to 0.1 neonates/bear), while the predation rate ranged from 16.1% to 91.3% of all caribou calves being killed by bears (Fig. 2). To kill the full cohort of neonates, approximately 1 out of every 9 bears would need to kill one neonate each. The mean hourly sample size of bears from peak calving (May 6-12) onwards was 40.3 bears per hour (Appendix D), so each kill could be extrapolated, on average, to ~41 kills or 23% of neonates killed by the bear population. However, this ability of bear density to drive predation rate was limited by low detection distances. For example, with a 20 m detection distance, only 16.1% (95% CI: 10-24%) of neonates were killed despite bears being 9-fold more abundant than neonates in our study area (Fig. 2B). The pattern of low kill rates scaling to high predation rates and the limiting effect of small detection distances on predation rate were also observed in the reduced bear density scenarios (Appendix F).

To test the effect of reducing bear density on neonate predation rate, we focused on one detection distance (100 m) with an intermediate predation rate (Fig. 2) so that the effect of density was not limited by the minimum or maximum limits of the predation rate. Reducing the bear population from 1649 to 1072 bears reduced the mean neonate predation rate from 48.1% to 44.3%, which was much less than the ~35% decrease in bear density (Fig. 3). The observed mean difference in predation rate between paired iterations comparing average versus reduced bear density was 3.8 percentage points (95% CI: -6.8 to 14.5 percentage points), or about 7 fewer neonates being killed on average at the reduced bear density. In contrast, a directly proportional (35%) reduction in predation rate would have amounted to a mean difference in predation rate of ~17 percentage points. The predation rate was not always lower in the reduced than in the average bear density scenario, as indicated by the 95% CI overlapping zero. The other detection distances did not substantially alter the simulation inferences (Appendix F).

Across either bear density scenario, the movement and habitat-use of individual bears rarely resulted in a bear killing more than one neonate in a calving season (maximum of 4 neonates), and high rates of neonate predation were not due to just a few bears (27 unique bears killed at least one neonate in high-quality habitat). Further, there did not appear to be a sex bias in the bears that killed at least one neonate ($\chi^2 = 0.074$, df = 1, p = 0.79).

3.2 Spatial Separation Hypothesis

To assess the spatial separation hypothesis, we used the average bear density with one detection distance (100 m) and kill success probability (0.8) so that the effect of neonate distribution was not limited by the minimum or maximum limits of the predation rate. The neonate predation rate due to bears was lower on average when caribou calved in high-quality calving habitat (48.1%) compared to when they calved throughout caribou range (60.6%; Fig. 4). The mean difference between paired iterations comparing the two neonate distributions was 12.5 percentage points (95% CI: 2.6 to 22.6 percentage points), or ~22 fewer neonates killed, on average, when caribou calved in high-quality habitat. The mean differences in predation rate were smaller than 12.5 percentage points in most scenarios, but were positive in all but one scenario (average bear density, 50 m detection distance, 0.2 kill success; Appendix F).

The lower rate of neonate predation in high-quality calving habitat versus throughout caribou range was reflected by a much lower proportion of bear GPS locations occurring within high-quality habitat (1.4%) than within caribou range (58.4%). Including the bear movement paths between locations did not substantially alter these proportions (Appendix G). Additionally, high-quality habitat had fewer bear GPS locations for its areal coverage (3.0 fixes/km^2) than caribou range or broader categories of calving habitat (Appendix G). However, neonates were less dispersed on average when calving in high-quality habitat than when calving throughout caribou range. For example, during peak parturition (May 6-12; scenario in Fig. 4), neonates born in high-quality calving habitat were a median distance of 3.2 km from the nearest neonate, while neonates born throughout caribou range were a median distance of 6.3 km from the nearest neonate (Appendix H).

4. Discussion

Predator-caused mortality of boreal caribou is driven primarily by predator-caribou spatial overlap and predator density (McLoughlin et al. 2005, Fryxell et al. 2020, Serrouya et al.

2021, DeMars et al. 2023). Although high densities of black bears have been suggested as the driver of high rates of bear predation on boreal caribou neonates (Bastille-Rousseau et al. 2011, Pinard et al. 2012, Leblond et al. 2016), the interactive effect of bear-neonate spatial overlap and bear density on predation rates is understudied. Our use of simulations allowed us to understand both the predator and prey perspective of the predation process while accounting for bear density. Bear movement and habitat-use led to low spatial overlap between bears and neonates in high-quality calving habitat, resulting in low average kill rates by individual bears. However, these low kill rates could cause high neonate mortality when scaled to our average or reduced bear density estimates. Finally, as predicted, neonate survival was higher on average when female caribou calved in high-quality habitat compared to when they had no habitat preference during calving.

In low-density caribou populations, predators can be a major source of caribou mortality even if caribou are an unimportant food source for these predators (Wittmer et al. 2005, Boisjoly et al. 2010, Latham et al. 2011b, Found et al. 2017). Our simulation results supported this relationship for black bears and boreal caribou neonates. From the caribou perspective, more than half of neonate calves could be killed by bears at moderate to high detection distances (Fig. 2). However, the ability of high bear densities to drive high rates of predation on neonates was limited by low detection distances, suggesting that there should be a selective pressure for maternal-neonate pairs to reduce their detectability to bears. In forested environments where bears may detect neonates using olfactory rather than visual cues, wet calving habitats (i.e., peatlands) may degrade olfactory cues more quickly than drier habitats (Reed et al. 2011).

From the bear perspective, it seems unlikely that neonate presence encourages bears to forage in calving habitat as proposed by Latham et al. (2011a) given that kills were infrequent and stochastic for bears and the small size of caribou neonates (5-13 kg; Kojola 1993, Adams 2005). Bears may be able to actively hunt and kill ungulate neonates in systems where neonates are high-density and/or congregated at calving grounds (Brockman et al. 2017, Rayl et al. 2018, Twynham et al. 2021, Ruprecht et al. 2022, Bonin et al. 2023), but where neonates are low-density and dispersed, it is more likely that they opportunistically kill neonates (Bastille-Rousseau et al. 2011). Indeed, <6% of the average density bear population in this study could kill >1 neonate each without extirpating all neonates, while bears killed an average of 14.1 and 27 caribou calves each during the calving season in Alaska and Newfoundland, respectively (Brockman et al. 2017, Rayl et al. 2018). Therefore, proportions of black bear populations that select for caribou calving habitat (33%; Latham et al. 2011a, 8%; Bastille-Rousseau et al. 2011) could not realistically have high success in killing caribou neonates, and are likely selecting these areas for reasons other than caribou neonates.

Bear density was the primary driver of the neonate predation rate at either the average or reduced density estimates in our simulation, which were 87 and 57 times higher than wolf densities above which boreal caribou populations tend to decline (1.8 wolves/1000 km2; Serrouya et al. 2021). Bears can exist at higher densities than wolves and caribou because their omnivorous diet enables them to obtain energy from multiple trophic levels (Mosnier et al. 2008, McCauley et al. 2018). Such ‘top-heavy’ communities (*sensu* McCauley et al. 2018) are counterintuitive to our understanding of classical biomass pyramids (Elton 1927, Lindeman 1942), and not explicitly accounting for such high bear densities can lead to erroneous conclusions about the importance of black bear predation on caribou. For example, McLaren et al. (2021) attributed the absence of caribou in black bear scat in Ontario to regional variability in bear predation without addressing how rare it would be for a bear to kill a neonate and to collect that scat given their reported bear (125 bears/1000 km^2) and caribou (minimum 4.5 caribou/1000 km^2) densities. Accounting for bear density provides an alternative explanation to regional variability for how caribou can comprise <0.5% of black bear diet (Mosnier et al. 2008b, Lesmerises et al. 2015, McLaren et al. 2021, Rioux et al. 2022), but kill 30-55% of calves (Dussault et al. 2012, Pinard et al. 2012, Leclerc et al. 2014) in the eastern boreal forest.

Black bear densities used in our simulations were comparable or lower than those reported elsewhere for the boreal forest (120 bears/1000 km^2 (Mosnier et al. 2008a); 200-400 bears/1000 km^2 (Walker et al. 2021); 220 bears/1000 km^2 (Bastille-Rousseau et al. 2011, Pinard et al. 2012, Leblond et al. 2016)). Density estimates from adjacent systems were more variable, but also suggest that our estimates were plausible: the interior mountains of British Columbia (257 bears/1000 km^2; Mowat et al. 2005); the southern Alberta Rockies (104.1 bears/1000 km^2 on Crown land; Loosen et al. 2019); Newfoundland (48.5 bears/1000 km^2; Rayl et al. 2018); and the northern range of Yellowstone National Park (200 bears/1000 km^2; Bowersock et al. 2023). Finally, black bears may be most abundant in areas without grizzly bears, as in our study area (Mowat et al. 2005, Bradley et al. 2024).

Bear density was positively related to the rate of predation on neonates, but the change in predation rate was not proportional to the change in density. Given our assumption that bear behaviour did not change in response to bear density, this result directly contradicts the prediction that rates of predation on caribou should change in direct proportion to changes in predator density (James et al. 2004). This non-linear effect was due to the combination of high bear densities and the real-time depletion of neonates. Depletion of prey is the simplest way that changing predator densities can influence prey availability and thus encounter rates (Rogers 1972, Charnov et al. 1976), with important but often ignored implications for predator-prey dynamics (Rogers 1972, Sih et al. 1998, McCoy et al. 2012). Although bear behaviour presumably does change with conspecific density, a key assumption of scaling up to the density of the bear population was that black bears do not exclude conspecifics from their home ranges. This assumption was met for our study (Appendix C) and in other boreal forest systems (Samson and Huot 2001, Mosnier et al. 2008a). Our simulation did not account for the hypothesized positive relationship between predator density and predator-prey spatial overlap (i.e., “spill over”; Rand and Louda 2006, DeCesare et al. 2010, Frost et al. 2015), which means we may have underestimated the difference in neonate predation rate between bear densities. However, any differences in predation rate caused by spatial overlap would likely be smaller than that observed in our test of the spatial separation hypothesis (see 3.2), in which we contrasted the two extremes of spatial overlap. Thus, we believe that our methods were appropriate to highlight that at the densities used in this study, reducing bear density may have limited effect on predation rates due to compensatory predation of neonates that would have been killed at higher bear densities.

Parturient caribou and other ungulates employ various strategies to reduce predation risk to their offspring while balancing other factors such as nutritional demands and their own survival (Bergerud and Page 1987, Bowyer et al. 1999, Barten et al. 2001, Duquette et al. 2014, Berg et al. 2021). Boreal caribou select habitat to decrease neonate predation risk from wolves (Bergerud et al. 1990, Leclerc et al. 2014, Leblond et al. 2016, Viejou et al. 2018), but it was unclear whether spatial separation could simultaneously reduce predation risk from black bears (Rettie and Messier 1998, Leclerc et al. 2014, Leblond et al. 2016). Our results do not imply that all caribou calve exclusively in the highest quality calving habitat, but rather that boreal caribou with a calf at-heel select habitat within caribou range in part to reduce predation risk from black bears – a finding consistent with differences in bear and caribou habitat selection in our study area (Latham et al. 2011a). Even if caribou mothers are not as effective at avoiding predation from bears as wolves (Leclerc et al. 2014, Leblond et al. 2016), we demonstrated that habitat selection by parturient females may increase neonate survival compared to having no habitat preference, even with high rates of bear predation. Boreal caribou also disperse at calving to reduce predation risk to neonates (DeMars et al. 2016), but our results show that dispersal and spatial separation can be interactive. By dispersing in high-quality habitat, parturient caribou were able to reduce predation risk to neonates more effectively than if they were just maximally dispersed.

Our simulated predation rates were above and below reported rates of bear predation, but not all our results were biologically realistic. Using mean demographic rates for the CL and ESAR populations (adult female survival: 0.83, recruitment rate: 12 calves/100 adult females; Hervieux 2013), we would expect ~87% of calves to be dead by late winter $\left(1 - \frac{228\ adult\ females \times 0.83 \times 0.12}{177\ calves}\right)$. Although juvenile caribou mortality can be low from post-calving to late-winter (Seip 1992, Stuart-Smith et al. 1997, Pinard et al. 2012), predation rates near or greater than 87% were likely unrealistic given we only monitored the first 2 weeks of neonate life and one source of mortality. Accordingly, it is also unlikely that bears can effectively detect and kill neonate caribou at distances >300 meters, despite bear's ability to detect scents from long-distances (Bacon and Burghardt 1976). The highest reported black bear-specific predation rate for boreal caribou calves (up to 8 weeks old) is 55% (Dussault et al. 2012), while studies that monitored survival up to 2 weeks old reported 20% of calves killed by black bears (Leclerc et al. 2014) and 15% general mortality rates (Walker et al. 2021) (Fig. 2). However, it is difficult to directly compare rates of bear predation between populations because the impact on caribou is contingent upon caribou population size and adult female survival (DeCesare et al. 2012). Continuing our above example, 44% neonate survival (56% predation rate) would leave enough female calves to replace the adult females that die in our study area (assuming an equal sex ratio of calves), but not enough in populations with lower adult female survival (e.g., Gaspésie caribou; Environment and Climate Change Canada 2022).

