

## RESEARCH ARTICLE

# Harvest of transboundary grey wolves from Yellowstone National Park is largely additive

Brenna Cassidy<sup>1</sup>  | Douglas W. Smith<sup>2,†</sup> | Kira Cassidy<sup>2</sup> | Daniel Stahler<sup>2</sup> | Mark Hebblewhite<sup>1</sup> 

<sup>1</sup>Wildlife Biology Program, Department of Ecosystem and Conservation Sciences, Franke College of Forestry and Conservation, University of Montana, Missoula, Montana, USA

<sup>2</sup>National Park Service, Yellowstone Center for Resources, Yellowstone National Park, Wyoming, USA

**Correspondence**

Brenna Cassidy

Email: [brenna.cassidy@umontana.edu](mailto:brenna.cassidy@umontana.edu)

**Funding information**

National Science Foundation, Grant/Award Number: 366330, DEB-06137730 and DEB-1245373; Yellowstone National Park, Yellowstone Forever, V. Gates, A. and B. Graham, University of Montana Wilderness Institute Meier Graduate Research Fellowship; University of Montana; Living With Wolves Foundation

**Handling Editor:** Abishek Harihar

**Abstract**

1. Large carnivores are globally threatened due to habitat fragmentation and loss, prey depletion and human exploitation. Human exploitation includes both legal and illegal hunting and trapping. Protected areas can create refugia from hunting and trapping; however, hunting can still threaten wide-ranging large carnivores when they leave these areas. Large carnivore reintroductions to protected areas are often motivated to restore ecological processes, including wolf reintroduction to Yellowstone National Park (YNP). Determining if harvest is compensatory or additive is essential for informed conservation strategies, as it influences the overall impact on wolf populations and their ecosystems.
2. If harvest was compensatory, then increasing harvest pressure outside YNP should not decrease overall survival for transboundary wolves. Alternatively, if increasing harvest was additive, then increasing harvest pressure outside YNP should decrease overall survival for transboundary wolves. We tested the effects of variable harvest pressure following delisting on the survival of YNP grey wolves (*Canis lupus*) from 1995 to 2022. We defined three harvest levels: no harvest, harvest with limited quotas and unlimited harvest. We used Cox-proportional hazards models and cumulative incidence functions to estimate survival rates, factors affecting survival and cause-specific mortality between these three harvest periods to test predictions of the additive mortality hypothesis.
3. Most harvested wolves that primarily lived in YNP were killed adjacent to the park border. Cox-proportional hazards models revealed that mortality was highest during years of unlimited harvest during winter outside YNP. Cause-specific mortality analyses showed that natural mortality from other wolves and harvest were the two leading causes of death, but that harvest mortality had additive effects on wolf mortality. Wolf survival decreased with increased harvest mortality, while natural mortality remained relatively unchanged.
4. *Synthesis and applications.* High rates of additive harvest mortality of wolves could negatively impact wolf survival in YNP. Harvest mortality of transboundary wolves is additive possibly due to source-sink dynamics of uneven spatial susceptibility

<sup>†</sup>Retired.

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of wolves to harvest mortality across protected area borders, as well as effects of harvest on complex social dynamics of wolves in YNP. Transboundary management of large carnivores is challenging, yet cooperation between agencies is vital for wolf management in and around YNP. Our results support the use of small quota zones surrounding protected areas, that minimize transboundary mortality impacts on large carnivores living primarily inside protected areas.

#### KEYWORDS

additive mortality, *Canis lupus*, carnivore, compensatory mortality, protected areas, survival, transboundary, wolves

## 1 | INTRODUCTION

Large carnivores are among the most threatened and endangered species globally (Ripple et al., 2014; Tilman et al., 2017). Carnivores are threatened by habitat fragmentation and loss, prey depletion and human exploitation and persecution (Ripple et al., 2014). Protected areas are seldom large enough to insulate large carnivore populations from these threats (Fritts & Carbyn, 1995; Santini et al., 2016). In Europe, no Special Areas of Conservation were large enough to support viable populations of lynx (*Lynx lynx*), grey wolves (*Canis lupus*) or brown bears (*Ursus arctos*) (Santini et al., 2016). Although protected areas can provide refugia from human-caused threats, wide-ranging large carnivores often cross land management authority boundaries, creating transboundary challenges due to differences in management policies across jurisdictions (Forbes & Theberge, 1996; Hebblewhite & Whittington, 2020). Ranging outside protected areas into population sinks, not population size, was the most important predictor for extinction risk for 10 African carnivores (Woodroffe & Ginsberg, 1998).

Large carnivores also often have disproportionately important effects on ecological processes (Carbone & Gittleman, 2002). These include influencing the abundance and distribution of other predators and prey, altering disease dynamics and precipitating trophic cascades throughout food webs (Ripple et al., 2014, 2016; Ritchie & Johnson, 2009). Species like wolves are often considered keystone species (Smith et al., 2020), with disproportionately large impacts on ecosystems on a per capita basis. Thus, understanding effects of human harvest on wolves, and their population dynamics, could be important to understand potential ecosystem impacts in protected areas which often are more preservation focused. Due, in part, to these ecological effects (Ripple et al., 2016), reintroduction of large carnivores has gained attention worldwide.

Grey wolves have naturally recolonized or been reintroduced to numerous places around the world. This includes in the Great Lakes region of the United States, central Europe, and recently to Colorado, USA. Following successful wolf recovery, numerous jurisdictions have or are considering reinstating harvest seasons. The reintroduction of grey wolves to the Northern Rocky Mountains in Yellowstone National Park (YNP) and central Idaho, beginning in 1995, aimed to reverse their endangerment and restore the ecological process of

predation in the contiguous United States (Smith et al., 2010). Grey wolves were extirpated from the Greater Yellowstone Ecosystem (GYE) by 1926 (Smith et al., 2010), but following restoration, quickly recovered to hundreds of wolves within the GYE by the early 2000's. Wolves were subsequently delisted from the Endangered Species Act (ESA) in the Northern Rocky Mountains between 2009 and 2012, becoming one of the world's leading examples of carnivore recovery. Wolf restoration also highlighted the effects wolves have on ecosystems, including their pivotal contribution to food webs and biodiversity (Smith et al., 2020). Some species such as coyotes (*C. latrans*), grizzly bears (*Ursus arctos horribilis*), ravens (*Corvus corax*) and magpies (*Pica hudsonia*) benefitted from wolf restoration with increased carrion availability (Wilmers et al., 2003), while other species such as elk (*Cervus canadensis*; Metz et al., 2020) and coyotes (Berger & Gese, 2007) declined due in part to the effect of wolves.

Since removal from the ESA, variable harvest management of wolves in the Northern Rocky Mountains has prompted concerns about the effects of harvest on wolves, particularly in protected areas. The United States Fish and Wildlife Service's (USFWS) recovery goal was to establish a sustainable population of wolves to the Northern Rocky Mountains. Then to return wolf management to the states bordering YNP (Montana, Wyoming and Idaho) with approved state management plans (Smith et al., 2010). After wolves were federally delisted from the ESA in 2009, Montana and Idaho initiated hunting and trapping seasons. Wyoming, however, did not yet have an approved state management plan and, therefore, did not have a hunting or trapping season until 2012. Wolves were temporarily relisted in 2010 due to a court case, pausing harvest seasons, but Montana and Idaho reinstated hunting and trapping seasons in 2011. Wolves were briefly relisted in Wyoming from 2014 to 2016, with hunting and trapping seasons reinstated in 2017. Thus, harvest quotas, season length and number of management units varied between states and years between 2009 and 2022 (Table 1). Intermittent changes to harvest regulations, including longer seasons, higher overall harvest levels and more flexible policies, prompted concerns about potential harvest impacts on wolves that primarily live in YNP. This spatiotemporal variation in regulations provided an ideal setting to test effects of variable harvest rates on wolves. Researchers in other protected areas have documented significant impacts on wolf survival due to harvest of transboundary wolves (Barber-Meyer et al., 2021; Forbes

**TABLE 1** Harvest level classification, quotas and wolf management units (WMU's) for grey wolves (*Canis lupus*) in and around to Yellowstone National Park from 1995 to 2022, showing changes in harvest level over time, by state and by wolf management units (WMU) within the states of Montana (MT), Wyoming (WY) and Idaho (ID). Years of WMU's with n/a indicate the WMU did not exist.

