

SPECIAL SECTION

Moose and white-tailed deer mortality peaks in fall and late winter

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Abstract

The Grand Portage Band of Lake Superior Chippewa manages for sustainable subsistence harvests of moose (mooz; *Alces alces*) and white-tailed deer (waawaashkeshi; *Odocoileus virginianus*). Moose populations in northern Minnesota, USA, are declining, which may necessitate alterations to Indigenous subsistence practices. Moose and deer exhibit seasonal behaviors such as altered space use and movement strategies, to which gray wolves (ma'ingan; *Canis lupus*) and humans may adapt, resulting in seasonal mortality patterns. Identifying periods of increased moose and deer vulnerability is important for achieving tribal conservation objectives. We assessed seasonal cause-specific mortality of adult moose (2010–2021) and deer (2016–2022) fitted with global positioning system collars on and near the Grand Portage Indian Reservation (Gichi Onigaming; GPIR) in Minnesota and hypothesized mortality risk would be influenced by species-specific space use patterns and weather. We estimated survival rates and mortality risk using time-to-event models. We recorded 42 moose mortalities (17 health issues, 8 predations, 4 subsistence harvests, 13 unknown causes) and 49 deer mortalities (26 predations, 13 harvests, 4 other causes, 6 unknown causes). Mean annual moose survival was 83.2%, and mortality risk peaked during late winter (~25 April) and fall (~8 October). Mean annual deer survival was 48.0%, and mortality risk peaked during late winter (~25 March) and during their fall migration period (~11 November). Mortality

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timing coincided with transitions between space use states (i.e., periods of spatial stability), suggesting ungulates are at greater risk during these transitional periods, though movement strategy (i.e., resident vs. migratory) did not influence mortality risk. Further, increased winter severity corresponded with increased deer mortality. We observed similar temporal peaks in mortality risk when harvest mortalities were censored, suggesting our observed seasonal mortality peaks occur naturally despite harvest comprising most fall deer mortality. Our results can inform population models and harvest regulations by identifying periods of mortality risk on GPIR under Anishinaabe principles of seventh-generation conservation planning.

KEYWORDS

cause-specific, harvest, hunting, Indigenous, migration, predator–prey, survival, telemetry

Located on the ancestral and present homelands of the Anishinaabe people, the Grand Portage Indian Reservation (Gichi Onigaming; GPIR) in Minnesota is the present home of the Grand Portage Band of Lake Superior Chippewa, a federally recognized sovereign nation within the United States. In 1854, the Lake Superior Chippewa signed a treaty ceding lands in northeastern Minnesota to the United States. Under the 1854 Treaty, members of the Grand Portage, Fond du Lac, and Bois Forte bands of Lake Superior Chippewa can exercise their usufructuary rights to hunt, fish, and gather throughout the 1854 Ceded Territory (Thompson 2020), which spans northeastern Minnesota from Grand Portage to Moose Lake to Crane Lake (1854 Treaty Authority 2023). These practices cannot be regulated by Minnesota state law but may be governed by United States federal law, such as the Endangered Species Act of 1973. Within GPIR, resource harvest (e.g., wild fish and game, timber, and wild rice [manoomin; *Zizania palustris*]) is managed by the elected Tribal Council of the Grand Portage Band.

Moose (mooz; *Alces alces*) and white-tailed deer (waawaashkeshi; *Odocoileus virginianus*) are 2 culturally important species to the Anishinaabe seventh-generation planning approach to environmental stewardship. Moose populations in northeastern Minnesota are declining (Severud et al. 2022), and these declines are concerning because moose remain a primary subsistence species for Anishinaabe people. Deer are also an important subsistence species for Anishinaabe people. Deer populations are growing in northeastern Minnesota, but an increased presence of deer may negatively influence moose populations via parasite transmission and apparent competition (Barber-Meyer and Mech 2016, Oliveira-Santos et al. 2021, Severud et al. 2023). Moose and deer mortality occurs concurrent to seasonal disease and predation risk (Musante et al. 2010, Vucetich et al. 2012), warranting improved understanding of seasonal cause-specific mortality among these species of Indigenous conservation interest.

Seasonal mortality can be influenced by seasonal space use and species-specific movement strategies, which often change in response to shifting environmental conditions (Basille et al. 2013). Predator–prey interactions can also vary seasonally in response to species-specific space use within local communities via mechanisms such as migratory coupling (Furey et al. 2018). Exemplifying these changes, ungulates often alter space and resource use seasonally to maximize energetic gain (Avgar et al. 2014). Wildebeest (*Connochaetes taurinus*; Hopcraft et al. 2014) and caribou (*Rangifer tarandus*; Couriot et al. 2023) exhibit large-scale space use changes via migration, whereas roe deer (*Capreolus capreolus*) exhibit this pattern at smaller spatial extents by shifting their functional home ranges (Couriot et al. 2018). Resource selection by range-resident populations of sika deer (*Cervus nippon*; Latham

et al. 2015) and feral horses (*Equus caballus*; Schoenecker et al. 2023) also demonstrates seasonal changes in response to forage availability. Space use change is often risky (Avgar et al. 2014, Forrester et al. 2015) and, among partially migratory populations, migratory individuals generally incur greater mortality risk (Hebblewhite and Merrill 2007, Robinson et al. 2010).

Legal hunter harvest is a predominant source of anthropogenic large-mammal mortality and is usually concentrated during fall hunting seasons designated by regulatory agencies (Collins and Kays 2011, Dellinger et al. 2018, Hill et al. 2019). Wild boar (*Sus scrofa*; Lagos et al. 2012), elk (*Cervus canadensis*; Unsworth et al. 1993), and mule deer (*Odocoileus hemionus*; Dellinger et al. 2018) mortality was greatest during legal fall hunting seasons. Hunting pressure may also influence natural mortality; Eurasian lynx (*Lynx lynx*) increased roe deer predation during the fall hunting season as roe deer increased use of forests to avoid humans (Gehr et al. 2018). Comparatively, natural adult ungulate mortality is most common during winter (Dellinger et al. 2018) as demonstrated by greater winter mortality among red deer (*C. elaphus*), roe deer, and wild boar (Jedrzejewski et al. 1991, Warchalowski et al. 2015).

Moose and white-tailed deer alter their space and resource use seasonally (Basille et al. 2013, Severud et al. 2019, Darlington et al. 2022). Moose exhibit behavioral changes in spring associated with parturition and forage availability (Basille et al. 2013, Francis et al. 2021) and in winter by reducing movement rates and selecting snow depths and habitats that optimize energetic requirements and lessen predation risk (Dussault et al. 2005, Cunningham et al. 2022). Deer alter their behavior during late winter by switching from lower movement rates on south-facing slopes to higher movement rates in deciduous forests in response to forage availability and snow depth (Massé and Côté 2013, Darlington et al. 2022). Moose and deer mortality varies temporally, with greater natural mortality during winter than summer, corresponding to nutritional deficiencies and increased snow depth (Modafferi and Becker 1997, Musante et al. 2010, Vucetich et al. 2012, Dellinger et al. 2018).

Mortality studies generally use pre-defined or descriptive seasons, with few examining mortality in relation to seasonal space use or ecological seasons (Basille et al. 2013, Bastille-Rousseau et al. 2016). Roe deer mortality, for example, was assessed using 3 solstice-defined seasons: summer, autumn, and winter (Steiner et al. 2021). Comparatively, space use states are temporally delineated periods defined by relatively stable seasonal population-level space use (i.e., movements and resource selection) resulting from species-specific responses to changing biotic and abiotic conditions (e.g., available forage, reproductive activities, snowfall; Wehr 2023).

We examined seasonal moose and white-tailed deer mortality in a predominantly subsistence harvest system within the context of seasonal space use states, movement strategies, and Indigenous-led conservation efforts. Moose in our study area exhibit 4 space use states (summer, winter, spring, and pre-parturition) and 3 movement strategies (resident, migratory, or nomadic; Wehr 2023). Deer exhibit 2 space use states (summer and winter) and 2 movement strategies (resident or migratory; Wehr 2023). We hypothesized moose and deer mortality risk would be 1) similar among seasonal space use states because natural winter mortality and fall subsistence harvest would each contribute to their respective space use states, 2) greater among migratory individuals because of increased vulnerability during migration, 3) greater during winters and subsequent summers of greater winter severity as associated with cumulative malnutrition, and 4) lower during summers and subsequent winters with more growing degree-days (GDD) as associated with greater forage availability. Additionally, we predicted 5) the removal of hunter harvest mortalities from our models would result in winter being the only seasonal space use state with greater mortality risk corresponding to a single natural seasonal mortality peak.

