Original Research Article

Wolves without borders: Transboundary survival of wolves in Banff National Park over three decades

Mark Hebblewhite [a], [*], Jesse Whittington [b]

[a] *Wildlife Biology Program, Department of Ecosystem and Conservation Sciences, W.A. Franke College of Forestry and Conservation, University of Montana, 32 Campus Drive, Missoula, MT, 59801, USA*
[b] *Parks Canada Agency, Banff National Park, Banff, Alberta, T1L 1K2, Canada*

A B S T R A C T

Large carnivores are important ecological drivers of ecosystem dynamics when they occur at ecologically effective densities. They are also challenging to conserve, especially in transboundary settings such as along borders of parks and protected areas. Here, we tested for effects of transboundary movements on survival of 72 radiocollared gray wolves from 1987 to 2018 in and adjacent to Banff National Park, Canada. We fit Bayesian counting-process survival models to known-fate radiotelemetry data and tested for the influence of intrinsic covariates such as sex and age, time, and movements outside of protected areas on survival of wolves. We also estimated cause-specific mortality. Non-parametric survival was 0.733 (95% CI 0.622–0.816), and the top Bayesian survival model indicated that wolves outside the park had much lower annual survival rates (0.44, 95% BCI = 0.24–0.65) compared to wolves inside the park (0.84, 95% BCI = 0.73–0.91). The cumulative risk of mortality was on average 6.7 times higher (odds ratio 95% BCI = 2.2–21.4) for wolves outside the park, peaking during the winter hunting and trapping seasons. We found weak evidence for declining survival over time, opposite to patterns predicted by density-dependence. Bayesian cause-specific mortality indicated that the top three sources of mortality were trapping (rate = 0.080, 36% of mortality), followed by hunting (0.053, 18%), and highway (0.046, 18%) mortality. Surprisingly, we found no intraspecific mortality, and low dispersal from Banff National Park. This demographic profile is akin to other exploited populations across North America. While we were unable to combine survival rates with reproduction to estimate population trends, the overall mortality rates within our study area are consistent with a stable wolf population. Nonetheless, the long-term stability and ecological effectiveness of wolves likely differed inside and outside of protected areas, which highlights a challenge with managing transboundary carnivores exposed to different management regimes.

1. Introduction

Large carnivores are disproportionately important for ecosystem function and biodiversity conservation (Ripple et al., 2014), and their importance is tied to ecologically effective population sizes (Soule et al., 2003). There is a growing body

* Corresponding author.
  E-mail address: mark.hebblewhite@umontana.edu (M. Hebblewhite).

of studies that clearly demonstrate the widespread ecological effects of large carnivores (Ford and Goheen, 2015; Ripple et al., 2014). For example, large carnivores have direct effects on reducing large ungulate prey through predation and indirect effects on lower food web levels through the phenomenon of trophic cascades. These effects have been documented through the globe, such as jaguars (*Panthera onca*) in Venezuela (Terborgh et al., 2001), gray wolves (*Canis lupus*) in North America (Hebblewhite et al., 2005), and dingo's (*C. familiaris*) in Africa (Letnic et al., 2012). Human activities can exert strong effects on carnivore survival, and thus the ecological effectiveness of large carnivores, both inside and outside of protected areas (Thurber et al., 1994; Woodroffe et al., 2001). Understanding how human activities in and outside of protected areas affect survival and cause-specific mortality rates of transboundary carnivores is a key component for assessing their population resilience, and, secondarily, ecological effectiveness.

Despite the ecological importance of large carnivores, they are experiencing large-scale global declines with many species experiencing imperiled status (Ripple et al., 2014). Large carnivores are challenging to conserve, ultimately because of persecution by humans (Musiani and Paquet, 2004). Large carnivores are sensitive to human-caused mortality because of their low densities and numbers, wide-ranging behavior, and penchant for direct conflict with humans either through depredation on livestock, competition (real or perceived) with wild ungulate prey, and even direct attacks on humans (Dhanwatey et al., 2013; Gittleman et al., 2001; Woodroffe et al., 2005). These challenges are acute for social carnivores, who have lower effective population sizes, and because human persecution disrupts social behavior which often is crucial for survival or reproduction (Borg et al., 2014; Vucetich and Creel, 1999).

Because of their vulnerability to human persecution, parks and protected areas have played an important role in protecting populations of large carnivores around the globe (Burton et al., 2011; Laliberte and Ripple, 2004). Most tigers (*Panthera tigris*), for example, occur in or near large protected area landscapes in Asia (Wikramanayake et al., 2004). African wild dogs (*Cuon albicus*) are crucially dependent on large protected area complexes in Africa (Woodroffe and Ginsberg, 2001; Woodroffe et al., 2007). In North America, parks and protected areas harbor many of the last intact populations of large carnivores (Laliberte and Ripple, 2004). Despite the important role of protected areas, most protected areas are too small to completely protect large carnivores, who are vulnerable to edge effects, transboundary mortality and ultimately extirpation (Newmark, 1995; Woodroffe and Ginsberg, 2001). For example, Thurber et al. (1994) showed that wolves in a transboundary protected area in Alaska were vulnerable to hunting and trapping outside the Park. Recent studies have demonstrated significant impacts on wolf population dynamics of harvest due to their sociality (Brainerd et al., 2008), and pervasive effects of mortality outside parks and protected areas on wolf-prey ecology. Transboundary mortality even reduced the quality of visitor experiences within Denali and Yellowstone National Parks (Borg et al., 2016; Borg et al., 2014). Transboundary mortality poses a challenge to carnivore conservation around the globe (Smith et al., 2016; Woodroffe and Ginsberg, 2001).