Despite speculation about increasing black bear density in the boreal forest (Leblond et al. 2016), the extent of bear population growth in response to human-caused landscape alteration is poorly understood. As omnivores, bears can have demographic responses to increases in both ungulate availability (Schwartz and Franzmann 1991) and forage availability (Reynolds-Hogland et al. 2007, Mowat et al. 2013, Bradley et al. 2024), both of which have increased in our study area over recent decades due to landscape alteration and climate change (Laurent et al. 2021, Serrouya et al. 2021). Both linear disturbances (Dawe et al. 2017) and polygonal disturbances (Brodeur et al. 2008) can increase berry availability, a predictor of bear population growth (Reynolds-Hogland et al. 2007), but this relationship is untested in the low productivity boreal forest (Mosnier et al. 2008b). Similarly, it is unknown if bear density has increased in response to the 17.5-fold increase in white-tailed deer density (Latham et al. 2011b). Black bear reproduction increased in response to an increased twinning rate and a 12-fold increase in moose density following fire disturbance in Alaska (Schwartz and Franzmann 1991); however, McLellan (2011) suggested that grizzly bear populations exhibit lower densities with increased terrestrial meat consumption.

Regardless of whether bear density has increased, at high bear densities even a marginal increase in the average bear’s use of calving habitat translates to many bears with an increased probability of encountering a neonate. Linear disturbances may directly facilitate bears moving into calving habitat (DeMars and Boutin 2018, Dickie et al. 2020). Increased graminoids and forbs on linear (Finnegan et al. 2018) and polygonal disturbances (Bork et al. 2021), i.e., spring forage for bears (Mosnier et al. 2008b, Lesmerises et al. 2015, McLaren et al. 2021), may also facilitate frequent bear movements among high-quality forage patches that increase bear-neonate encounters (Bastille-Rousseau et al. 2011). Despite the potential for increased bear-caribou encounters due to increased bear-neonate spatial overlap and high bear density in our industrialized study area, we showed that high-quality caribou habitat continues to represent the area on the landscape with the lowest risk of bear predation.

Our simulation demonstrated a wide range of plausible rates of bear predation, but even in scenarios with lower average predations rates, predation varied stochastically among iterations (i.e., calving seasons). This variation reflected the likely opportunistic nature of bear predation on boreal caribou (Bastille-Rousseau et al. 2011) and is consistent with the high variability in juvenile survival for most ungulate populations (Gaillard et al. 1998). Additionally, bears can track spring green-up (Bowersock et al. 2021), and stochastic events like delayed green-up could increase rates of bear predation if they are foraging over larger and/or less productive areas (i.e., calving habitat) to meet nutritional demands during the spring growth period (Noyce and Garshelis 1998). Small ungulate populations are vulnerable to stochastic bouts of high predation (Festa-Bianchet et al. 2006), so efforts to increase caribou population size will likely make them more resilient to the impacts of stochastic bear predation.

4.1 Conservation Implications

Our results emphasize that predator density estimates are critical to contextualize the potential impact of small changes in encounter rates between predators and secondary, low-density prey, such as boreal caribou. Recent density estimates for large predators are often based on genetic mark-recapture techniques, but the TIFC method used here (Becker et al. 2022) may be an alternative that could improve the availability of predator density estimates by using an existing and multi-purpose data source (i.e., remote cameras). However, the TIFC method should be validated using multiple predator species in multiple regions to assess its accuracy. Studies of predator diets (e.g., via scat, isotope analysis, or video-collars) are ill-suited to understanding the importance of predation for boreal caribou. These studies have a low chance of sampling the individual predator that killed the prey, especially for high-density predators like bears. Studies of cause-specific mortality are helpful to identify important predators of caribou (Wittmer et al. 2005, Gustine et al. 2006, Pinard et al. 2012, Mahoney et al. 2016), but effective management strategies need to account for the influence of predator density from both the predator and prey perspectives. Simulations are not meant to be perfectly realistic, but for high density predators they may be the only feasible way to estimate the population-level impacts of small changes in predator use of caribou habitat that may otherwise seem unimportant (Mosnier et al. 2008a).

Conservation actions to improve caribou population demography are expensive (Schneider et al. 2010), and need to understand the mechanisms of decline to be effective (DeMars et al. 2023). Bear removal programs, for example, are poorly suited for boreal caribou systems because many bears would likely need to be removed, but setting a target bear density would be challenging given the effects of bear predation were not linear with bear density. Many more total bears than wolves would need to be removed for a bear reduction to be comparable to that of wolf culls (45-80% reduction; Boertje et al. 1988, Hayes et al. 2003, Hervieux et al. 2014). Such removals would be expensive and possibly unacceptable to the public at large, especially given that most bears killed in a cull would not have killed a neonate (Fig. 2A) and removals would have to be continuous to be effective (Mosnier et al. 2008a).

If bear predation is influenced by bear density and spatial overlap with neonates, then addressing the factors that increase bear density and spatial overlap is relevant to boreal caribou conservation. Human-caused landscape alteration can increase bear overlap with boreal caribou calving habitat (DeMars and Boutin 2018). Avoiding future alterations and remediating existing alterations in and near high-quality calving habitat could benefit neonate survival by reducing spatial overlap with bears (Dickie et al. 2021, Keim et al. 2021), and lends support to the "gain-in-refugia" caribou management approach when allocating limited conservation dollars (DeMars et al. 2023). Conversely, little is known about the link between landscape alteration and bear demography in the boreal forest, with patterns of habitat selection often used as a proxy (e.g., Brodeur et al. 2008). Future studies could use bear densities in comparable but unaltered boreal forest (e.g., northern Saskatchewan; Neufeld et al. 2021), metrics of bear hunter effort and success (Wolfe et al. 2016, Frenette et al. 2020, Trump et al. 2022), and/or traditional/local ecological knowledge (Ferguson and Messier 1997, Anadón et al. 2009) to understand the relationship between bear density and increased landscape alteration over recent decades.

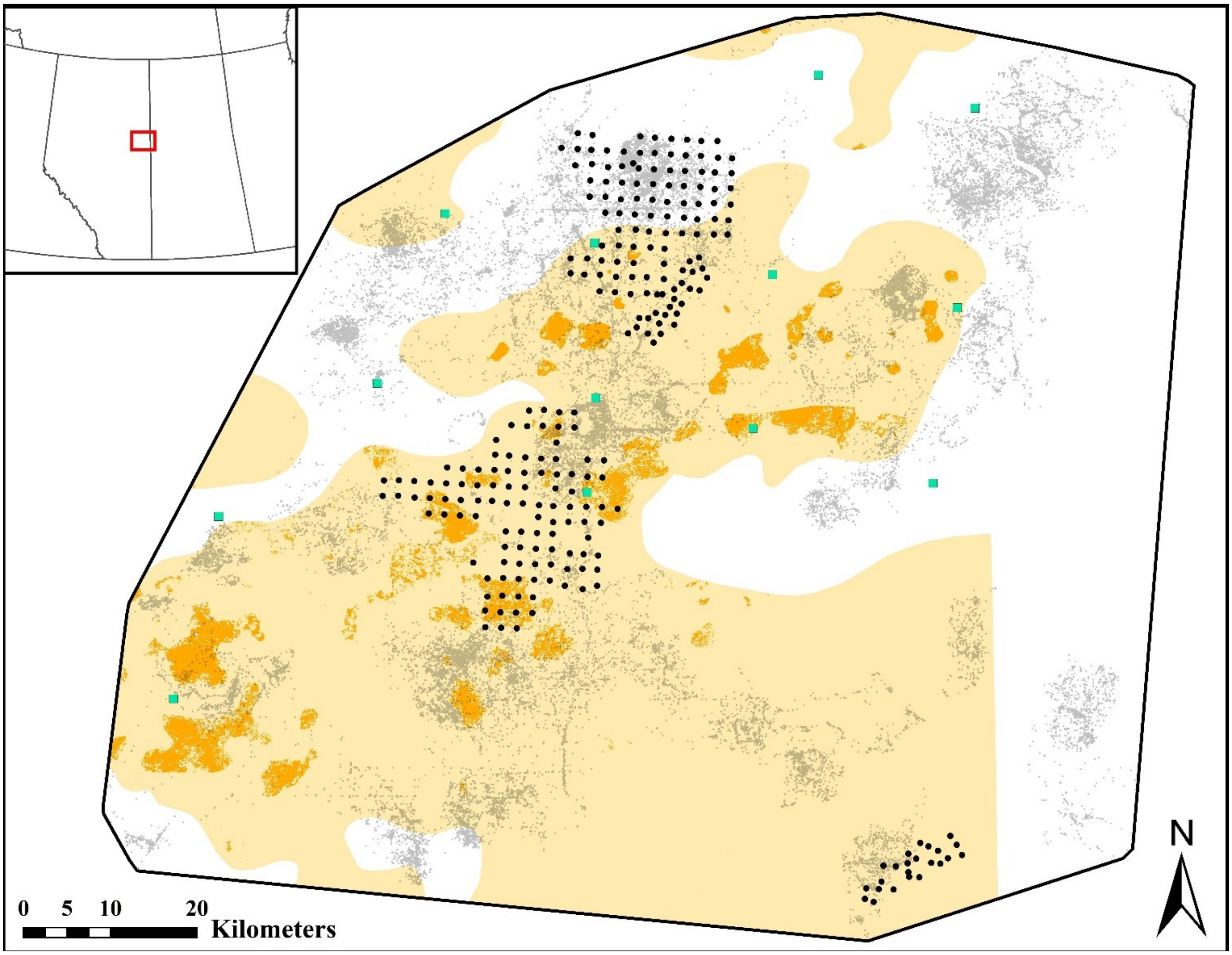

Figure 1. Black bear GPS locations (grey dots with 100 meter radii) relative to caribou range (light orange) and high-quality calving habitat (dark orange) within our study area (black polygon). The black circles and green squares represent the camera locations (n=288) used to estimate bear density in our study area. The squares represent clusters of up to 4 cameras that are 600 meters apart from one another. The extent of our study area with respect to provincial boundaries is represented by the red box in the map inset.

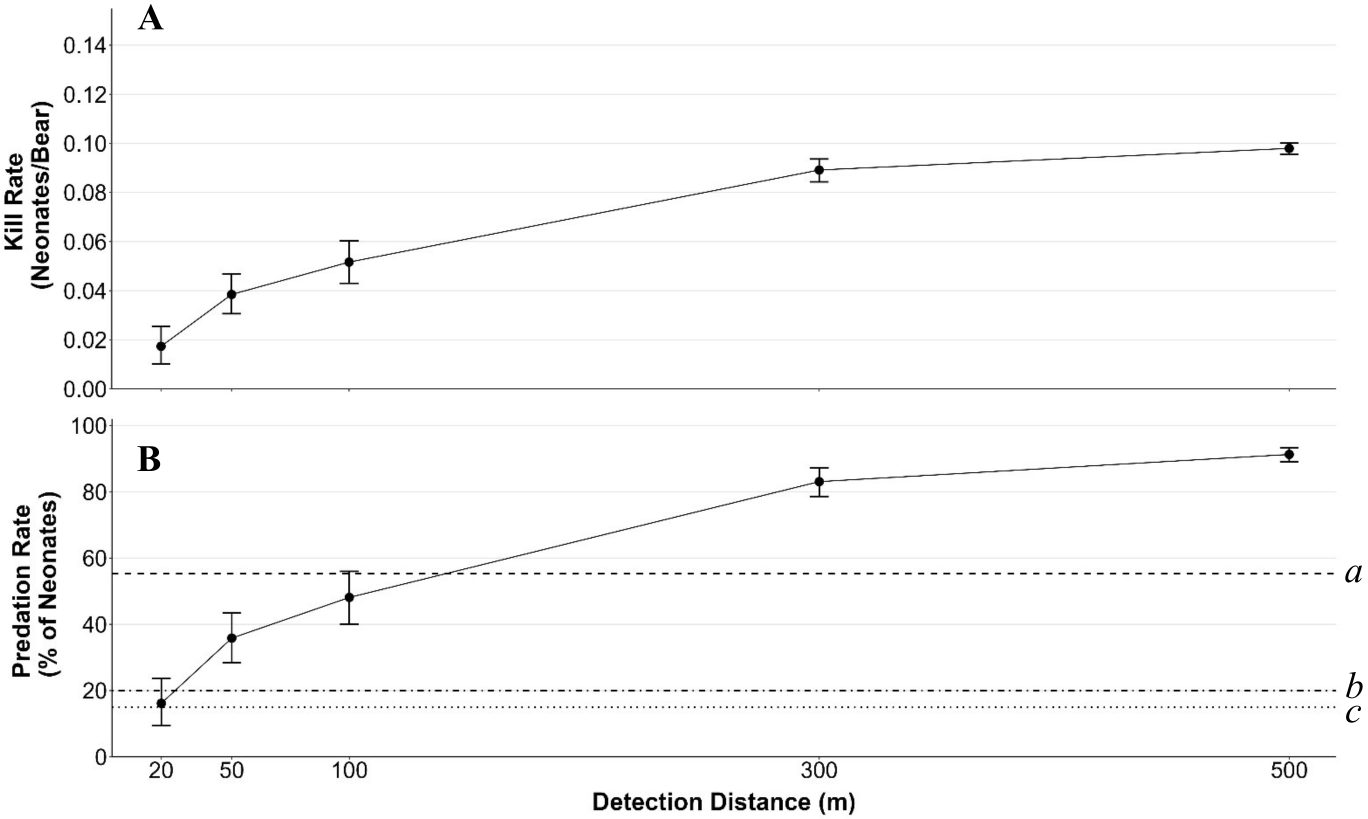

Figure 4. The mean kill rate (average number of neonates killed per bear; A), and the mean predation rate (percentage of neonates killed by bears; B) for a population of 1649 bears (157 bears/1000 km^2). Simulations tracked bear kills of neonate caribou (≤ 2 weeks old; n=177) born in high-quality calving habitat during the caribou calving season (n = 30 iterations/scenario). The scenarios shown here varied detection distance (meters; x-axis), while kill success probability was held constant at 0.8. Error bars are bootstrapped 95% confidence intervals (n=10,000 iterations). *a* - percent of calves up to 8 weeks old that were killed by black bears (Dussault et al. 2012); *b* - percent of calves up to 2 weeks old that were killed by black bears (Leclerc et al. 2014); *c* – percent mortality of calves up to 2 weeks old (Walker et al. 2021).

