

Original Article

The importance of wilderness to wolf (*Canis lupus*) survival and cause-specific mortality over 50 years

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ABSTRACT

We assessed the relative importance of wilderness to gray wolf (*Canis lupus*) population dynamics over 50 years in a population that 1) was long extant (i.e., not reintroduced or recolonized), 2) was not subject to harvest in our study area until recently, and 3) used both wilderness and adjacent, mainly public, non-wilderness. We analyzed the survival of radiocollared wolves ($n = 756$ collared-wolf tenures) during 1968–2018 in the Superior National Forest, Minnesota, USA, including the Boundary Waters Canoe Area Wilderness. Over 50 years, adult annual survival was 78%. Wolves captured in wilderness tended to exhibit higher survival than those captured in non-wilderness, but the difference was more pronounced during harvest years and post-harvest years when wilderness wolf survival remained relatively high and non-wilderness wolf survival dropped (relative to pre-harvest). During Nov–Apr of pre-harvest years for adults, the natural mortality rate was similar for non-wilderness wolves and wilderness wolves (both 6%), but the anthropogenic mortality rate was higher for non-wilderness wolves than wilderness wolves (7% versus 1%), as was the illegal mortality rate (5% versus 1%). During Nov–Apr of pre-harvest years, wilderness wolves were less likely to die than non-wilderness wolves ($p = 0.042$; hazard ratio = 0.59), pups were more likely to die than adults ($p = 0.002$; hazard ratio = 1.84), and males were less likely to die than females ($p = 0.053$; hazard ratio = 0.73). Our long-term wolf survival, cause-specific mortality, and hazard results will inform management agencies whenever wolves are delisted, and jurisdiction for them passes to states.

1. Introduction

By the late 1960s gray wolves (*Canis lupus*) were extirpated throughout the contiguous United States except for a relatively isolated and small island population in Isle Royale National Park (about 20–30 wolves; Mech, 1966; Vucetich and Peterson, 2012) and a larger population in northeastern Minnesota (about 700 wolves) adjacent to a source population farther north in Ontario, Canada (Mech, 2009, 2017). Following Endangered Species Act (ESA) protections, wolves in Minnesota expanded their distribution, reclaimed some of their historic range, and eventually spread to Wisconsin and Michigan (Beyer et al., 2009; Wydeven et al., 2009). Since 1968 wolves in the Superior National Forest (SNF) of northeastern Minnesota, USA have been radiocollared as part of a long-term wolf-prey study (Mech, 2009). This ongoing study has resulted in 50 years of wolf radiotelemetry data and annual winter resident wolf counts (Mech, 2009). These long-term SNF wolf data have not been comprehensively examined for survival and cause-specific mortality.

A better understanding of wolf population dynamics is of particular importance to management across the contiguous United States where wolves are recolonizing and increasing in various areas where formerly extirpated (Gude et al., 2012; Jimenez et al., 2017; Mech, 2017; Mesler, 2015; Treves and Bruskotter, 2011). Although most wolf populations in the contiguous United States have been delisted, controversy persists partly due to public wolf harvests that commenced soon after delisting (Ausband, 2016; Creel and Rotella, 2010; Epstein, 2017; Hogberg et al., 2016; Mech, 2017; Olson et al., 2015). Well-informed wolf management requires understanding of key vital rates, including survival and cause-specific mortality (Adams et al., 2008; Creel and Rotella, 2010; Gude et al., 2012; Murray et al., 2010; O'Neil et al., 2017; Smith et al., 2010, 2020; Stenglein et al., 2015, 2018). Because wolves may have “a survival-driven life history compared to the recruitment-driven strategy of most harvested species” (Murray et al., 2010), information on anthropogenic (human-caused) mortality sources, such as harvest, based on estimates from individual-based models (rather than only population-level studies), is especially needed (Murray et al., 2010;

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Stenglein et al., 2015).

Our primary objectives were 1) to report survival and cause-specific mortality rates and 2) to investigate proportional hazards to determine what factors influenced mortality risk of radiocollared wolves in the SNF from 1968 through 2018, focusing on the potential influence of wilderness. Our study area in the SNF included part of the federally-designated Boundary Waters Canoe Area Wilderness, with no roads or motorized conveyances and with limited and regulated access during high human-use periods. The importance of wilderness, refugia, and/or protected areas to wolf population dynamics has been examined (Adams et al., 2008; Benson et al., 2014; Hebblewhite and Whittington, 2020; Mech, 1989; Smith et al., 2010, 2020), but our 50-year study was unique in that the wolf population 1) was long extant (i.e., not reintroduced or recolonized), 2) was not subject to harvest in our study area until recently, and 3) used both wilderness and adjacent, mainly public, non-wilderness. Because federally-designated wilderness (as defined in The 1964 Wilderness Act, Public Law 88-577, 16 U.S.C. 1131-1136) represents some of the least human-affected landscapes, assessments of wolf population dynamics there and in adjacent non-wilderness areas are important for better understanding human impacts on otherwise natural variation in wolf vital rates (Smith et al., 2010, 2020).

Although adult survival in longer-lived animals has greater potential effect on population dynamics than juvenile survival, it is often juvenile survival that has higher realized influence on trajectories, because adult survival is usually high and less variable (Eberhardt, 2002; Gaillard et al., 1998; Gude et al., 2012; Smith et al., 2020). Thus, we predicted that adult survival would be higher than juvenile survival (Smith et al., 2020). Given observations in Yellowstone of males having increased involvement in aggressive conflicts (Cassidy et al., 2017), we assessed whether survival of males and females differed.

We hypothesized that survival would be higher and that cause-specific mortality rates would differ for wolves that lived primarily in wilderness (Benson et al., 2014; Smith et al., 2010, 2020) compared to those that lived in the rest of the SNF. In the wilderness there are no roads so there should be no vehicle-strike mortality (Mech, 1989). There should also be less harvest, less opportunistic poaching, and less legal human-wildlife conflict mortalities due to relative difficulty of human access (Mech, 1989; Mladenoff et al., 1995). Similarly, there may be less exposure to domestic dogs (*C. l. familiaris*) and their diseases in the wilderness.

We suspected that most natural mortality would be intraspecific strife (wolf-killed wolf, hereafter “strife”) (Adams et al., 2008; Cubaynes et al., 2014; Mech, 1977), and we predicted that starvation and disease rates would be greater for pups than adults (Mech and Goyal, 1993, 1995, 2011; Mech et al., 2008; Smith et al., 2020). Based on our field observations, we also expected increased illegal mortality to coincide with fall ungulate harvest seasons when higher opportunistic poaching was likely to occur.

We also investigated whether wolf mortality varied with annual weather trends. We hypothesized that during severe winters there could be increased rates of disease-related mortality (e.g., mange) but decreased rates of starvation due to potentially increased prey vulnerability (Mech et al., 1971; Peterson and Allen, 1974; Post et al., 1999; Wilmers et al., 2020). We further hypothesized that mortality rates could vary in a density-dependent manner with the resident wolf population (Cubaynes et al., 2014; O’Neil et al., 2017, 2019; Post et al., 1999; Smith et al., 2015, 2020; Stenglein et al., 2018; Vucetich and Peterson, 2004).

Although our study population was only subject to legal harvest for a few months each year during 2012–2014 while it was delisted, we were interested in how survival and cause-specific mortality differed during that period. Due to limited data, we could not investigate proportional hazards during harvest years or post-harvest years.

The U.S. Fish and Wildlife Service (USFWS) proposed a rule in the Federal Register on March 15, 2019 to delist gray wolves in the Western Great Lakes region from protection of the ESA (USFWS, 2019). On

November 3, 2020 the USFWS published the final rule (USFWS, 2020) to remove gray wolves from the ESA effective January 4, 2021. Environmental groups subsequently filed a lawsuit challenging the delisting (Center for Biological Diversity, 2021). The results from our analysis will help inform potential ensuing state management of gray wolves (Creel and Rotella, 2010; Mech, 2017; Olson et al., 2015) by better defining rates of survival and sources of mortality for them.

2. Methods

2.1. Study area

Our study area (Fig. 1) consisted of 2060 km² of the SNF, generally east of Ely, Minnesota, USA (48°N, 92°W) extending just into the southern portion of Ontario, Canada (see Nelson and Mech, 1981 and Mech, 2009 for detailed descriptions). Temperatures rarely exceeded 35 °C, while average monthly temperatures ranged from approximately –18 °C to 2 °C during November through April and 4 °C to 18 °C during May through October (Heinselman, 1996). From mid-November through mid-April snowfall averaged approximately 150 cm, with snowpack typically present from December through April (Heinselman, 1996; Nelson and Mech, 2006). The area was in a transition zone between the southern boreal forest of neighboring Ontario, Canada and the hardwood forests typical of areas just south (Pastor and Mladenoff, 1992). Vegetation was predominately conifers (e.g., jack pine [*Pinus banksiana*], white pine [*P. strobus*], red pine [*P. resinosa*], black spruce [*Picea mariana*], white spruce [*P. glauca*], balsam fir [*Abies balsamea*], white cedar [*Thuja occidentalis*], and tamarack [*Larix laricina*]) in the forest overstory with white birch (*Betula papyrifera*) and quaking aspen (*Populus tremuloides*) interspersed (Heinselman, 1996). The landscape generally included uneven uplands, numerous lakes, swamps, and rocky ridges with elevations mainly 325 m to 600 m above sea level (Heinselman, 1996).