Gray wolves first recolonized the Canadian Rockies in the 1970's and 1980's from natural dispersal following persecution across Canada (Carbyn, 1974; Gunson, 1992). Wolves colonized the Bow Valley of Banff National Park in 1985, where they subsequently established important ecosystem effects (Hebblewhite et al., 2005). It was areas outside Banff and Jasper National Parks from which wolves were captured for the Yellowstone wolf reintroduction of 1995 (Smith et al., 2006). Wolves in this region also naturally recolonized northwestern Montana through natural dispersal in the 1980s (Boyd et al., 1995). Early reports suggested a stable wolf population in Banff National Park (Paquet et al., 1996), but with high human-caused mortality from transportation corridors and transboundary mortality. Parks Canada invested in highway overpasses and underpasses to mitigate the negative effects of highway mortality on wildlife (Clevenger et al., 2001). Wolves also recolonized provincial lands east of Banff National Park in the late 1980's (Cullingham et al., 2016). These wolves were subject to trapping and hunting mortality but occurred at higher densities likely due to greater ungulate densities (Webb et al., 2011). Although wolf demography is known to change during wolf recovery due to density-dependence (Cubaynes et al., 2014), no studies have examined survival rates of Banff National Park's transboundary wolf population.

Our goals were to examine wolf survival and cause-specific mortality in Banff National Park (BNP) from 1987 to 2018. Specifically, we tested for broad changes in survival across three decadal time periods roughly corresponding to the early increasing phase associated with an expanding population, high prey abundance, and concurrent ecological restoration and highway mitigation actions; a decline phase associated with a declining prey abundance; and a longer-term stable phase associated with stable prey abundance. We hypothesized wolf survival would initially be high, decline, and then stabilize accordingly (Cubaynes et al., 2014). If highway mitigation was successful at reducing wolf mortality, we also predicted that wolf survival would increase corresponding to a cumulative increase in highway fencing over time. Similarly, we predicted that with the liberal harvest seasons for wolves in adjacent provincial lands (~9 months of legal harvest with no bag limits), wolves that spent greater amounts of time outside BNP would experience higher human-caused trapping and hunting mortality. Finally, previous studies occasionally found differences in survival across different age and sex-classes, which we also investigated.

2. Materials and methods

2.1. Study area

The study occurred from 1987 to 2019 in and adjacent to Banff National Park (BNP, 51°30''/115°30″) in an area defined by the movements of radiocollared wolves over a ~7000 km² study area (Fig. 1). Elevations range from 1400 m to 3500 m, with a cold, continental climate with long (October–April) snowy winters, and a brief summer (May–September) (Holland and

Coen, 1983). Vegetation is dominated by lodgepole pine (*Pinus contorta*) forests at lower elevations grading to Englemann spruce (*Picea englemanni*) and alpine herbaceous communities at higher elevations. Fifty percent of BNP is rock and ice, with the best ungulate winter ranges of montane rough fescue (*Festuca campestris*) grasslands occurring in the lower elevation montane region along the eastern slopes of the Rocky Mountains. For more details of the predator-prey community see Hebblewhite et al. (2004).