STUDY AREA

We conducted our study during 2010–2022 on about 1,200 km² including GPIR (47.9614°N, 89.7594°W) and a 30-km buffer that included the migratory range of our study populations (Wehr 2023). This area includes portions of the 1854 Ceded Territory in Minnesota west of GPIR and Ontario, Canada, north of GPIR, and is bordered by

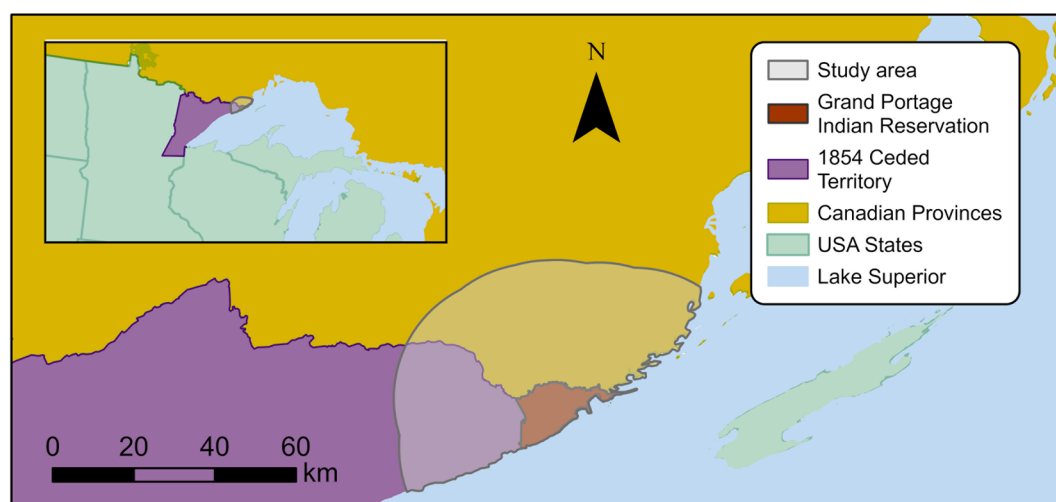


FIGURE 1 Study area on and near the Grand Portage Indian Reservation (GPIR), Minnesota, USA. Our study area included mainland areas near the coast of Lake Superior on GPIR, in the 1854 Ceded Territory within Minnesota, and in Ontario, Canada.

Lake Superior to the southeast (Figure 1). Topography is characterized by broad valleys between steep ridges, with elevations 183–674 m above sea level (U.S. Geological Survey 2020). The area contains 17% deciduous forest, 11% coniferous forest, 44% mixed forest, 9% shrubland, 7% wetland, and $\leq 5\%$ each of other land covers (Canada Centre for Remote Sensing et al. 2020), which is managed primarily for silviculture, hunter harvest, and recreation. Mean daily temperatures during 2009–2019 ranged from $23.3 \pm 1.7^\circ\text{C}$ (mean \pm SD) in July to $-17.8 \pm 3.5^\circ\text{C}$ in January (National Oceanic and Atmospheric Administration [NOAA] 2022). Annual average rainfall was 83.8 ± 11.7 cm, and annual average snowfall was 150.2 ± 80.8 cm (NOAA 2022).

Moose and white-tailed deer are the only wild ungulates in our study system (Wehr et al. 2023), and gray wolves (*ma'iingan*; *Canis lupus*) are their primary predator as adults. Moose can be harvested in Minnesota by tribal band members (1854 Treaty Authority 2023) and in Ontario by Ontario residents (Ontario Ministry of Natural Resources and Forestry [OMNRF] 2023). Minnesota tribal harvests are primarily antlered (Grand Portage Band of Lake Superior Chippewa, unpublished data) while antlered and antlerless Ontario moose harvests are more evenly distributed (Government of Ontario 2023a). The public can obtain permits to harvest deer in Minnesota and Ontario (Minnesota Department of Natural Resources [MNDNR] 2023b, OMNRF 2023), with greater antlered than antlerless harvests (Government of Ontario 2023b, MNDNR 2023a). Annual moose and deer hunting seasons occur during September–December (1854 Treaty Authority 2023, MNDNR 2023b, OMNRF 2023).

METHODS

Data collection

We used data collected by the Grand Portage Band of Lake Superior Chippewa Department of Biology and Environment. We included data from collared moose captured using aerial darting during February 2010–March 2020 and collared white-tailed deer captured using Clover traps during March 2016–April 2021 (VerCauteren et al. 1999, Barros et al. 2018, Oliveira-Santos et al. 2021). We monitored moose and deer through 28 February 2021 and 28 February 2022, respectively. We assessed sex and pregnancy at time of capture using physical characteristics and progesterone blood tests (Struck et al. 2023).

We programmed collars to send mortality alerts following 6 hours of inactivity. We assessed mortalities as soon as practical, typically ≤ 4 days from receipt of the mortality alert. We assessed dates and causes of mortality using data from collars, carcass remains, and other evidence at mortality sites (Kautz et al. 2019, 2020). Evidence of predation included predator tracks and scat, canine puncture wounds, hemorrhaging of punctured tissues, and caching (Petroelje et al. 2020). If we determined a mortality was a predation, we assigned it to a specific predator or otherwise considered it an unidentified predation (Kautz et al. 2019, 2020). Evidence of anthropogenic mortalities included proximity to roads, hemorrhaging of intact tissues, and bullet wounds; many anthropogenic mortalities were reported directly by hunters and vehicle operators. All moose harvest mortalities were from subsistence hunters, but some white-tailed deer harvests were not; for clarity, we refer to each as subsistence moose harvests and deer harvests, respectively. Evidence of health-related mortalities included decreased movement rates before death, hair loss, and infected tissues (Wünschmann et al. 2015). When available, we submitted organ samples to the University of Minnesota Veterinary Diagnostic Laboratory in St. Paul, Minnesota for pathogen evaluation (Carstensen et al. 2018). We excluded mortalities occurring within 7 days of capture because animal behavior and mortality risk may be altered during this period (Northrup et al. 2014).

Seasonal space use states and movement strategies were previously determined for moose and white-tailed deer on and near GPIR using cluster analyses (Basille et al. 2013) and Brownian bridge movement models (Merkle et al. 2022), respectively (Wehr 2023). Moose space use states were spring (11 March–13 April), pre-parturition (14 April–6 May), summer (7 May–17 October), and winter (18 October–10 March; Wehr 2023). Deer space use states were summer (24 April–18 November) and winter (19 November–23 April; Wehr 2023). Though not previously identified as separate space use states, we also considered deer spring migration (4 April–2 May) and fall migration (10 October–28 November) as distinct periods because they describe seasonal deer movements for 67% of the population (Wehr 2023). Using seasonal movements, we categorized individuals as resident (single year-round home range), migratory (seasonally shifting among 2–3 home ranges), nomadic (shifting among ≥ 4 home ranges), or unknown (movement strategy could not be assessed, typically because of mortality or collar failure soon after capture; Wehr 2023).

We used the NOAA Climate Data Online tool to extract mean daily snow depth and temperature from weather stations within our study area (Cook County, Minnesota) during 2010–2022 (NOAA 2022). We calculated a cumulative winter severity index (CWSI) by summing 1 point for each day snow depth was >38 cm and 1 point for each day mean ambient temperature was $<-17.7^{\circ}\text{C}$ (DeGiudice et al. 2002, Kautz et al. 2020). We summed scores continuously beginning 19 November to coincide with the onset of the winter space use state for white-tailed deer (Wehr 2023) and the median first day of CWSI accumulation during 2010–2022. We calculated GDD from mean daily temperatures with a latitudinal correction (van Wijk et al. 2012). We calculated GDD cumulatively beginning on 24 April to coincide with the onset of the summer space use state for deer (Wehr 2023) and the end of CWSI accrual. We used the same CWSI and GDD values for moose and deer.

Data analysis

To test our hypothesis that space use state, movement strategy, and weather influenced seasonal mortality risk, we modeled weekly survival separately for moose and white-tailed deer using staggered entry extended Cox proportional hazards models in R (version 4.2.1; Therneau and Grambsch 2000, R Core Team 2023). Cox proportional hazards models fit a baseline hazard function using time-to-event and a covariate matrix (Lin and Wei 1989). To prepare our time-to-event data, we grouped monitoring data into individual-years from 1 March (the approximate mean capture date of moose and deer) to 28 February of the following year and assigned individuals monitored for multiple years unique individual-year identifiers. We reformatted monitoring data from daily to weekly steps and right-censored weeks in which an animal recorded zero locations. We concluded monitoring if the animal died or was censored (individual alive on 28 February, collar failed, or collar intentionally removed). When an animal died, we recorded a mortality event and concluded monitoring (Kautz et al. 2020, Therneau et al. 2023).

We included covariates for each of our first 4 predictions in our covariate matrix. We included moose (winter, spring, pre-parturition, and summer) and white-tailed deer (winter, summer, spring migration, and fall migration) space use states, moose (resident, nomadic, migratory, or unknown) and deer (resident, migratory, or unknown) movement strategies, mean weekly CWSI, and mean weekly GDD. We additionally included nuisance covariates for sex and pregnancy status of moose (male or female positive, negative, or unknown) and sex of deer (female or male) because of their potential influences on survival among harvested populations (Nelson and Mech 1986, Ballard et al. 1991). To assess our final prediction, we developed models including and excluding hunter harvest mortalities. We developed 2 moose and 4 deer models (Table 1). We produced the 2 additional deer models to account for potential migration-specific peaks in seasonal mortality (Wehr 2023). We fit all models using the coxph function in the survival R package (Andersen and Gill 1982, Therneau 2022, Therneau et al. 2023). We reported hazard ratios for each covariate and considered covariates statistically significant if the *P*-value was <0.05 and the hazard ratio 95% confidence interval (CI) did not overlap 1.00. We displayed results using Kaplan-Meier estimates in the survminer R package (Rich et al. 2010, Kassambra et al. 2021). For deer, we compared the models including only the summer and winter space use states to those including all 4 seasons using Akaike's Information Criterion for small samples (AIC_c; Hurvich and Tsai 1989, Mazerolle 2023).