Biological year	Harvest level classification	Montana WMU quotas			State harvest		
		WMU 313	WMU 316	WMU 313/316 combined	WY	ID	MT
1994–2008	No harvest	n/a	n/a	n/a	No	No	No
2009	Unlimited	n/a	n/a	No quota	No	Yes	Yes
2010	No harvest	no hunt	No hunt	No hunt	No	No	No
2011	Quota	n/a	4 <sup>a</sup>	n/a	No	Yes	Yes
2012	Unlimited	No quota	3	n/a	Yes	Yes	Yes
2013	Quota	4	3	n/a	Yes	Yes	Yes
2014	Quota	3	3	n/a	No	Yes	Yes
2015	Quota	2	2	n/a	No	Yes	Yes
2016	Quota	2	2	n/a	No	Yes	Yes
2017	Quota	2	2	n/a	Yes	Yes	Yes
2018	Quota	2	2	n/a	Yes	Yes	Yes
2019	Quota	2	2	n/a	Yes	Yes	Yes
2020	Quota	1	1	n/a	Yes	Yes	Yes
2021	Unlimited	No quota	No quota	n/a	Yes	Yes	Yes

<sup>a</sup>While not originally a quoted WMU, Montana Fish, Wildlife and Parks shut down WMU 316 after 4 wolves were harvested.

& Theberge, 1996; Hebblewhite & Whittington, 2020). For example, wolves radiocollared inside Banff National Park that left park boundaries had much lower survival rates (0.44) than wolves inside the park (0.84) (Hebblewhite & Whittington, 2020).

Harvest of large carnivores such as wolves is largely thought to be compensatory with other forms of mortality (Arnold, 2021; Errington, 1946). Thus populations of wolves are considered resilient to harvest (Fuller et al., 2003). Conversely, mountain lion (*Puma concolor*) harvest had an additive effect on mortality as well as negative effect on population growth (Robinson et al., 2014). This suggests that the assumptions of harvest mortality being compensatory for wolves does not hold true for other carnivore species and study areas, and thus should be closely examined in other studies. Several studies show that wolves can sustain harvest rates anywhere from 22% (Fuller et al., 2003) to 48% (Gude et al., 2012) before population growth rate declines with possible impacts on natural mortality. The wide variation in these harvest thresholds can depend on differing levels of immigration (Adams et al., 2008) and recruitment (Gude et al., 2012). Thus, what level of human-caused mortality is sustainable or does not cause a population decline, especially in different phases of wolf colonization, is uncertain. Immigration is often thought to offset losses (Adams et al., 2008), but Bassing et al. (2020) found immigration did not compensate for harvest mortality in two wolf populations in Idaho, USA and Alberta, Canada. Understanding harvest effects is especially important to monitor in recently recovered wolf populations such as YNP and the broader GYE, where state reinstatement of harvest quickly followed ESA delisting. This is particularly important when the wolves in question lived primarily inside a national park where the National Park Service (NPS) policy is to preserve natural systems (e.g. Smith et al., 2016).

Despite the 12 years of state harvest of wolves surrounding YNP, effects on Yellowstone wolf survival or demography have not yet been investigated. For example, Cubaynes et al. (2014) showed wolf survival from 1995 to 2010 in YNP was high at 80%, yet that study only included one hunting season. In addition to debates about direct impacts of harvest on wolf survival, there is also growing evidence of indirect effects of harvest on wolves such as decreased probability of reproduction, disrupted social structure and decreased pack persistence (Ausband et al., 2015, 2017; Benson et al., 2014; Borg et al., 2015; Brainerd et al., 2008; Cassidy et al., 2023; Rutledge et al., 2010, 2012). A recent study showed that harvests of transboundary wolves from five U.S. National Parks (including YNP) had strong negative effects on wolf pack persistence and reproduction. These effects could potentially lead to ecosystem consequences arising from altered predator–prey processes due to differences in wolf social behaviour (Cassidy et al., 2023). Thus, understanding the effects of harvest on transboundary wolves living primarily in YNP is increasingly important for the management of both ecosystem processes and the NPS goal of ecosystem preservation.

The compensatory or additive nature of harvest mortality plays a crucial role in determining harvest's impact on population viability (Boyce et al., 1999). If harvest mortality is compensatory, non-harvest mortality is reduced as harvest mortality increases, with overall survival remaining relatively constant (Sandercock et al., 2011). In this case, compensatory harvest mortalities may have minimal impact on the population size and persistence. In contrast, if the harvest mortality is additive and non-harvest mortality does not decrease as harvest mortality increases, then overall survival will decrease, and harvest mortality may cause a population decline and threaten population viability (Sandercock et al., 2011). In a pseudo-experimental test of the

compensatory mortality hypothesis in mountain lions, mortality was almost completely additive (Robinson et al., 2014), raising questions if this pattern extends to other large carnivores such as wolves. Additive mortality combined with insufficient adult female survival, may have indicated a declining mountain lion population (Robinson et al., 2014).

Density-dependent processes also affect wolf survival and the degree to which harvest of transboundary wolves was additive (see Cubaynes et al., 2014). Before legal harvest occurred in the Northern Rocky Mountains of the USA, wolves experienced partially compensatory anthropogenic mortality (Murray et al., 2010). Anthropogenic mortality included vehicle collisions, illegal poaching, and control actions, which were lethal removals due to conflict with humans or livestock outside protected areas. At high wolf densities, other studies determined anthropogenic mortality of wolves as partially compensatory (Boertje et al., 1996; Sparkman et al., 2011; Stenglein et al., 2018). Most wolf studies cannot fully examine compensatory and additive mortality due to their short study duration, lack of variability in harvest rates or incompleteness of mortality data. Additionally, few studies have focused on how harvest affects transboundary populations surrounding a protected core. With a high proportion of the YNP wolf population radiocollared since 1995, and variable harvest rates over 12 years, this transboundary study system provided an ideal and unique opportunity to test the compensatory mortality hypothesis in a globally significant large carnivore population.

Our goal was to test how changes to harvest levels surrounding YNP affected the survival of wolves primarily living in YNP, while accounting for other factors known to influence wolf survival (Cubaynes et al., 2014; Fuller et al., 2003; Hebblewhite & Whittington, 2020; Schweizer et al., 2018; Smith et al., 2010). We also estimated cause-specific mortality and tested if harvest mortality was compensatory or additive by comparing changes in annual harvest mortality, natural mortality and survival rates. We hypothesized based on the previous studies we note above that harvest mortality would be compensatory and that as harvest mortality increased, natural mortality would decrease, leading to similar net annual survival rates between years (Boertje et al., 1996; Sparkman et al., 2011; Stenglein et al., 2018). Alternatively, net annual survival could be different between years if harvest is additive and harvest mortality varies between years, therefore, net annual survival would also vary (Sandercock et al., 2011). Our results have implications for improving the development of transboundary management strategies for large carnivores around the globe.