Two towns (~10 000), a national railway (Canadian Pacific Railway), a national highway (Trans-Canada Highway, TCH), secondary roads, and human developments (ski resorts, golf courses) fragment the study area. The Bow Valley of BNP is used by more than 4 million visitors per year, causing direct mortality from railways and highways, but also indirectly through food conditioning. In contrast, remote areas of BNP experience low human activity. Trapping and hunting are prohibited within BNP. Outside BNP, wolves are exposed to hunting and trapping mortality during liberal hunting and trapping seasons with no bag limits and long seasons (~9 months, Robichaud and Boyce, 2010). Trapping occurred on registered trap lines that provided trappers exclusive trapping rights within a registered fur management area (Robichaud and Boyce, 2010). Human settlements and agriculture lands further east constrain wolf distribution to occur along the main ranges and foothills of the Canadian Rocky Mountains, but there was little to no conflicts with livestock in our study area. Wolf densities in BNP went through 3 broad time-periods following recolonization. Wolf density increased from approximately 2 to 6 wolves per 1000 km^2 from
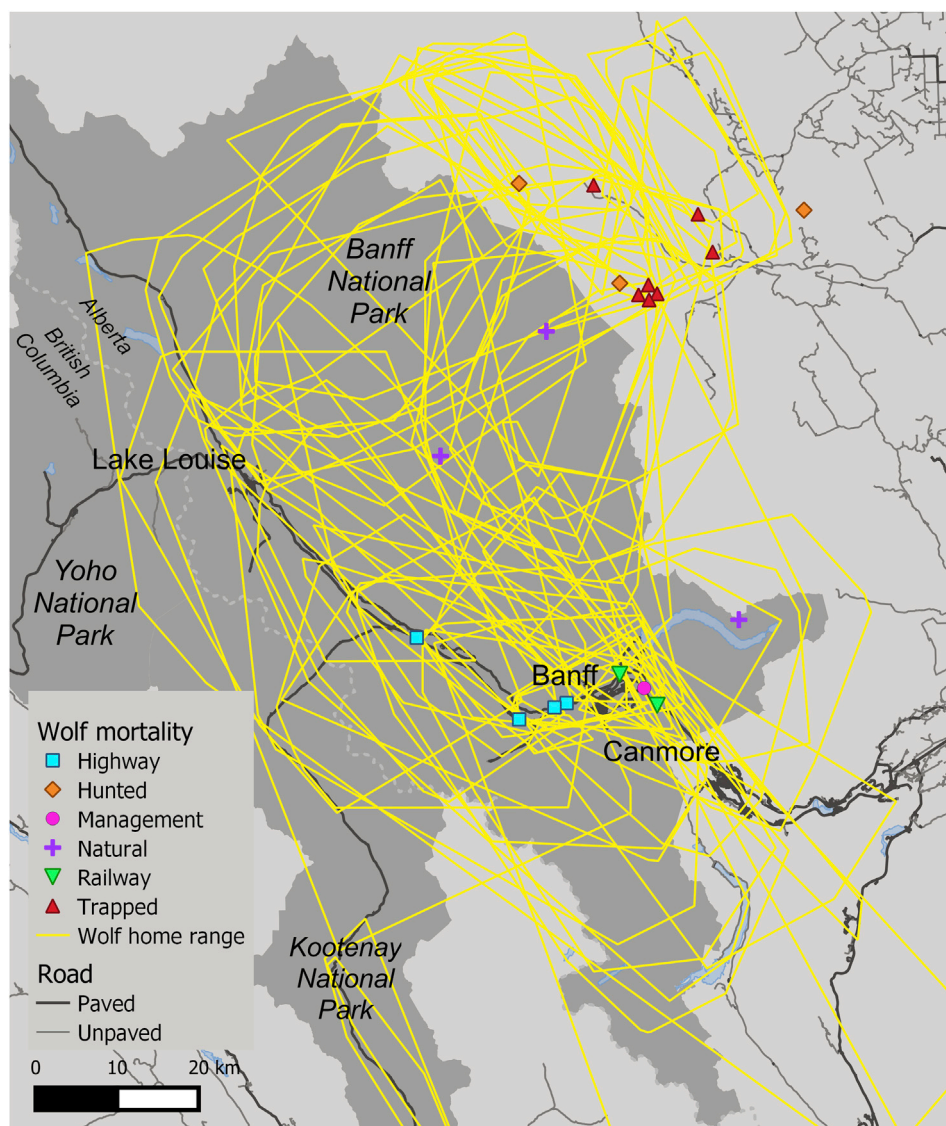
Fig. 1. Mortality locations and home ranges of radiocollared wolves (95% minimum convex polygon) collected from 1987 to 2019 in and around Banff National Park, Alberta.

1987 to 1994 (increase phase), then declined to approximately 3 wolves per 1000 km^2 in 2005 (decline phase), and has since stabilized at approximately three wolves per 1000 km^2 (stable phase, Supporting Information, Fig. S1).

2.2. Wolf capture and handling

We captured wolves using foot-hold traps in summer, and helicopter netgunning and aerial darting during winter (University of Alberta Animal care protocol ID# 353112, University of Montana Institutional Animal Care Protocol # 059-08MHECS-120908, 004-16MHECS-020916, 066-18MHWB-123118, Parks Canada Research and Collection Permits LL-2010-4392, BAN-2015-18276, BAN-2018-30898). Wolves were outfitted with VHF radiocollars (LMRT-3, LOTEK Ltd. Newmarket, ON, Canada) exclusively during early years of the study. Two wolves were outfitted with ARGOS satellite radiocollars in the early 1990's. Starting around 2001, wolves were largely outfitted with Global Positioning System (GPS) radiocollars of a variety of brands, models and fix-rate schedules (e.g., LOTEK GPS3300sw, SirTrack, Vectronic). Wolf GPS collars were programmed to obtain anywhere from 2 to 96 locations/day. During 1987−2005, all collared wolves were relocated aerially from a Cessna Skymaster 337 or Helicopter every 1−2 weeks. Wolves with VHF collars or store-on-board GPS collars were monitored almost daily in road-accessible areas using ground telemetry. Few wolves were radio-collared between 2005 and 2012. Our study switched to satellite-based GPS collars from 2012 to 2019, which enabled staff to monitor wolf movements and mortality events on a daily basis.

2.3. Wolf monitoring

All radiocollars were outfitted with mortality sensors. VHF radiocollars were monitored manually via ground or aerial telemetry to detect mortalities, and GPS radiocollars communicated mortality signals via satellite uploads. Once a mortality was detected via VHF or GPS signals, we endeavored to investigate each mortality in the field as soon as possible. We determined cause and date of death using standard field necropsy protocols combined with information about the midpoint between successive VHF locations. We classified mortalities into three broad categories, natural, human-caused, and unknown. Natural mortalities included disease, accidents, and injuries sustained while hunting. Human-caused mortalities were classified into road kill, railway, habituation-related, hunting and trapping. Unknown mortalities included all cases where cause could not be determined. Furthermore, we also classified when wolves permanently left the study area as dispersal (Boyd et al., 1995), and used the dispersal date to censor those animals from our survival analyses.