We used multi-modal flexible parametric periodic hazard functions in the cyclomort R package to estimate the number of mortality peaks and the dates and durations of those peaks with 95% confidence intervals (Gurarie et al. 2020). The utility of these models is the temporal estimation of the hazard function, which describes periods of greater mortality risk (Gurarie et al. 2020). We used the same individual-year delineations from our Cox proportional hazards models in these multi-modal models and similarly included and excluded harvest mortalities.

TABLE 1 Covariates included in each candidate Cox proportional hazards model of moose and white-tailed deer mortality on and near the grand Portage Indian Reservation, Minnesota, USA, 2010–2022. Space use states, movement strategies, and sex were categorical variables with available categories included. Cumulative winter severity index (CWSI) and growing degree days (GDD) were continuous covariates. Hunter harvest mortalities were either included or excluded from respective models.

Species	Space use states	Movement strategies	Sex	Continuous covariates	Harvest
Moose	Winter, spring, pre-parturition, summer	Resident, nomadic, migratory, unknown	Male, female positive, female negative, unknown	CWSI, GDD	Included
Moose	Winter, spring, pre-parturition, summer	Resident, nomadic, migratory, unknown	Male, female positive, female negative, unknown	CWSI, GDD	Excluded
Deer	Winter, summer	Resident, migratory, unknown	Male, female	CWSI, GDD	Included
Deer	Winter, spring migration, summer, fall migration	Resident, migratory, unknown	Male, female	CWSI, GDD	Included
Deer	Winter, summer	Resident, migratory, unknown	Male, female	CWSI, GDD	Excluded
Deer	Winter, spring migration, summer, fall migration	Resident, migratory, unknown	Male, female	CWSI, GDD	Excluded

We input individual-year mortality data for both species into each of 6 periodic hazard functions with 0–5 possible mortality peaks representing the number of possible transitions between space use states. We assessed model fit using Akaike's Information Criterion (AIC; Gurarie et al. 2020, Ewing et al. 2023).

RESULTS

Moose

We monitored 109 adult moose over 11 years, resulting in 283 moose-years (10,972 moose-weeks), and we recorded 42 mortalities. In moose-years, our sample included 51 males (18.0%), 88 pregnant females (31.1%), 22 non-pregnant females (7.8%), and 122 females of unknown pregnancy (43.1%). Our sample represented 149 nomadic (52.7%), 89 resident (31.4%), 24 migratory (8.5%), and 21 unknown movement strategy (7.4%) moose-years. Proximate causes of moose mortality included 17 health issues (40.5%; 5 brainworm parasite [*Parelaphostrongylus tenuis*], 5 winter tick [*Dermacentor albipictus*], 7 non-specific health issues), 8 gray wolf predations (19.0%), 4 subsistence hunter harvests (9.5%), and 13 unknown causes (31.0%).

Mean annual moose survival was 83.2% (95% CI = 78.7, 88.0; Figure 2). Our Cox proportional hazards models indicated the spring (reference category) and pre-parturition (95% CI = 0.01, 1.10; $P = 0.06$) space use states had the greatest hazard ratios, followed by the summer (95% CI = <0.01, 0.04; $P < 0.01$) and winter (95% CI = <0.01, <0.01; $P < 0.01$) space use states (Table 2; Table S1, available in Supporting Information). The multi-modal cyclomort model corroborated this result, indicating there were 2 mortality peaks (Table S2, available in Supporting Information): one centered on 25 April (95% CI = 9 April, 12 May) for 54 days (95% CI = 29, 90) during the spring and pre-parturition space use states, and one during the transition between summer and winter space use states centered on 8 October (95% CI = 17 September, 19 October) for 25 days (95% CI = 11, 55). Spring and pre-parturition mortalities ($n = 17$) were predominantly health issues (52.9%), gray wolf predations (17.6%), or unknown causes (29.4%), whereas summer–winter transition mortalities were from 5 sources (Figure S1, available in Supporting Information).

Hazard ratios for resident (95% CI = 0.23, 2.11; $P = 0.52$), nomadic (95% CI = 0.16, 1.30; $P = 0.14$), and migratory (reference category) moose were similar, but moose of unknown movement strategy had greater mortality (95% CI = 6.27, 61.80; $P < 0.01$). No weather covariates were related to mortality (Table 2; Figure S1; Table S1). Pregnant moose had lower hazard ratios than males (95% CI = 0.14, 0.81; $P = 0.02$), but non-pregnant (95% CI = 0.48, 3.36; $P = 0.63$) and unknown pregnancy moose (95% CI = 0.33, 1.84; $P = 0.56$) exhibited similar mortality to males (Table S3; Figure S2, available in Supporting Information). When harvested moose were censored, model estimates remained similar for Cox proportional hazards models (Table 2; Table S1) and multi-modal cyclomort models (Figure 3). But nomadic moose had lower hazard ratios (95% CI = 0.10, 0.94; $P = 0.04$) than migratory moose, and pregnant moose no longer exhibited lower hazard ratios (95% CI = 0.47, 3.44; $P = 0.63$) than males (Table 2; Table S1).

White-tailed deer

We monitored 75 adult white-tailed deer (2 dispersed outside the study area and were removed from our analyses) for 6 years, resulting in 124 deer-years (3,745 deer-weeks) and 49 mortalities. In deer-years, our sample included 34 males (27.4%) and 90 females (72.6%). Our sample included 69 migratory (55.6%), 30 resident (24.2%), and 25 unknown movement strategy (20.2%) deer-years. Deer mortalities included 25 gray wolf predations (51.0%), 13 hunter harvests (26.5%), 3 vehicle collisions (6.1%), 1 black bear (*Ursus americanus*) predation (2.0%), 1 accident (2.0%; fell from cliff), and 6 unknown causes (12.2%).