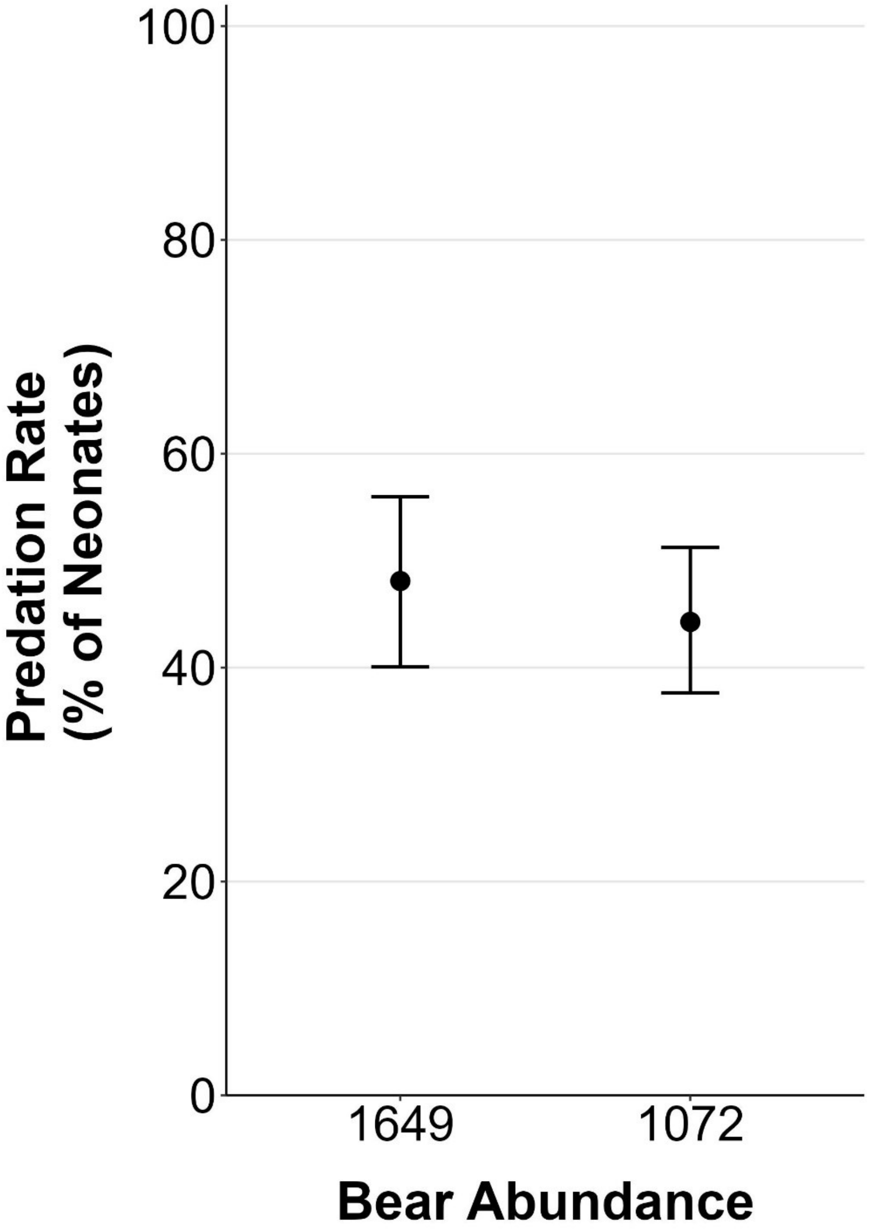

Figure 5. The mean rates of black bear predation (percentage of neonates killed by bears) on caribou neonates (≤ 2 weeks old; n=177) by populations of 1649 bears (157 bears/1000 km^2) and 1072 bears (102 bears/1000 km^2). Simulations tracked bear kills of neonates in high-quality calving habitat during the caribou calving season (n=30 iterations/scenario). Error bars are bootstrapped 95% confidence intervals (n=10,000) of mean predation rates. For the scenario in this figure, detection distance and kill success probability were held constant at 100 meters and 0.8, respectively.

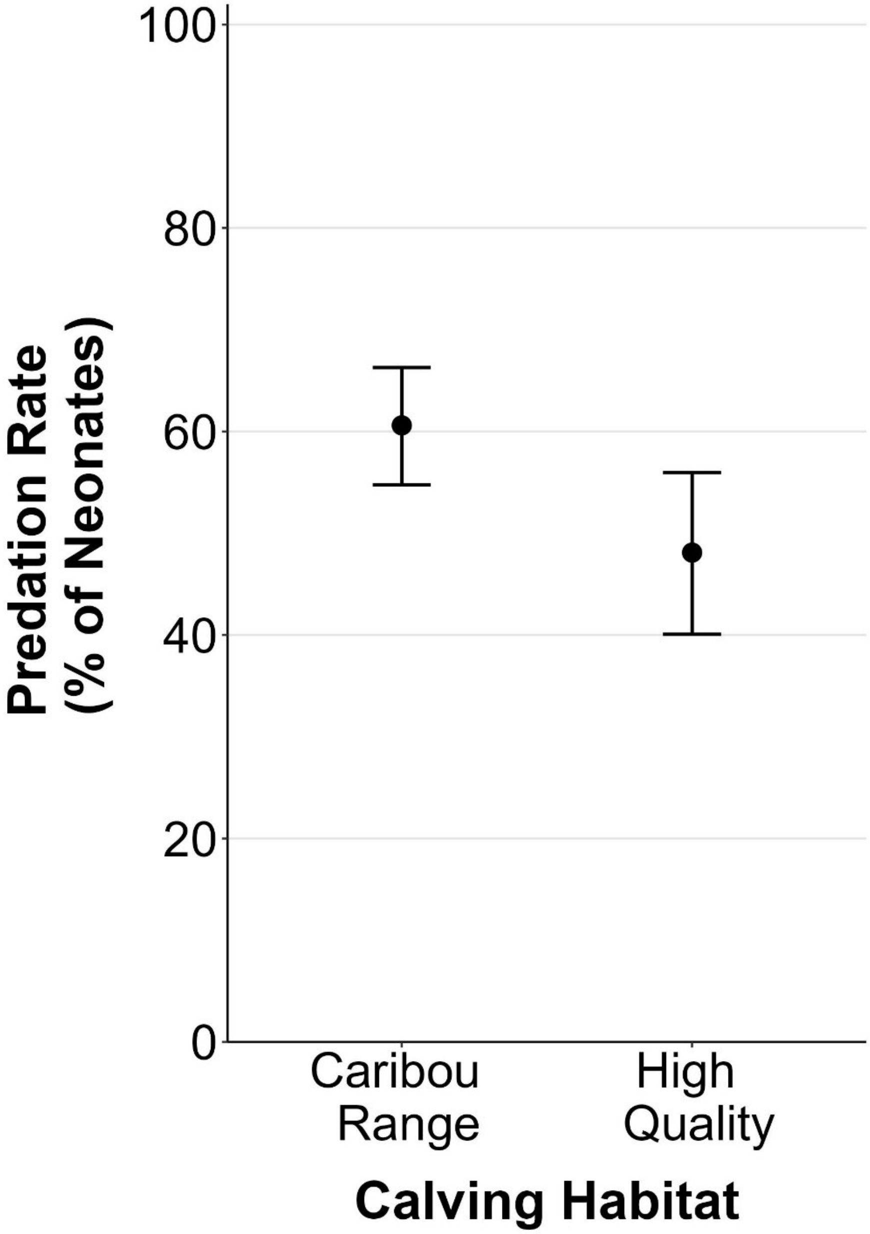

Figure 7. The mean rates of black bear predation (percentage of neonates killed by bears) on caribou neonates (≤ 2 weeks old; n=177) that were distributed throughout caribou range or in high-quality calving habitat. Simulations tracked neonate kills by a population of 1649 bears (157 bears/1000 km^2) during the caribou calving season (n=30 iterations/scenario). Error bars are bootstrapped 95% confidence intervals (n=10,000) of mean predation rates. For the scenario in this figure, detection distance and kill success probability were held constant at 100 meters and 0.8, respectively.

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Appendix A – GPS Data Preparation

Before all analyses, we removed the first 3 days of black bear GPS-collar data post-capture to account for potential impacts of capture on bear behaviour (Rode et al. 2014), and we screened the remaining data for potential errors. First, we removed GPS locations (i.e., "fixes") with coordinates far outside our study area (n = 3 fixes). Second, we removed two-dimensional fixes with Dilution of Precision (DOP) >5 and three-dimensional fixes with DOP >10 (i.e., fixes with low positional accuracy; Lewis et al. 2007). Finally, we removed fixes associated with biologically unrealistic bear movements (Bjørneraas et al. 2010).

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Appendix B – Spring Den Departure

We used data from bears fitted with GPS-collars before hibernation to determine the timing of bear emergence and departure from their dens (n=26 bear-years; 14M:12F). We classified den emergence as an increase in successful GPS fixes and/or movement distinct from existing in-den GPS fixes, and classified bears as departed from their dens when they moved beyond a 50 meter buffer of their den emergence location and remained outside the buffer for at ≥24 hours (Fig. B1). Black bears are unlikely to encounter caribou calves if they do not move >50 m of their den sites, which are not typically located in lowland habitats associated with caribou (Tietje and Ruff 1980). Therefore, we excluded fixes on and before the den departure date for each denning bear, and we used the proportion of departed bears by date to correct our bear population abundance estimates (Fig. B2). The observed phenology of black bear den emergence and departure was consistent with that of Tietje and Ruff (1980) in northeastern Alberta.

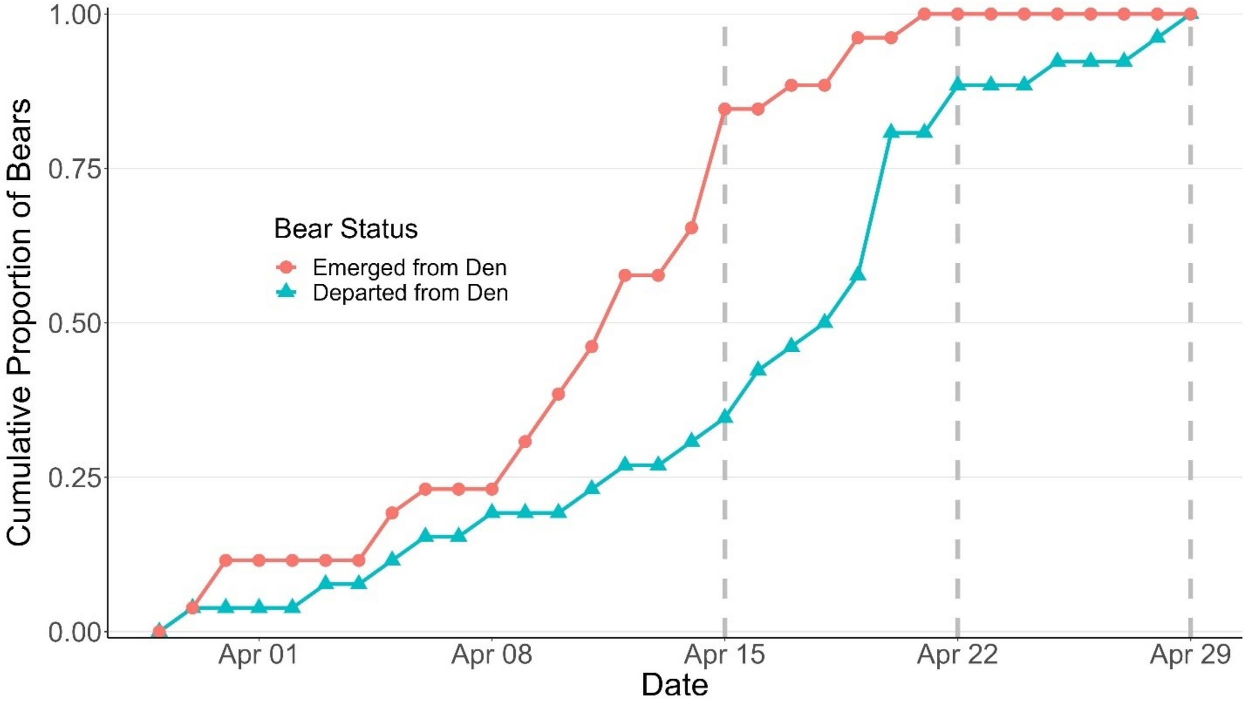

Figure B1. The timing of den emergence and departure for black bears (n=26 bear-years) in northeastern Alberta. The vertical dashed lines indicate the 7-day periods used for the caribou parturition distribution over the calving season (April 15- July 15).

