Persistent Increase in Human-Caused Wolf Mortality Following the Minnesota 2012-2014 Hunting Seasons

Roman Teo Oliynyk[1,2*]

[1*]Department of Genetics, Harvard Medical School, Boston, MA, USA.

[2]Department of Computer Science, University of Auckland, Auckland, New Zealand.

Corresponding author(s). E-mail(s): roli573@aucklanduni.ac.nz;

Abstract

By the mid-twentieth century, wolves were nearly extinct in the lower 48 states, with a small number surviving in Northern Minnesota. After wolves were placed on the endangered species list, the Northern Minnesota wolf population increased and stabilized by the early 2000s. A wolf trophy hunt was introduced in 2012-2014 and halted by a court order in December 2014. The Minnesota Department of Natural Resources collected wolf radiotelemetry data for the years 2004–2019. Our statistical analysis showed that wolf mortality was close to constant from 2004 until the initiation of the hunt, and mortality doubled with the initiation of the first hunting and trapping season in 2012 and remained at an almost constantly elevated level through 2019. Notably, the average annual wolf mortality increased from 21.7% before wolf hunt seasons (10.0% by human causes and 11.7% naturally) to 43.4% (35.8% by human causes and 7.6% naturally). The fine-grained statistical trend implies that human-caused mortality increased sharply during hunting seasons, while naturally attributable mortality initially dropped. The human-caused mortality, while gradually diminishing after the hunt discontinuation, remained high, perhaps indicating a lasting shift in human attitudes and a post-hunt change in wolf pack composition and size as well as wolf behavior.

Keywords: wolf,radiotelemetry,hunt,survival,mortality,statistical trend

Introduction

By the mid-twentieth century, wolves were nearly extinct in the lower 48 states of the United States, with only 450–700 wolves remaining in northern Minnesota in the 1950s [1, 2]. After wolves were protected by the federal Endangered Species Act of 1973, the Northern MN wolf population gradually increased and stabilized in early 2000s [3]. In late December 2011, the US Fish and Wildlife Service removed wolves in the western Great Lakes region from the federal endangered species list [4]. The following year, Minnesota and other states established a wolf trophy hunting and trapping season, which was extended in 2013 and 2014 [5–8]. In December 2014, a Federal Judge placed wolves back on the endangered species list, thus halting further Minnesota hunting and trapping [9].

According to Minnesota Department of Natural Resources (MN DNR) wolf population surveys [3, 10, 11], wolf population estimates varied in years 2012–2014 from approximately 2,200 to 2,400. MN DNR *Minnesota Wolf Season Reports* [6–8] accounted for 413 wolves killed in 2012, 238 in 2013, and 264 in 2014. In this paper, for conciseness, we will tend to abbreviate "hunting and trapping season" to "hunting season" – inclusive with trapping.

MN DNR have collected radiotelemetry data recording wolf movements and mortality between the years 2004 and 2019. To our knowledge, the only study that performed survival analysis based on these data was 2022 paper by Chakrabarti et al. [12], who failed to observe evidence that wolf survival was markedly reduced during 2012–2014 hunting seasons. While our findings disagree with this conclusion, we recommend Chakrabarti et al. [12] paper for the reference on the wolf population, wolf pack sizes, territories, and the descriptions of the DNR radiotelemetry data collection methods that are relevant to our analysis.

In this research, we endeavored to analyze how wolf survival and mortality compared for two specific time ranges, before and after initiation of the first 2012 wolf hunting season. Our statistical analysis showed that wolf mortality was close to constant from 2004 until the hunt, followed by doubling of wolf mortality after initiation of the first hunting season in 2012, and mortality remained at almost constantly high level through 2019. The finer grained trend implies that human-caused mortality increased sharply during hunting seasons, while naturally attributable mortality initially dropped. The human-caused mortality, while gradually diminishing after the hunting discontinuation, persisted on higher level than before initiating of the hunting seasons.