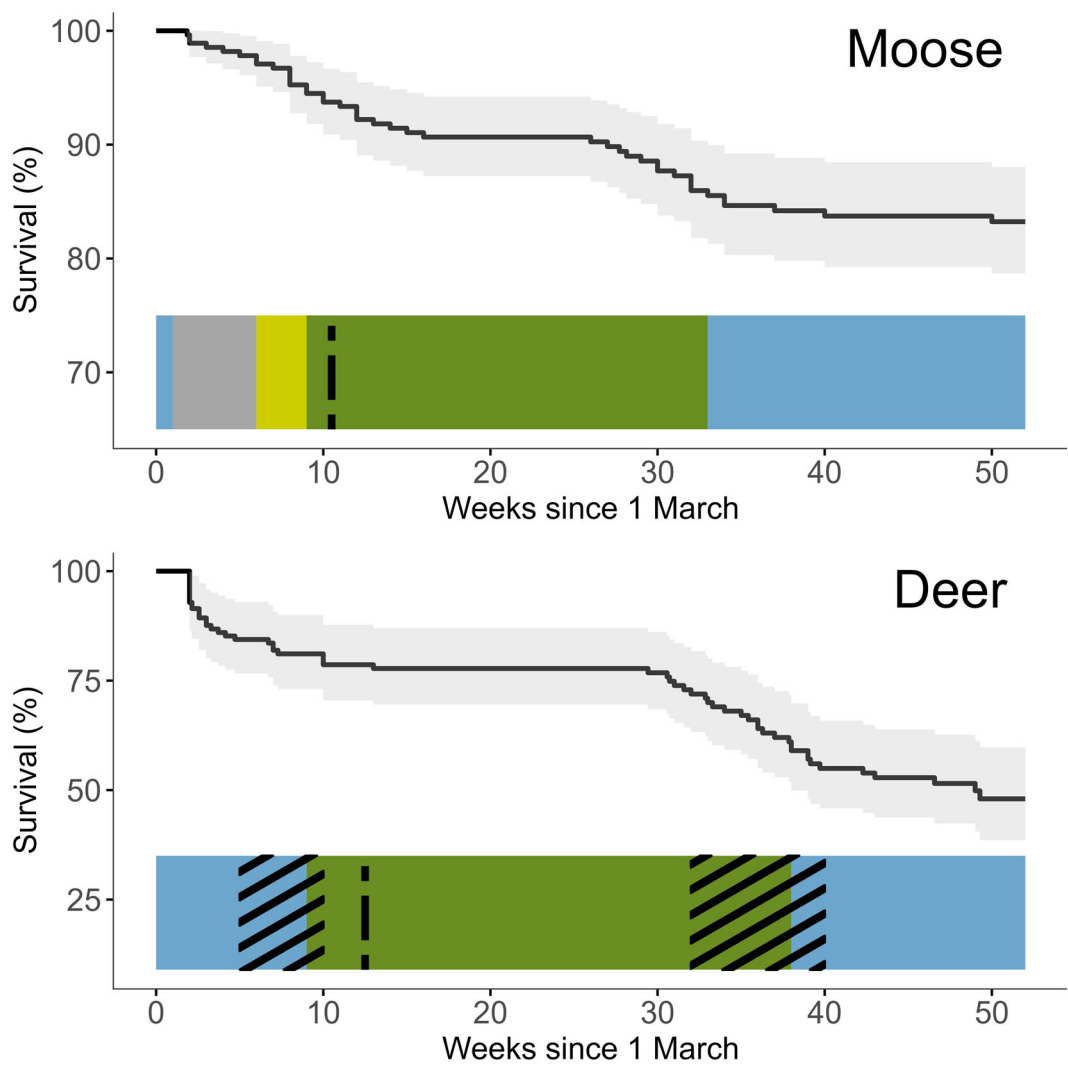


FIGURE 2 Moose (2010–2021) and white-tailed deer (2016–2022) survival on and near the Grand Portage Indian Reservation, Minnesota, USA. Solid black lines indicate mean percent population survival with gray shading representing 95% confidence intervals of Kaplan-Meier estimates. Colors represent space use states where gray is spring, yellow is pre-parturition, green is summer, and blue is winter. Black dashed lines represent median annual parturition dates, and black diagonal lines represent spring and fall migration periods. Models include harvest mortalities.

Mean annual white-tailed deer survival was 48.0% (95% CI = 38.6, 59.8; Figure 2). Our Cox proportional hazards 2- and 4-season models including hunter harvest were not different ($\Delta AIC_c = 0.25$, favoring the 2-season model), and covariate estimates did not result in competing interpretations (Table 3; Table S4, available in Supporting Information). Hazard ratios from the summer (reference category) and winter (95% CI = 0.06, 8.52; $P = 0.79$) space use states indicated similar mortality. Our multi-modal cyclomort model indicated deer mortality was best described by 2 peaks (Table S2). Both mortality peaks occurred during transitions between space use states and migration periods (i.e., winter, spring migration, summer, and fall migration). There was a late winter mortality peak centered on 25 March (95% CI = 11 March, 8 April) for 41 days (95% CI = 23, 69) and a fall mortality

TABLE 2 Hazard ratios for staggered entry extended Cox proportional hazards models of moose mortality on and near the Grand Portage Indian Reservation, Minnesota, USA, 2010–2021. Hazard ratios >1.00 indicate increased mortality, and hazard ratios <1.00 represent decreased mortality.

Covariate ^a	Including hunter harvest			Excluding hunter harvest		
	Hazard ratio	Lower CI	Upper CI	Hazard ratio	Lower CI	Upper CI
Pregnant: no	1.27	0.48	3.36	1.80	0.64	5.10
Pregnant: yes	0.34	0.14	0.81	0.49	0.47	3.44
Pregnant: unknown	0.77	0.33	1.84	1.28	0.19	1.26
Movement: nomadic	0.46	0.16	1.30	0.31	0.10	0.94
Movement: resident	0.69	0.23	2.11	0.53	0.17	1.67
Movement: unknown	19.69	6.27	61.80	17.91	5.63	56.98
Space use state: pre-parturition	0.12	0.01	1.10	0.12	0.01	1.14
Space use state: summer	<0.01	<0.01	0.04	<0.01	<0.01	0.04
Space use state: winter	<0.01	<0.01	<0.01	<0.01	<0.01	<0.01
GDD	0.73	0.46	1.15	0.73	0.46	1.15
CWSI	0.85	0.44	1.64	0.69	0.33	1.45

^aReference category for sex was males (compared to females by pregnancy status), reference category for movement status was migratory, and reference category for space use state was spring. Growing degree days (GDD) and cumulative winter severity index (CWSI) were continuous covariates.

peak centered on 11 November (95% CI = 5 November, 17 November) for 19 days (95% CI = 10, 35). Gray wolf predation accounted for most late winter mortality ($n = 13$, 76.5%) and harvests accounted for most fall mortality ($n = 11$, 78.6%; Figure S1).

Hazard ratios of resident (95% CI = 0.67, 2.99; $P = 0.37$) and migratory (reference category) white-tailed deer were similar in our Cox proportional hazards model, but unknown movement strategy deer had greater hazard ratios (95% CI = 2.82, 11.96; $P < 0.01$) as did all deer when CWSI was greater (95% CI = 1.20, 4.38; $P = 0.01$; Table 3; Figure S1). Females (reference category) and males (95% CI = 0.83, 2.92; $P = 0.16$) experienced similar hazard ratios (Figure S2), and GDD (95% CI = 0.53, 3.70; $P = 0.50$) did not influence mortality.

When harvest mortalities were censored, the 2- and 4-season models were not different ($\Delta AIC_c = 0.87$, favoring the 4-season model) and produced similar coefficients and interpretations (Table 3; Table S5, available in Supporting Information). The exception was that mortality was greater during the winter space use state in the 4-season model without harvest (95% CI = 1.18, 115.25; $P = 0.04$). Matching this exception, the timing, 7 November (95% CI = 11 October, 3 December), and duration, 47 days (95% CI = 16, 103), of the fall mortality peak in our multi-modal cyclomort model without harvest differed from the 2-season model (Figure 4).

DISCUSSION

Mortality risk of moose and white-tailed deer was greatest during transitional periods between space use states, which partially supported our first prediction. Moose mortality risk peaked in April during the spring–pre-parturition–summer space use state transitions and in October during the summer–winter space use state transition. Deer mortality risk peaked in March immediately before spring migration movements and in November during the fall migration period. Moose and deer mortality elsewhere was also greatest in late winter and during fall

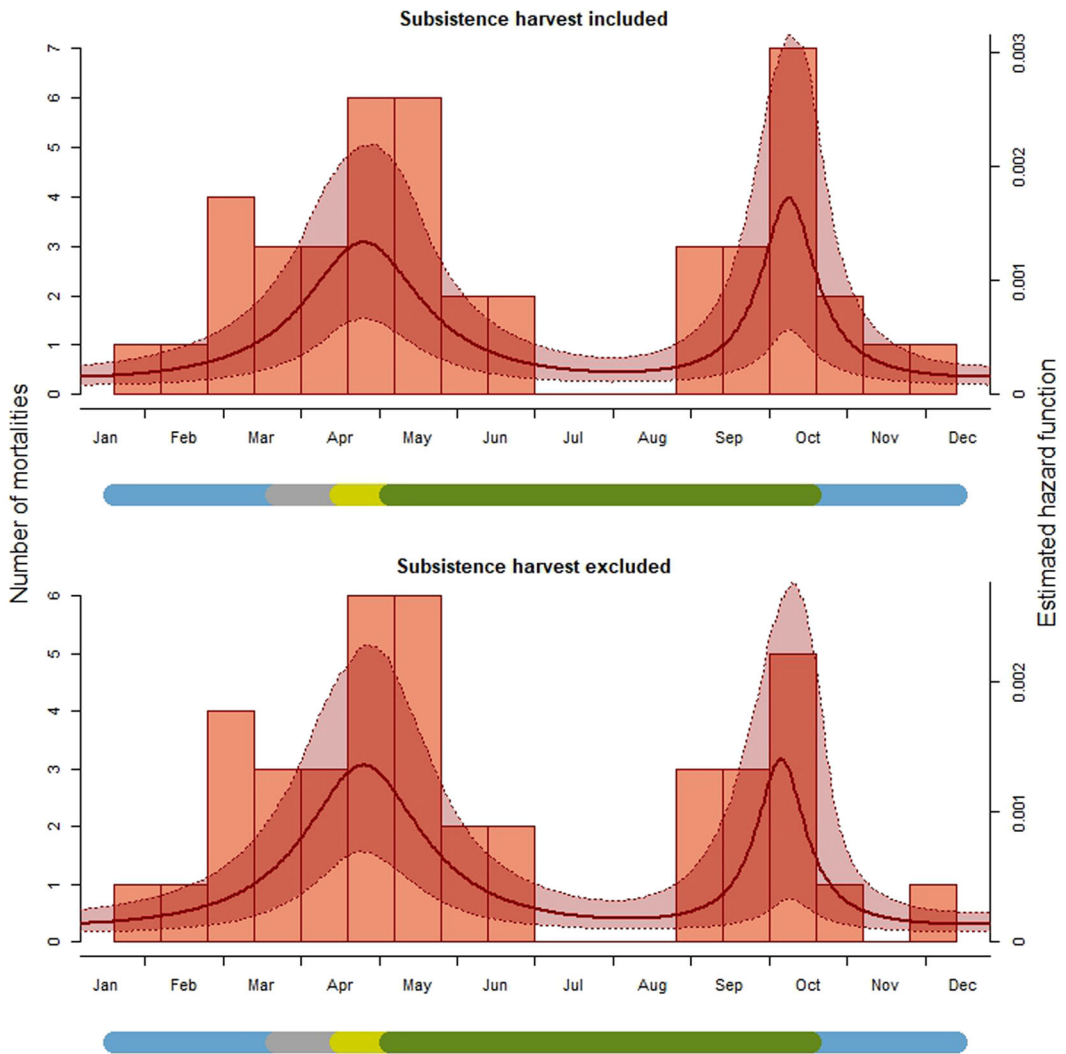


FIGURE 3 Periodic hazard function describing seasonal moose mortality risk on and near the Grand Portage Indian Reservation, Minnesota, USA, 2010–2021. The upper panel represents mortality risk with subsistence harvest included and the lower panel excludes subsistence harvest. Histograms represent the number of mortalities in a given time period; solid lines represent the estimated hazard function with shading indicating 95% confidence intervals. Colored bars beneath months represent space use states where gray is spring, yellow is pre-parturition, green is summer, and blue is winter.