## 2 | MATERIALS AND METHODS

### 2.1 | Study area

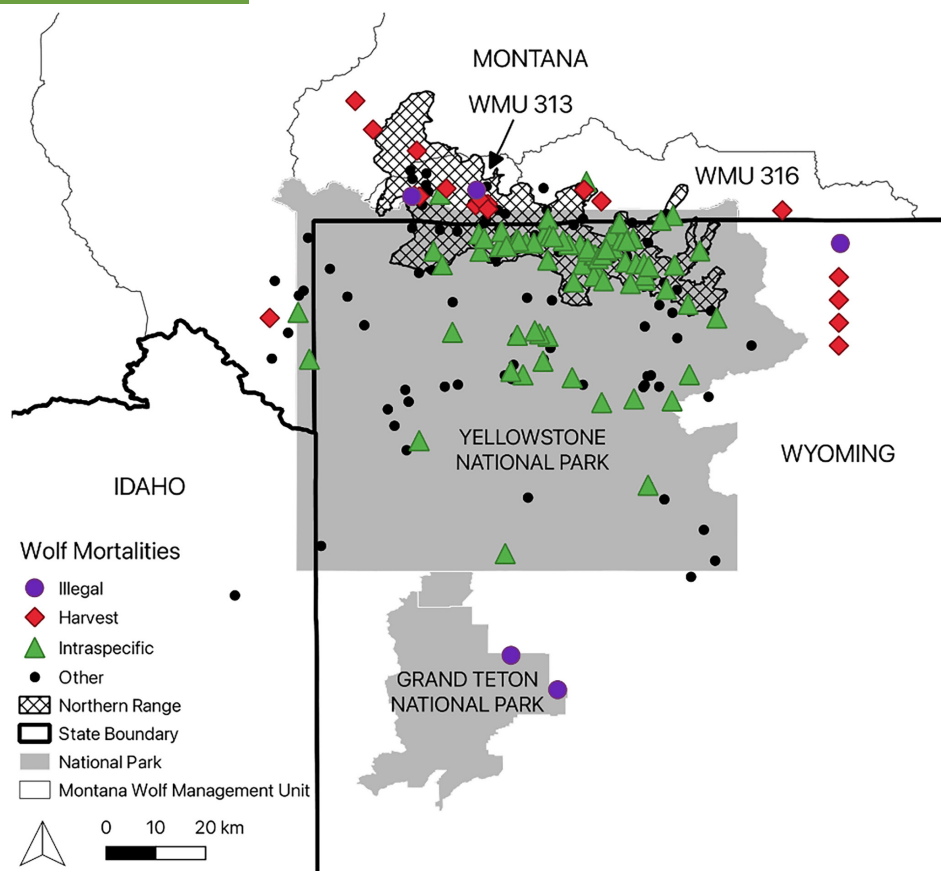
YNP is an 8991 km<sup>2</sup> national park in Wyoming, Montana and Idaho, USA. The surrounding area of the GYE is a patchwork of federal, state, tribal and private lands with differing land use and hunting regulations. Wolves in this study area are descendants of wolves

reintroduced to YNP from Canada and northwest Montana in 1995–1997 (vonHoldt et al., 2008). Wolf abundance in YNP initially increased to a peak of 174 near 2004, declined, then stabilized from 2009 to 2022 at an average of 98.4 wolves. See Smith et al. (2020) for more details on the study system.

Wolf hunting and trapping occurred most years since 2009 in the three states surrounding YNP (Montana, Wyoming and Idaho), but resource exploitation, including hunting and trapping of wildlife, is prohibited in YNP. Hunting outside YNP has occurred since wolves were delisted as an endangered species from the ESA in 2009, although quotas and wolf management units (WMU's) varied between years and states (Table 1). Here, harvest includes archery hunting, rifle hunting and trapping. While wolf packs primarily living in YNP may cross any part of the park boundary, the northern border of YNP shared with Montana is particularly important for wolf vulnerability to anthropogenic mortality (Figure 1). This area, known as the northern range, includes the associated road and trail networks surrounding the towns of Gardiner and Jardine, Montana, which provides human access to the area during the hunting season. The northern range is primary winter range for migratory ungulates, particularly the northern Yellowstone elk herd, and has the highest densities of wolves in YNP (Smith et al., 2020). Wolves primarily living in YNP spend 96% of their time inside YNP's boundaries, and 4% outside the boundary, with most of the transboundary movement across the northern boundary (Smith et al., 2020). We defined three harvest levels for wolves in YNP based on Montana's harvest seasons as no harvest, harvest with quotas and unlimited harvest (harvest with no quotas, Table 1). The state harvest regimes of both Idaho and Wyoming were reasonably consistent and represent a low proportion of annual wolf harvest of wolves living primarily in YNP (Table 1; Figure 1).

### 2.2 | Wolf capture and monitoring

Between 10 and 20 wolves were captured every winter from 1995 to 2022 via aerial darting or netgunning and fitted with radiocollars with Very High Frequency (VHF) or, starting in 2000, with Global Positioning System (GPS) radiocollars (Smith et al., 2020). All capture and handling protocols were conducted in accordance with the NPS (IACUC permit IMR\_YELL\_Smith\_wolves\_2012) and University of Montana protocols (University of Montana IACUC AUP MH046-21). On average, 30% of the wolves in YNP were radiocollared each year. All radiocollars contained mortality sensors, and mortality events were investigated as quickly as possible to determine cause of death (median to cause of death determination = 2 days). Cause of death was determined by field or lab necropsy. We monitored radiocollared wolves with aerial VHF telemetry every 7–10 days. More wolves were radiocollared in the prey-rich northern range where overall wolf density is higher (20–99 wolves per 1000 km<sup>2</sup> vs. 2–11 wolves per 1000 km<sup>2</sup> in the remainder of YNP; Cubaynes et al., 2014; Smith et al., 2020).



**FIGURE 1** Yellowstone National Park, Montana wolf management units (WMU's), and all mortality locations of grey wolves (*Canis lupus*) collected from 1995 to 2022 in and around Yellowstone National Park, USA. Other causes of wolf mortality include, but are not limited to, interspecific conflicts, unknown natural mortality and vehicle strikes. Note that exact wolf harvest locations outside Yellowstone National Park in Wyoming are not known.

## 2.3 | Survival analyses

We used Kaplan–Meier, Cox-proportional hazards models and cumulative incidence functions (CIF; Heisey & Patterson, 2006; Hosmer et al., 2008; Kaplan & Meier, 1958) to estimate wolf survival rates, mortality factors and cause-specific mortality rates in YNP. We considered only known mortalities of wolves classified as residents of YNP. To determine residency, we identified wolves within a pack that spent more than 50% of their time in YNP. We based this determination on location data from radiocollars each year. We included wolves in our study that were captured and fitted with radiocollars as part of the reintroduction program initiated in 1995 until February 28, 2022. We defined the start of the biological year as September 1, with a recurring biological year beginning September 1 and ending August 31 (Fieberg & DelGiudice, 2009). We chose this biological year to begin with the hunting season and when wolves are leaving homesites with that year's offspring to measure the effects from the hunting season in the fall on survival over the rest of the biological year. We used staggered entry to allow wolves to enter the model following capture. We right-censored individuals in cases of collar failure, dispersal out of the study area or disappearance (DeCesare et al., 2014). We only included wolf mortalities within 60 days of the

last known location to minimize effects of bias on survival estimates because fates of radiocollared wolves were not always known with certainty in our study (DeCesare et al., 2015).

We used non-parametric Kaplan–Meier models to estimate annual survival rates of wolves (Kaplan & Meier, 1958) at three different harvest levels (Table 1). We then used semi-parametric time-to-event Cox-proportional hazard models (Hosmer et al., 2008) in the 'survival' package (Therneau, 2021) in R Statistical Software (v4.1.1; R Core Team, 2021) to test for factors affecting wolf mortality (Cox & Oakes, 1984; Hosmer et al., 2008). Cox-proportional hazards models (Cox models hereafter) estimate the instantaneous hazard rate  $h(t)$  as a function of a non-parametric baseline hazard function ( $h_0$ ) with covariate ( $X_i$ ) effects on the hazard specified by proportional beta ( $b$ ) coefficients ( $e^{(\beta_1 X_1 + \epsilon)}$ ) (DeCesare et al., 2014; Smith et al., 2010) following:

$$h(t|bs) = h_{0t} \times e^{(\beta_1 X_1 + BnXn + \epsilon)}. \quad (1)$$

Survival ( $\Phi$ ) over some time period ( $\Delta t$ ) and mortality hazard in a Cox model are related by taking the inverse of the total mortality rate ( $\Sigma h(t)$ ) over time  $t$  following:

$$\Phi_{\Delta t} = 1 - \Sigma h(t|bs). \quad (2)$$



We accounted for non-independence between individual wolves by using robust standard errors in the default function of `coxph()` in the 'survival' package in R (Therneau, 2021). And finally, we also tested for violation of the proportionality assumption using the `cox.zph()` test in the same package (Therneau, 2021).