About 40% of our study area included non-wilderness (national forest land with private inholdings) and the other 60% included wilderness that was comprised of the Boundary Waters Canoe Area Wilderness (57%) and a small portion of Quetico Provincial Park, Canada to the north (~3%) (Fig. 1). The vast majority of our study area was public land, with private residences primarily clustered around a narrow corridor extending east about 19 km along the northwest corner of our study area from a town about 6.5 km west-northwest of our study area (Winton, Minnesota, 2020 population = 168; <https://worldpopulationreview.com/us-cities/winton-mn-population>, accessed 30 December 2020). Our study area included no towns, no agricultural land, and no livestock operations. Non-wilderness included a network of paved and unpaved roads and trails used by automobiles and recreational vehicles (ATVs, snowmobiles). Road density (including U.S. Forest Service Road types A, B, and C; U.S. Forest Service, 1986) in the core of the non-wilderness of our study area averaged 0.73 km/km² (Mech, 1989). About 80% of those roads and trails in the non-wilderness were impassable during winter by vehicle except by snowmobiles (Mech, 1989). Density of snow-compacting trails and roads in the wider non-wilderness averaged 1.19 km/km² and ranged from 0.69–1.83 km/km² in relevant Lynx Analysis Units during 2020 (USDA Forest Service, 2020). There were no roads or motorized vehicles permitted in wilderness. Human impacts on wilderness were further limited through regulated access during peak-visitation periods. Wolf prey (white-tailed deer [*Odocoileus virginianus*], moose [*Alces americanus*], and beaver [*Castor canadensis*]) in the non-wilderness were legally harvested. Both male and female moose were harvested from 1993 until 2007 (Mech et al., 2018). From 2007 to 2012, “only males were harvested except for a few females harvested by Native American hunters” (Mech et al., 2018). After 2012, the moose harvest was restricted to Native Americans, and few were taken. Although harvest was allowed in the wilderness, moose and beaver did not face as significant harvest pressure there, likely in part due to limited access (Barber-Meyer, 2019). Wilderness was also not

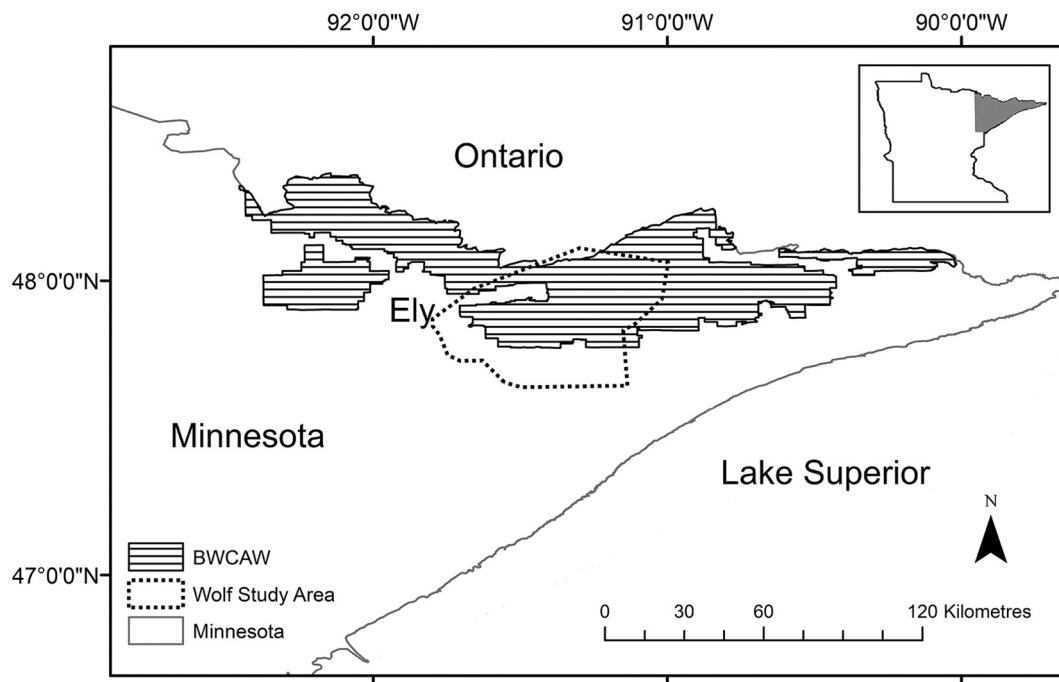


Fig. 1. The Superior National Forest wolf study area in northeastern Minnesota, USA. The Boundary Waters Canoe Area Wilderness (BWCAW) and the town of Ely, Minnesota are also shown.

subject to logging, had more water features and higher beaver density, and generally included more moose than white-tailed deer, relative to non-wilderness (Barber-Meyer, 2019). Both areas were subject to wildfires, but they were managed to protect human developments in non-wilderness, whereas they were generally allowed to burn in wilderness.

Minnesota wolves were federally listed as endangered in 1967, protected as endangered in 1974, downlisted to threatened in 1978, temporarily delisted and relisted twice, delisted from 2012 to 2014 and managed then by Minnesota including a regulated public harvest during November through January each year except in 2014 when the harvest ended in mid-December when wolves were relisted again. Wolves in this study were part of a larger contiguous population that included wolves in Ontario, Canada. While wolves in Quetico Provincial Park (directly north of our study area) were legally protected, elsewhere in Ontario they experienced hunting and trapping pressure. During our study, wolf density varied between 11 and 47 wolves per 1000 km² (Mech and Barber-Meyer, 2019). Other medium-large mammals present in the study area, but in unknown abundance, included lynx (*Lynx canadensis*) (Barber-Meyer et al., 2018; Burdett et al., 2007; Mech, 1973a, 1980), coyote (*Canis latrans*), and black bear (*Ursus americanus*) (Rogers, 1987). Wolf packs in the northeast of our study area fed primarily on moose (Mech and Frenzel, 1971; Mech and Nelson, 2013), whereas those in the southwest fed mainly on white-tailed deer (Barber-Meyer and Mech, 2016; Frenzel, 1974; Mech, 2009; Mech and Frenzel, 1971; Nelson and Mech, 1981, 1986). Beaver and snowshoe hare (*Lepus americanus*) were also prey for resident carnivores (Barber-Meyer and Mech, 2016; Mech and Karns, 1977; O'Donoghue et al., 1997).

2.2. Capture and handling

We live-trapped wolves with modified foot-hold traps from 1968 to 2017, mostly May through November, drugging the animals intramuscularly with anesthetics via syringe-pole (Barber-Meyer and Mech, 2014; Kreeger and Arnemo, 2018; Mech, 1974, 2009). Traps were baited with standard natural and commercial baits and lures, and they were generally placed along logging roads, trails, or canoe portages, and checked at least daily. We followed the guidelines of the American

Society of Mammalogists for use of wild mammals in research (Sikes and the Animal Care and Use Committee of the American Society of Mammalogists, 2016) under USFWS permits PRT831774 and TE3886A-0 and the approval of the U.S. Geological Survey, Northern Prairie Wildlife Research Center Animal Care and Use Committee.

We weighed, measured, determined sex, ear-tagged, and collected biologic samples from wolves, and fitted them with radiocollars that pulsed either continuously or just throughout the day, and since 1987 radiocollars included mortality signals that pulsed approximately 3 times as rapidly after 4 h of inactivity (e.g., Telonics, Inc., Mesa, AZ). Pups were generally not radiocollared until late summer or fall. Almost all radiocollars (96%) were standard very high frequency (VHF) collars; 4% were Global Positioning System (GPS) collars equipped with VHF beacons. We handled wolves for approximately 1 h. For additional capture and handling details see Mech (1974) and Barber-Meyer and Mech (2014).

Starting in 2000, we estimated ages of all non-pup wolves by tooth wear comparing with the chart in Gipson et al. (2000). Previously, we assigned a minimum age of 1 year to non-pup wolves at their initial capture. If a wolf was later recaptured, we updated each wolf's known-minimum age by adding the ensuing years (Mech et al., 2016). In some cases, tooth wear information recorded at the time of capture from wolves captured prior to 2000 allowed us to retroactively assign a more precise age based on Gipson et al. (2000) (Mech et al., 2016).