hunting seasons (Lenarz et al. 2009, Musante et al. 2010, Dellinger et al. 2018, Kautz et al. 2020). Moose and deer in our study area exhibited similar ecological seasons (defined by space use states in this study) to populations in other locations (Basille et al. 2013, Francis et al. 2021, Petroelje et al. 2021). Caribou mortality in the Northwest Territories, Canada peaked in late April and mid-July (Gurarie et al. 2020, Kelly 2020), likely transition periods between ecological seasons (i.e., spring dispersal, pre-calving, calving, and late summer) as identified among caribou in Quebec, Canada (Basille et al. 2013). Hazard function assessments of seasonal mortality peaks are rarely conducted (Gurarie et al. 2020, Kelly 2020, Ewing et al. 2023), and we deepened this approach by examining mortality in direct relation to ecological seasons.

TABLE 3 Hazard ratios for staggered entry extended Cox proportional hazards models of white-tailed deer mortality on and near the Grand Portage Indian Reservation, Minnesota, USA, 2010–2021. Models either include or exclude hunter harvest and either exclude spring and fall migration as space use states (2 seasons) or include them (4 seasons). Hazard ratios >1.00 indicate increased mortality, and hazard ratios <1.00 represent decreased mortality. We report Akaike's Information Criterion for small samples (AIC_c) parenthetically alongside model names.

Covariate ^a	Including hunter harvest: 2 seasons (392.48)				Including hunter harvest: 4 seasons (392.73)				Excluding hunter harvest: 2 seasons (286.19)				Excluding hunter harvest: 4 seasons (285.32)			
	Hazard ratio	Lower CI	Upper CI		Hazard ratio	Lower CI	Upper CI		Hazard ratio	Lower CI	Upper CI		Hazard ratio	Lower CI	Upper CI	
Sex: male	1.56	0.83	2.92		1.51	0.81	2.81		1.22	0.54	2.72		1.19	0.53	2.66	
Movement: resident	1.41	0.67	2.99		1.41	0.67	2.98		1.21	0.46	3.13		1.23	0.47	3.18	
Movement: unknown	5.81	2.82	11.96		5.64	2.76	11.54		5.82	2.67	12.67		5.95	2.76	12.85	
Space use state: spring migration					2.80	0.47	8.10						4.37	0.61	31.22	
Space use state: fall migration					2.16	0.58	16.65						1.76	0.37	8.31	
Space use state: winter	0.71	0.06	8.52		6.19	0.81	47.41		2.27	0.13	40.44		11.68	1.18	115.25	
GDD	1.40	0.53	3.70		1.03	0.54	1.95		0.96	0.31	2.90		0.99	0.52	1.86	
CWSI	2.30	1.20	4.38		2.95	1.53	5.69		2.14	0.99	4.66		2.72	1.22	6.07	

^aReference category for sex was females, reference category for movement status was migratory, and reference category for space use state was summer. Growing degree days (GDD) and cumulative winter severity index (CWSI) were continuous covariates.

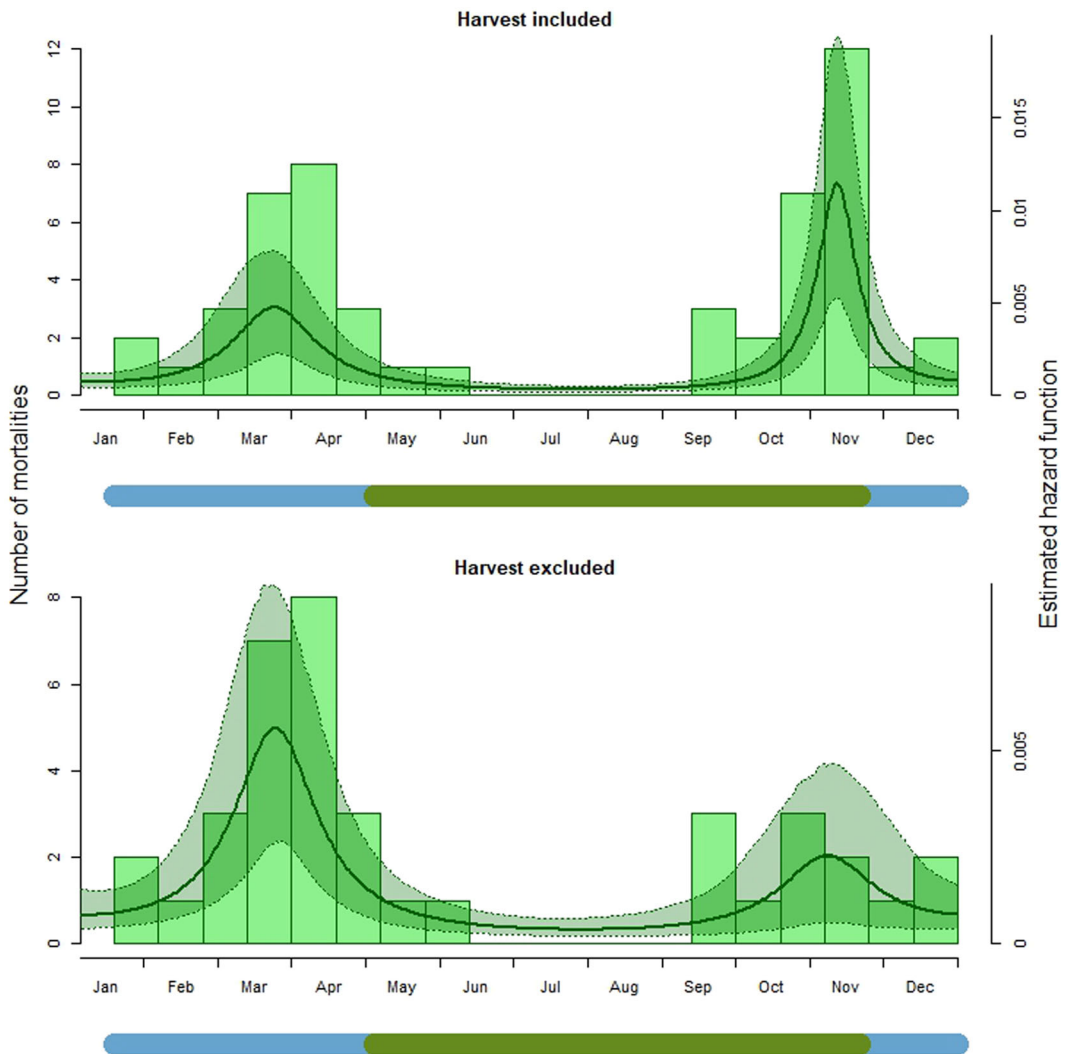


FIGURE 4 Periodic hazard function describing seasonal mortality risk of white-tailed deer on and near the Grand Portage Indian Reservation, Minnesota, USA, 2016–2022. The upper panel models mortality risk with harvest included and the lower panel excludes harvest. Histograms represent number of mortalities in a given time period; solid lines represent the estimated hazard function with shading indicating 95% confidence intervals. Colored bars beneath months represent space use states where green is summer and blue is winter.

Opposing our second prediction, movement strategy largely did not influence mortality. Migratory, nomadic, and resident moose exhibited similar mortality as did migratory and resident white-tailed deer. Migration is often risky because of decreased vigilance and lessened familiarity with new areas (Hebblewhite and Merrill 2007, Hopcraft et al. 2014, Forrester et al. 2015, Gehr et al. 2020). In partially migratory elk populations, migratory individuals generally incur greater risk than residents (Hebblewhite and Merrill 2009, Robinson et al. 2010), and migratory deer in our study system experience greater spatial overlap with wolves (Wehr 2023). A potential explanation for our contrasting results is the scale of migratory movements in our study system. Winter and summer ranges of migratory moose are from 1–20 km apart and from 3–33 km apart for deer (Wehr 2023). Comparatively, elk migration distances are typically greater, and predation pressure may vary more between their

seasonal ranges (Kauffman et al. 2020, Hebblewhite et al. 2021). Alternatively, spatial overlap may not equate to risk in our study system (Hebblewhite et al. 2005, Wehr 2023) or resident deer may experience mortality risks unassessed in this study as 3 of 4 fall deer mortalities of unknown cause were residents. That migratory deer did not experience greater mortality than residents has important implications for disease transmission in the context of declining Minnesota moose populations (Oliveira-Santos et al. 2021, Severud et al. 2023). Moose and deer with unknown movement strategies experienced greater mortality in our analyses, but this was likely an artefact of moose and deer with unknown movement strategies dying before their movement strategy could be adequately assessed (Wehr 2023).