## 2.4 | Survival covariates

We considered a suite of covariates as mortality risk factors in Cox models. We classified harvest levels into three categories (Table 1) and predicted that wolf survival would be highest during periods with no harvest and lowest during periods of unlimited harvest with no quotas. We also tested for the instantaneous effects of a wolf being outside YNP where at each location a wolf was assigned to either inside YNP or outside YNP, and thus exposed to a higher risk of anthropogenic mortality than wolves inside YNP (Barber-Meyer et al., 2021; Forbes & Theberge, 1996; Hebblewhite & Whittington, 2020). We considered differences in seasons (winter September 1–March 31, summer April 1–August 31) to capture differences in when seasonal harvest outside YNP boundaries occurs (i.e. in winter) and during wolf pup-rearing seasons, by assigning each wolf location to one of those seasons. We also considered annual predicted elk abundance from a discrete time Gompertz state-space model (Tallian et al., 2017) and a measure of winter wolf abundance from annual wolf surveys conducted by NPS (Cassidy et al., 2022). Higher elk abundance has been shown to increase wolf abundance (Fuller et al., 2003). However, higher wolf abundance has been shown to increase intraspecific mortality (Cubaynes et al., 2014).

Finally, we included factors known previously to affect wolf survival in YNP and other populations including fixed individual-level covariates of sex and coat colour, as well as a time-varying category of age class in our analyses (Cubaynes et al., 2014, 2022; Schweizer et al., 2018; Smith et al., 2010). We assessed sex, coat colour and age during capture and radiocollaring operations. We assigned sex and coat colour to be fixed throughout a wolf's life and changed age class with time. Age class was separated into three classes: juvenile (<2 years old), adult (3–5 years old) and old adult (6 years and older). In other studies, sex had negligible impacts on wolf survival (Fuller et al., 2003); however, coat colour is a significant driver of wolf survival (Cubaynes et al., 2022). Black heterozygote wolves in YNP have higher survival compared with grey wolves in individuals infected with canine distemper virus (Cubaynes et al., 2022).

## 2.5 | Model selection

We compared competing Cox models of factors affecting wolf mortality hazard using Akaike Information Criterion corrected for small sample size (AICc; Akaike, 1973). We adopted a hierarchical, manual

forward stepwise model building approach (Hosmer et al., 2008) to identify the top model(s). To begin our model building approach, we first fit univariate models to evaluate the significance of potential covariates using AICc and model diagnostics. We then combined all marginally significant covariates (at  $p=0.10$ ) to a multiple covariate Cox model and used forward model selection to select the top model(s) whilst screening against multicollinearity using  $|r|<0.5$ . We also considered important biological interactions such as harvest level  $\times$  season and harvest level  $\times$  being in or out of park to account for differences in survival in the winter season during harvest and the fact that wolves could only be harvested when physically outside of YNP (see Hebblewhite & Whittington, 2020). Finally, to confirm our forward model selection approach we also conducted best subsets selection using the `MuMIn::dredge` function in package 'MuMIn' (Bartoń, 2022).

## 2.6 | Testing additive and compensatory mortality hypotheses

Mortality is additive if survival declines as mortality from a cause increases or, conversely, if there is no relationship between two mortality types (i.e. mortality from harvest vs. natural causes, Arnold, 2021; Errington, 1946). Mortality is compensatory if survival remains relatively constant while mortality from one type leads to a reduction in another type of mortality (Sandercock et al., 2011). We tested whether harvest mortality was additive or compensatory by estimating cause-specific mortality rates (e.g. Arnold, 2021). We did so using the same time-to-event framework as for mortality hazard with CIFs (Heisey & Patterson, 2006) using the R package 'survival' (Therneau, 2021). CIFs estimate cause-specific mortality rates while accounting for competing risks of sources of mortality (Heisey & Patterson, 2006). We used linear regression models using R Statistical Software (v4.1.1; R Core Team, 2021) to test predictions of compensatory or additive mortality by examining the relationships between annual survival rate, natural mortality and harvest mortality.

We tested whether harvest mortality was additive or compensatory based on the slope of the relationship between survival and mortality source  $i$  (Arnold, 2021; Burnham et al., 1984). We used the 'corrected slope' method by dividing the model slope by the intercept (i.e. baseline survival when mortality type  $i=0$ ), to ensure the slope term is relative to the absolute magnitude of mortality (Burnham et al., 1984). A corrected slope of negative one indicates fully additive mortality, while a corrected slope of zero indicates fully compensatory mortality. Intermediate slope values indicate partial compensation (Arnold, 2021; Murray et al., 2010). When testing for additive or compensatory relationships between two different mortality sources, the same logic applies, but mortality is said to be fully compensatory if the slope of the regression between mortality type 1 and 2 is negative one, and additive if there is a slope of zero (Burnham et al., 1984).

### 3 | RESULTS

#### 3.1 | Survival analyses

We monitored 457 VHF and GPS radiocollared wolves captured 668 times from 1995 to 2022. Individual wolves were captured an average of 1.5 times each (range 1–6) and were monitored a median of once every 2 days via VHF and daily via GPS. We monitored these wolves for a total of 1445 wolf-years. We censored 11 mortalities that occurred >60 days after the last known location to minimize effects of bias on survival estimates since fates of radiocollared wolves are not always certain (DeCesare et al., 2015). This left 177 mortalities of wolves living primarily in YNP with working radiocollars at the time of death.

Overall, the non-parametric annual Kaplan–Meier survival estimate was 0.83 (95% CI 0.81–0.85). Annual survival was highest for periods of no harvest at 0.86 (95% CI 0.84–0.89), followed by periods of harvest with quotas at 0.78 (95% CI 0.72–0.83), and periods of unlimited harvest had the lowest survival at 0.72 (95% CI 0.62–0.81). The log-rank tests showed sufficient evidence ( $\chi^2_{(2,n=177)} = 13.2, p=0.001$ ) for significant differences between the three harvest levels. Survival rates were higher within YNP at 0.83 (95% CI 0.80–0.86) versus outside YNP at 0.70 (95% CI 0.62–0.78; Figure S1).

#### 3.2 | Cox-proportional hazards models

The top Cox model included the main effects of harvest level, season and an interaction of harvest level and season, an interaction of harvest level and mortality location in or out in the park such that harvest mortality hazard increased with increased harvest intensity. The top model also included wolf age class, coat colour, YNP wolf count and elk count, as well as whether wolves were located in or out of the park (Table 2; Figure S2). While there was some model selection uncertainty with 3 other potential models within 0–5  $\Delta\text{AICc}$  (Table 2), the primary differences between these 4 top models were minor. Model 2 did not include the effect of wolf abundance and model 4 did not include the effect of wolf abundance but included an effect of sex that was not statistically significant ( $\beta_{\text{sex}} = -0.005, p=0.075$ ). Model 3 was the only other model within 0–5  $\Delta\text{AICc}$ , which was the global model with all covariates and interactions, with the same non-significant variables (e.g. sex, season). We chose to continue with the top ranked model since parameter estimates for model 1 or model 2 were quite close and note that the extra parameter in model 1 (wolf abundance) was significant ( $p=0.018$ ; Arnold, 2010). We also chose to include the extra parameter due to the challenge of disentangling the effect of wolf versus elk abundance in lower ranked models with only one or the other of wolf or elk abundance on survival without a more mechanistic approach