Results

The regression analysis was applied to MN DNR wolf radiotelemetry statistics for years 2004-2019, as described in Methods (see Table A1 for wolf radiotelemetry summary by calendar year). The goal was to compare two time periods represented in the data. The first period we will call for brevity "before hunt", starting from middle of 2004, when first two wolves were radio-collared for this DNR tracking study, with larger representative number added starting 2005, and up to October 31st, 2012 — before the initiation of the first wolf hunting and trapping season. The second period, which we will call "after hunt", starts November 1st, 2012, when the hunting season started in the second week of November and trapping continued throughout January 2013. Similarly, the second- and third-year hunting seasons started in November of these years. Thus, statistical comparison years covered from November 1st up to October 31st next year; see Table A2 for wolf radiotelemetry summary with time reference offset to November 1st. The regression discontinuity analysis, described below, validates and necessitates this choice of time frames.

Table 1: Wolf survival and mortality summary.

		Yearly mortality				**Wolf deaths by cause**	
Period	**Survival**	**all**	**human**	**natural**	**R-days**	**human**	**natural**
			All wolves				
Before	0.783 (0.69-0.89)	21.7%	10.0%	11.7%	22373	6.92	8.08
After	0.566 (0.48-0.67)	43.4%	35.8%	7.6%	28233	36.30	7.70
All	0.653 (0.59-0.73)	34.7%	25.4%	9.3%	50606	43.22	15.78
			Adult				
Before	0.773 (0.67-0.89)	22.7%	11.3%	11.3%	18440	6.50	6.50
After	0.574 (0.48-0.69)	42.6%	33.0%	9.6%	22341	26.32	7.68
All	0.656 (0.58-0.74)	34.4%	24.0%	10.4%	40781	32.82	14.18
			Male				
Before	0.754 (0.61-0.93)	24.6%	14.1%	10.6%	9035	4.00	3.00
After	0.583 (0.45-0.76)	41.7%	23.8%	17.9%	10841	9.14	6.86
All	0.655 (0.55-0.78)	34.5%	19.7%	14.8%	19876	13.14	9.86
			Female				
Before	0.792 (0.66-0.95)	20.8%	8.3%	12.5%	9405	2.40	3.60
After	0.565 (0.43-0.74)	43.5%	41.0%	2.6%	11500	16.94	1.06
All	0.658 (0.56-0.78)	34.2%	27.6%	6.6%	20905	19.34	4.66
			Juvenile				
Before	0.831 (0.64-1.07)	16.9%	0.0%	16.9%	3933	0.00	2.00
After	0.538 (0.37-0.79)	46.2%	46.2%	0.0%	5892	10.00	0.00
All	0.640 (0.50-0.82)	36.0%	30.0%	6.0%	9825	10.00	2.00

Wolf hunting seasons always commenced in November of 2012–2014, therefore all statistics are offset to start each year on November 1st. Periods 'before' include 2004 to October 31, 2012, 'after' – November 1st 2012 to the end of 2019, all years calculated for the entire data time span combining before and after periods. The range in parentheses following 'Survival' is 95% confidence interval range. R-days stands for radiotelemetry days for each time interval. Fractional wolf death counts are the result of six wolf deaths that were of unknown causes, imputed proportionately to the known mortality causes for each period.

There were 150 wolves tracked with over 50 thousands radio-days in the time period of almost 16 years. This amount of data allowed for accurate summary survival statistics for the entire time period, and separately for before and after hunt periods, displayed in Table 1.