2.3. Aerial telemetry and necropsy investigations

Generally, we aerially located radiocollared wolves weekly year-round and observed them and their pack-mates mostly in winter but occasionally at other times. We recorded maximum winter pack sizes observed during aerial surveys from 1968 to 2018 (Barber-Meyer et al., 2016; Mech, 1973b, 2009). Occasionally, packs within our study area were not radiocollared, and we used information such as aerial or ground track counts, aerial or ground observations of wolves, and camera-trap images to generate a probable pack-size range. For individual packs that straddled our study area border, we prorated their pack size by the proportion of their winter territory included in our

study area to generate that pack's maximum winter pack size. We added the maximum winter pack sizes to determine the annual winter resident wolf count (Fig. 2). When the annual result was a range because of pack-size uncertainty, we used the mean. Pack wolf density was determined by dividing our annual winter resident wolf count by our study area. Because our annual winter count only included packs, lone wolves were not included.

We determined that a wolf might be dead when its location did not change for consecutive tracking sessions, or as of 1987 when mortality switches in collars indicated lack of movement for at least 4 h. We investigated the carcass (or what remained of it) from the ground as soon as possible to determine cause of death. Mortality categories included natural (starvation/disease, strife, natural-other, or natural-unknown), anthropogenic (vehicle strike, illegal, legal-take, anthropogenic-other, or anthropogenic-unknown), and unknown. Illegal anthropogenic mortality could have also included deaths caused by snares/traps that were legally set for other species, but wolves died in them outside of a legal wolf harvest season. Provisional mortality causes were identified in the field and reviewed by long-term project biologists. We judged the most significant factor affecting mortality to be the cause of death (Stenglein et al., 2015). Some examples of evidence used to assign categories included bite marks consistent with wolf canines to the face, neck, shoulders, rump, groin, or legs (i.e., strife, Mech and Barber-Meyer, 2017), proximity to road, blunt trauma, and skin abrasion (i.e., vehicle strike), and emaciation, poor marrow fat, or extreme hair loss (i.e., starvation/disease). We note that determining precise cause of death is typically more difficult for mortalities in remote areas (generally wilderness in our study area).

2.4. Statistical analyses

We classed wolves as adults or pups from 1968 to 1999. After that we classed wolves as adults (≥ 3 years), subadults (1–2 years), or pups (< 1 year). Except as specified for some exploratory analyses (see below), adults and subadults were pooled to increase samples.

We used capture location (wilderness or non-wilderness) as a proxy for wilderness use because we were unable to precisely calculate wilderness use due to data limitations. To assess whether this was reasonable before conducting our analyses, we compared capture versus mortality locations ($n = 302$ mortalities). Of 264 wolves captured in

non-wilderness, 239 (91%) died there, and 8 more (3%) died within 1.6 km of non-wilderness. Of 38 wolves captured in wilderness, 24 (63%) died there, and 4 more (11%) died within 1.6 km of wilderness. While most of our data were from VHF collars, we had GPS-collar location data that spanned the tenures of three wolves captured in wilderness. These GPS data were not sufficient to analyze wilderness use out of 756 collared-wolf tenures (see Hebblewhite and Whittington, 2020), but lend support for our use of capture-location as a proxy. The first wolf was a resident female in a pack with a territory that included primarily wilderness, but also included some non-wilderness. Her tenure was from October 2013 to January 2016 with 4333 locations recorded (72% in wilderness). The second wolf was a resident male that remained almost entirely in wilderness throughout his tenure from October 2014 to March 2016 with 2707 locations recorded (96% in wilderness). The third wolf was a male that at first was a wilderness resident with a mate, then later made large movements north into Quetico Provincial Park wilderness, returned to wilderness in our study area, then moved out of the wilderness and out of our study area to the southwest and then to the southeast of our study area along Lake Superior, followed by its collar expiring. His tenure was from September 2016 to December 2018 with 4477 locations recorded (57% in wilderness). Generally, these location patterns from the 3 GPS-collared, wilderness-captured wolves show that wilderness-captured wolves tended to use wilderness areas, though not exclusively. Hereafter, we refer to wilderness wolves and non-wilderness wolves based on where they were captured.

Our radiotelemetry data consisted of generally weekly locations that represented collared-wolf tenures. We structured our radiotelemetry data with either an annually or seasonally recurrent time of origin for statistical analyses. We defined the biological year as May (year) through April (year+1) to coincide with pup birth. We defined two seasons based on when wolves primarily den and use rendezvous sites (season 1, May 1–Oct 31) and when they move more widely after pups are more fully grown (season 2, Nov 1–Apr 30) (Barber-Meyer and Mech, 2015). Radiotelemetry outcomes included either mortality or censored. If the date of death was unknown or could not be reasonably estimated, we used the midpoint between the date of the last active radio location and the date of the mortality signal. Censored animals included those (1) that survived to the end of the study, and (2) whose signals were lost. The latter could have resulted from radios malfunctioning or expiring, wolves dispersing out of detectable range, or individuals being

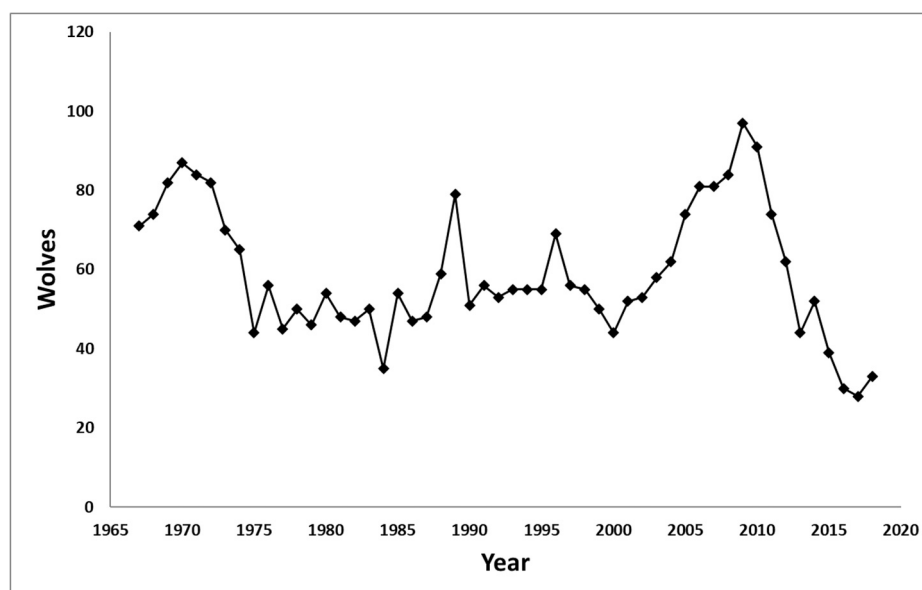


Fig. 2. Annual winter resident wolf counts from 1967 to 2018 in the Superior National Forest 2060 km² wolf study area, Minnesota, USA (Barber-Meyer et al., 2021; Mech, 2009). In cases where the annual result was a range, we plotted the mean. Note that radiocollaring commenced in 1968. Thus, the 1967 winter count was obtained through 124 h of aerial observations of wolves and their tracks (Mech and Frenzel, 1971).

illegally killed whose radios were destroyed. Animals could re-enter the study as a separate collared-wolf tenure with new entry and exit dates after censoring if recaptured and recollared (e.g., collar failed, later animal recaptured). If an animal was recaptured and its collar was replaced while it was currently being tracked, we considered that a continuation of the existing tenure. To minimize possible capture effects on wolf fates, we only analyzed data for wolves confirmed active at least 14 days post-capture. Data were pooled across biological years for statistical analyses due to small samples within them. Also, pups were assessed only during Nov–Apr for statistical analyses because most pups were not radiocollared until late summer or fall. Due to data limitations, we could not analyze several variables that may affect survival, including resident or transient status (Benson et al., 2014; O’Neil et al., 2017), pack size (Almberg et al., 2015), pack demographics (Cassidy et al., 2015), and interactions among variables (e.g., sex and age class) (Cassidy et al., 2017). We also did not analyze canine parvovirus’ influence on mortality because there were too many missing values, it has been reported on extensively in this study area, and it mainly affects pups younger than those that we radiocollared (Mech and Goyal, 1993, 1995, 2011; Mech et al., 2008). Given that our study was longer than most other wolf studies, a primary aim of ours was to report survival and cause-specific mortality rates over various periods and within various strata. In general, because subsamples were small and confidence intervals were large, we refer to point estimates as higher or lower than others throughout the manuscript without necessarily implying statistical significance, except where we note statistical significance (readers are invited to examine corresponding confidence intervals).

Individual wolf data and annual winter resident wolf counts are available at doi:<https://doi.org/10.5066/P9KVM4IH> (Barber-Meyer et al., 2021). We conducted all analyses in R version 3.5.1 (R Core Team, 2018) using the “survival” package (Therneau, 2015) and the “wild1” package (Sargeant, 2011). We considered results significant at $\alpha = 0.05$ and marginally significant (suggestive) at $\alpha = 0.10$.

2.5. Survival analysis

We generated survival functions for radiocollared wolves using the nonparametric Kaplan-Meier estimator modified for staggered entry of individuals (Pollock et al., 1989). We compared survival based on sex, age class (adults, pups), and wilderness capture (yes or no). From 2000 to 2018, we also assessed subadult survival (i.e., age classes included pups, subadults, and adults). We estimated annual and seasonal survival rates for radiocollared wolves during different periods, including the entire study (1968–2018), pre-harvest years (1968–2012), harvest years (2012–2015), and post-harvest years (2015–2018). We report survival rates as decimals and percents interchangeably.