**TABLE 2** Top Cox-proportional hazards models for grey wolf (*Canis lupus*) survival in and around Yellowstone National Park (YNP) from 1995 to 2022 ( $n=177$ ) from models based on demographic, spatial and temporal variables. We provide model selection results from a hierarchical, manual stepwise model building approach for top ranked models based on Akaike's Information Criterion (AICc), including number of model parameters (K), difference in AICc from top model ( $\Delta\text{AICc}$ ), proportion of the total amount of predictive power (AICcWt), log-likelihood (LL) and sum of the AICc weights (Cum.Wt).<sup>a</sup>

Model	Model number	K	$\Delta\text{AICc}$	AICcWt	LL	Cum.Wt
age class + colour + harvest level + season + in/out park + harvest $\times$ in/out park + harvest $\times$ season + nr elk + wolf	1	13	0	0.54	–1142.77	0.54
age class + colour + harvest level + season + in/out park + harvest $\times$ in/out park + harvest $\times$ season + nr elk	2	12	1.92	0.20	–1142.74	0.74
sex + age class + colour + harvest level + season + in/out park + harvest $\times$ in/out park + harvest $\times$ season + nr elk + wolf	3	14	3.62	0.09	–1145.58	0.83
sex + age class + colour + harvest level + season + in/out park + harvest $\times$ in/out park + harvest $\times$ season + nr elk	4	13	4.30	0.06	–1145.93	0.89
age class + colour + harvest level + season + in/out park + harvest $\times$ in/out park + harvest $\times$ season	5	11	5.44	0.04	–1147.49	0.93
age class + colour + harvest level + season + in/out park + harvest $\times$ in/out park + harvest $\times$ season + wolf	6	12	5.49	0.03	–1145.52	0.96
sex + age class + colour + harvest level + season + in/out park + harvest $\times$ in/out park + harvest $\times$ season	7	12	6.20	0.02	–1145.87	0.98

<sup>a</sup>Covariates descriptions: age class = age, colour = coat colour, harvest level = no, unlimited or quota harvest, season = winter or summer, in/out park = in or out of YNP, harvest  $\times$  in/out park = in or out of YNP interaction with harvest level, harvest  $\times$  season = season interaction with harvest level, nr elk = Northern Range annual predicted elk abundance, wolf = annual wolf abundance.

(Smith & Cassidy, 2024). Thus, we proceeded using the top model, model number 1 (Table 3). Both model selection approaches, manual forward stepwise 'dredging', revealed the same top model structure.

Mortality risk was 2.6 times higher in winter (e.g. when harvest occurs) than summer (Table 3). There were effects of age (i.e. older age classes had higher risk of mortality, especially wolves  $\geq 6$  years old,  $\beta = 0.61$ ,  $p = 0.004$ ) and coat colour (grey wolves with higher risk of mortality,  $\beta = -0.32$ ,  $p = 0.040$ ) on wolf survival that were consistent with previous studies. The baseline reference category was young grey wolves in summer inside YNP. During unlimited harvest years, risk of mortality was 16.1 times higher outside YNP compared to inside YNP, and when there were harvest quotas, risk of mortality was 5.5 times higher outside YNP compared to inside YNP (Table 3; Figure 2). The interaction between harvest type and season (Table 3) indicated that mortality risk was higher in winter (when wolf hunting and trapping seasons occurred) for years with unlimited harvest. See Supporting Information for additional discussion of non-harvest related wolf mortality factors, as we focus on harvest in the discussion.

### 3.3 | Additive and compensatory mortality

Wolves from YNP died of natural ( $n = 133$ ), anthropogenic ( $n = 37$ ), and unknown causes ( $n = 7$ ). Harvest was the leading type of anthropogenic cause of death for wolves primarily living in YNP ( $n = 18$ ), with the other types of anthropogenic mortality including vehicles ( $n = 9$ ), illegal poaching ( $n = 8$ ) and control action ( $n = 2$ ). Mortality due to harvest varied greatly with annual state-defined harvest level regulations. Wolves died of harvest at the highest rate during periods of unlimited harvest ( $n = 11$ , CIF mortality rate = 0.120, 95% CI 0.064–0.196; Table S1) compared to periods of harvest with quotas ( $n = 7$ , rate = 0.018, 95% CI 0.010–0.030; Figure 3; Figure S3). Instances of illegal poaching varied with harvest level. Most illegal poaching of wolves took place during periods of harvest with quotas (rate = 0.020, 95% CI 0.005–0.052,  $n = 5$ ) and unlimited harvest (rate = 0.011, 95% CI 0.001–0.054,  $n = 1$ ), and least in periods without harvest (rate = 0.003, 95% CI 0.0006–0.010,  $n = 2$ ; Figure 3). Intraspecific mortality was the leading natural cause of death for wolves living in YNP, and intraspecific mortality rates did not statistically differ between the three levels of harvest (Figure 3). Wolves died at the highest rate from intraspecific mortality during periods of harvest with quotas (rate = 0.093, 95% CI 0.060–0.136,  $n = 23$ ), followed by during periods of unlimited harvest (rate = 0.068, 95% CI 0.028–0.133,  $n = 6$ ) and no harvest (rate = 0.061, 95% CI 0.045–0.081,  $n = 45$ ; Figure 3). Intraspecific mortality did not decrease with increased harvest (years with quotas or unlimited harvest) as would be expected with compensatory mortality.

Correcting for bias following Burnham et al., 1984, we observed a significant relationship between the annual survival rate and annual harvest mortality rate (Figure 4a;  $\beta_{\text{uncorrected}} = -0.78$ ,  $\beta_{\text{corrected}} = -0.93$ ,  $p = 0.028$ ). The estimated slope of  $-0.93$  closely approached a slope of negative one, indicating that harvest mortality was an almost completely additive mortality source. Natural (disease, malnutrition,

interspecific, intraspecific and other natural causes) mortality rate did not exhibit a significant relationship with the harvest mortality rate (Figure 4b;  $\beta = 0.38$ ,  $p = 0.272$ ). Additionally, natural mortality rate and anthropogenic (harvest, vehicle collision, control action and poaching) mortality rate ( $\beta = 0.21$ ,  $p = 0.431$ ; Supporting Information) did not exhibit a significant relationship. These analogous findings indicate higher levels of harvest mortality were associated with reduced annual survival rates, an additive relationship (Figure S4a,b).

## 4 | DISCUSSION

Contrary to our hypothesis that harvest mortality would be partially compensatory, harvest mortality was almost entirely additive. Our results showed clear differences in overall survival for wolves primarily living in YNP between different levels of harvest outside of YNP borders. Survival was highest in years with no harvest (0.86), followed by years with quotas (0.78) and lowest in years with unlimited harvest (0.72). Our results found the overall YNP wolf survival of 0.83 (95% CI 0.81–0.85) was higher or similar than other harvested wolf populations in North America, which ranged from 0.32 to 0.84 which is highly dependent on the amount of anthropogenic mortality the population was subject to (Fuller et al., 2003). Prior to reinstatement of state harvest in the greater Montana, Idaho and Wyoming region, Smith et al. (2010) found that wolf survival was 0.75 (95% CI 0.728–0.772). Previous studies in YNP similarly reported an annual survival rate of 0.80 during the period largely without harvest (Cubaynes et al., 2014). These previous studies align with our overall findings, although in our analysis survival varied by 14% between harvest levels. Similar to our study, Hebblewhite and Whittington (2020) found that wolves inside Banff National Park experienced much lower mortality rates than outside protected areas boundaries, wolves outside Banff National Park were 6.7 times more likely to die (odds ratio 95% BCI = 2.2–21.4) than wolves in the protected area (year-end survival rates and 95% BCI, Out of Park = 0.44, 0.24–0.65; In Park = 0.84, 0.73–0.91). We next review potential mechanisms generating the additive mortality we observed in our study area, and how are results compare with previous studies. While the levels of additive harvest we observed are likely not affecting overall wolf population size, they are significant in the context of transboundary management of controversial threatened species, such as wolves.