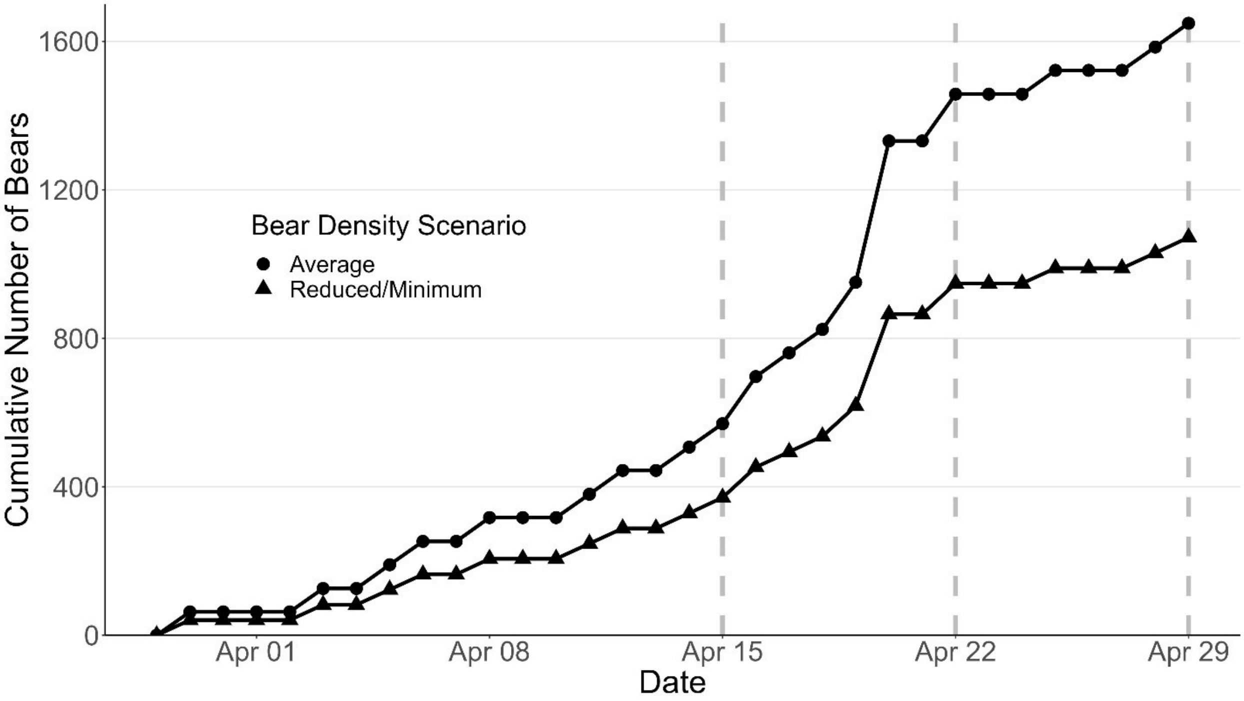

Figure B2. The population abundance of bears in our study area corrected for the proportion of bears (n=26 bear-years) that departed their dens each day. All bears had departed their dens by April 29. The shapes indicate bear abundance based on different bear density estimates for our study area: average density (circles; 157 bears/1000 km^2; 1649 bears total) and minimum (reduced) density (triangles; 102 bears/1000 km^2; 1072 bears total). The vertical dashed lines indicate the start of the 7-day periods used to define the caribou parturition distribution over the calving season (April 15- July 15).

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Appendix C – Home Range Overlap

We compared the home range overlap (100% MCP) between GPS-collared black bears to investigate i) whether bear-years could be considered an independent sample unit, and ii) whether bears exclude conspecifics from their home ranges, which would violate an assumption of extrapolating kills from a sample of bears to the population. We used the *spatsoc* package in R

(Robitaille et al. 2019) to determine reciprocal home range overlaps between each bear pair. We excluded home ranges with zero overlap from these analyses because we were interested in the extent to which home ranges do overlap, and long distances between home ranges in our study (rather than conspecific interactions) could be the reason for zero overlap. There were home range overlaps between different bears in the same year that were comparable to the home range overlap between years for a given bear, thus suggesting that bear-years could be considered independently (Fig. C1). Bears in a given year did not appear to exclude conspecifics of either sex from their home ranges in our study area (Fig. C2).

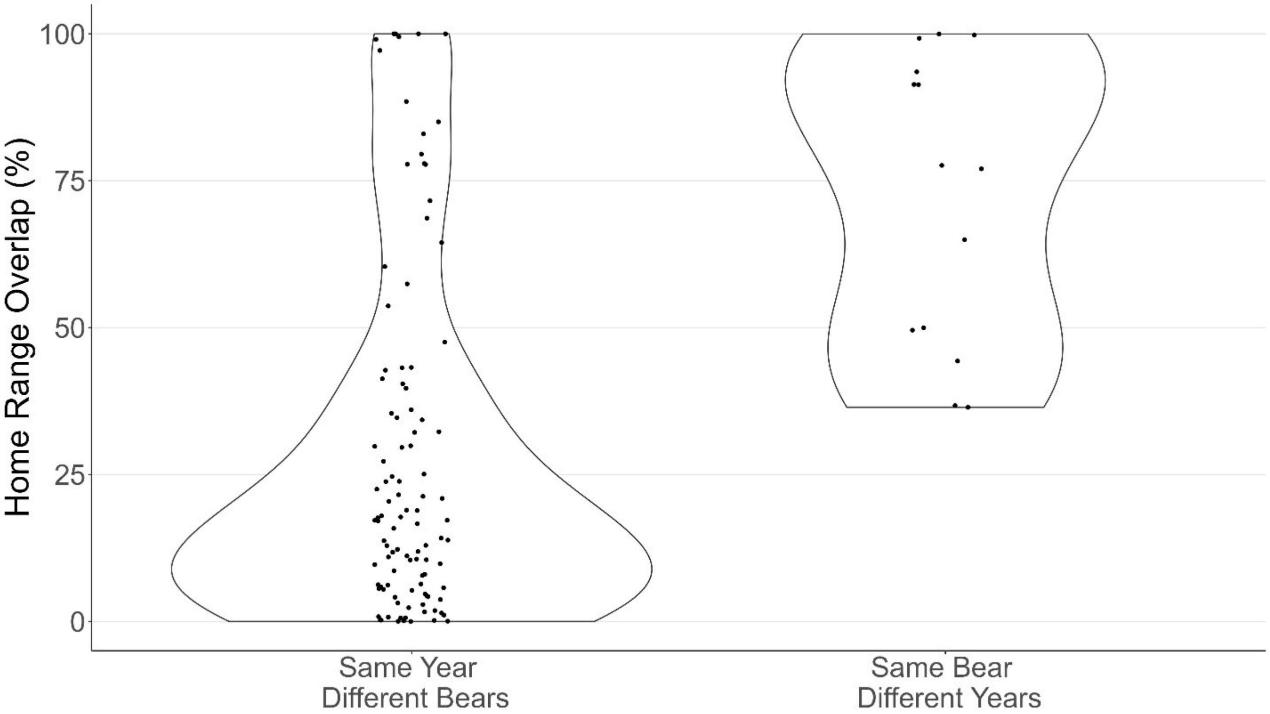

Figure C1. Violin plots showing the percent home range overlap (100% Minimum Convex Polygons) between different bears in the same year (n=48 bears, n=106 overlap measures) and between different years for the same bear (n=7 bears, n=14 overlap measures) from April 15-July 15.

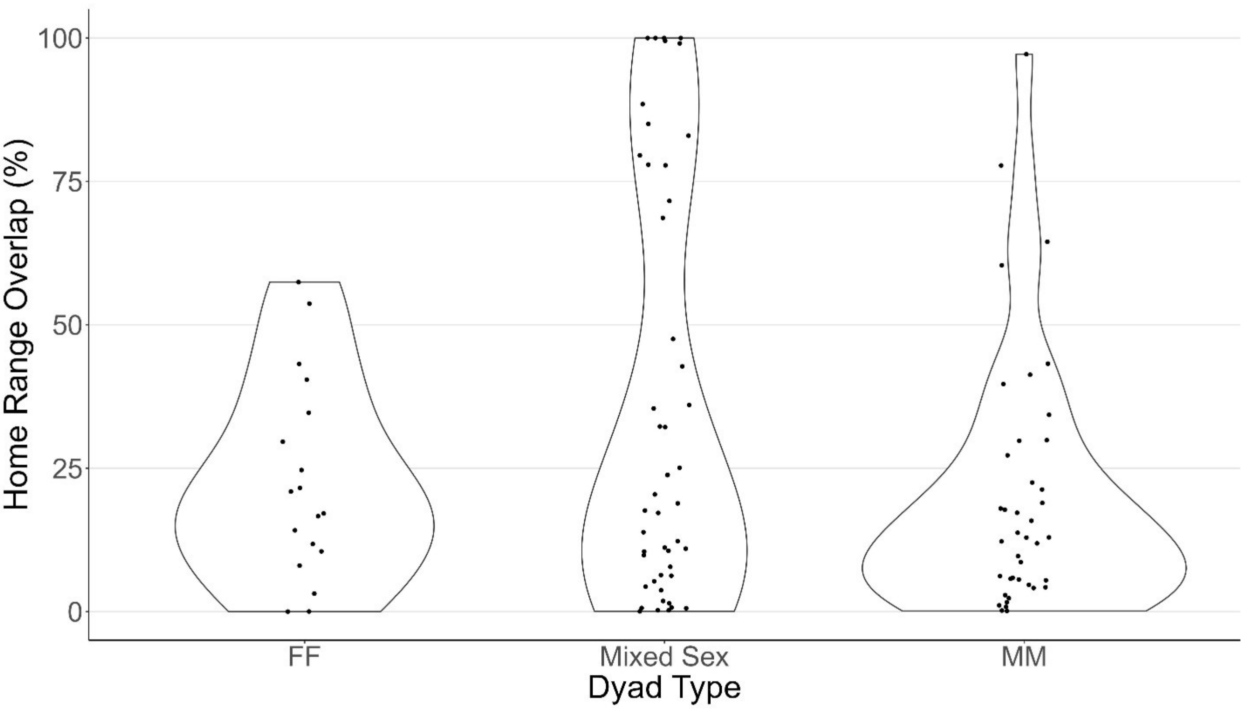

Figure C2. Violin plots showing the percent home range overlap (100% Minimum Convex Polygons) between different bear dyad types in the same year from April 15-July 15 in 2014, 2015, 2019, or 2021. Home range overlaps were calculated for female-female (FF; n=11 bear-years; n=18 overlaps), mixed-sex (n=34 bear-years; n=48 overlaps), and male-male dyads (MM; n=25 bear-years; n=40 overlaps).