Our third prediction regarding winter severity received mixed support. Moose experienced a late winter mortality peak due primarily to gray wolf predation and health issues. Moose are likely more susceptible to the cumulative effects of seasonal malnutrition and parasites (i.e., winter ticks; Wolf et al. 2021) during late winter, putting them at greater risk of predation and health-related mortality (Musante et al. 2010). Increased winter severity did not predict increased moose mortality risk in our study; this may be because moose can use greater snow depths to reduce gray wolf predation risk (Fuller 1991, Dussault et al. 2005). Comparatively, white-tailed deer in our study experienced greater mortality risk in more severe winters and in summers following more severe winters. This result matches prior work indicating winter severity during the current and preceding year can cause late-winter survival bottlenecks and reduce survival (Mech et al. 1987, Kautz et al. 2020). This result also supports models indicating northern deer distributions will expand as winter severity decreases with climate change (Kennedy-Slaney et al. 2018, Hinton et al. 2022), which may have negative effects on moose populations (Barber-Meyer and Mech 2016, Carstensen et al. 2018, Oliveira-Santos et al. 2021). We acknowledge, however, that the metric we used to assess winter severity (CWSI; DelGiudice et al. 2002) may not sufficiently explain winter weather variability and its influence on moose and deer. Threshold levels of snow depth considered by CWSI (38 cm) may be too low to influence moose mortality. Further, CWSI weighs all snow depths above the threshold equally and does not consider snow quality (i.e., density or top layer crustiness), which likely influences moose, deer, and gray wolf mobility.

Though our fourth prediction that increased GDD would decrease mortality risk was not supported, it is possible the moose mortality peak in late summer reflected a second period of moose susceptibility to parasites (e.g., brainworm), seasonal malnutrition, and predation. Supporting this possibility, others have reported moose in Minnesota experienced heat stress in summer and selected for thermal cover (Street et al. 2016, Carstensen et al. 2018). A further analysis of moose mortality using thermal metabolic threshold as a heat stress indicator reported decreased survival under warmer conditions (Lenarz et al. 2009). Increased GDD also did not decrease white-tailed deer mortality during summer or through the subsequent winter. This result contrasts with mule deer survival (Hobbs 1989) and evidence indicating white-tailed deer body mass is improved by earlier green-up (McGraw et al. 2020). Though GDD is a good predictor of forest growth, other climatic variables unassessed in our study (e.g., precipitation) influence forage availability (Dox et al. 2022). We recommend future analyses consider improved summer forage metrics (e.g., individual resource use or annual vegetation surveys) as predictors of mortality risk.

Our models produced generally similar results when harvest mortalities were removed, which counters our fifth prediction and suggests fall mortality peaks could represent periods of greater natural mortality similar to late winter mortality peaks. A difference between the multi-modal models with and without harvest was the increased width of the fall white-tailed deer mortality peak when harvest was excluded. A potential explanation for this difference is that hunting seasons typically occur in similar timeframes each year. Our estimated fall deer mortality peak with harvest (11 November) coincided with the midpoints of annual rifle deer hunting seasons in Ontario (e.g., 7 October–15 December in 2023; OMNRF 2023) and Minnesota (e.g., 4–18 November in 2023; MNDNR 2023b), periods during which Grand Portage Band members also exhibit peak effort and harvest (Grand Portage Band of Lake Superior Chippewa, unpublished data). That this fall deer mortality peak remained present when harvest mortalities were censored, despite harvest being the primary cause of mortality during this period, was unexpected.

The presence of a second natural mortality peak may support evidence that migratory deer experience greater gray wolf predation risk during the fall migration period (Wehr 2023), similar to other ungulates (Kojola et al. 2004, Hebblewhite and Merrill 2007), as the 6 non-harvest migratory deer mortalities of known cause that occurred during fall were directly or indirectly attributed to gray wolves.

MANAGEMENT IMPLICATIONS

Moose and white-tailed deer exhibited natural mortality peaks in fall and late winter. Winter mortality peaks likely result from winter resource scarcity. The natural fall mortality peak of moose was likely due to summer-induced heat stress, and most natural fall deer mortality was attributed to gray wolf predation of migratory individuals. Change in the moose hazard ratio during fall was negligible when subsistence hunter harvests were included. This result indicates Indigenous subsistence moose harvests by Grand Portage band members are likely compensatory, supporting their continued sustainable use of this resource. Comparatively, fall deer hazard ratios changed markedly when hunter harvests were included, suggesting these harvests are partially additive and may reduce disease transmission by deer to moose and aid moose conservation efforts led by the Grand Portage Band.

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CONFLICT OF INTEREST STATEMENT

The authors declare no conflicts of interest.

ETHICS STATEMENT

All animal capture and handling followed protocols approved by the Grand Portage Band of Lake Superior Chippewa Tribal Council, Michigan State University institutional animal care and use committee (PRO-TO202200266), and State University of New York College of Environmental Science and Forestry Institutional Animal Care and Use Committee (210702).

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REFERENCES

- 1854 Treaty Authority. 2023. Treaty harvest. <https://www.1854treatyauthority.org/treaty-harvest/treaty-harvest.html>. Accessed 11 Nov 2023.
- Andersen, P. K., and R. D. Gill. 1982. Cox's regression model for counting processes: a large sample study. *Annals of Statistics* 10:1100–1120.
- Avgar, T., G. Street, and J. M. Fryxell. 2014. On the adaptive benefits of mammal migration. *Canadian Journal of Zoology* 92:481–490.
- Ballard, W. B., J. S. Whitman, and D. J. Reed. 1991. Population dynamics of moose in south-central Alaska. *Wildlife Monographs* 114:3–49.
- Barber-Meyer, S. M., and L. D. Mech. 2016. White-tailed deer (*Odocoileus virginianus*) subsidize gray wolves (*Canis lupus*) during a moose (*Alces americanus*) decline: a case of apparent competition? *Canadian Field Naturalist* 130:308–314.