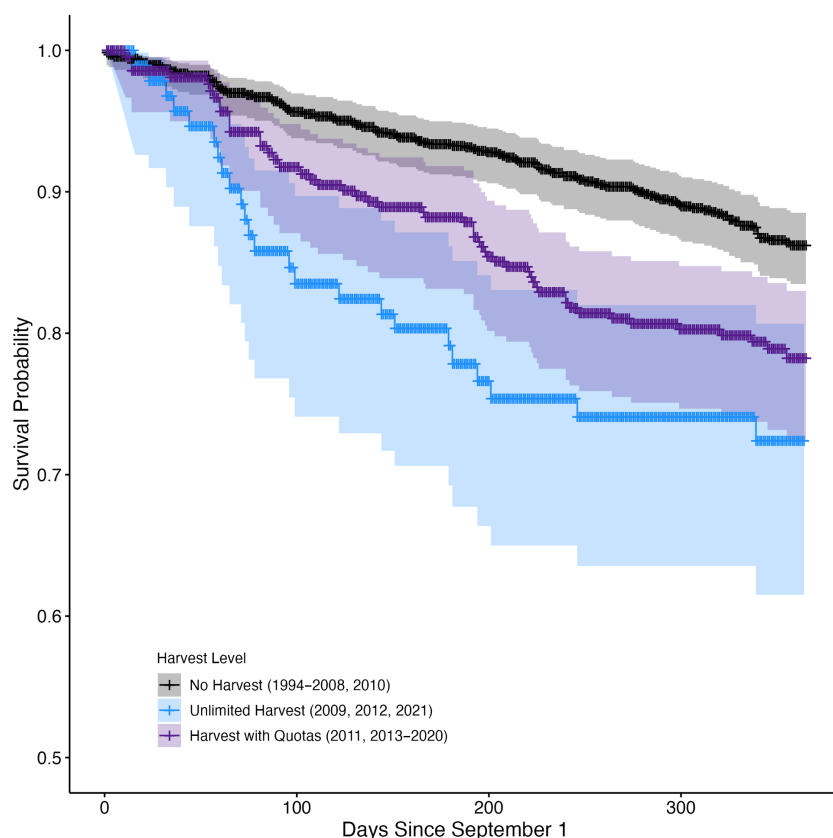
Theory predicts compensation of anthropogenic mortality under density-dependent conditions (Lebreton, 2005), where increased levels of anthropogenic mortality are counteracted by reductions in natural mortality (Benson et al., 2023). Under this hypothesis, there is an assumption that there is a certain number of individuals that will die without changing the overall survival of the population (Benson et al., 2023). In northern YNP, at one of the highest known wolf densities in North America (20–99 wolves per 1000 km<sup>2</sup>), we found harvest mortality to be mostly additive. Our study contributes to the lack of consensus on whether anthropogenic mortality is additive or compensatory for wolves. Several studies showed trends which



**TABLE 3** Mortality covariate estimates ( $\beta$ ) from the top Cox-proportional hazards model for grey wolf (*Canis lupus*) survival in and around Yellowstone National Park (YNP) from 1995 to 2022 ( $n=177$ ) from models based on demographic, spatial and temporal variables ( $\beta$  coefficients, standard deviation, hazard ratios, 95% confidence intervals and  $p$ -value with significant covariates bolded). The baseline hazard described a grey, <2-year-old wolf inside YNP boundaries during the summer of a year without harvest occurring outside park boundaries. Hazard ratio >1.0 signify increased mortality risk.<sup>a</sup>

Covariate	$\beta$	SE (coef)	Hazard ratio (HR)	Lower 95% CI (HR)	Upper 95% CI (HR)	$p$
Age class (2–5 years)	0.02	0.190	1.02	0.70	1.48	0.927
<b>Age class (&gt;6 years)</b>	<b>0.61</b>	0.209	<b>1.83</b>	<b>1.22</b>	<b>2.76</b>	<b>0.004</b>
<b>Colour (black)</b>	<b>−0.32</b>	0.154	<b>0.72</b>	<b>0.54</b>	<b>0.99</b>	<b>0.040</b>
Harvest (unlimited)	0.16	0.379	1.17	0.55	2.47	0.674
Harvest (quota)	−0.19	0.322	0.82	0.44	1.55	0.548
Season (winter)	0.96	0.747	2.62	0.61	11.32	0.197
Out of park	−0.16	0.343	0.85	0.43	1.66	0.632
<b>Harvest × in/out park (unlimited)</b>	<b>2.78</b>	0.540	<b>16.09</b>	<b>5.58</b>	<b>46.39</b>	<b>&lt;0.001</b>
<b>Harvest × in/out park (quota)</b>	<b>1.71</b>	0.459	<b>5.51</b>	<b>2.24</b>	<b>13.54</b>	<b>&lt;0.001</b>
<b>Harvest × season (unlimited)</b>	<b>−1.58</b>	0.550	<b>0.20</b>	<b>0.07</b>	<b>13.54</b>	<b>0.004</b>
Harvest × season (quota)	10.12	0.345	0.88	0.45	1.74	0.722
<b>Elk count</b>	<b>−0.08</b>	0.033	<b>0.92</b>	<b>0.86</b>	<b>0.98</b>	<b>0.012</b>
<b>Wolf count</b>	<b>−0.01</b>	0.003	<b>0.99</b>	<b>0.99</b>	<b>0.99</b>	<b>0.018</b>

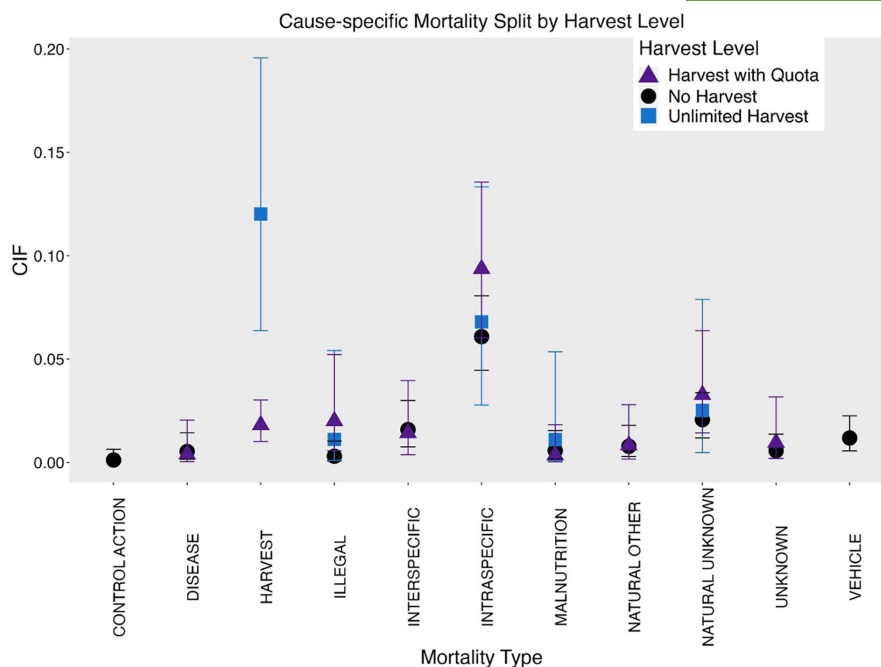
<sup>a</sup>Covariates descriptions: age class=age, colour=coat colour, harvest level=no, unlimited or quota harvest, season=winter or summer, in/out park=in or out of YNP, harvest × in/out park=in or out of YNP interacting with harvest level, harvest × season=season interacting with harvest level, nr elk=Northern Range annual predicted elk abundance, wolf=annual wolf abundance.