2.6. Cause-specific mortality analysis

We used the nonparametric, cumulative-incidence-function estimator (Heisey and Patterson, 2006) to generate cause-specific mortality rates and 95% confidence intervals for radiocollared wolves. We compared cause-specific mortality rates based on sex, age class (adults, pups), and wilderness capture (yes or no). We estimated annual and seasonal cause-specific mortality rates for radiocollared wolves during different periods, including the entire study (1968–2018), pre-harvest years (1968–2012), harvest years (2012–2015), and post-harvest years (2015–2018). We report cause-specific mortality rates as decimals and percents interchangeably.

2.7. Cox proportional hazards regression analysis

We used the Anderson-Gill extension to the Cox Proportional Hazards (CPH) regression model (Therneau and Grambsch, 2000) to assess factors potentially influencing mortality risk of radiocollared wolves, including annual continuous variables (weather and wolf-density index)

and individual categorical variables (sex, age class, and wilderness capture). We assessed these factors annually and seasonally (May–Oct, Nov–Apr) during the entire study and pre-harvest years; note that age class was only assessed during Nov–Apr, when pups were included. Due to small samples, we could not reliably assess these factors during harvest years and post-harvest years. We first assessed the annual continuous variables (weather and wolf-density index) for outliers and then standardized those variables by transforming them to mean = 0 and variance = 1. For the weather variable we used the Northern Atlantic Oscillation (NAO) winter index (DJFM; December January February March) (NAO, 2003) because 1) inconsistent methods were used to calculate the winter severity index (WSI; MN DNR, 2015) during our study and 2) not all years of WSI were available for our study area. Positive values of the NAO winter index correlated with a less severe winter (decreased snow depth) in this study area and in nearby Isle Royale National Park (Post and Stenseth, 1998; Post et al., 1999). We used the annual winter resident wolf count in our fixed-boundary study area as a wolf-density index (Fig. 2). We tested for effects of the variables on mortality risk using additive models that included 4–5 variables (age class was only relevant for the Nov–Apr assessment). We assessed significance of variables across models based on robust z-tests and hazard ratios (exponentiated β coefficients) with 95% confidence intervals; we computed robust standard errors for regression coefficients by clustering observations by individual (Therneau and Grambsch, 2000). We tested the proportional-hazards assumption for significant or marginally significant variables across models using the statistical test based on scaled Schoenfeld residuals (Therneau and Grambsch, 2000).

We also tested for an effect of any significant or marginally significant variable from CPH regression modeling on cause-specific mortality of radiocollared wolves using a previously described approach (Heisey and Patterson, 2006). First, we replicated the dataset within a single data table once for each category of mortality and created an associated stratification variable indicating the category of mortality (Lunn and McNeil, 1995). Second, we coded dummy variables representing interactions between a given significant or marginally significant variable and the stratification variable. Third, we ran a stratified CPH regression model using the dataset and including the dummy variables.

3. Results

We radiocollared 690 wolves from 1968 to 2017 and analyzed 756 collared-wolf tenures from 1968 to 2018. Based on the collared-wolf tenures, we tracked more females (381) than males (375) and more adults (555) than pups (201) and had more non-wilderness captures (629) than wilderness captures (127). We documented 261 mortalities and censored 495 tenures.

3.1. Survival

During the entire study, annual survival of adults was 0.78 (95% confidence interval [CI] = 0.76–0.81), with higher survival during May–Oct than Nov–Apr, higher survival in wilderness wolves than non-wilderness wolves, and similar survival between sexes (Table 1). Seasonal (Nov–Apr) survival of pups was lower than that of adults during the entire study (Table 1).

During pre-harvest years, annual survival of adults was 0.79 (95% CI = 0.77–0.82), which was similar to that during the entire study, and the seasonal and group-specific survival trends were also similar (Table 1). The annual survival rate for adults during pre-harvest years was higher than that during harvest years (0.68, 95% CI = 0.58–0.79) and post-harvest years (0.74, 95% CI = 0.62–0.88). Seasonal (Nov–Apr) survival rates for both pups (0.79, 95% CI = 0.72–0.85) and adults (0.86, 95% CI = 0.84–0.89) during pre-harvest years were similar to those during the entire study (Table 1).

Because the harvest only lasted 3 years and only occurred during Nov–Apr, sample sizes were small (adults = 49, subadults = 22, pups =

Table 1

Estimated annual and seasonal survival rates (95% confidence interval) for radiocollared wolves of different groups during various periods in the Superior National Forest wolf study area, Minnesota, USA. Pups could only be assessed during Nov–Apr. Subadults are pooled with adults. N/A = not applicable.

Age class	Group	Season	1968–2018	1968–2012	2012–2015	2015–2018
			Entire study	Pre-harvest	Harvest	Post-harvest
Adult	All	Annual	0.78 (0.76–0.81)	0.79 (0.77–0.82)	0.68 (0.58–0.79)	0.74 (0.62–0.88)
Adult	Female	Annual	0.78 (0.74–0.81)	0.78 (0.75–0.82)	0.68 (0.55–0.83)	0.81 (0.68–0.98)
Adult	Male	Annual	0.79 (0.75–0.83)	0.80 (0.77–0.84)	0.67 (0.52–0.88)	0.64 (0.46–0.89)
Adult	Wilderness	Annual	0.83 (0.78–0.89)	0.83 (0.77–0.90)	0.79 (0.60–1.00)	1.00 (no deaths)
Adult	Non-wilderness	Annual	0.77 (0.74–0.80)	0.79 (0.76–0.82)	0.65 (0.53–0.78)	0.69 (0.56–0.85)
Adult	All	May–Oct	0.92 (0.90–0.94)	0.92 (0.90–0.94)	0.89 (0.81–0.96)	0.93 (0.86–1.00)
Adult	Wilderness	May–Oct	0.92 (0.88–0.97)	0.92 (0.87–0.97)	0.91 (0.75–1.00)	1.00 (no deaths)
Adult	Non-wilderness	May–Oct	0.92 (0.90–0.94)	0.92 (0.90–0.94)	0.88 (0.80–0.97)	0.92 (0.84–1.00)
Adult	All	Nov–Apr	0.85 (0.83–0.87)	0.86 (0.84–0.89)	0.76 (0.67–0.87)	0.79 (0.68–0.92)
Adult	Wilderness	Nov–Apr	0.90 (0.86–0.95)	0.90 (0.85–0.96)	0.87 (0.71–1.00)	1.00 (no deaths)
Adult	Non-wilderness	Nov–Apr	0.84 (0.82–0.87)	0.85 (0.83–0.88)	0.73 (0.62–0.86)	0.75 (0.62–0.91)
Pup	All	Nov–Apr	0.78 (0.72–0.85)	0.79 (0.72–0.85)	0.67 (0.30–1.00)	N/A (no pups)
Pup	Wilderness	Nov–Apr	0.87 (0.77–0.98)	0.87 (0.77–0.98)	N/A (no pups)	N/A (no pups)
Pup	Non-wilderness	Nov–Apr	0.76 (0.68–0.84)	0.76 (0.68–0.84)	0.67 (0.30–1.00)	N/A (no pups)
Adult + pup	All	Nov–Apr	0.84 (0.82–0.86)	0.85 (0.83–0.87)	0.76 (0.67–0.87)	0.79 (0.68–0.92) ^a
Adult + pup	Wilderness	Nov–Apr	0.90 (0.86–0.94)	0.90 (0.85–0.94)	0.87 (0.71–1.00) ^b	1.00 (no deaths) ^a
Adult + pup	Non-wilderness	Nov–Apr	0.83 (0.81–0.85)	0.84 (0.81–0.87)	0.73 (0.62–0.86)	0.75 (0.62–0.91) ^a

^a There were no pups radiocollared during Nov–Apr of 2015–2018, so these estimates reflect adults only.

^b There were no wilderness pups radiocollared during Nov–Apr of 2012–2015, so these estimates reflect adults only.

3) resulting in relatively wide confidence intervals. Nevertheless, the survival estimates reflect biologically reasonable results (Table 1). Pooling data across age classes, survival was similar between sexes (female = 0.75, 95% CI = 0.63–0.89; male = 0.78, 95% CI = 0.63–0.95) during Nov–Apr of harvest years. Seasonal (Nov–Apr) survival rates dropped during harvest years, and wilderness wolves survived better than non-wilderness wolves (Fig. 3).

Subadults could only be assessed as a separate age class post 1999. Annual survival rates for subadults and adults during 2000–2018 were 0.82 (95% CI = 0.73–0.92) and 0.79 (95% CI = 0.74–0.84), respectively.