2.4. Survival modeling

We used a continuous-time survival monitoring framework to estimate the survival and cause-specific mortality of wolves in BNP. We set the annual biological calendar to start every year on May 1 (approximately the time of denning), and used a recurrent time-horizon following Fieberg and DelGuidice (2009) to model annual survival of wolves. We only included known mortalities that occurred during regular monitoring either with GPS or VHF locations. We considered interval truncation when the time period between locations exceeded 30 days to avoid potential biases in survival estimation due to dispersing wolves or failed collars (DeCesare et al., 2016). We used left- and right-staggered entry and exit approaches to introduce wolves into the analysis on their capture date and to censored wolves when they dispersed or when their collar failed or was remotely removed. We assumed censoring occurred independently of fate.

With these constraints, we estimated survival rates using non-parametric Kaplan-Meier (Hosmer et al., 2008) methods in R (R Core Team, 2020) using the survival package (Therneau, 2019; Therneau and Grambsch, 2000) using 95% log-log confidence intervals. We first analyzed the data using Frequentist methods to help guide our understanding of factors influencing survival, but because of confounding between season and park status (see Supporting Information Appendix S2 for frequentist details), we proceeded to use more flexible Bayesian methods which we report here in text.

We tested our hypotheses regarding survival using a Bayesian counting-process modelling framework (Plummer and Carstensen, 2011; Whittington et al., 2011) with parametric seasonal mortality pulses following Gurarie et al. (2019). We estimated the baseline hazard (h_0) for all individuals and additive effects on mortality rates ($e^{\beta X}$) by determining whether individual wolf i was alive or dead (y_{it}) for every day t it was monitored. We modelled daily mortality status y_{it} as a Poisson-process driven by the instantaneous hazard of mortality (h_t) at time t where:

$$y_{it} \sim \text{Poisson}(h_t(\gamma, \rho, \mu, \beta, \mathbf{X_i}, t)),$$
$$h_t(\gamma, \rho, \mu, \beta, \mathbf{X_i}, t) = h_0(\gamma, \rho, \mu, t)\, e^{\beta \mathbf{X}},$$
$$h_0(\gamma, \rho, \mu, t) = (\gamma\, (1 - \rho^2)) / (1 + \rho^2 - 2\rho \cos(t - \mu)), \qquad \text{(Equation 1)}$$

were h_t was the daily risk of mortality at time t, $\beta \mathbf{X}$ were additive fixed effects affecting mortality for 1 to j parameters, and h_0 was the daily hazard affecting all individuals.

While some studies estimate the daily hazard h_0 using splines (or ignore it using Cox-proportional hazards regression), we estimated the daily hazard using the wrapped Cauchy distribution (Gurarie et al., 2019). The advantage of the wrapped Cauchy distribution is that it estimates seasonal pulses in mortality and models the hazard as a circular distribution,

appropriate for recurrent time-horizons in survival models (Fieberg and DelGiudice, 2009). Based on Kaplan-Meier analyses described above, we estimated up to one seasonal pulse in mortality where γ was the average hazard across the year, μ was the seasonal timing for the peak in mortality measured in radians, ρ was the clustering coefficient that varied between 0 (no peak) and 1 (infinite hazard) (Gurarie et al., 2019).

2.5. Ecological covariates and model selection

We developed survival models using Markov chain Monte Carlo (MCMC) sampling and compared competing models using WAIC (Watanabe, 2010). We considered the following additive covariates affecting survival: time periods during general increasing (1987−1994), decreasing (1995−2004), and stable (2005−2019) wolf population trends (methods described in Eggeman et al., 2016; Fig. S1), year as a linear covariate centered on 2002, the age class young-of-year as a dummy variable, sex, and whether a wolf was inside BNP at time t. Age has affected wolf survival in some studies, but not others (Fuller et al., 2003). We estimated wolf age at time of capture based on body morphology and tooth wear and then classified wolves as being a young-of-year or adult. We re-classified the age of wolves for each year of monitoring. We included sex in our candidate set of models, although sex in other studies has had minimal effects on wolf survival (Fuller et al., 2003).

Wolves travelling inside versus outside protected areas incur differing mortality risk (Thurber et al., 1994; Schmidt et al., 2017). We determined whether each telemetry location was inside or outside BNP, and used the instantaneous Park status k as a categorical covariate (In/Out) to test whether leaving BNP reduced survival. Our counting-process model required a value for park status every day a wolf was monitored. For intervening days between telemetry fixes, we generated random latent values for park status based on the proportion of known telemetry locations within the park ψ for each wolf such that $Park_{it} \sim$ Bernoulli (ψ_i). We hypothesized that the seasonal pulse in mortality differed for wolves travelling in versus outside of BNP. We tested for differences in seasonal mortality risk by including models where the baseline hazard h_0 differed by park status. We allowed all wrapped Cauchy parameters (γ, μ, and ρ) to vary by park status (*sensu* Gurarie et al., 2019).