**FIGURE 2** Cumulative probability of annual (September 1–August 31) survival of grey wolf (*Canis lupus*) survival for wolves in and around Yellowstone National Park, USA from 1995 to 2022.

categorized anthropogenic mortality as at least partially compensatory at high wolf densities in mostly saturated, and unprotected and harvested populations (Adams et al., 2008; Murray et al., 2010). In

contrast, in recovering or low-density wolf populations, other studies reported anthropogenic mortality as additive (Adams et al., 2008; Murray et al., 2010; Sparkman et al., 2011; Stenglein et al., 2018). For



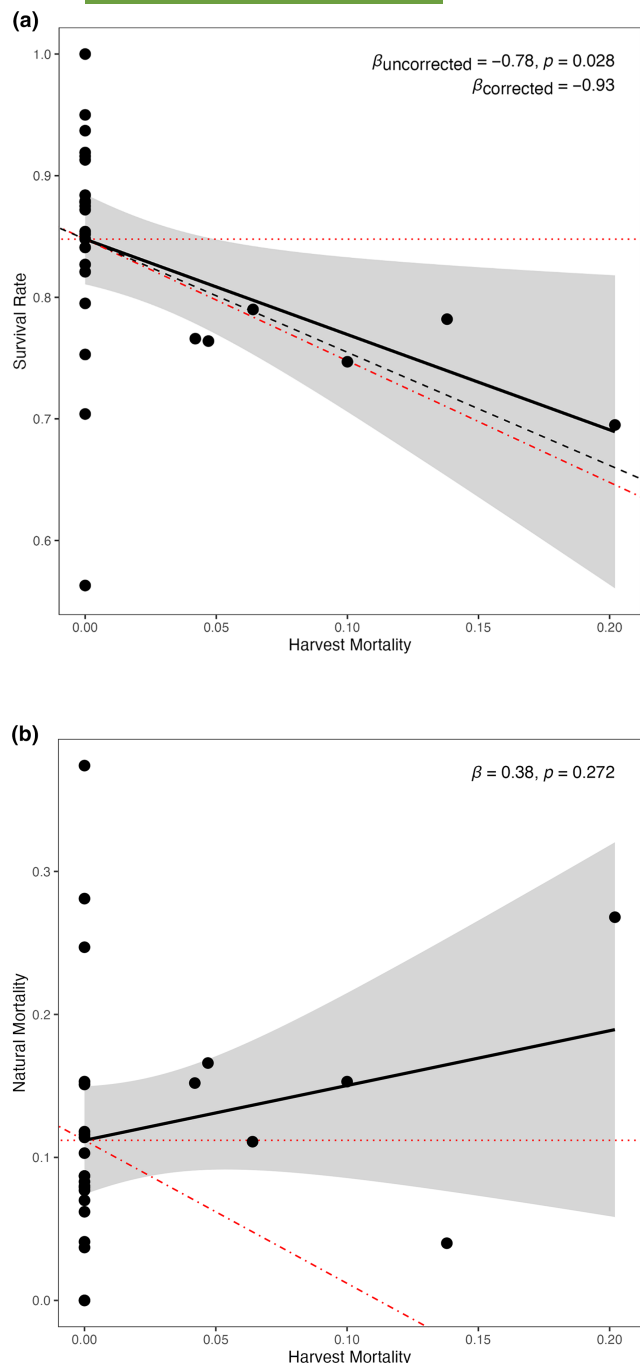
**FIGURE 3** Cumulative incidence function (CIF) estimates for different causes of mortality for grey wolves (*Canis lupus*) in and around Yellowstone National Park from 1995 to 2022 ( $n = 177$ ) split by different levels of harvest intensity.

example, Sparkman et al. (2011) detected additive anthropogenic mortality in the protected red wolf population (*C. rufus*). Similar results have been seen in the recovering Wisconsin wolf population, but as the population size and density increased, anthropogenic mortality became increasingly compensatory (Stenglein et al., 2018). In the entire Northern Rocky Mountains (including YNP, but mostly unprotected wolves in the states) from 1995 to 2004, Murray et al. (2010) found that anthropogenic mortality was partially compensatory but increasingly additive at higher density. In this former study, natural processes such as natural mortality, were disrupted by high rates of anthropogenic mortality (Murray et al., 2010). These results demonstrate the close link between density-dependence and increasingly compensatory mortality as density increases. In an unprotected population in northern Alaska, Adams et al. (2008) found evidence for compensation from immigration into the study area, not a reduction in natural mortality, if anthropogenic mortality was below 29%. These previous studies highlight the unique finding in our study for support for additive mortality in a high density, but largely protected wolf population in contrast where previous studies only found additive mortality at lower densities.

Our study area differs from previous studies in two primary ways that may provide plausible mechanisms for the additive mortality we report. First, unlike many other previously studied wolf populations, the wolves of YNP are protected within park boundaries. YNP wolves spent an average of 96% of their time in the park, leaving only 4% of their time susceptible to legal harvest outside YNP boundaries (Smith et al., 2020). Consequently, this may create local source-sink dynamics where wolves inhabiting YNP at high densities move from the protected park to outside the park where they are vulnerable to harvest (Benson et al., 2024). When wolves left YNP, the risk of

mortality greatly increased by 5.5 times when quotas were in place and 16.1 times in years with unlimited harvest. However, due to the small scale of such transboundary movements, studies at the larger state- and region-level scale (Murray et al., 2010; Smith et al., 2010) may not detect the presence of similar small scale, source-sink dynamics driving additive mortality within protected populations.

Secondly, protected wolf populations like YNP likely have larger packs with more complex social structures and traits (Horne et al., 2019; Smith et al., 2020) than highly exploited wolf populations (Hayes & Harestad, 2000). Protected wolf populations can attain larger group sizes, older ages and other social traits such as multiple breeding females per pack. These factors may facilitate the relatively stable intraspecific mortality rates of wolves in YNP, regardless of harvest, unlike in studies in harvested populations. Within YNP, the social dynamics of wolves were characterized by both high population densities and the formation of large, complex packs, which consisted of anywhere from 2 to 37 members, with an average of approximately 12 members (Cassidy et al., 2022). In contrast, wolf packs in Idaho averaged only 5.5 wolves per pack (Horne et al., 2019). Furthermore, social dynamics can be affected as more wolves reach advanced ages (Smith et al., 2020). Larger packs composed of older individuals ( $\geq 6$  years old) were more successful in interpack conflicts (Cassidy et al., 2015). It is likely that many highly exploited wolf populations do not have large packs or many individuals that reach the advanced age of 6 years old (Hayes & Harestad, 2000). In YNP where wolf packs are larger and more complex than in highly exploited populations, intraspecific mortality remains the primary cause of death among wolves, and there has never been a documented instance of a wolf killed in YNP by less than four other wolves (Cassidy, K., unpublished). These observations suggest



**FIGURE 4** Relationships between (a) harvest mortality and annual wolf survival with uncorrected slope as the solid line and the corrected slope as the dashed line ( $\beta_{\text{uncorrected}} = -0.78, \beta_{\text{corrected}} = -0.93, p = 0.028$ ) and (b) harvest mortality and natural mortality ( $\beta = 0.38, p = 0.272$ ). On panel (a) a slope of negative one indicates fully additive mortality (red dot-dash line) and zero indicates fully compensatory mortality (dotted line). On panel (b) a slope of zero indicates fully additive mortality, and negative one indicates fully compensatory mortality. Natural mortality includes mortality from disease, malnutrition, interspecific, intraspecific and other natural causes.

that fatal interpack conflicts necessitate involvement of multiple wolves, and therefore, may not commonly exist in exploited populations. Additionally, a pack with at least one human-caused mortality

had a 71% lower likelihood of persisting until the following year, leading to the isolated individuals being more susceptible to intra-specific conflict and mortality (Cassidy et al., 2023). Consequently, our study suggests that the wolves of YNP experienced additive effects of harvest mortality for two reasons: (1) the concentrated local spatial susceptibility to harvest and (2) the complex social structure of wolf packs in YNP leading to intraspecific mortality when packs are disrupted due to human-caused mortality.