- Barros, D. S., A. L. Evans, J. M. Arnemo, F. Stenbacka, and G. Ericsson. 2018. Effective thiafentanil immobilization and physiological responses of free-ranging moose (*Alces alces*) in northern Sweden. *Veterinary Anaesthesia and Analgesia* 45:502–509.
- Basille, M., D. Fortin, C. Dussault, J. P. Ouellet, and R. Courtois. 2013. Ecologically based definition of seasons clarifies predator–prey interactions. *Ecography* 36:220–229.
- Bastille-Rousseau, G., N. D. Rayl, E. H. Ellington, J. A. Schaefer, M. J. L. Peers, M. A. Mumma, S. P. Mahoney, and D. L. Murray. 2016. Temporal variation in habitat use, co-occurrence, and risk among generalist predators and a shared prey. *Canadian Journal of Zoology* 94:191–198.
- Canada Centre for Remote Sensing, Canada Centre for Mapping and Earth Observation, Natural Resources Canada, Comisión Nacional para el Conocimiento y Uso de la Biodiversidad, Comisión Nacional Forestal, Instituto Nacional de Estadística y Geografía, and United States Geological Survey. 2020. 2015 land cover of North America at 30 meters. Canada Centre for Remote Sensing, Ottawa, Ontario, Canada.
- Carstensen, M., E. C. Hildebrand, D. Plattner, M. Dexter, V. St-Louis, C. Jennelle, and R. G. Wright. 2018. Determining cause-specific mortality of adult moose in northeast Minnesota, February 2013–July 2017. Pages 236–247 in L. Cornicelli, M. Carstensen, M. A. Larson, N. Davros, and B. Davis, editors. *Summaries of wildlife research findings 2016*. Minnesota Department of Natural Resources, St. Paul, USA.
- Collins, C., and R. Kays. 2011. Causes of mortality in North American populations of large and medium-sized mammals. *Animal Conservation* 14:474–483.
- Couriot, O. H., M. D. Cameron, K. Joly, J. Adamczewski, M. W. Campbell, T. Davison, A. Gunn, A. P. Kelly, M. Leblond, J. Williams, et al. 2023. Continental synchrony and local responses: climatic effects on spatiotemporal patterns of calving in a social ungulate. *Ecosphere* 14:e4399.
- Couriot, O. H., A. J. M. Hewison, S. Saïd, F. Cagnacci, S. Chamaillé-Jammes, J. D. C. Linnell, A. Mysterud, W. Peters, F. Urbano, and M. Heurich. 2018. Truly sedentary? The multi-range tactic as a response to resource heterogeneity and unpredictability in a large herbivore. *Oecologia* 187:47–60.
- Cunningham, C. X., G. E. Liston, A. K. Reinking, N. T. Boelman, T. J. Brinkman, K. Joly, M. Hebblewhite, S. Boutin, S. Czetwertynski, and L. E. Sielecki. 2022. Human and animal movements combine with snow to increase moose-vehicle collisions in winter. *Environmental Research Letters* 17:125007.
- Darlington, S., A. Ladle, A. C. Burton, J. P. Volpe, and J. T. Fisher. 2022. Cumulative effects of human footprint, natural features and predation risk best predict seasonal resource selection by white-tailed deer. *Scientific Reports* 12:1072.
- DelGiudice, G. D., M. R. Riggs, P. Joly, and W. Pan. 2002. Winter severity, survival, and cause-specific mortality of female white-tailed deer in north-central Minnesota. *Journal of Wildlife Management* 66:698–717.
- Dellinger, J., C. Shores, M. Marsh, M. Heithaus, W. Ripple, and A. Wirsing. 2018. Impacts of recolonizing gray wolves (*Canis lupus*) on survival and mortality in two sympatric ungulates. *Canadian Journal of Zoology* 96:760–768.
- Dox, I., B. Marien, P. Zuccarini, L. J. Marchand, P. Prislan, J. Gricar, O. Flores, F. Gehrman, P. Fonti, H. Lange, et al. 2022. Wood growth phenology and its relationship with leaf phenology in deciduous forest trees of the temperate zone of Western Europe. *Agricultural and Forest Meteorology* 327:109229.
- Dussault, C., J. P. Ouellet, R. Courtois, J. Huot, L. Breton, and H. Jolicœur. 2005. Linking moose habitat selection to limiting factors. *Ecography* 28:619–628.
- Ewing, S. R., C. E. Thomas, N. Butcher, B. Denman, D. J. T. Douglas, D. I. K. Anderson, G. Q. A. Anderson, J. Bray, S. Downing, and R. Dugan. 2023. Illegal killing associated with gamebird management accounts for up to three-quarters of annual mortality in hen harriers *Circus cyaneus*. *Biological Conservation* 283:110072.
- Forrester, T. D., D. S. Casady, and H. U. Wittmer. 2015. Home sweet home: fitness consequences of site familiarity in female black-tailed deer. *Behavioral Ecology and Sociobiology* 69:603–612.
- Francis, A. L., C. Procter, G. Kuzyk, and J. T. Fisher. 2021. Female moose prioritize forage over mortality risk in harvested landscapes. *Journal of Wildlife Management* 85:156–168.
- Fuller, T. K. 1991. Effect of snow depth on wolf activity and prey selection in north central Minnesota. *Canadian Journal of Zoology* 69:283–287.
- Furey, N. B., J. B. Armstrong, D. A. Beauchamp, and S. G. Hinch. 2018. Migratory coupling between predators and prey. *Nature Ecology & Evolution* 2:1846–1853.
- Gehr, B., N. C. Bonnot, M. Heurich, F. Cagnacci, S. Ciuti, A. M. Hewison, J. M. Gaillard, N. Ranc, J. Premier, and K. Vogt. 2020. Stay home, stay safe—site familiarity reduces predation risk in a large herbivore in two contrasting study sites. *Journal of Animal Ecology* 89:1329–1339.
- Gehr, B., E. J. Hofer, M. Pewsner, A. Ryser, E. Vimercati, K. Vogt, and L. F. Keller. 2018. Hunting-mediated predator facilitation and superadditive mortality in a European ungulate. *Ecology and Evolution* 8:109–119.
- Government of Ontario. 2023a. Moose hunting activity and harvests. <https://data.ontario.ca/dataset/moose-hunting-activity-and-harvests>. Accessed 25 Jan 2024.

- Government of Ontario. 2023b. White-tailed deer hunting activity and harvest. <https://data.ontario.ca/dataset/white-tailed-deer-hunting-activity-and-harvest>. Accessed 25 Jan 2024.
- Gurarie, E., P. R. Thompson, A. P. Kelly, N. C. Larter, W. F. Fagan, and K. Joly. 2020. For everything there is a season: analysing periodic mortality patterns with the cyclomort R package. *Methods in Ecology and Evolution* 11:129–138.
- Hebblewhite, M., H. Martin, S. Williams, G. Coulombe, M. Hessami, B. Gano, E. Merrill, M. Trottier, J. Normandeau, M. Flowers, et al. 2021. Ya Ha Tinda elk project: long-term monitoring of the partially migratory Ya Ha Tinda elk population, predators, and foraging resources. University of Montana, Missoula, USA.
- Hebblewhite, M., and E. H. Merrill. 2007. Multiscale wolf predation risk for elk: does migration reduce risk? *Oecologia* 152: 377–387.
- Hebblewhite, M., and E. H. Merrill. 2009. Trade-offs between predation risk and forage differ between migrant strategies in a migratory ungulate. *Ecology* 90:3445–3454.
- Hebblewhite, M., E. H. Merrill, and T. L. McDonald. 2005. Spatial decomposition of predation risk using resource selection functions: an example in a wolf–elk predator–prey system. *Oikos* 111:101–111.
- Hill, J. E., T. L. DeVault, and J. L. Belant. 2019. Cause-specific mortality of the world's terrestrial vertebrates. *Global Ecology and Biogeography* 28:680–689.
- Hinton, J. W., J. E. Hurst, D. W. Kramer, J. H. Stickles, and J. L. Frair. 2022. A model-based estimate of winter distribution and abundance of white-tailed deer in the Adirondack Park. *PLoS One* 17:e0273707.
- Hobbs, N. T. 1989. Linking energy balance to survival in mule deer: development and test of a simulation model. *Wildlife Monographs* 101:3–39.
- Hopcraft, J. G. C., J. M. Morales, H. Beyer, M. Borner, E. Mwangomo, A. Sinclair, H. Olff, and D. T. Haydon. 2014. Competition, predation, and migration: individual choice patterns of Serengeti migrants captured by hierarchical models. *Ecological Monographs* 84:355–372.
- Hurvich, C. M., and C. L. Tsai. 1989. Regression and time series model selection in small samples. *Biometrika* 76:297–307.
- Jedrzejewski, W., B. Jedrzejewska, H. Okarma, and A. L. Ruprecht. 1991. Wolf predation and snow cover as mortality factors in the ungulate community of the Białowieża National Park, Poland. *Oecologia* 90:27–36.
- Kassambara, A., M. Kosinski, and P. Biecek. 2021. survminer: drawing survival curves using 'ggplot2'. R package version 0.4.9. <https://cran.r-project.org/package=survminer>
- Kauffman, M. J., H. E. Copeland, E. Cole, M. Cuzzocreo, S. Dewey, J. Fattebert, J. Gagnon, E. Gelzer, T. A. Graves, K. Hersey, et al. 2020. Ungulate migrations of the western United States, volume 1. United States Geological Survey, Laramie, Wyoming, USA.
- Kautz, T. M., J. L. Belant, D. E. Beyer Jr., B. K. Strickland, and J. F. Duquette. 2020. Influence of body mass and environmental conditions on winter mortality risk of a northern ungulate: evidence for a late-winter survival bottleneck. *Ecology and Evolution* 10:1666–1677.
- Kautz, T. M., J. L. Belant, D. E. Beyer Jr., B. K. Strickland, T. R. Petroelje, and R. Sollmann. 2019. Predator densities and white-tailed deer fawn survival. *Journal of Wildlife Management* 83:1261–1270.
- Kelly, A. 2020. Seasonal patterns of mortality for boreal caribou (*Rangifer tarandus caribou*) in an intact environment. Thesis, University of Alberta, Edmonton, Canada.
- Kennedy-Slay, L., J. Bowman, A. A. Walpole, and B. A. Pond. 2018. Northward bound: the distribution of white-tailed deer in Ontario under a changing climate. *Wildlife Research* 45:220–228.
- Kojala, I., O. Huitu, K. Toppinen, K. Heikura, S. Heikkinen, and S. Ronkainen. 2004. Predation on European wild forest reindeer (*Rangifer tarandus*) by wolves (*Canis lupus*) in Finland. *Journal of Zoology* 263:229–235.
- Lagos, L., J. Picos, and E. Valero. 2012. Temporal pattern of wild ungulate-related traffic accidents in northwest Spain. *European Journal of Wildlife Research* 58:661–668.
- Latham, A. D. M., D. Herries, and M. C. Latham. 2015. Seasonal patterns of resource selection by introduced sika deer (*Cervus nippon*) in Kaweka Forest Park Recreational Hunting Area, New Zealand. *New Zealand Journal of Ecology* 39: 291–302.
- Lenarz, M. S., M. E. Nelson, M. W. Schrage, and A. J. Edwards. 2009. Temperature mediated moose survival in northeastern Minnesota. *Journal of Wildlife Management* 73:503–510.
- Lin, D. Y., and L. J. Wei. 1989. The robust inference for the Cox proportional hazards model. *Journal of the American Statistical Association* 84:1074–1078.
- Massé, A., and S. D. Côté. 2013. Spatiotemporal variations in resources affect activity and movement patterns of white-tailed deer (*Odocoileus virginianus*) at high density. *Canadian Journal of Zoology* 91:252–263.
- Mazerolle, M. J. 2023. AICcmodavg: model selection and multimodel inference based on (Q)AIC(c). R package version 2.3.2. <https://cran.r-project.org/package=AICcmodavg>
- McGraw, A. M., D. J. Storm, D. R. Bronson, and T. Pearson. 2020. Habitat and weather influence body condition in white-tailed deer, Wisconsin, USA. *Journal of Wildlife Management* 86:e22176.