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Appendix D – Alignment of Caribou Parturition Timing and Bear-Year Sample Size

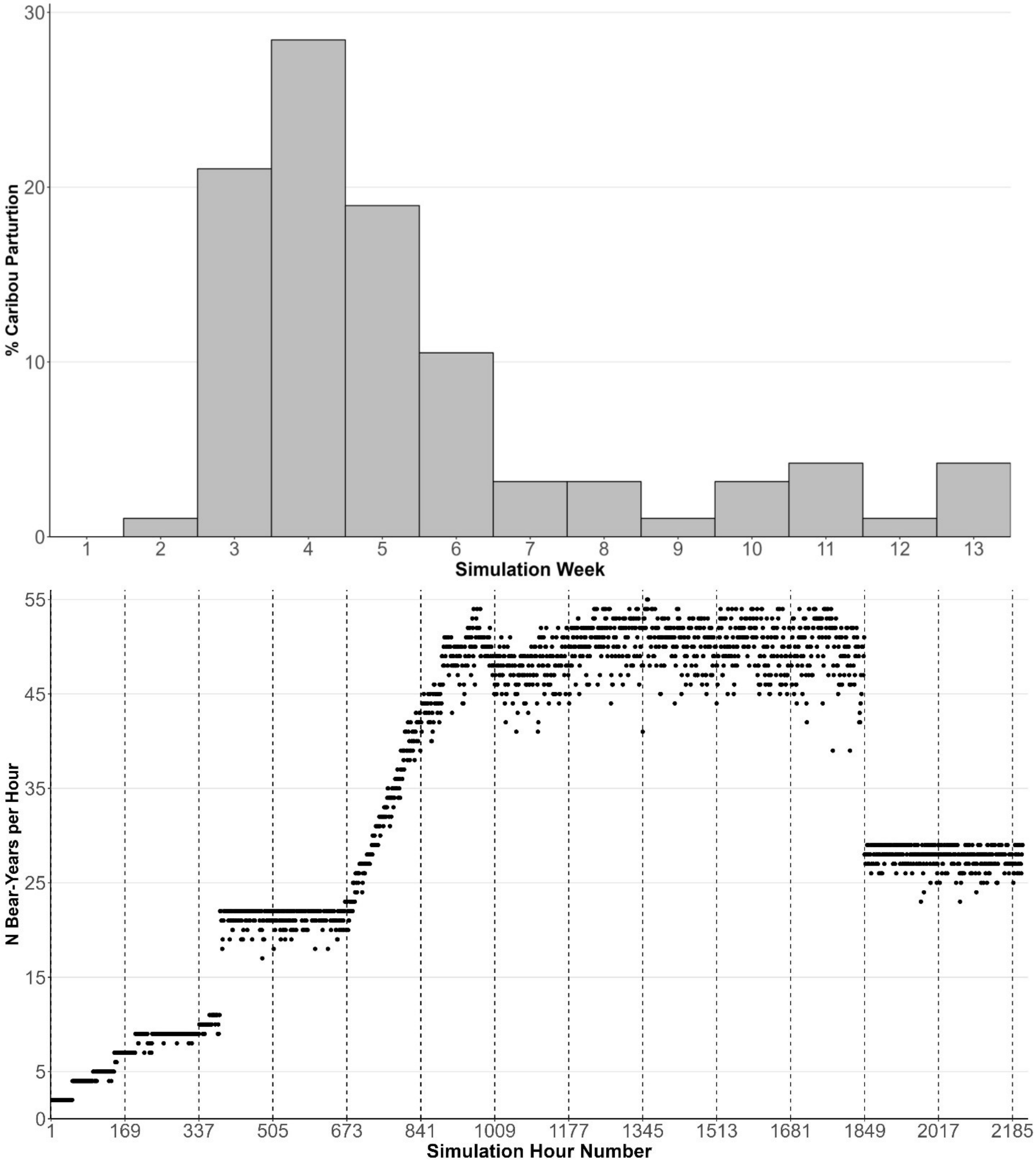

Figure D1. Empirical distribution of caribou parturition dates by week during the caribou calving season (April 15-July 15; top), and the sample size of bear-years in each hour of the calving season (2208 hours total; bottom). The vertical dashed lines (bottom) indicate the start of the 7-day periods used to define the caribou parturition distribution over the calving season. The parturition distribution was used to determine birth timing for simulated neonates, which could be killed by bears up to two weeks after their birth.

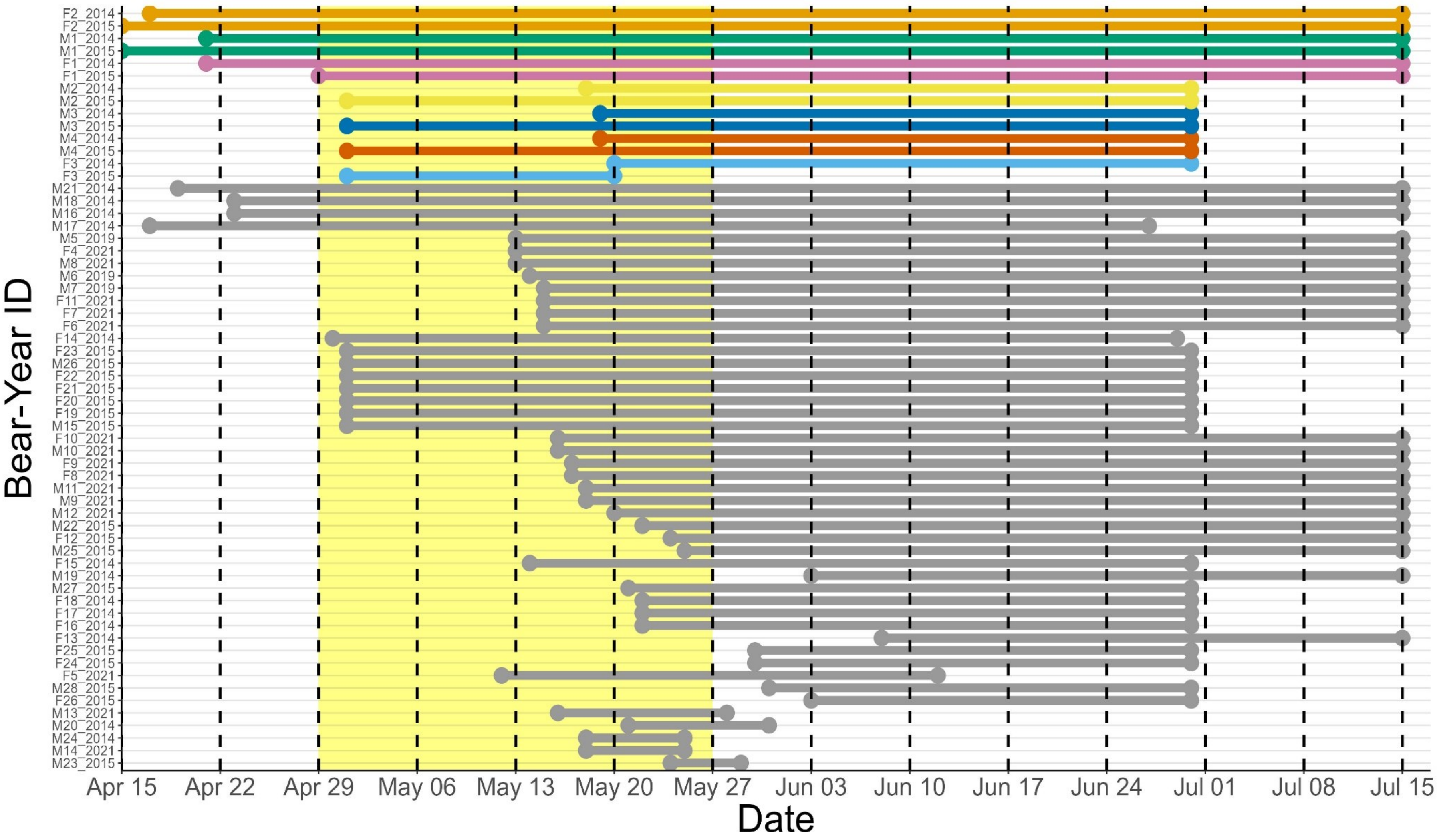

Figure D2. The duration of collar deployments for each bear-year (n=61). Bear-year ID indicates the sex (M/F) and year of deployment. The vertical dashed lines indicate the start of the 7-day periods used to define the caribou parturition distribution over the calving season (April 15-July 15). Most bear-years were recording GPS locations over the period when ~80% of caribou calves were born (April 29-May 26; yellow rectangle). Colours indicate bears with multiple years of data. Three bears were recollared during a bear-year, but the 3-day data gap is not shown for simplicity.

Appendix E – Caribou Calving Resource Selection Functions

We developed range-specific second-order (*sensu* Johnson 1980) resource selection functions (RSFs) using location data collected from GPS-collared female caribou with a calf at-heel (≤ 4 weeks old) in the Cold Lake (CL; $n = 8$ caribou) and East Side Athabasca River (ESAR; $n = 42$ caribou) boreal caribou ranges. The RSFs were developed using environmental variables hypothesized to influence calving habitat selection (Table E1). To model land cover, we used the Enhanced Wetland Classification (Ducks Unlimited Canada 2009) data, which we collapsed into eight classes that were biologically relevant to caribou (Table E1, Table E2). To model anthropogenic disturbance, we used the Human Footprint Inventory from the Alberta Biodiversity Monitoring Institute which combines existing baseline datasets with SPOT6 satellite imagery to identify and classify anthropogenic disturbances such as roads, pipelines, seismic lines, well pads, and cut blocks. Timber harvest cut blocks and forest fires <50 years old were considered together to represent early seral habitats that may be avoided by caribou (Dalerum et al. 2007).

RSFs were estimated using generalized linear mixed effect models (GLMMs; Gillies *et al.* 2006), which account for the hierarchical structure inherent in GPS location data and unequal sample sizes among individual caribou. In all GLMMs, we assigned individual caribou-year as a random grouping effect (i.e., a random intercept). This formulation of caribou-year accounts for yearly differences in calving area selection for individuals calving in more than one season. We standardized all continuous variables prior to model fitting. For all models, we assessed for multicollinearity using variance inflation factors (VIFs) and none of the considered variables were significantly correlated (VIFs < 2; Zuur, Ieno & Elphick 2010).

For each range, we first estimated a base model that consisted of only local land cover (30 m x 30 m resolution) variables, setting treed bog as the reference category. We then used a forward variable model selection process that considered AIC and model fit for each added variable. Variables were retained if AIC was lowered by > 2 units and if the variable improved model fit. We assessed model fit by using the fixed-effects output from a given model to predict values for both the random locations generated within each range and the caribou GPS locations. Predicted values of the range-specific random points were then partitioned into deciles (i.e., 10 ordinal bins containing an equal number of random points). We compared the proportional frequency of predicted values for the caribou GPS locations falling within a given bin to the bin rank using Spearman's correlation coefficient as a measure of model fit (r_S; DeCesare et al. 2012).

Using outputs from each range's top model, we developed spatially explicit maps of caribou calving habitat, binning predicted RSF values into ten ordinal bins as outlined above. Model fit was excellent for ESAR ($r_S = 0.91$), but only fair for Cold Lake ($r_S = 0.55$), likely due to the small sample size ($n = 8$ caribou) that resulted in few GPS locations falling within bin 10. We considered bin 10 to be high-quality calving habitat and this bin comprised 5.6% of the combined caribou range (6152 km^2) within our study area (Fig. E1). In the CL range, relative calving habitat suitability was highest in nutrient-rich and nutrient-poor fens that had a high proportion of nutrient-poor fens, conifer swamps, and upland deciduous forest in the surrounding area. Additionally, CL maternal-neonate pairs selected for areas closer to early seral habitat, but only when the proportion of nutrient-poor fen and conifer swamp were high in the surrounding area (Table E3). In the ESAR range, relative calving habitat suitability was highest in nutrient-rich and nutrient-poor fens that had a high proportion of nutrient-poor fens in the surrounding area, and all other land cover types were selected less than bogs (Table E4).

Table E1. Environmental variables used in the development of range-specific resource selection functions using location data collected from GPS-collared female caribou with a calf at-heel in the Cold Lake and East Side Athabasca River boreal caribou ranges in northeastern Alberta.

Variable	**Description**	**Source**
Land cover	The dominant vegetation type at a given location. The simplified classes were treed bog, nutrient-poor fen, nutrient-rich fen, conifer swamp, deciduous swamp, upland coniferous forest, upland deciduous forest, and other (combines rare classes such as anthropogenic disturbances, mudflats, gravel bars, and recent forest fires).	Enhanced Wetland Classification (EWC) from Ducks Unlimited Canada (2009)
Landscape context	The proportion of a given land cover type in a 1.5 km radius.	EWC
Slope	Derived from a digital elevation model from Shuttle Radar Topography Mission data	https://www2.jpl.nasa.gov/srtm/
Normalized difference vegetation index (NDVI)	An index of plant greenness that is often used to model food quality and/or quantity. The NDVI was derived from MODIS images taken over a 16-day window. This analysis used NDVI values averaged over May 1 – June 30.	U.S. National Aeronautics and Space Administration MODIS database
Distance to nearest river	N/A	Government of Alberta
Distance to nearest lake	N/A	Government of Alberta
Distance to early seral habitat	As of 2014, the distance to nearest timber harvest cut block or forest fire < 50 years old.	Alberta Biodiversity Monitoring Institute (ABMI) Geospatial Centre (cut blocks), Government of Alberta (forest fires)

Distance to nearest well site	Well sites are polygonal disturbances associated with petroleum extraction	ABMI 2012 human footprint data
Density of linear disturbances	Density of seismic lines, pipelines, and roads in a 400 m radius	ABMI 2012 human footprint data

Table E2. The reduction of land cover classes from the Enhanced Wetlands Classification (EWC; Ducks Unlimited Canda 2009) to model resource selection by caribou with a calf at-heel in the Cold Lake and East Side Athabasca River boreal caribou ranges in northeastern Alberta.