There are important limitations to studies that quantify the effects of wolf harvest levels on population growth rates (Adams et al., 2008; Fuller et al., 2003; Gude et al., 2012; Keith, 1983). Estimates of sustainable harvest of wolves range from 22% in an analysis of multiple populations (Fuller et al., 2003) to 48% in Montana (Gude et al., 2012). The harvest rate of the YNP population (12% during unlimited harvest) is well below the reported manageable harvest level of other populations, and the wolf population was evidently stable or increasing during this period despite additive harvest (Smith et al., 2020). Introduction of harvest also corresponded to an increase in illegal harvest, suggesting social tolerance for wolves in this area did not increase with the implementation of wolf harvest (Hogberg et al., 2015). For example, illegal poaching was highest in periods of harvest with quotas and lowest in periods of no harvest, suggesting that we would have underestimated total (legal + illegal) harvest by 8% under unlimited and 53% under quota periods if wolf harvest managers only used reported wolf harvest reports (from Figure 3). Our work also likely underestimated wolf mortality due to cryptic poaching mortality, which refers to poaching mortality that remained undetected by conventional methods (Liberg et al., 2012). In Sweden, cryptic poaching mortality was estimated to be as high as 69% of total illegal mortality and 51% of total mortality (Liberg et al., 2012). Cryptic poaching rates were likely much lower in YNP than Sweden but could have occurred in unknown or censored animals where collars were potentially destroyed. While cryptic poaching may not have significant population level effects in YNP, there may be significant effects on wolf social dynamics (e.g. see Cassidy et al., 2023).

Adams et al. (2008) highlighted immigration from outside the study area as a likely mechanism to offset harvest within a population. Genetic analyses on YNP's wolves have indicated that there have been relatively low levels of gene flow into the population. Instead, YNP acts largely as a source population of wolves that disperse into more heavily harvested adjacent areas of Montana, Wyoming and Idaho (vonHoldt et al., 2008, 2023). Lower survival of individuals living in YNP may mean there are fewer wolves dispersing to the surrounding states, especially in periods of unlimited wolf harvest surrounding YNP. Understanding such regional source-sink dynamics may be important to understand the role of immigration to state-level wolf harvest management.

In addition to the direct effects of harvest mortality, indirect effects of anthropogenic mortality are detrimental to pack persistence, probability of reproduction and natural social structure in packs (Ausband et al., 2015, 2017; Borg et al., 2015; Brainerd et al., 2008; Cassidy et al., 2023; Rutledge et al., 2010). Potential

mechanisms of indirect effects include disrupted social structure, breeding dynamics and altered genetic relatedness due to losing members of a wolf pack to anthropogenic mortality (Ausband & Waits, 2020; Brainerd et al., 2008; Cassidy et al., 2023; Jędrzejewski et al., 2005). In five U.S. National Parks, including YNP, packs that experienced an anthropogenic loss persisted to the next year only 76.3% of the time while packs experiencing no anthropogenic mortality persisted 91.6% of the time (Cassidy et al., 2023). Breeder loss specifically decreased the chance of pack reproduction the following year, with only 46.8% of packs reproducing following the loss of a breeder (Brainerd et al., 2008). In Denali National Park, 77% of wolf pack dissolutions were preceded by breeder loss due to harvest (Borg et al., 2015). Additionally, high levels of harvest can disrupt social dynamics, breeding structure and genetic relatedness within and between wolf packs with implications for the maintenance of genetic diversity (Ausband & Waits, 2020; Jędrzejewski et al., 2005). In Idaho (Ausband & Waits, 2020) and the Polish-Belarusian border (Jędrzejewski et al., 2005), heavily exploited wolf populations created additional breeding opportunities, increased genetic relatedness between groups but decreased genetic relatedness within groups. Contrarily, levels of harvest that isolate a population can significantly reduce gene flow and effective population sizes, negatively impacting genetic viability in wolf populations (vonHoldt et al., 2024). Thus, the additive mortality we report here adds to the increasing evidence that harvest of transboundary wolves in YNP may affect social, genetic and ecological dynamics of wolf populations inside YNP. This has implications for not only the resiliency of YNP's wolf population, but for its role as a source population for successful dispersal and genetic connectivity outside of YNP (vonHoldt et al., 2023).

This study emphasizes the difficulties of reconciling differing policy objectives for wildlife hunting in transboundary management settings. Differences between the NPS policy of preservation and state agency policies of conservation, as well as consideration of other state industries and economies highlight the challenge of transboundary wolf population management. A 2021 study estimated that the presence of wolves in YNP brought an extra \$82.7 million dollars to the communities in the GYE every year (RRC Associates and University of Montana Institute for Tourism and Recreation Research, 2021). These economic benefits highlight the role the population of wolves in YNP plays in the local economy, underscoring the importance of conservation of wolves in YNP.

Our results are relevant to recent policy compromise that supports transboundary management. As a result of the discussions between state and federal agencies, and input from scientific research and public comment, in 2022 the Montana Fish, Wildlife and Parks Commission reinstated restricted quotas of six wolves per year for the combined wolf management unit WMU 313/316 adjacent to YNP for the 2022–2023 Montana wolf hunting season. Future wolf hunting season regulations that limit and disperse harvest adjacent to YNP strike a compromise among stakeholders while recognizing the value of minimizing human-caused mortality to wolves living

inside YNP (Smith et al., 2016). While there is no simple solution to transboundary management challenges, the reinstatement of quotas provides a scientifically supported compromise between state and federal objectives that could be a model for carnivore conservation worldwide.

## AUTHOR CONTRIBUTIONS

Brenna Cassidy and Mark Hebblewhite conceived the ideas and designed methodology; Brenna Cassidy, Douglas W. Smith, Kira Cassidy and Daniel Stahler collected the data; Brenna Cassidy and Mark Hebblewhite analysed the data; Brenna Cassidy and Mark Hebblewhite led the writing of the manuscript. All authors contributed critically to the drafts and gave final approval for publication.

## ACKNOWLEDGEMENTS

We would like to thank the dedicated employees and volunteers of the Yellowstone National Park Wolf Project for their countless hours of wolf monitoring. Support for the study came from the National Science Foundation (36630, DEB-06137730, DEB-1245373), Yellowstone National Park, Yellowstone Forever, V. Gates, A. and B. Graham, University of Montana Wilderness Institute Meier Graduate Research Fellowship, the University of Montana and the Living With Wolves Foundation. We would like to additionally thank pilots R. Stradley, S. Ard, M. Packila, J. Pope, T. Woydziak and R. Hawkins for safe aerial support during capturing and monitoring flights. Finally, we thank associate editor Dr. Abishek Harihar and two anonymous reviewers for their insightful feedback which greatly contributed to the refinement of this manuscript.

## CONFLICT OF INTEREST STATEMENT

The authors have no conflict of interest to declare.

## DATA AVAILABILITY STATEMENT

Data available from the Dryad Digital Repository <https://doi.org/10.5061/dryad.x3ffb7tc> (Cassidy et al., 2024).

## ORCID

Brenna Cassidy  <https://orcid.org/0000-0003-3488-7001>

Mark Hebblewhite  <https://orcid.org/0000-0001-5382-1361>

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## SUPPORTING INFORMATION

Additional supporting information can be found online in the Supporting Information section at the end of this article.

**Appendix S1.** Extended discussion on non-harvest related wolf mortality factors, complementing the primary focus on harvest-related factors in the main discussion.

**How to cite this article:** Cassidy, B., Smith, D. W., Cassidy, K., Stahler, D., & Hebblewhite, M. (2024). Harvest of transboundary grey wolves from Yellowstone National Park is largely additive. *Journal of Applied Ecology*, 61, 2180–2193. <https://doi.org/10.1111/1365-2664.14720>