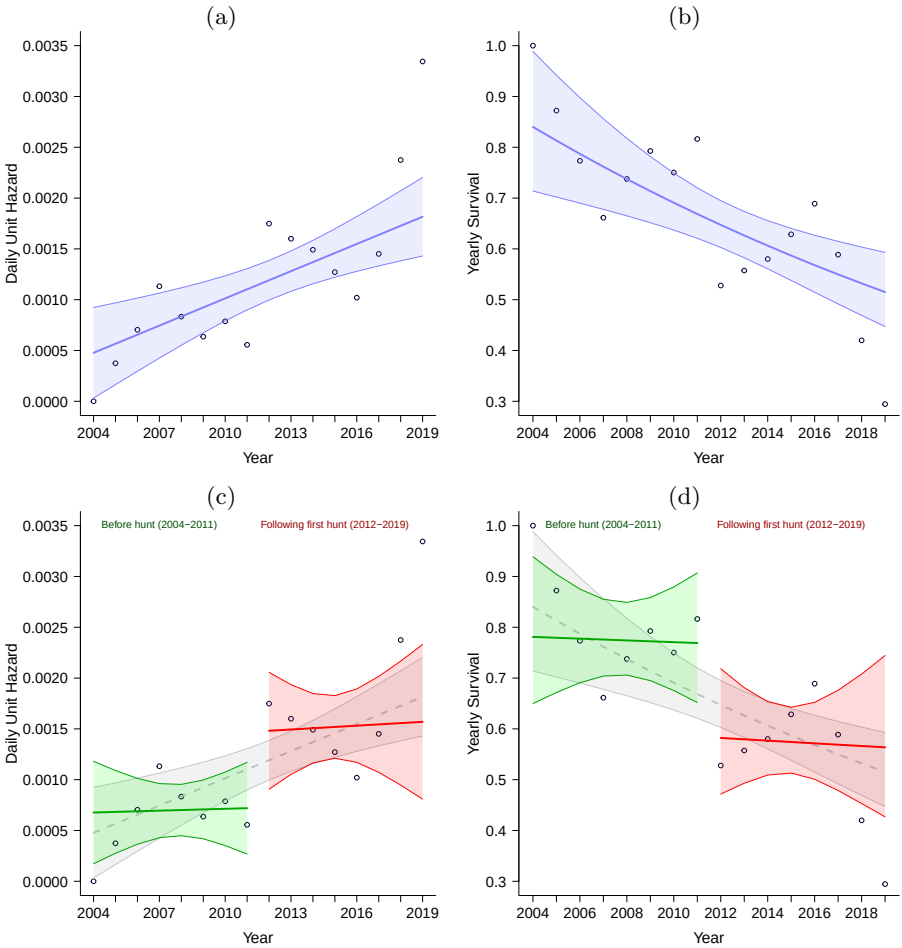

Fig. 1: **Survival statistics summary.** Wolf hunting seasons always commenced in November 2012–2014, therefore all statistics are offset to start each year on November 1st. **(a)** Linear regression of daily unit hazard across entire 2004-2019 period. Blue line – regression; blue shaded area – 95% confidence interval. **(b)** Linear regression of yearly survival across entire 2004-2019 period. Blue line – regression; blue shaded area – 95% confidence interval. **(c)** Daily unit hazard regressions, separately for before (2004–2011) and following first hunting season (2012–2019). Green line – trend before hunt, red line – trend after hunt; corresponding shaded areas – 95% confidence interval. **(d)** Yearly survival regressions, separately for before (2004–2011) and following first hunting season (2012–2019). Green line – trend before hunt, red line - trend after hunt; corresponding shaded areas – 95% confidence interval.

As can be seen in Table 1 section titled *All wolves*, the overall wolf mortality (all wolf ages and sexes) doubled from before to after hunt period. The trend was similar for the *Adult*, *Male* and *Female* sections, with male wolves showing little less than double the mortality increase from before to after hunt, while overall female wolf mortality more than doubled, and in *Juveniles* section wolves' mortality almost tripled. human-caused mortality increased after hunt for all wolves' categories, but most notably for juveniles, followed by female wolves. Natural cause mortality percentage decreased after hunt for all categories with exception of male wolves, whose natural mortality also increased, potentially due to conflict caused by wolf pack disruption during and following hunts.