We first ran univariate analyses with all covariates described above and then combined covariates in a forward-stepwise manner if they improved model performance and the 75th percentile of Bayesian confidence intervals (BCI) excluded 0. Because of our modest sample size, we only considered models with ≤3 or fewer parameters to minimize risk of overfitting. We selected the model with the lowest WAIC as the most parsimonious model (Watanabe, 2010), a Bayesian generalization of AIC calculated from the posterior distribution of the MCMC samples (Gelman et al., 2014). Further supporting our approach, our top model selected with WAIC was equivalent to the top frequentist model selected using AIC (see Supporting Information Appenxi S2). We analyzed the data using the R package Nimble version 0.8.0 (de Valpine et al., 2017). We used vague priors for all parameters including log(γ) ~ Normal (0, 10), μ ~ Uniform (-2π, 2π) so that proposed values for the circular parameter could cross the $-\pi:\pi$ boundary, ρ ~ Uniform (0, 1), and β_j ~ Normal (0, 10). We ran 5 chains for each model with an adaption phase of 1000 iterations followed by 30 000 iterations. We removed the first 5000 iterations as the burn-in phase and thinned posterior samples to every fifth sample. We assessed model convergence by examining Gelman-Rubin statistics (values less than 1.1 indicated lack of convergence) and by visually examining trace plots. We provide an R script to simulate data and estimate a wrapped Cauchy survival model in Supporting Information Appendix S4, and refer readers for more details to Jones et al. (2020) for full details on the Bayesian survival modeling approach.

2.6. Cause-specific mortality

We estimated cause-specific mortality rates with Bayesian cumulative incidence functions (CIFs, Heisey and Patterson, 2006). CIFs estimate the probability of death from a mortality cause, accounting for competing risks between different mortality sources and the number of animals at risk of mortality (Heisey and Patterson, 2006). We adapted a Bayesian approach recently developed by Jones et al. (2020) based on Heisey and Patterson (2006).

3. Results

3.1. Wolf monitoring

We included 72 radiocollared wolves from 1987 to 2019 in our final survival models, with an average of 4.1 new wolves radiocollared per year and 5.3 wolves monitored per year. Individual wolves were monitored an average of 1.4 years (SD = 1.51, range 1 day−6.44 years) for a total of 155 wolf-years of monitoring. Of our initial sample, 22 wolves died while they were monitored and the remaining 50 wolves were censored when their collar failed, their collar was removed, or when they had not been located for >30 days. Only 3 known radiocollared wolves dispersed from BNP during monitoring: two short dispersals from BNP to adjacent provincial parks to the southeast and one dispersal westward where the wolf was shot within 15 days of dispersal. None of the wolves radiocollared east of Banff National Park dispersed. Our dataset included 33 females and 39 males, 21 of the wolves were initially radiocollared as young-of-year, and 55 (76%) of the wolves spent greater than 50% of their time in BNP. We obtained and average of 96 VHF (during pre-GPS era) and 235 GPS daily locations per wolf, resulting in average monitoring intervals of 4.8 days for VHF and 1.2 days for GPS data.

3.2. Survival modeling

Non-parametric Kaplan-Meier survival estimates were 0.733 (95% CI 0.622−0.816, Supporting Information Appendix S2). The top Bayesian model for wolf survival contained distinct seasonal hazards for wolves inside and outside of Banff National Park (Table 1). Overall, the daily risk of mortality (γ) was 4.7 times higher for wolves outside the park than inside the park (Table 1, hazard ratio $\gamma_{OutOfPark}/\gamma_{InPark}$, 95% BCI = 1.9−11.2). Daily mortality rates were most similar and not significantly different for wolves outside and inside the park around June 29 (Fig. 2, hazard ratio = 1.4, 95% BCI = 0.3−5.2). The hazard ratio peaked on January 1 when wolves were 12.7 times more likely to die outside the park (95% BCI = 3.7−44.7). Cumulatively, wolves outside the park were 6.7 times likely to die (odds ratio 95% BCI = 2.2−21.4) by the end of the year compared to wolves inside the park (year-end survival rates and 95% BCI, Out of Park = 0.44, 0.24−0.65; In Park = 0.84, 0.73−0.91). The second ranked model suggested a weak effect of year on wolf mortality rates (Table 1). Wolf mortality rates increased both in and outside of parks over the course of the study (Odds ratios β_{Year} = 1.038, 95% BCI = 0.986−1.092) (see Table 2).

3.3. Cause-specific mortality

Wolves died of the following causes: trapping (n = 8), hunting (n = 4), highways (n = 4), railway (n = 2), natural (n = 3; one each of avalanche, fall from a cliff, unknown), and management (n = 1). Bayesian cause-specific mortality indicated that the leading cause was trapping (rate = 0.080, 95% BCI 0.036−0.152, 36% of mortality), followed by hunting (0.053, 0.016−0.131, 18%), highway (0.046, 0.013−0.114, 18%), natural (0.032, 0.007−0.088, 14%), railways (0.018, 0.003−0.061, 9%), and management (0.011, 0.001−0.056, 5%). All trapping and hunting mortality occurred during winter, whereas other sources of human-caused mortality occurred year-round inside BNP (Fig. S3, Supporting Information).