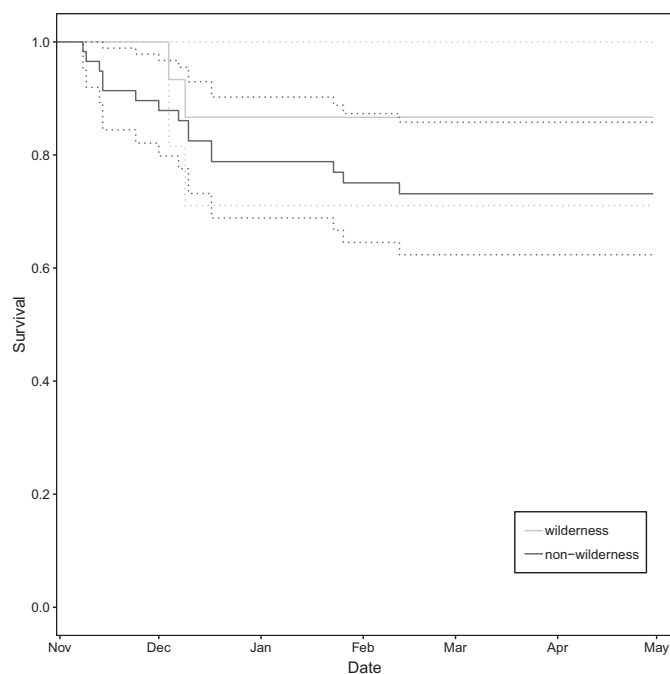


Fig. 3. Seasonal (Nov–Apr) survival estimates during 2012–2015 (harvest) for wolves (age classes pooled) captured in the Boundary Waters Canoe Area Wilderness (light gray solid line) and those captured in non-wilderness (dark gray solid line) of the Superior National Forest wolf study area, Minnesota, USA. Associated confidence intervals are shown as dotted lines. Note there were no wilderness pups radiocollared during Nov–Apr of 2012–2015, so the wilderness-specific survival curve reflects adults only.

Seasonal (Nov–Apr) survival rates for pups, subadults, and adults during 2000–2018 were 0.81 (95% CI = 0.63–1.00), 0.86 (95% CI = 0.79–0.94), and 0.86 (95% CI = 0.82–0.90), respectively. During harvest years, seasonal (Nov–Apr) survival of subadults (0.69, 95% CI = 0.51–0.93) was nearer to that of pups (0.67, 95% CI = 0.30–1.00) than that of adults (0.79, 95% CI = 0.69–0.92).

3.2. Cause-specific mortality

We recorded 261 mortalities of radiocollared wolves (excluding mortalities that occurred after being censored), including 102 natural (51 strife, 41 starvation/disease, 6 natural-unknown, and 4 natural-other), 111 anthropogenic (67 illegal, 17 vehicle strike, 14 legal-take, 8 anthropogenic-other, and 5 anthropogenic-unknown), and 48 unknown. Non-wilderness wolves died from 38% natural (87/229), 45% anthropogenic (103/229), and 17% unknown (39/229) causes, whereas wilderness wolves died from 47% natural (15/32), 25% anthropogenic (8/32), and 28% unknown (9/32) causes.

During 1968–2018, annual cause-specific mortality rates (95% CI) among the 3 main categories (natural, anthropogenic, and unknown) for adults ranged from 0.04 (0.02–0.05) for unknown to 0.09 (0.07–0.11) for both natural and anthropogenic (Table 2). During the same years, seasonal (Nov–Apr) cause-specific mortality rates for pups ranged from 0.05 (0.01–0.09) for unknown to 0.10 (0.05–0.16) for anthropogenic (Table 2). Some confidence intervals were wide, reflecting that generally few events occurred for specific causes of death within that stratum. Annually, natural mortality (9%) and anthropogenic mortality (9%) was similar for adults, with strife (5%) the highest source of natural mortality and illegal mortality (5%) the highest source of anthropogenic mortality (Table 2). During May–Oct, natural mortality (4%) was about twice that of anthropogenic mortality (2%) for adults, whereas, during Nov–Apr, anthropogenic mortality (7%) was higher than natural mortality (6%) for adults, with illegal mortality (4%) the highest source of anthropogenic mortality (Table 2). During Nov–Apr, natural mortality (6%) of pups was similar to that of adults, with starvation/disease (6%) the highest source of natural mortality, but anthropogenic mortality (10%) of pups was higher than that of adults, which was partly attributable to more illegal mortality (8%) (Table 2).

Annual anthropogenic mortality rates for adults were highest during the 3 harvest years and remained high for 3 years after (Table 3). Interestingly, the highest annual illegal mortality rate for adults was during the 3 post-harvest years (Table 3). The annual strife rate for

Table 2

Estimated annual and seasonal cause-specific mortality rates (95% confidence interval) for radiocollared adult and pup wolves during 1968–2018 in the Superior National Forest wolf study area, Minnesota, USA. Pups could only be assessed during Nov–Apr. Subadults are pooled with adults.

Cause-specific mortality	Adult annual	Adult May–Oct	Adult Nov–Apr	Pup Nov–Apr
Natural – all	0.09 (0.07–0.11)	0.04 (0.02–0.05)	0.06 (0.04–0.08)	0.06 (0.02–0.11)
Natural – strife ^a	0.05 (0.03–0.07)	0.02 (0.01–0.03)	0.03 (0.02–0.05)	0.01 (0.00–0.02)
Natural – starvation and disease	0.03 (0.02–0.05)	0.01 (0.00–0.02)	0.02 (0.01–0.04)	0.06 (0.01–0.10)
Anthropogenic – all	0.09 (0.07–0.11)	0.02 (0.01–0.03)	0.07 (0.05–0.09)	0.10 (0.05–0.16)
Anthropogenic – illegal	0.05 (0.03–0.07)	0.01 (0.00–0.02)	0.04 (0.03–0.06)	0.08 (0.03–0.12)
Anthropogenic – legal-take ^b	0.01 (0.00–0.02)	0.00 (0.00–0.00) ^c	0.01 (0.00–0.02)	0.01 (0.00–0.04)
Unknown	0.04 (0.02–0.05)	0.02 (0.01–0.03)	0.02 (0.00–0.03)	0.05 (0.01–0.09)

^a Strife deaths are intraspecific mortalities (i.e., wolf-killed-wolves).

^b Also includes wolves killed legally by state and federal officers for conflict or nuisance issues.

^c Rate value and upper 95% CI value are actually non-zero, but do not appear so due to rounding.

Table 3

Estimated annual cause-specific mortality rates (95% confidence interval) for radiocollared adult wolves during different periods in the Superior National Forest wolf study area, Minnesota, USA. Subadults are pooled with adults. N/A = not applicable.

Cause-specific mortality	1968–2018	1968–2012	2012–2015	2015–2018
	Entire study	Pre-harvest	Harvest	Post-harvest
Natural – all	0.09 (0.07–0.11)	0.09 (0.07–0.11)	0.11 (0.03–0.19)	0.09 (0.00–0.18)
Natural – strife ^a	0.05 (0.03–0.07)	0.05 (0.03–0.07)	0.04 (0.00–0.09)	0.02 (0.00–0.07)
Natural – starvation and disease	0.03 (0.02–0.05)	0.03 (0.01–0.04)	0.06 (0.00–0.12)	0.05 (0.00–0.11)
Anthropogenic – all	0.09 (0.07–0.11)	0.08 (0.06–0.10)	0.18 (0.10–0.27)	0.15 (0.04–0.26)
Anthropogenic – illegal	0.05 (0.03–0.07)	0.05 (0.03–0.06)	0.07 (0.00–0.13)	0.11 (0.01–0.20)
Anthropogenic – legal-take ^b	0.01 (0.00–0.02)	0.01 (0.00–0.01)	0.09 (0.02–0.16)	N/A (no deaths)
Unknown	0.04 (0.02–0.05)	0.04 (0.02–0.06)	0.03 (0.00–0.08)	0.02 (0.00–0.06)

^a Strife deaths are intraspecific mortalities (i.e., wolf-killed-wolves).

^b Also includes wolves killed legally by state and federal officers for conflict or nuisance issues.

adults declined from pre-harvest years through harvest years through post-harvest years (Table 3), although, as noted above, confidence intervals around some point estimates were wide (especially during shorter periods with smaller samples such as harvest years and post-harvest years) and overlapping.

During Nov–Apr of harvest years, adults and pups together experienced relatively high anthropogenic mortality (18%; including 4% illegal mortality) and relatively low natural mortality (4%; including 1% strife, which was the lowest rate of such observed during the study) and unknown mortality (1%) (Table 4). During Nov–Apr of post-harvest years, illegal mortality (11%) reached its highest level (Table 4). There were no unknown or legal-take deaths during post-harvest years, but high illegal mortality resulted in anthropogenic mortality (14%) remaining high then (Table 4).

During pre-harvest years for adults, annual anthropogenic mortality was higher for non-wilderness wolves than wilderness wolves (9% versus 3%), but annual natural mortality and unknown mortality were similar for both groups (9% and 4%, respectively) (Fig. 4, Table 5). During Nov–Apr of pre-harvest years for adults, anthropogenic mortality

was higher for non-wilderness wolves than wilderness wolves (7% versus 1%), as was illegal mortality (5% versus 1%), whereas natural mortality was similar for both groups (6%) (Table 6).