Land cover	**EWC classes**	**Description**
Treed bog	Treed bog, Open bog, Shrubby bog	Black spruce (*Picea mariana*) and Sphagnum moss dominated peatland areas with no hydrodynamic flow or standing water. Treed bogs (25-60% black spruce cover, <10 m tall) dominate.
Nutrient-poor fen	Graminoid poor fen, Shrubby poor fen, Treed poor fen	Low nutrient peatland soils with standing water and components of both bogs and fens. Treed poor fens (25-60% tree cover) dominate, comprised of black spruce and tamarack (*Larix laricina*). Short shrubs (<2 m) are more common than in bogs (bog birch (*Betula glandulosa*), willow (*Salix* spp.*)*, and Ericaceous shrubs).
Nutrient-rich fen	Graminoid rich fen, Shrubby rich fen, Treed rich fen	High nutrient peatland soils influenced by groundwater flows. Treed and shrubby rich fens dominate, comprised of black spruce, tamarack, bog birch, sweet gale (*Myrica gale*), and willow. Rich fen indicators species are buckbean (*Menyanthes trifoliata*) and wire sedges (*Carex* spp.).
Conifer swamp	Conifer swamp, Tamarack swamp	Can occur on peatland or mineral soils, often at transitions between bog/fen and upland habitats. Pools of water present. Dominant tree species are black spruce or tamarack (tree heights >10 m).
Deciduous swamp	Shrub swamp, Hardwood swamp, Mixed-wood swamp	Mineral soils with pools of water often present. Dominant species are paper birch (*Betula papyrifera*), balsam popular (*Populus balsamifera*), and tall (>2 m) willow and alder (*Alnus* spp.) shrubs.
Upland conifer	Upland conifer	Mineral soils with >25% tree cover and at least 80% conifer species, mainly black spruce, white spruce (*Picea glauca*), balsam fir (*Abies balsamea*), and jack pine (*Pinus banksiana*).

Upland deciduous	Upland deciduous, Upland mixed-wood	Mineral soils with >25% tree cover and <80% conifer species. Dominant deciduous tree species: trembling aspen (*Populus tremuloides*), balsam poplar, and paper birch.
Other	Upland other, Anthropogenic, Burn, Aquatic, Cloud shadow	Upland other: mineral soils with tree cover <25%. Anthropogenic: urban areas, roads and cut blocks. Burns: vegetation is limited or covered by burn Aquatic: a continuum of aquatic classes from open water to meadow marshes that occur on non-peatland soils (i.e., mineral or deposited organic soil). Open water is the dominant aquatic class. Cloud shadow was rare.

Table E3. Resource selection function coefficients for female caribou with a calf at-heel (n=8) in the Cold Lake range in northeastern Alberta. Statistically significant coefficients are in bold.

Variable	**Estimate**	**Std Error**	**z value**	**Pr(>|z|)**
(Intercept)	-5.40866	0.257716	-20.9869	8.64E-98
Nutrient poor fen	**0.859393**	0.179509	4.787477	1.69E-06
Nutrient rich fen	**0.962503**	0.183958	5.232201	1.68E-07
Conifer Swamp	-0.60577	0.235506	-2.57218	0.010105962
Upland Conifer	0.006383	0.198257	0.032197	0.974314612
Upland Deciduous	-0.15365	0.202309	-0.7595	0.447555578
Other	0.069559	0.261541	0.26596	0.790270118
Proportion of Nutrient Poor Fen	**1.276141**	0.043071	29.62855	6.41E-193
Proportion of Conifer Swamp	**0.586261**	0.03385	17.31948	3.35E-67
Proportion of Upland Deciduous	**0.714451**	0.036014	19.83815	1.39E-87
Distance to Early Seral	**-0.68702**	0.04773	-14.394	5.64E-47
Proportion of Nutrient Poor Fen × Distance to Early Seral	**0.757912**	0.035993	21.05734	1.96E-98
Proportion of Conifer Swamp × Distance to Early Seral	**0.129294**	0.033069	3.909825	9.24E-05

Treed bog is the reference category for land cover.

Distance to Early Seral was transformed via an exponential decay function:

$$1 - e^{(-0.002 \times \text{distance to early seral})}$$

Table E4. Resource selection function coefficients for female caribou with a calf at-heel (n=42) in the East Side Athabasca River range in northeastern Alberta. Statistically significant coefficients are in bold.

Variable	**Estimate**	**Std Error**	**z value**	**Pr(>|z|)**
(Intercept)	-4.35057	0.098697	-44.0801	0
Nutrient poor fen	**0.094677**	0.043443	2.179337	0.029307
Nutrient rich fen	**0.17863**	0.041092	4.34713	1.38E-05
Conifer Swamp	-1.07818	0.08429	-12.7913	1.83E-37
Deciduous Swamp	-1.2098	0.106936	-11.3133	1.13E-29
Upland Conifer	-1.69855	0.110864	-15.321	5.53E-53
Upland Deciduous	-1.25567	0.074583	-16.8358	1.33E-63
Other	-1.17019	0.083614	-13.9951	1.67E-44
Proportion of Nutrient Rich Fen	**0.935338**	0.011321	82.6173	0

Treed bog is the reference category for land cover.

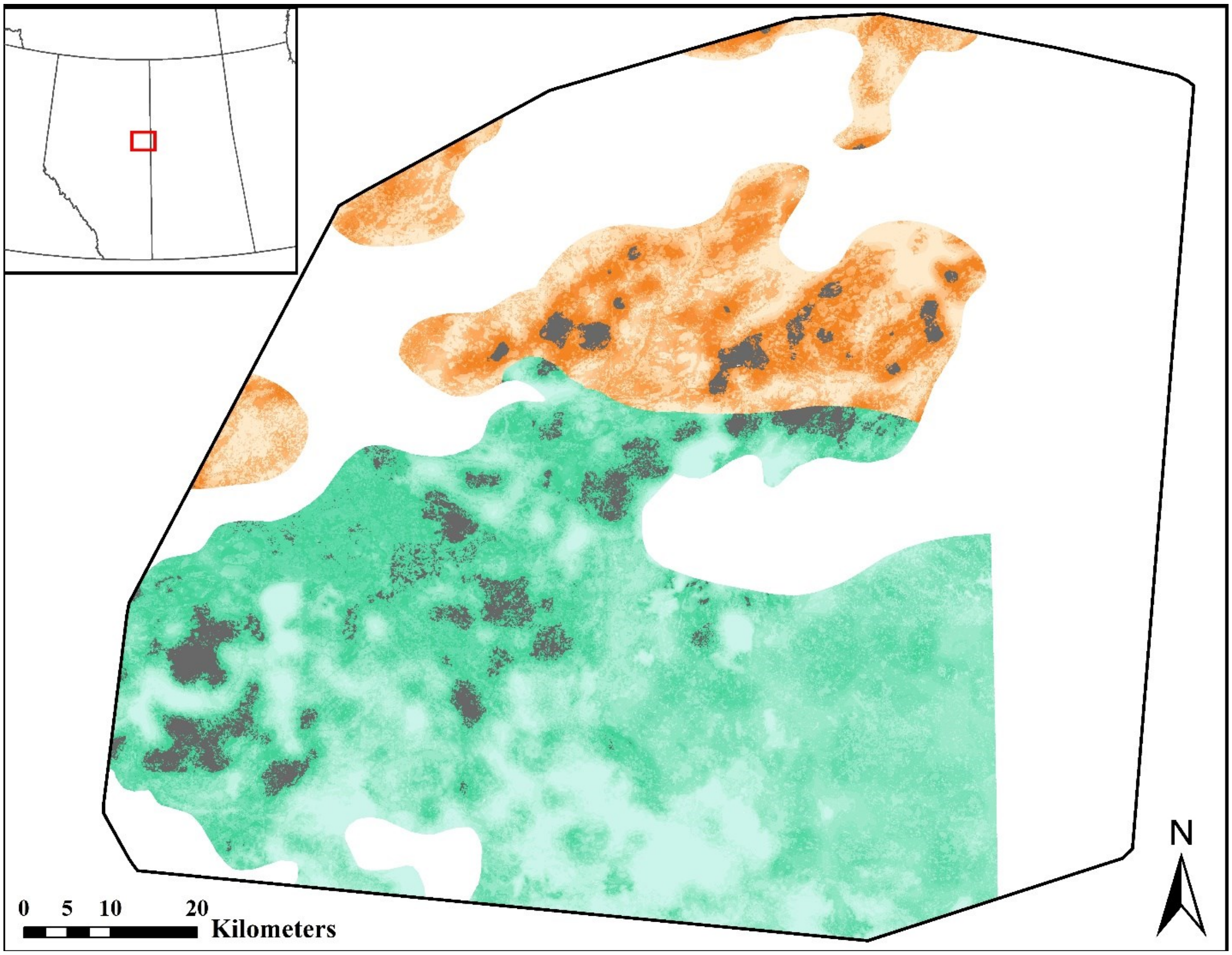

Figure E1. Relative calving habitat suitability for female caribou with a calf at-heel in the Cold Lake (green) and East Side Athabasca River (orange) boreal caribou ranges in northeastern Alberta. Darker shades indicate higher relative habitat suitability, and dark grey indicates "high-quality" calving habitat used in our simulation. The extent of our study area with respect to provincial boundaries is represented by the red box in the map inset.

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Appendix F – Sensitivity Analyses

Influence of Bear Movement, Habitat-Use, and Density on Neonate Predation Rate

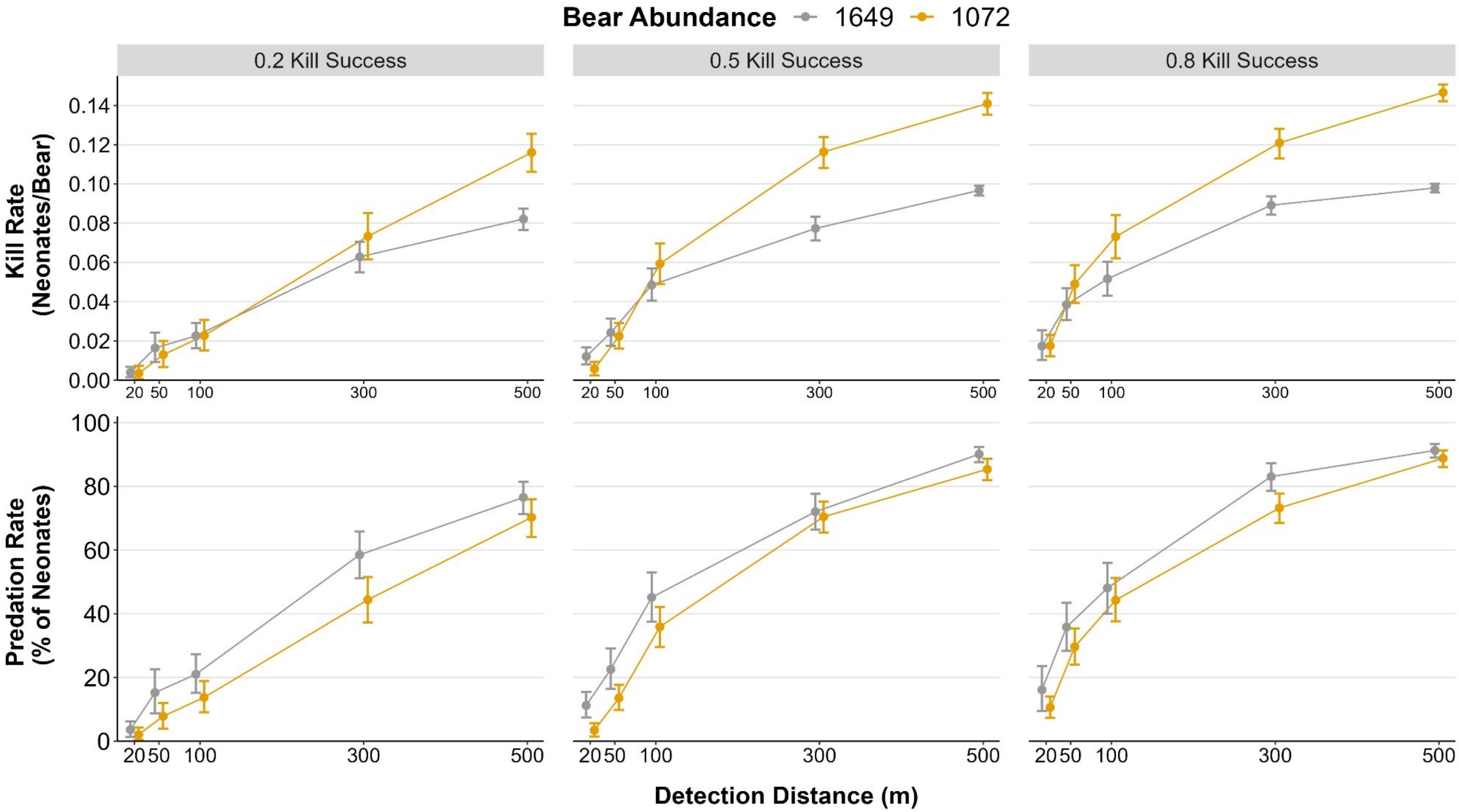

Figure F1. The mean kill rate (average number of neonates killed per bear; top row), and the mean predation rate (percentage of neonates killed by bears; bottom row) for a population of 1649 bears (grey lines; 157 bears/1000 km^2) versus 1072 bears (orange lines; 102 bears/1000 km^2). Simulations tracked bear kills of neonate caribou (≤ 2 weeks old; n=177) born in high-quality calving habitat during the caribou calving season (n = 30 iterations/scenario). Error bars are bootstrapped 95% confidence intervals (n=10,000 iterations). Scenarios also varied detection distance (meters; x-axis) and kill success probability (columns).