4. Discussion

Our results revealed that wolves in BNP experienced similar survival rates and cause-specific mortality to harvested populations throughout North America. Overall survival was 0.73, human-caused mortality dominated known mortality both inside and outside BNP (90% of all known mortality), and, unlike other protected populations, we found no intraspecific mortality. Indeed, the greatest risk factor in our study was whether wolves left the protection of the park in winter during the hunting and trapping season on adjacent provincial lands. Wolves that did experienced up to 12.7 times higher daily risk of mortality, especially from trapping, and ~7 times higher annual risk of mortality. Despite the risks outside BNP, wolves also experienced human-caused mortality inside BNP from highway, railway, and management related causes. Our differential survival rates were similar to endangered African wild dogs (_Lycaon pictus_) where mortality rates and the ratio of human-caused to natural mortalities increased outside of protected areas (Woodroffe et al. 2001; 2007).

Our wolf survival rates were similar to survival rates in other harvested populations. For example, Cubaynes et al. (2014) found wolf survival in the mostly protected Yellowstone population varied from 0.70 to 0.94 from 1998 to 2008. Most mortality was caused by wolf-caused mortality in this protected population (~40% of all mortality rates were intraspecific wolf caused mortality). In comparison, it is remarkable that we found zero wolf-caused mortality in BNP, yet low intraspecific mortality is a hallmark of exploited populations (Adams et al., 2008; Webb et al., 2011). In a similar transboundary protected area setting, Benson et al. (2014) studied survival of 147 wolves in Algonquin PP in Ontario, Canada, and found that wolf survival declined outside of buffered protected areas as hunting and trapping access (secondary road) increased. For non-eastern wolves, survival was ~0.67−0.72, with the bulk of mortality transboundary hunting/trapping mortality. Smith et al. (2010) report on survival of 711 wolves in Idaho, MT and Wyoming from 1982 to 2004 and found survival of wolves was 0.75, but much lower (~0.57) for wolves targeted for conflicts with livestock. In a follow-up analysis of cause-specific mortality, Murray et al. (2010) found 80% of all mortality was human-caused, and such mortality was partially compensatory. Schmidt et al. (2017) studied transboundary mortality of n = 146 wolves over 22 years in Yukon-Charley National Preserve in

Table 1
Top ranked models for wolf survival from 1987 to 2019 in Banff National Park (BNP) based on WAIC where $h_t = h_{0t}e^{\beta X}$. The daily hazard h_{0t} was modelled using a wrapped Cauchy distribution with parameters for the average hazard γ, timing of the seasonal pulse μ, and intensity of the seasonal pulse ρ. Hazards for the top ranked model depended on whether wolves were inside or outside BNP (Park).

Hazard h_{0t}	Additive Effects $e^{\beta X}$	WAIC	ΔWAIC
γ ~ Park, μ ~ Park, ρ ~ Park		342.5	0.0
γ ~ Park, μ ~ Park, ρ ~ Park	Year	342.6	0.1
γ ~ Park, μ ~ Park, ρ ~ Park	Year x Park	344.5	2.0
γ ~1, μ ~1, ρ ~1	Park	344.7	2.1
γ ~1, μ ~1, ρ ~1	Year	352.2	9.7
γ ~1, μ ~1, ρ ~1		355.0	12.4
γ ~1, μ ~1, ρ ~1	Male	356.6	14.1
γ ~ Park, μ ~ Park, ρ ~ Park	1995−2005 + 2006−2019	357.0	14.4
γ ~1, μ ~1, ρ ~1	YoungOfYear	357.3	14.8
γ ~1 (Constant Hazard)		357.3	14.8

Table 2

Posterior estimates (median, standard deviation, and 95% BCI's) for parameters in the top ranked model for wolf survival in and adjacent to Banff National Park, 1987 - 2018. The average hazard γ, timing of mortalities μ (circular variable in radians), and intensity of mortalities ρ depended on whether wolves travelled inside vs outside the park.

Parameter	Park	Median	SD	lcl	ucl
γ	Out of Park	0.00225	0.00071	0.00117	0.00393
γ	In Park	0.00048	0.00016	0.00024	0.00085
μ	Out of Park	-2.18	0.39	-3.01	-1.61
μ	In Park	1.88	2.05	-1.05	4.81
ρ	Out of Park	0.54	0.14	0.25	0.79
ρ	In Park	0.15	0.13	0.01	0.46
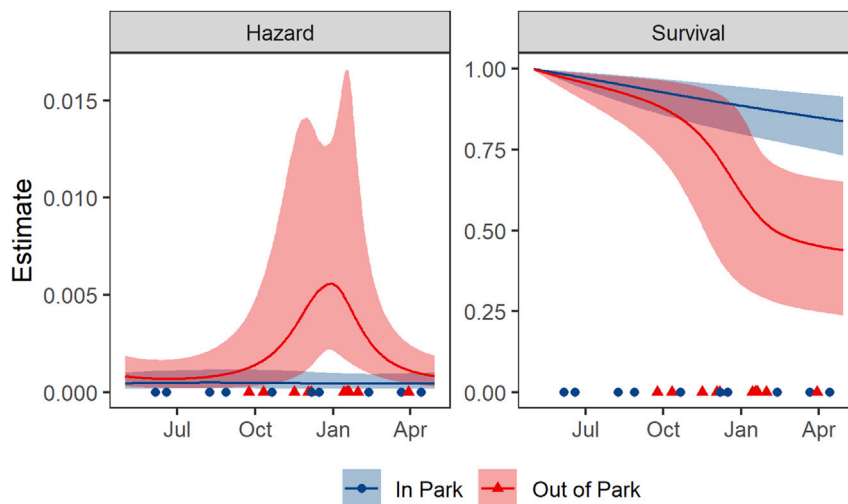
Fig. 2. Daily a) mortality hazard and b) cumulative probability of survival (median ± 95% BCI's) for wolves travelling in and outside of Banff National Park (BNP), 1987−2018. Points along the x-axis show mortality events inside (blue dot) and outside (red triangle) BNP. (For interpretation of the references to colour in this figure legend, the reader is referred to the Web version of this article.)