During harvest years for adults, there was no natural death and no unknown death in wilderness wolves compared to 14% annual natural mortality and 4% annual unknown mortality in non-wilderness wolves (Table 5). Annual anthropogenic mortality of adults was high during harvest years for both wilderness wolves and non-wilderness wolves (though confidence intervals were wide for estimates) (Table 5). Seasonal (Nov–Apr) anthropogenic mortality of adults was higher for non-wilderness wolves than wilderness wolves (19% versus 13%) during harvest years (Table 6).

3.3. Cox proportional hazards regression

Harvest was a significant predictor of adult annual survival during 1968–2015 ($z = 2.5, p = 0.013$), whereby individuals were more likely to die during harvest years than pre-harvest years (hazard ratio = 1.74, 95% CI = 1.13–2.70). Thus, to assess long-term predictors of mortality

Table 4

Estimated seasonal (Nov–Apr) cause-specific mortality rates (95% confidence interval) for radiocollared wolves of all age classes during different periods in the Superior National Forest wolf study area, Minnesota, USA. N/A = not applicable.

Cause-specific mortality	1968–2018	1968–2012	2012–2015	2015–2018
	Entire study	Pre-harvest	Harvest	Post-harvest
Natural – all	0.06 (0.04–0.08)	0.06 (0.04–0.08)	0.04 (0.00–0.10)	0.07 (0.00–0.16)
Natural – strife ^a	0.03 (0.01–0.04)	0.03 (0.02–0.04)	0.01 (0.00–0.05)	0.02 (0.00–0.07)
Natural – starvation and disease	0.03 (0.01–0.04)	0.03 (0.01–0.04)	0.03 (0.00–0.07)	0.02 (0.00–0.07)
Anthropogenic – all	0.08 (0.06–0.10)	0.07 (0.05–0.09)	0.18 (0.09–0.27)	0.14 (0.03–0.25)
Anthropogenic – illegal	0.05 (0.03–0.07)	0.05 (0.03–0.06)	0.04 (0.00–0.10)	0.11 (0.01–0.22)
Anthropogenic – legal-take ^b	0.01 (0.00–0.02)	0.01 (0.00–0.01)	0.11 (0.03–0.19)	N/A (no deaths)
Unknown	0.02 (0.01–0.03)	0.02 (0.01–0.04)	0.01 (0.00–0.05)	N/A (no deaths)

^a Strife deaths are intraspecific mortalities (i.e., wolf-killed-wolves).

^b Also includes wolves killed legally by state and federal officers for conflict or nuisance issues.

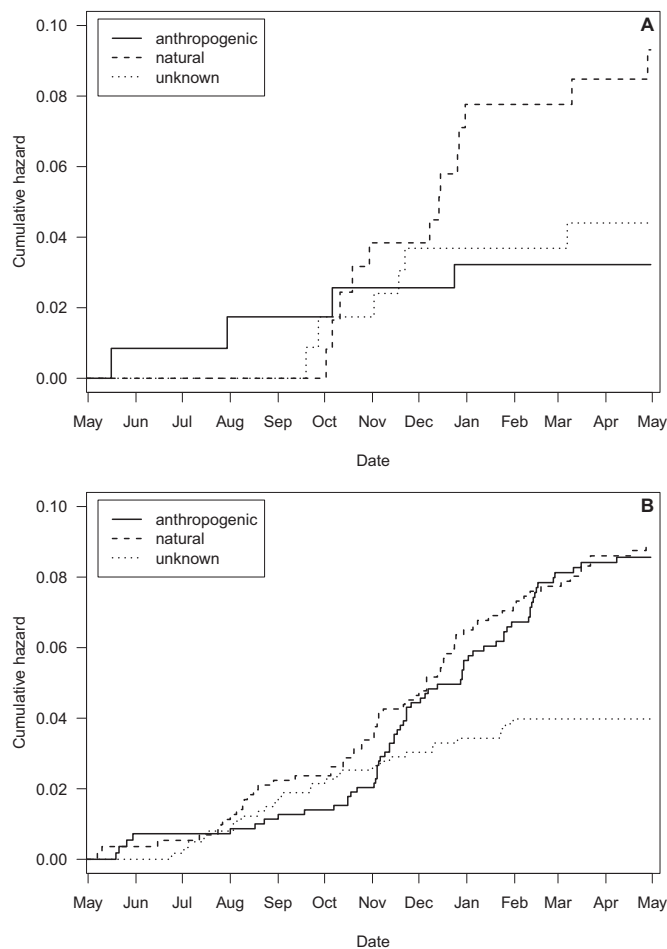


Fig. 4. Annual (May 1–Apr 30) cumulative hazard of cause-specific mortality (anthropogenic, natural, unknown) for radiocollared adult wolves during 1968–2012 (pre-harvest) classed by Boundary Waters Canoe Area Wilderness capture (A) or non-wilderness capture (B) in the Superior National Forest wolf study area, Minnesota, USA.

unaffected by the 3 harvest years, we analyzed data from 1968 to 2012 (pre-harvest). Samples (i.e., events per stratum) were too small to robustly model hazard ratios (i.e., survival curves crossed, hazards were not proportionally consistent) during 2012–2015 (harvest) and 2015–2018 (post-harvest).

For the additive model including sex, wilderness capture, wolf density index, and NAO, no variable was a significant predictor of adult annual survival. Annually, wolf density index was a marginally

significant ($z = -1.7, p = 0.098$; hazard ratio = 0.86, 95% CI = 0.72–1.03) predictor of adult survival. Similarly, for the same additive model, no variable was a significant predictor of adult seasonal survival during May–Oct or Nov–Apr. During May–Oct, wolf density index was a marginally significant ($z = -1.8, p = 0.078$; hazard ratio = 0.75, 95% CI = 0.54–1.03) predictor of adult survival. However, during Nov–Apr when pups were included, age class ($z = 3.1, p = 0.002$) and wilderness capture ($z = -2.0, p = 0.042$) were significant predictors of survival, whereby pups were more likely to die than adults (hazard ratio = 1.84, 95% CI = 1.25–2.71), and wilderness wolves were less likely to die than non-wilderness wolves (hazard ratio = 0.59, 95% CI = 0.35–0.98). We note that age class showed a significant violation of proportionality ($\chi^2 = 5.2, p = 0.023$); however, inspection of the survival curves showed that they did not cross; rather pup survival declined precipitously relative to adult survival early in the season. Additionally, during Nov–Apr when pups were included, sex was a marginally significant ($z = -1.9, p = 0.053$) predictor of survival, whereby males were less likely to die than females (hazard ratio = 0.73, 95% CI = 0.53–1.00).

Stratified CPH regression models indicated that wilderness capture, age class, and sex were significant predictors of cause-specific mortality of radiocollared wolves during Nov–Apr of 1968–2012. Wilderness capture was a significant predictor of anthropogenic mortality ($z = -2.6, p = 0.008$), whereby wilderness wolves were less likely than non-wilderness wolves to die of human causes (hazard ratio = 0.07, 95% CI = 0.01–0.50). Age class was a significant predictor of anthropogenic mortality ($z = 2.1, p = 0.035$) and unknown mortality ($z = 2.6, p = 0.009$), whereby pups were more likely than adults to die of human causes (hazard ratio = 1.84, 95% CI = 1.04–3.24) and unknown causes (hazard ratio = 3.10, 95% CI = 1.32–7.25). Sex was a significant predictor of anthropogenic mortality ($z = -2.2, p = 0.028$), whereby males were less likely than females to die of human causes (hazard ratio = 0.57, 95% CI = 0.34–0.94).

4. Discussion and conclusions

4.1. Survival

In longer-lived mammals such as wolves (Mech, 1988; Schmidt, 2020), survival of adults is usually much less variable than that of younger animals, with even small changes having a disproportionately large influence on population dynamics (Eberhardt, 2002; Gaillard et al., 1998; Patterson and Murray, 2008). In Yellowstone, adult survival had the strongest effect on wolf population dynamics (Smith et al., 2020). Adult survival in our study was generally high during pre-harvest years (79%) and was similar to rates reported in studies of wolves that also at least partially used protected areas such as Cubaynes et al. (2014), Hebblewhite and Whittington (2020) and Smith et al. (2010). Unsurprisingly, adult survival dropped in our study during harvest years (68%). Lower adult survival during harvest likely contributed to the

Table 5

Estimated annual cause-specific mortality rates (95% confidence interval) during 1968–2012 (pre-harvest) and 2012–2015 (harvest) for radiocollared adult wolves captured inside the Boundary Waters Canoe Area Wilderness and those captured in non-wilderness in the Superior National Forest wolf study area, Minnesota, USA. Subadults are pooled with adults. N/A = not applicable.