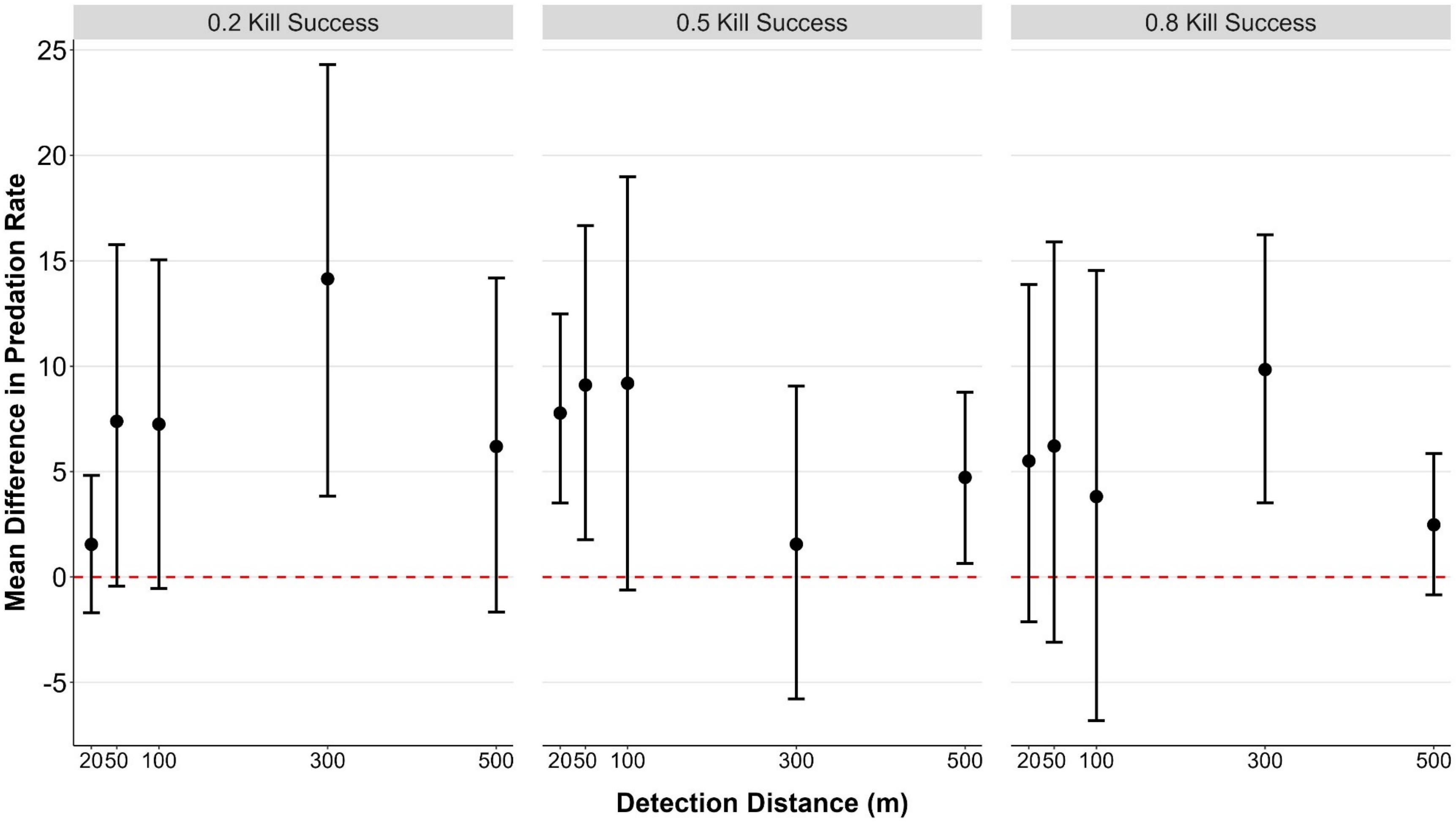

Figure F2. The mean difference in predation rate between a population of 1649 bears (157 bears/km^2) and 1072 bears (102 bears/km^2) during simulations that tracked bear kills of neonate caribou (≤ 2 weeks old) born in high-quality calving habitat from April 15-July 15 (n=30 iterations/scenario). The mean difference was calculated such that values greater than zero (red dotted line) indicate neonate predation rate was higher at the higher bear density. Error bars are bootstrapped 95% confidence intervals (n=10,000) of the mean difference in predation rates. Scenarios also varied detection distance (meters; x-axis) and kill success probability (columns).

Spatial Separation Hypothesis

Note: we excluded scenarios with 500 m detection distance from these plots because the resulting predation rates were unrealistic.

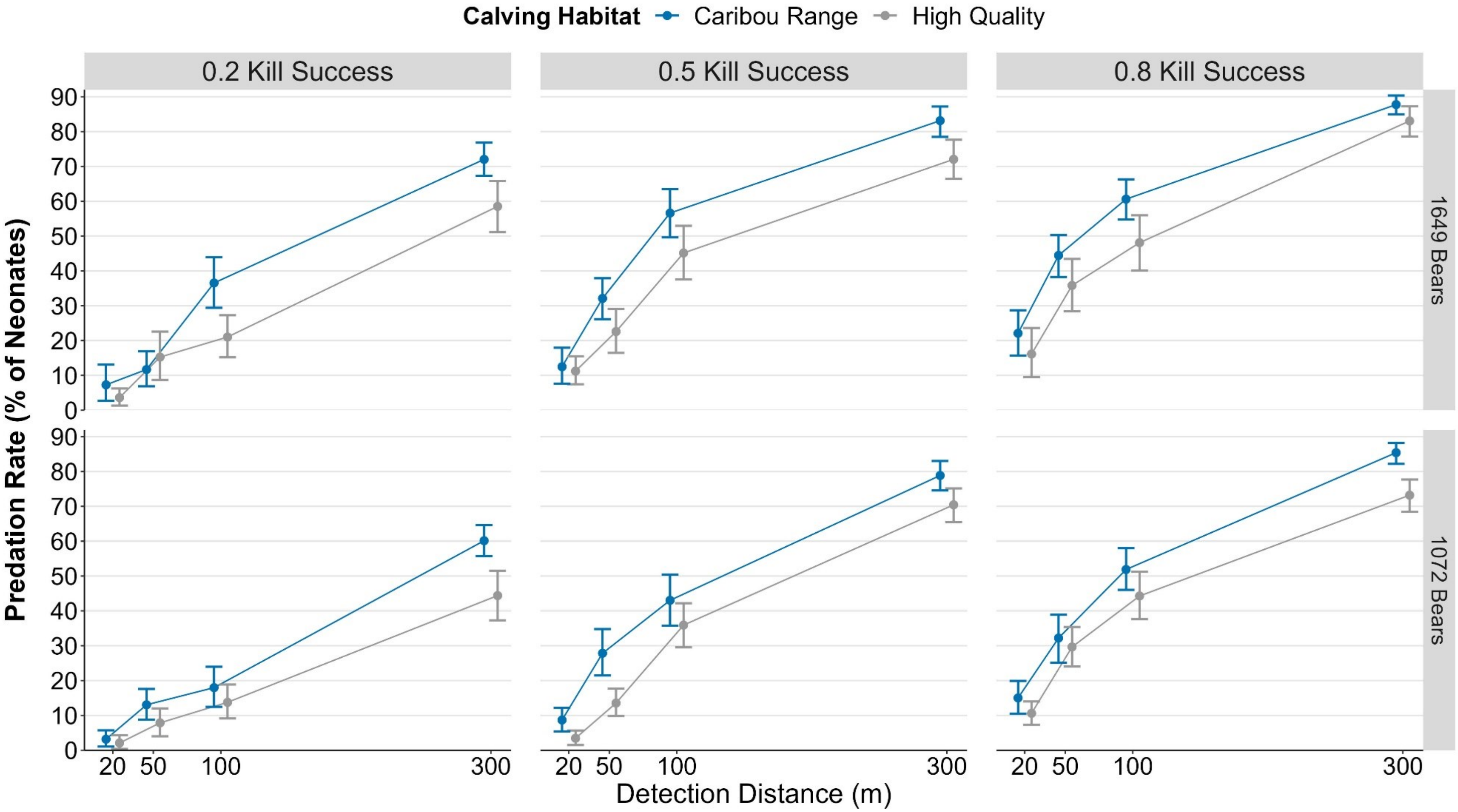

Figure F3. The mean rates of black bear predation (percentage of neonates killed by bears) on caribou neonates (≤ 2 weeks old; n=177) that were distributed throughout caribou range or in high-quality calving habitat. Simulations tracked neonate kills by a population of 1649 (top row; 157 bears/1000 km^2) or 1072 bears (bottom row; 102 bears/1000 km^2) during the caribou calving season (n=30 iterations/scenario). Error bars are bootstrapped 95% confidence intervals (n=10,000) of mean predation rates. Scenarios also varied detection distance (meters; x-axis) and kill success probability (columns).

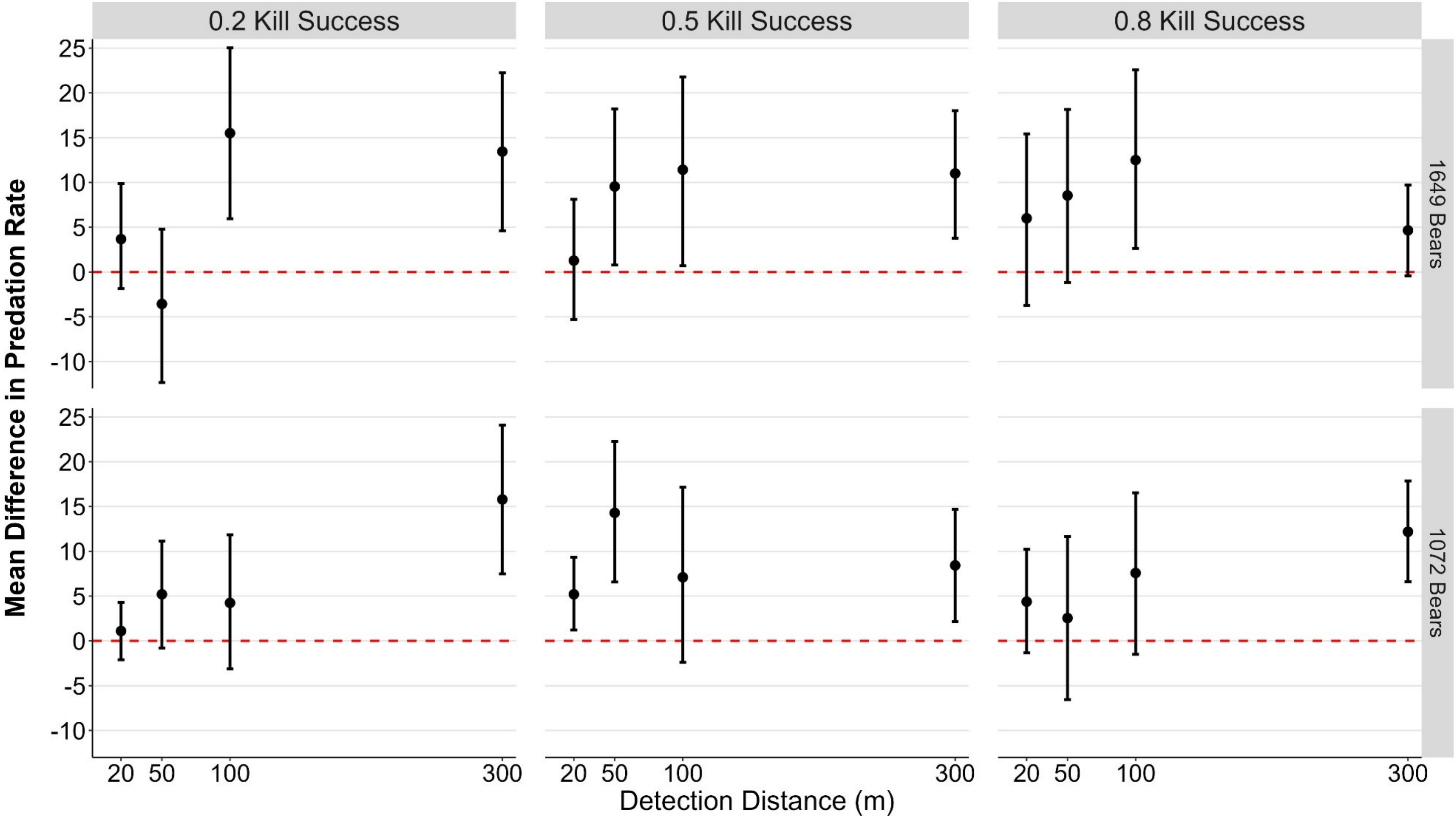

Figure F4. The mean difference in predation rate between scenarios where neonates were placed throughout caribou range versus in high-quality calving habitat. Simulations tracked neonate kills by a population of 1649 (top row; 157 bears/1000 km^2) or 1072 bears (bottom row; 102 bears/1000 km^2) during the caribou calving season (n=30 iterations/scenario). Values greater than zero (red dotted line) indicate that predation rates were higher when neonates were born throughout caribou range than in high-quality calving habitat. Error bars are bootstrapped 95% confidence intervals (n=10,000) of the mean difference in predation rates. Scenarios also varied detection distance (meters; x-axis) and kill success probability (columns).