- Mech, L. D., R. E. McRoberts, R. O. Peterson, and R. E. Page. 1987. Relationship of deer and moose populations to previous winters' snow. *Journal of Animal Ecology* 56:615–627.
- Merkle, J. A., J. Gage, H. Sawyer, B. Lowrey, and M. J. Kauffman. 2022. Migration Mapper: identifying movement corridors and seasonal ranges for large mammal conservation. *Methods in Ecology and Evolution* 13:2397–2403.
- Minnesota Department of Natural Resources [MNDNR]. 2023a. 2022 Minnesota deer harvest report. Minnesota Department of Natural Resources, St. Paul, USA.
- Minnesota Department of Natural Resources [MNDNR]. 2023b. Minnesota hunting & trapping regulations. Minnesota Department of Natural Resources, St. Paul, USA.
- Modafferi, R. D., and E. F. Becker. 1997. Survival of radiocollared adult moose in lower Susitna River Valley, southcentral Alaska. *Journal of Wildlife Management* 61:540–549.
- Musante, A. R., P. J. Pekins, and D. L. Scarpitti. 2010. Characteristics and dynamics of a regional moose *Alces alces* population in the northeastern United States. *Wildlife Biology* 16:185–204.
- National Oceanic and Atmospheric Administration [NOAA]. 2022. Climate Data Online (CDO). National Climatic Data Center, Asheville, North Carolina, USA.
- Nelson, M. E., and L. D. Mech. 1986. Mortality of white-tailed deer in northeastern Minnesota. *Journal of Wildlife Management* 50:691–698.
- Northrup, J. M., C. R. Anderson Jr., and G. Wittemyer. 2014. Effects of helicopter capture and handling on movement behavior of mule deer. *Journal of Wildlife Management* 78:731–738.
- Oliveira-Santos, L. G. R., S. A. Moore, W. J. Severud, J. D. Forester, E. J. Isaac, Y. Chenaux-Ibrahim, T. Garwood, L. E. Escobar, and T. M. Wolf. 2021. Spatial compartmentalization: a nonlethal predator mechanism to reduce parasite transmission between prey species. *Science Advances* 7:eabj5944.
- Ontario Ministry of Natural Resources and Forestry [OMNRF]. 2023. 2023 hunting regulations summary. Ontario Ministry of Natural Resources and Forestry, Peterborough, Canada.
- Petroelje, T. R., J. L. Belant, D. E. Beyer Jr., and N. J. Svoboda. 2020. Identification of carnivore kill sites is improved by verified accelerometer data. *Animal Biotelemetry* 8:18.
- Petroelje, T. R., T. M. Kautz, D. E. Beyer Jr., and J. L. Belant. 2021. Interference competition between wolves and coyotes during variable prey abundance. *Ecology and Evolution* 11:1413–1431.
- R Core Team. 2023. R: a language and environment for statistical computing. Version 4.2.1. R Foundation for Statistical Computing, Vienna, Austria.
- Rich, J. T., J. G. Neely, R. C. Paniello, C. C. J. Voelker, B. Nussenbaum, and E. W. Wang. 2010. A practical guide to understanding Kaplan-Meier curves. *Otolaryngology-Head and Neck Surgery* 143:331–336.
- Robinson, B. G., M. Hebblewhite, and E. H. Merrill. 2010. Are migrant and resident elk (*Cervus elaphus*) exposed to similar forage and predation risk on their sympatric winter range? *Oecologia* 164:265–275.
- Schoenecker, K. A., S. Esmaeili, and S. R. B. King. 2023. Seasonal resource selection and movement ecology of free-ranging horses in the western United States. *Journal of Wildlife Management* 87:e22341.
- Severud, W. J., S. S. Berg, C. A. Ernst, G. D. DelGiudice, S. A. Moore, S. K. Windels, R. A. Moen, E. J. Isaac, and T. M. Wolf. 2022. Statistical population reconstruction of moose (*Alces alces*) in northeastern Minnesota using integrated population models. *PLoS One* 17:e0270615.
- Severud, W. J., G. D. DelGiudice, and T. R. Obermoller. 2019. Association of moose parturition and post-parturition habitat with calf survival. *Journal of Wildlife Management* 83:175–183.
- Severud, W. J., T. M. Kautz, J. L. Belant, and S. A. Moore. 2023. Mineral licks as a potential nidus for parasite transmission. *Food Webs* 36:e00299.
- Steiner, W., E. M. Scholl, F. Leisch, and K. Hacklander. 2021. Temporal patterns of roe deer traffic accidents: effects of season, daytime and lunar phase. *PLoS One* 16:e0249082.
- Street, G. M., J. Fieberg, A. R. Rodgers, M. Carstensen, R. Moen, S. A. Moore, S. K. Windels, and J. D. Forester. 2016. Habitat functional response mitigates reduced foraging opportunity: implications for animal fitness and space use. *Landscape Ecology* 31:1939–1953.
- Struck, M., W. J. Severud, Y. M. Chenaux-Ibrahim, E. J. Isaac, J. L. Brown, S. A. Moore, and T. M. Wolf. 2023. Refining the moose serum progesterone threshold to diagnose pregnancy. *Conservation Physiology* 11:coad003.
- Therneau, T. M. 2022. Survival: survival analysis. R package version 3.3-1. <https://cran.r-project.org/package=survival>
- Therneau, T. M., C. Crowson, and E. Atkinson. 2023. Using time dependent covariates and time dependent coefficients in the Cox model. <https://stat.ethz.ch/R-manual/R-patched/library/survival/doc/timedep.pdf>. Accessed 6 Jun 2023.
- Therneau, T. M., and P. M. Grambsch. 2000. Modeling survival data: extending the Cox model. Springer, New York, New York, USA.
- Thompson, D. P. 2020. The right to hunt and fish therein: understanding Chippewa treaty rights in Minnesota's 1854 Ceded Territory. 1854 Treaty Authority, Duluth, Minnesota, USA.

- Unsworth, J. W., L. Kuck, M. D. Scott, and E. O. Garton. 1993. Elk mortality in the Clearwater drainage of northcentral Idaho. *Journal of Wildlife Management* 57:495–502.
- U.S. Geological Survey. 2020. 1 arc-second digital elevation models (DEMs)—USGS National Map 3DEP downloadable data collection. United States Geological Survey, Reston, Virginia, USA.
- van Wijk, R. E., A. Kölsch, H. Kruckenberg, B. S. Ebbinge, G. J. D. M. Müskens, and B. A. Nolet. 2012. Individually tracked geese follow peaks of temperature acceleration during spring migration. *Oikos* 121:655–664.
- VerCauteren, K. C., J. Beringer, and S. E. Hygnstrom. 1999. Use of netted cage traps for capturing white-tailed deer. Pages 155–164 in G. Proulx, editor. *Mammal trapping*. U.S. Department of Agriculture Animal and Plant Health Inspection Service, Fort Collins, Colorado, USA.
- Vucetich, J. A., B. A. Huntzinger, R. O. Peterson, L. M. Vucetich, J. H. Hammill, and D. E. Beyer Jr. 2012. Intra-seasonal variation in wolf *Canis lupus* kill rates. *Wildlife Biology* 18:235–245.
- Warchalowski, M., P. Nowakowski, and A. Dancewicz. 2015. Effect of winter conditions on wild ungulates mortality in the Owl Mountains (Poland). *Folia Forestalia Polonica* 54:187–193.
- Wehr, N. H. 2023. Seasonal movement, space use, and mortality of gray wolves, moose, and white-tailed deer in northeastern Minnesota. Dissertation, Michigan State University, East Lansing, USA.
- Wehr, N. H., H. M. Boone, S. R. Wehr, and J. L. Belant. 2023. Island characteristics and species traits predict mammal diversity across islands of the Great Lakes of North America. *Biodiversity and Conservation* 32:3465–3480.
- Wolf, T. M., Y. M. Chenaux-Ibrahim, E. J. Isaac, A. Wünschmann, and S. A. Moore. 2021. Neonate health and calf mortality in a declining population of North American moose (*Alces alces americanus*). *Journal of Wildlife Diseases* 57:40–50.
- Wünschmann, A., A. G. Armien, E. Butler, M. Schrage, B. Stromberg, J. B. Bender, A. M. Firshman, and M. Carstensen. 2015. Necropsy findings in 62 opportunistically collected free-ranging moose (*Alces alces*) from Minnesota, USA (2003–13). *Journal of Wildlife Diseases* 51:157–165.

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SUPPORTING INFORMATION

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

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