Cause-specific mortality	1968–2012	1968–2012	2012–2015	2012–2015
	Wilderness	Non-wilderness	Wilderness	Non-wilderness
Natural – all	0.09 (0.04–0.15)	0.09 (0.07–0.11)	N/A (no deaths)	0.14 (0.04–0.23)
Natural – strife ^a	0.06 (0.02–0.10)	0.05 (0.03–0.07)	N/A (no deaths)	0.05 (0.00–0.11)
Natural – starvation and disease	0.02 (0.00–0.05)	0.03 (0.01–0.05)	N/A (no deaths)	0.08 (0.00–0.15)
Anthropogenic – all	0.03 (0.00–0.07)	0.09 (0.06–0.11)	0.21 (0.00–0.43)	0.18 (0.08–0.28)
Anthropogenic – illegal	0.02 (0.00–0.05)	0.05 (0.03–0.07)	0.09 (0.00–0.26)	0.07 (0.00–0.14)
Anthropogenic – legal-take ^b	N/A (no deaths)	0.01 (0.00–0.01)	0.12 (0.00–0.28)	0.08 (0.00–0.16)
Unknown	0.04 (0.01–0.08)	0.04 (0.02–0.06)	N/A (no deaths)	0.04 (0.00–0.10)

^a Strife deaths are intraspecific mortalities (i.e., wolf-killed-wolves).

^b Also includes wolves killed legally by state and federal officers for conflict or nuisance issues.

Table 6

Estimated seasonal (Nov–Apr) cause-specific mortality rates (95% confidence interval) during 1968–2012 (pre-harvest) and 2012–2015 (harvest) for radiocollared adult wolves captured inside the Boundary Waters Canoe Area Wilderness and those captured in non-wilderness in the Superior National Forest wolf study area, Minnesota, USA. Subadults are pooled with adults. N/A = not applicable.

Cause-specific mortality	1968–2012	1968–2012	2012–2015	2012–2015
	Wilderness	Non-wilderness	Wilderness	Non-wilderness
Natural – all	0.06 (0.02–0.10)	0.06 (0.04–0.08)	N/A (no deaths)	0.06 (0.00–0.13)
Natural – strife ^a	0.05 (0.01–0.09)	0.03 (0.01–0.05)	N/A (no deaths)	0.02 (0.00–0.07)
Natural – starvation and disease	0.01 (0.00–0.02)	0.03 (0.01–0.04)	N/A (no deaths)	0.04 (0.00–0.09)
Anthropogenic – all	0.01 (0.00–0.02)	0.07 (0.05–0.09)	0.13 (0.00–0.31)	0.19 (0.08–0.29)
Anthropogenic – illegal	0.01 (0.00–0.02)	0.05 (0.03–0.07)	N/A (no deaths)	0.06 (0.00–0.13)
Anthropogenic – legal-take ^b	N/A (no deaths)	0.01 (0.00–0.01)	0.13 (0.00–0.31)	0.09 (0.00–0.18)
Unknown	0.03 (0.00–0.06)	0.02 (0.00–0.03)	N/A (no deaths)	0.02 (0.00–0.07)

^a Strife deaths are intraspecific mortalities (i.e., wolf-killed-wolves).

^b Also includes wolves killed legally by state and federal officers for conflict or nuisance issues.

ongoing population decline in our study (Fig. 2). Notably, annual survival of adults in our study was higher than that of radio-marked wolves ≥ 5 months old in north-central Minnesota during 1980–1986 (64%) (Fuller, 1989), but our annual survival estimate did not include pups. Similar to other studies, we did not find consistent support for sex-specific differences in wolf survival (Fuller, 1989; Smith et al., 2020; but see O'Neil et al., 2017 where males had lower survival rates). However, sex was marginally significant seasonally (Nov–Apr) during pre-harvest years, with males less likely to die than females. Although confidence intervals were wide, seasonal (Nov–Apr) survival of pups (81%) was lower than that of subadults and adults (both 86%) during 2000–2018. Seasonal (Nov–Apr) survival of pups (79%) was (as predicted) lower than that of adults (86%) during pre-harvest years, and similar to that observed in north-central Minnesota during 1980–1986 (Fuller, 1989). In Yellowstone, pups are monitored from 10 to 14 days of age with the majority of pup deaths occurring during summer (although over-winter pup mortality has increased in recent years so the annual timing of most pup deaths could be changing; Smith et al., 2020; Stahler et al., 2013). There, pup survival was usually $>70\%$ in most years (Smith et al., 2020; Stahler et al., 2013). Because our estimate of pup survival only included pups that already survived to November, it overestimates true pup survival.

While wilderness wolves tended to exhibit higher survival than non-wilderness wolves throughout the study, the difference was more pronounced during harvest years and post-harvest years when wilderness wolf survival remained relatively high (similar to pre-harvest levels) and non-wilderness wolf survival dropped (relative to pre-harvest levels). Annual wolf population levels are not always negatively affected by harvest, depending on factors such as the total harvest rate and the proportion of reproductive animals killed (Fuller et al., 2003). Still, reduced adult and pup survival during harvest years has biological implications beyond population levels - down to individual packs - as recruitment (Ausband et al., 2015; Rutledge et al., 2010), pack composition (Bassing et al., 2020; Rutledge et al., 2010), and social disorder (Borg et al., 2015; Rutledge et al., 2010) can be affected.

4.2. Cause-specific mortality

Throughout our study, annual natural and anthropogenic mortality rates for adults were largely balanced (9%), except anthropogenic mortality was much higher during harvest years (18%) and post-harvest years (15%), with illegal mortality peaking during post-harvest years (11%). Our annual wolf counts declined steeply following winter 2008/2009 (Fig. 2). Thus, while the highest rates of anthropogenic mortality occurred during harvest and remained high thereafter, harvest mortality that began in 2012 could not have caused the initial decline, though it likely contributed to the continuation of the decline. In the then newly-created Gates of the Arctic National Park and Preserve in Alaska, harvest mortality (12%) was approximately equal to natural mortality (11%)

(Adams et al., 2008). In Algonquin Provincial Park, Canada, natural mortality largely replaced anthropogenic mortality when harvesting was banned (Rutledge et al., 2010). In Yellowstone National Park, where wolves are protected and human impacts are reduced, most wolves died of natural causes (Smith et al., 2020). Despite legal protection, the human-caused mortality rate of radio-collared wolves ≥ 5 months old in north-central Minnesota during 1980–1986 was at least 29% (80% of identified mortality was human caused, including 30% shot and 21% killed by an undetermined human cause) (Fuller, 1989). Anthropogenic mortality (primarily legal control and illegal killing, but also vehicle collision, legal harvest in Canada, and other anthropogenic sources) was greater than natural mortality (68% versus 21%) across 3 recovering wolf populations (Idaho, Montana, Greater Yellowstone Area) in the northern Rocky Mountains (Murray et al., 2010). In Wisconsin, two-thirds (Treves et al., 2017b) and $\sim 60\%$ (Stenglein et al., 2018) total mortality was due to anthropogenic causes, and the ratio of anthropogenic to natural mortality was greatest at the edge of wolf range (Stenglein et al., 2018). Because our study population has long been extant, and harvest was only legal for 3 years, higher natural mortality (e.g., strife and/or starvation/disease) can be expected relative to a recovering population. Over the 50 years of our study, most anthropogenic mortality, including most illegal mortality, occurred during Nov–Apr, coinciding with ungulate harvest (firearm season for white-tailed deer occurs in November), and was higher for pups than adults. The rate of anthropogenic mortality for adults during Nov–Apr was more than three times higher than that during May–Oct. Other studies have similarly found higher mortality risk for adult wolves during winter (Adams et al., 2008; Hebblewhite and Whittington, 2020; O'Neil et al., 2017; Stenglein et al., 2015).

Based on our cause-specific mortality rates, adults were more likely to die of strife than were pups (Mech, 1994; Mech and Barber-Meyer, 2017), whereas pups were more likely to die of disease or starvation than were adults. Annual strife deaths of adults declined from pre-harvest years through harvest years through post-harvest years, suggesting a potential compensatory response (Fuller et al., 2003) and density-dependent mechanism (Cubaynes et al., 2014; O'Neil et al., 2017; Stenglein et al., 2015). However, considering only non-wilderness wolves, natural mortality of adults was lower during pre-harvest years than harvest years and unknown mortality of adults stayed the same between periods, suggesting that the increased anthropogenic mortality observed during harvest years was likely not compensatory (Adams et al., 2008), similar to what was found in a meta-analysis of 21 North American wolf populations by Creel and Rotella (2010), but see Gude et al. (2012). However, considering only wilderness wolves, there were no natural or unknown deaths of adults during harvest years, suggesting that the increased anthropogenic mortality observed during harvest years could have been at least partially compensatory (Stenglein et al., 2018), although our samples were small.