Appendix G – Bear Fixes and Movements within Caribou Range

We compared the extent to which black bear GPS locations (fixes) and straight-line movement paths between consecutive 60-minute fixes overlap with changing levels of calving habitat quality for boreal caribou. Relative calving habitat quality was derived from a 30 m × 30 m resolution resource selection function (RSF) for adult female caribou with a calf at-heel in the Cold Lake (CL) and East Side Athabasca River (ESAR) boreal caribou ranges in northeastern Alberta (Appendix E). Although GPS locations more accurately reflect where a bear was on the landscape, we included straight-line movement paths between fixes in a second analysis because bear fixes alone may underestimate spatial overlap with caribou neonates if bears move quickly across calving habitat to get between more productive forage patches (Bastille-Rousseau et al. 2011).

We used the *terra* package in R (Hijmans 2023) to extract the calving RSF value intersecting each bear fix. We used the *spatsoc* package in R (Robitaille et al. 2019) to connect a straight line between fixes within 60 minutes (± 2.5 minutes) of each other for each bear. We calculated the percentage and density of RSF cells intersected by the fixes or movement paths within habitat classes of decreasing relative calving habitat quality (Table G1). The movement path analysis included solitary fixes (no consecutive fix before or after) because movement paths require at least two fixes. All calculations were with respect to the combined CL and ESAR ranges within our study area.

Regardless of whether bear fixes or movement paths were used as the metric for bear locations, bears were located least often in "high-quality" calving habitat and increasingly more often as calving habitat quality decreased (Table G1). Bears also used high-quality calving habitat disproportionately less than expected based on the small amount of area covered by high-quality habitat compared to other habitat classes (Table G1). The density of bear fixes and movement paths increase with decreasing calving habitat quality, but density of both metrics qualitatively appears to peak for RSF bins 7-10 and subsequently stabilize.

Table G1. Relationship of black bear GPS locations (fixes) and movement paths with changing levels of caribou calving habitat quality, as determined by a resource selection function (RSF) of female caribou with a calf at-heel. Habitat size and percentage of habitat in range refer to combined values for the Cold Lake and East Side Athabasca River boreal caribou ranges within our study area. Units for the density of fixes and paths are the number of RSF cells intersected by fixes or paths per km^2 of habitat.

RSF bins for habitat	**Habitat size (km^2)**	**Percentage of habitat in range**	**Percentage of fixes in habitat**	**Density of fixes in habitat**	**Percentage of paths in habitat**	**Density of paths in habitat**
10	347.8	5.7	1.4	3.0	2.2	59.2
9-10	887.0	14.4	6.0	5.0	8.4	88.0
8-10	1372.7	22.3	10.6	5.7	13.7	92.3
7-10	1906.0	31.0	17.7	6.9	20.8	100.7
6-10	2604.1	42.3	24.0	6.8	27.4	97.4
5-10	3351.9	54.5	30.6	6.8	34.2	94.2
4-10	4117.6	66.9	37.2	6.7	40.9	91.7
3-10	4860.8	79.0	45.5	6.9	48.1	91.4
2-10	5488.4	89.2	52.5	7.1	54.4	91.5
1-10	6151.5	100	58.4	7.0	59.9	90.0

An RSF bin of 10 was “high-quality” calving habitat, and a bins 1-10 equates to the combined caribou range within our study area.

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Appendix H – Effect of Spatial Distribution on Neonate Spacing

We used neonate locations from April 29 – June 9 to compare neonate dispersion among scenarios because most neonates (~80%) were born from April 29 – May 26 (plus two weeks of availability to bears) and the number of neonates on the landscape is more variable later in the calving season due to predation. We excluded scenarios with 500 m detection distance from these plots because the resulting predation rates were unrealistic. To estimate the degree of dispersion among neonates in each scenario, we first calculated the mean distance to the closest neonate for each neonate in each hour that had at least two neonates on the landscape. We calculated the mean of these hourly average distances for each 7-day period in each iteration of each scenario. Thus, each 7-day period had a mean nearest neonate distance for each iteration and scenario (n=30), except for seven iterations that did not have any hours from June 3 – 9 with at least two neonates (i.e., n=29). Finally, we calculated the median nearest neonate distance for each 7-day period in each scenario to reduce sensitivity to outlier iterations with very large nearest neonate distances when comparing dispersion of neonates born in of high-quality calving habitat versus throughout caribou range (Fig. H1, Fig. H2).

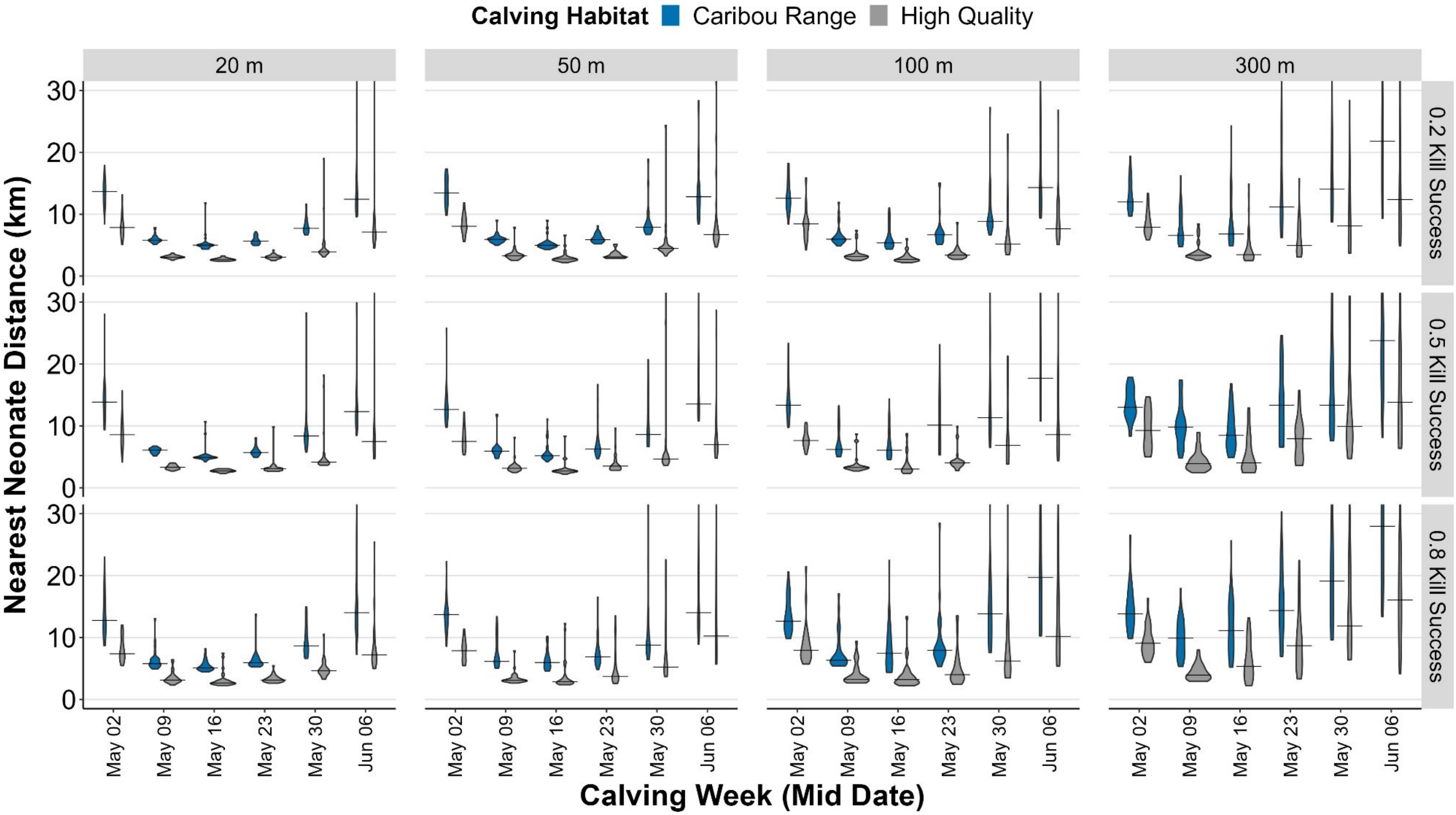

Figure H1. Violin plots of the mean distance (km) from each neonate to the nearest neonate across 7-day periods from April 29 – June 9 (i.e., many neonates on the landscape) during simulations where caribou neonates were placed throughout caribou range (blue) or in high-quality calving habitat (grey). The horizontal line in each week represents the median nearest neonate distance among the mean distances for that week (n=30, except for 5 weeks where n=29). Neonates were killed by black bears depending on the detection distance (meters; columns), kill success probability (rows), and bear population density (average density was used here (157 bears/1000 km^2; 1649 bears)). Note the y-axis excludes distances >30 km for the sake of visual clarity.

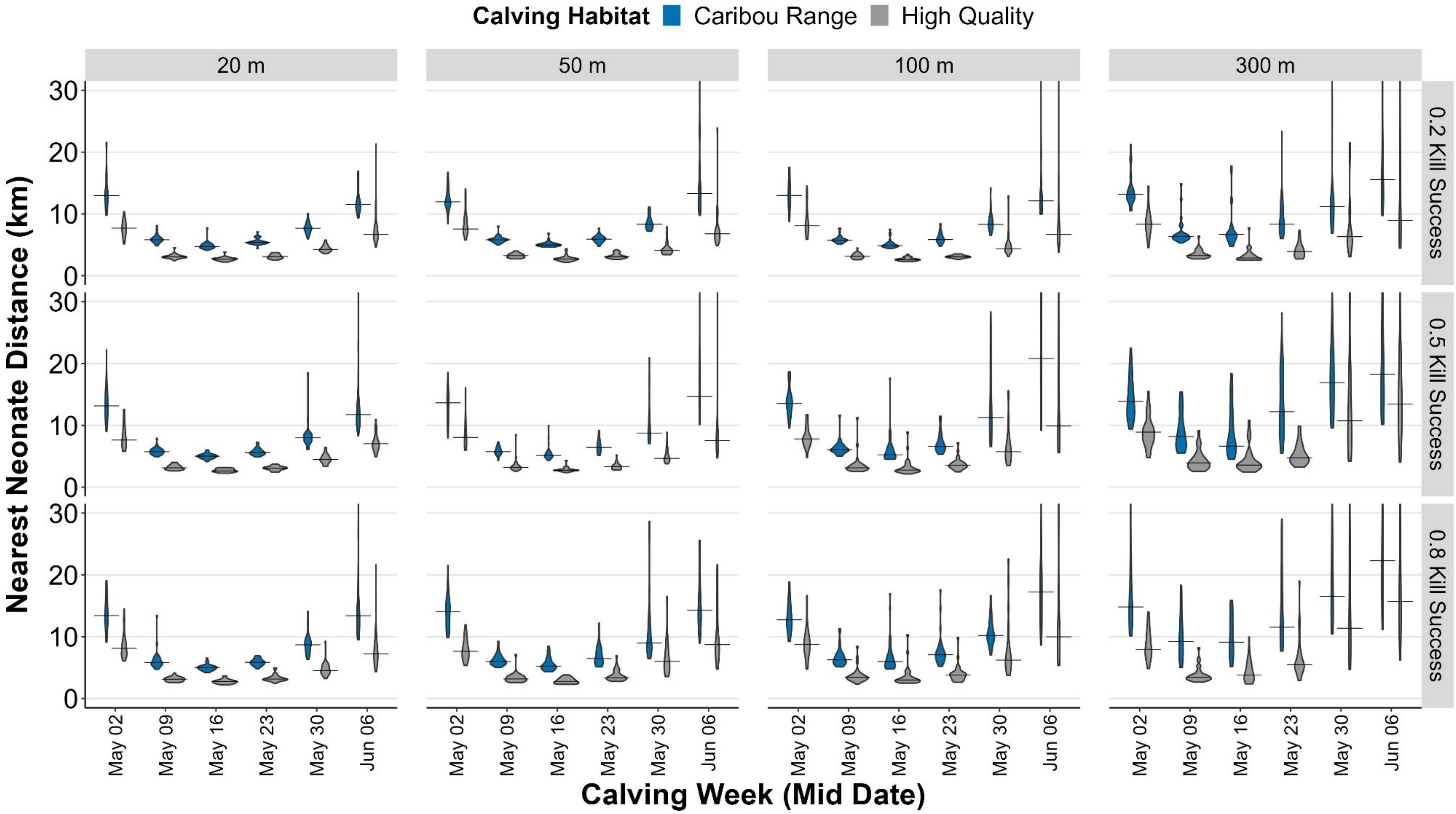

Figure H2. Violin plots of the mean distance (km) from each neonate to the nearest neonate across 7-day periods from April 29 – June 9 (i.e., many neonates on the landscape) during simulations where caribou neonates were placed throughout caribou range (blue) or in high-quality calving habitat (grey). The horizontal line in each week represents the median nearest neonate distance among the mean distances for that week (n=30, except for 2 weeks where n=29). Neonates were killed by black bears depending on the detection distance (meters; columns), kill success probability (rows), and bear population density (reduced density was used here (102 bears/1000 km^2; 1072 bears)). Note the y-axis excludes distances >30 km for the sake of visual clarity.