Alaska during 2 periods of ongoing wolf control outside park boundaries. Based on both radiocollared wolves and integrated population modeling, estimated survival was as low as 0.35−0.45 across all wolves, largely because of high levels of transboundary movements that exposed Preserve wolves to wolf control programs outside of NPS lands. Schmidt et al. (2017) found that such transboundary mortality caused population-level declines of wolves inside Yukon-Charley National Preserve. These studies confirm that survival of wolves in our study area was similar to other harvested wolf populations.

We found no differences in age- or sex-specific survival rates of wolves in BNP, but, did find some weak evidence for increasing mortality risk over time. This weak trend was in the opposite direction, however, to trends in survival that would be driven by density-dependent survival. For example, in Yellowstone, Cubaynes et al. (2014) reported decreasing survival with increasing wolf density, largely due to intraspecific mortality. In contrast, we found overall decreasing survival as wolf densities increased then declined in our study. O'Neil et al. (2017) found strong evidence for density-dependence in wolf survival rate across northern Michigan; survival was initially high, 0.92, but declined to 0.75 (still higher than ours). The mechanism for declines in Michigan wolf survival was increasing harvest and occupancy of wolves in areas with more exposure to hunting and trapping. We believe that commensurate with elk population declines in BNP (e.g., Hebblewhite, 2005), some wolf packs may have spent more time outside protected area boundaries during winter in a manner akin to O'Neil et al. (2017), increasing their mortality risk. Moreover, while construction of fencing paired with wildlife overpasses and underpasses has increased connectivity for wildlife (Sawaya et al., 2013), several wolf mortalities occurred when wolves travelled over cattle guards and onto the Trans-Canada Highway at secondary road junctions. Continued improvements to highway fence design coupled with electrified cattle guards have potential to reduce highway related mortality inside BNP.

Despite the heightened risk when outside BNP, our results are consistent with a stable, harvested wolf population. In a review of North American wolf studies, Fuller et al. (2003) generally found that wolf population growth rates were largely stable to increasing when human-caused mortality was <30%. This 30% threshold has been debated, with sustainable human-caused mortality rate thresholds estimated from 26% (Creel et al., 2015) to nearly 50% in large, contiguous populations (Fuller et al., 2003; Mitchell et al., 2016). Part of the debate has to do with the ability of wolf reproduction (and dispersal) to compensate for increased human-caused mortality. Another has to do with whether human-caused mortality compensates with mortality from 'natural', non-human causes such as disease, starvation or intraspecific mortality. In a review across

studies Adams et al. (2008) found little evidence for compensation between human-caused mortality and natural mortality if human-caused mortality is <29%. In adjacent provincial lands of Alberta, Webb et al. (2011) reported > 1-year old survival of 84 wolves was 0.62 and that trapping mortality (0.22) was twice that of hunting mortality (0.12). But when Webb et al. (2011) considered demographic data on reproduction, they concluded that wolf harvest was largely balanced with reproduction. Consistent with other exploited populations, they also found no wolf-caused mortality. Callaghan (2002) reported median litter size of ~5.2 pups/pack from 1989 to 2011, similar to Webb et al. (2011)'s reported 5.6 pups/pack as sufficient to balance mortality. Further, wolves entirely within BNP had high survival rates even though prey density was relatively low. In contrast, wolves outside BNP occurred in an area with higher prey density (Webb et al., 2011), which likely influenced wolf re-colonization rates, reproduction rates, pup survival rates, and their ability to recover from winters with high mortality. Moreover, long-term stability of wolf trapping on most traplines in Alberta (Robichaud and Boyce, 2010), combined with non-invasive monitoring of wolves in Alberta adjacent to BNP (Bassing et al., 2018) suggests the levels of human-caused mortality observed in our study are consistent with a stable wolf population.