During harvest years, there were no natural or unknown deaths of

wilderness wolves, but anthropogenic mortality increased in both wilderness wolves and non-wilderness wolves. In non-wilderness wolves, natural and unknown mortality were both still important. Harvest mortality can be additive, partially compensatory, or fully compensatory (Adams et al., 2008; Creel and Rotella, 2010; Fuller et al., 2003; Murray et al., 2010; Rutledge et al., 2010), and can become progressively more additive with increasing wolf density (Murray et al., 2010). Thus, increasing harvest quotas may be effective in reducing and maintaining wolf populations at lower levels than may otherwise be determined by a combination of prey base, social regulation, and environmental conditions (Stenglein et al., 2015).

While we expected the highest levels of anthropogenic mortality to occur during harvest years, we did not predict that this would remain high during post-harvest years, with the highest levels of adult annual illegal mortality (11%) occurring post-harvest. This suggests that the closure of the wolf harvest after 3 seasons may have prompted increased poaching (Olson et al., 2015). Some have contended that wolf-harvest seasons may increase social tolerance of wolves (see Epstein, 2017 for review) and thereby reduce poaching. There was a trend of increasing illegal mortality from pre-harvest (5%) to harvest (7%) to post-harvest (11%), although we note that the confidence intervals of all estimates overlapped. Thus, harvest did not appear to increase social tolerance in our study, but termination of harvest appeared to decrease social tolerance. In Wisconsin, poaching accounted for an estimated 39–45% of total mortality from 1979 to 2012 in one study (Treves et al., 2017b), whereas Stenglein et al. (2018) used a different analysis method to estimate an annual mortality rate of 9.4% due to poaching over a similar period. Our poaching estimates are likely underestimates (Stenglein et al., 2015; Treves et al., 2017a, 2017b) because we could not always differentiate between dispersers, expired or failed collars, and collars that were destroyed when wolves were killed illegally.

4.3. Cox proportional hazards regression

Seasonal (Nov–Apr) hazard ratios during pre-harvest years indicated that (as predicted) pups were more likely to die than adults (Eberhardt, 2002), wilderness wolves were less likely to die than non-wilderness wolves, and males were less likely to die than females (in contrast to O'Neil et al., 2017 where males had lower survival rates). Pups were more likely than adults to die of anthropogenic causes and unknown causes, but not natural causes, which likely is an artifact that the pups in our study already survived through to November (many natural deaths of pups occur prior to November; Smith et al., 2020; Stahler et al., 2013). Wilderness wolves were less likely than non-wilderness wolves to die of anthropogenic causes (as we predicted), presumably due largely to human-access issues. We note, though, that 28% of wilderness wolf deaths were due to an unknown cause. Possibly some of these deaths were anthropogenic, but because there are no roads and limited human access (and therefore reduced harvest and poaching opportunities) in the wilderness in our study area, anthropogenic deaths are less likely there. Also, because we used capture location as a proxy for use, possibly dispersal differences between wilderness wolves and non-wilderness wolves affected our results, though we were unable to examine this due to data limitations. Still, because most of our data were from VHF collars, dispersing wolves were generally “lost” from our study when they dispersed and contributed less to our data than resident wolves. Males were less likely than females to die of anthropogenic causes, but we do not know of a biological reason for this result.

While we did not find clear support for annual weather trends, sex, or wolf density as predictors of mortality, our analyses were limited by small samples, so these factors may be important to certain causes of death (e.g., strife, starvation/disease) but in contrasting ways, thus muddling our analyses that necessarily pooled mortality causes. For example, we surmise that consecutive years of severe winter could stabilize, increase, or decrease cause-specific mortality rates depending on the particular cause of death, as DelGiudice et al. (2006) found with

white-tailed deer. If sample sizes were sufficient, testing the above factors would be informative.

4.4. The importance of wilderness

Smith et al. (2010) examined the influence of core protected areas (relative to adjacent, less secure areas) on wolf vital rates in the Northern Rocky Mountains during 1982–2004. In that study, wolves in larger core areas and in areas with less agriculture and less private land had higher survival. In and around Banff National Park, Canada, wolves outside the park had a much lower annual survival rate (44%) than park wolves (84%), where trapping and hunting were prohibited (Hebblewhite and Whittington, 2020). In other studies in the Great Lakes region wolf survival rates and/or occupancy were affected by habitat quality, winter prey availability, human development, livestock proximity, and spatiotemporally varying population density (Mech, 1989; Mech et al., 2019; Mladenoff et al., 1995, 2009; O'Neil et al., 2019, 2020; Potvin et al., 2005; Stenglein et al., 2015, 2018). Our study consisted of designated-wilderness adjacent to non-wilderness national forest that included only limited private land and no agricultural or livestock operations. Even so, we also found support for the importance of core protected areas with wilderness wolves tending toward higher survival and less anthropogenic mortality than non-wilderness wolves. Our study area did not include many factors that were important determinants of wolf survival or occupancy elsewhere (e.g., agricultural land cover, livestock operations, a recolonizing population; Mech, 1989, 1995; Mladenoff et al., 1995, 2009; O'Neil et al., 2017, 2019, 2020; Potvin et al., 2005), but the non-wilderness national forest in our study did host a significant network of trails and roads that increased human accessibility. Road density and human accessibility have been important determinants of wolf persistence in other studies (Mech, 1989, 1995; O'Neil et al., 2019, 2020; Potvin et al., 2005; Thiel, 1985). In Wisconsin during the 1980s, areas with road densities >0.58 km/km² failed to support wolves (Thiel, 1985). In Upper Michigan, occupancy declined at higher road densities with a predicted threshold of 0.7 km/km² (Potvin et al., 2005). Our average road density estimate across the non-wilderness portion of our study area was higher than these thresholds, but our estimate also included snow-compacting trails. Mech (1989) concluded in a subsection of our study area that areas of higher road density can sustain wolves provided there are nearby roadless areas.

Our wolf survival was generally high, but it was higher in the wilderness, especially during Nov–Apr of harvest years and post-harvest years. While we studied designated-wilderness as compared to non-wilderness national forest, wilderness (or other protected areas) would likely be more important as a refuge and source population if adjacent to a non-protected area or when the population is at least partially subject to regular harvest (Benson et al., 2014; Hebblewhite and Whittington, 2020; Mech, 2017, 2021; Smith et al., 2010).

Our study spanned 50 years, but how might these long-term results vary in the context of future climate change? In the Great Lakes region, autumn and winter temperatures are predicted to increase by 5–8 °C within the next 100 years (Kling et al., 2003). Spring and summer temperatures are predicted to rise by 1.5–2 °C by 2025–2035 (Kling et al., 2003). Fewer snow days, longer growing seasons, and increased variability and increases in winter and spring precipitation are also predicted (Hayhoe et al., 2009, 2010; IPCC, 2007). Wolves historically lived from latitudes extending from central Mexico to the High Arctic (Mech, 1970), so they may be considered highly adaptable regarding climate change with effects largely realized through prey (Mahoney et al., 2020; Mech, 2000, 2004; Post and Stenseth, 1998; Post et al., 1999; Weiskopf et al., 2019; Wilmers et al., 2020). In general, distributions of species in the northern hemisphere at the southern end of their range will shift northward (Humphries et al., 2004; Parmesan and Yohe, 2003) (e.g., such as moose in our study area; Pastor and Mladenoff, 1992; Weiskopf et al., 2019). Climate change may also influence prey vulnerability to wolves (Wilmers et al., 2020), particularly through

changes in snowfall (Mech et al., 1987; Post et al., 1999), disease dynamics (e.g., potentially increased white-tailed deer *Parelaphostrongylus tenuis*, brainworm, transmission to moose; Weiskopf et al., 2019), and heat stress (Lenarz et al., 2009, but see Mech and Fieberg, 2014; Weiskopf et al., 2019). Depending on how these effects are realized in prey populations, we expect important factors in our wolf population (survival, reproduction, dispersal) to ultimately reflect lagged adjustments to their prey populations (Barber-Meyer and Mech, 2016; Mech and Barber-Meyer, 2015), as well as density-dependent social regulation (Cubaynes et al., 2014; O'Neil et al., 2017; Smith et al., 2015, 2020; Stenglein et al., 2018). Long-term habitat changes (e.g., logging and fire) and climatic conditions have already altered the ungulate composition of our study area such that white-tailed deer occupy much former moose range (Lenarz et al., 2009), and moose occupy some former white-tailed deer range (Nelson and Mech, 2006). Because wolves are opportunistic and highly adaptable predators (Gable et al., 2018; Mech et al., 2015), we expect our general results over the 50-year study are fairly robust to near-term climate change. Still, the establishment and maintenance of wilderness refuges (Mech, 2021) could help wolf populations increase their resilience when their prey (such as white-tailed deer) are affected by climate change due to habitat and longer-term weather changes (e.g., annual depth and duration of snow cover). Our long-term wolf survival, cause-specific mortality, and hazard results will inform land managers, the USFWS, and states, as they progress through the challenging process of gray wolf delisting to state management (Creel and Rotella, 2010; Olson et al., 2015) and into the future as potential climate change effects on prey are realized (Mahoney et al., 2020; Mech, 2000, 2004; Post et al., 1999; Weiskopf et al., 2019; Wilmers et al., 2020).

Declaration of competing interest

The authors declare no conflict of interest.

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