Despite this, it is notable that transboundary wolves in Canada's oldest National Park face high levels of mortality from hunting and trapping. Wolf packs with home ranges entirely within BNP had high annual survival rates close ~0.84 with relatively stable pack structure, which aligns with Parks Canada's mandate to prioritize ecological integrity (Government of Canada, 2000). High levels of harvest on transboundary and unprotected wolf packs may not threaten the long-term viability of the broader wolf population. However, high mortality rates of transboundary wolves could affect ecological integrity in adjacent protected areas. First, the high mortality rates of transboundary wolves could create source-sink population dynamics along the Canadian Rocky Mountains (Webb et al., 2011; Cullingham et al., 2016). Our dispersal rates (3 of 72 wolves) were lower than wolf dispersal rates immediately to the north (0.25, Webb et al., 2011) and the proportion of wolves that disperse along the Rocky Mountains in the Western United States (10%, Jimenez et al., 2017). Some dispersal may have been included in censoring, but either way, our dispersal remains low. Thus, the high levels of mortality likely limit BNP's putative role as a protected area source population, consistent with no evidence for directional gene flow out of BNP in Cullingham et al. (2016). Second, the high rates of mortality we report suggest that wolf age structure is likely more akin to those in harvested populations towards younger ages. Studies in Yellowstone demonstrate important effects of age on wolf predatory abilities, reproductive success, and pack stability that may affect the ecological effectiveness of wolves. For example, large male wolves >5 years old were particularly important to attack success in YNP (MacNulty et al., 2012; Stahler et al., 2013). Juvenile wolves may be more susceptible to trapping than adults (Webb et al., 2011), however all 8 wolves trapped in our study were at least one year old. Furthermore, large packs with multiple large wolves were often more successful in attacking and subduing large prey species such as bison (*Bison bison*). And large packs were more likely to have multiple litters, guarding against negative effects of breeder loss if the breeding female is subjected to harvest during the winter breeding season (Brainerd et al., 2008). These subtle effects of wolf harvest may reduce the ecological effectiveness (for example, magnitude of their predation on ungulates; Soule et al., 2003) of wolves inside BNP. Previous studies have clearly demonstrated an important keystone role of wolf predation in BNP in structuring ungulate population dynamics (Hebblewhite, 2005), relationships amongst the predator guild (Hebblewhite and Smith, 2010), and in restoring vegetation such as aspen and willow (Hebblewhite et al., 2005). For these reasons, additional attention to the demographic and ecosystem effects of transboundary harvest in BNP may be warranted.

Addressing transboundary mortality of large carnivores is challenging because of difficulties of reconciling different management paradigms, policies, and social pressures across park and non-park lands around the globe (Hebblewhite, 2007; Smith et al., 2016; Woodroffe and Ginsberg, 2001). Transboundary management agreements elsewhere provide an array of options ranging from the status quo to increased protection for wolves. In Yellowstone and Glacier National Parks in Montana, state and Federal agencies reached a compromise of a quota system of 2 wolves/management unit on state lands immediately adjacent to park boundaries (Smith et al., 2016). In Algonquin provincial park, a buffer zone the width of one township protects the endangered eastern Red wolf (*C. lycaon*) from trapping and hunting. This buffer has helped reverse genetic threats to the species and has bolstered survival (Benson et al., 2014). Given the wide-open and very liberal seasons on wolves in most of Canada, other options could involve limits in space and/or time on hunting or trapping mortality. Fig. 1 suggests such spatiotemporal quotas could be effective if implemented in a small area. Nonetheless, it is also true such transboundary management ultimately depends on societal objectives and goals, and such approaches often are controversial across Park boundaries.

Of course, there are a number of considerations when interpreting our results. Despite the long-time frame of our study, given the challenging nature of studying wolves, sample sizes of radiocollared wolves were modest. This may have obscured biological effects such as age- or sex-differences in survival. Previous studies of wolf survival ranged across a similar sample size from ~30 to 711 (Smith et al., 2010). Yet the magnitude of the transboundary survival effect was strong, and, consistent with previous studies (Benson et al., 2014; Schmidt et al., 2017; Thurber et al., 1994), confirming our interpretation. Bayesian analyses lend themselves well to modest such datasets, but Frequentist analyses provided additional confirmation of the strong transboundary survival gradient. Differences over time in monitoring approaches between VHF and GPS provided challenges which we addressed with restrictive interval censoring rules when animals went >30 days without monitoring that should effectively address conflation between unknown fates and specific mortality causes (DeCesare et al., 2016). The biggest challenge to interpreting our results is the lack of reproductive data with which to put our survival rates in the context of wolf demography in BNP. With long-term monitoring of wolf pack counts and pup counts available through a cost-effective

remote-camera trapping approach, new approaches such as integrated population modeling (Schmidt et al., 2017) could provide this context for transboundary management in the future.

Nevertheless, our results were consistent with wolves in and adjacent to BNP operating essentially as a harvested wolf population with demography akin to exploited populations across North America. Annual risk of mortality was ~7 times higher for wolves outside BNP due to trapping and hunting. Wolves within BNP continued to die from human sources of mortality along transportation corridors (roads and railways) and more recent challenges with food conditioning. How these levels of mortality influence the ecological effectiveness of wolves is unclear (Soule et al., 2003), but future studies could consider evaluating effects of these mortality rates on wolf demography and ecological integrity.

Declaration of competing interest

None.

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Appendix A. Supplementary data

Supplementary data to this article can be found online at https://doi.org/10.1016/j.gecco.2020.e01293.

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