The Table 1 showed that all-cause mortality across wolf categories was within a close range, with juveniles showing lowest mortality before hunt and highest after hunt, with all recorded after hunt mortality being of human causes. With 23 recorded deaths for male wolves over entire span of 16 years, 24 for female wolves and 12 for juveniles, it made sense to perform the regression analysis on the overall tracked population. The 95% confidence intervals, showing the tightest fit for 'All wolves' in Table 1. The 95% confidence intervals widen (along with fractionalizing radio-days) when splitting statistics by males, females and juveniles, discouraging the granular by age regression on yearly scale separately for these categories.

The summary of the linear regression analysis is presented in Fig. 1. The daily unit hazard was calculated for each tracked year, and linear regression across entire period was performed in Fig. 1a, and corresponding yearly survival derived from this result on Fig. 1b. The survival would be 0.83 in 2004 decreasing to 0.51 in 2019, however there appears to be a distinct grouping of the survival data points (and daily unit hazard) for the periods before and after hunt. We performed regression discontinuity analysis which showed a significant trend cut-point [13] with p-value of 0.02–0.04 exclusively within October–December 2012 span (see Regression discontinuity analysis in Methods and Appendix A.3, Table A9). Independently, statistical year offset for each of 12 months in Appendix A.2 showed the lowest standard error of linear regression for statistical year starting on November 1st for all three regression periods: before hunt, after hunt, and even for single regression over the entire period.

Trends tend to behave differently on both sides of a discontinuity, calling separate regression analyses for these two periods. The regression analyses in Fig. 1c demonstrated a relatively constant hazard/mortality periods before hunt, (shown in green); daily hazard approximately doubling in the first hunt year, and continuing on this new and almost constant hazard level after the hunt (red). Gray outline is retained for comparison with the entire 2004-2019 period regression from Fig. 1a. The corresponding analysis for yearly survival is shown in Fig. 1d, showing two approximately constant survival levels before and after hunt, with the sharp 22% survival drop in the year 2012.

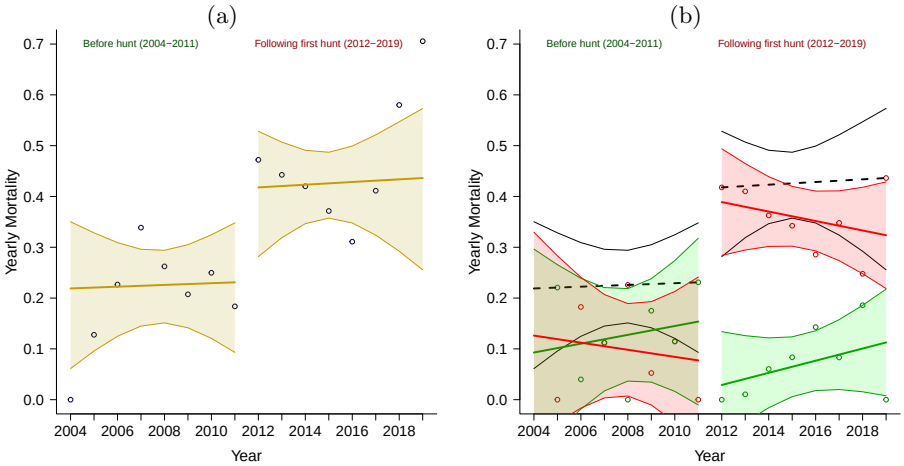

Fig. 2: **Wolf mortality for period before and following the first hunt.** (a) All-cause mortality before and following hunting seasons. Beige line – trend, before and after hunt indicated near the top of the figure; corresponding shaded areas – 95% confidence interval. (b) Same as (a), with mortality share by natural and human causes. Green lines and data points – mortality trend by natural causes, red lines and data points - mortality trend by human causes; corresponding shaded areas – 95% confidence interval. Black dashed line – trend and confidence interval outline sum of all-cause mortality, as shown on plot (a). Before and after hunt periods are indicated near the top of the figure.

The mortality analysis presented in Fig. 2a, matches with the regression discontinuity analysis in Fig. A1b. The Fig. 2b shows the analysis with the data points and regression trend separated into human and natural causes, with their corresponding data points and confidence intervals by cause of death using as a reference the overall mortality trend (dashed black line). The human-caused and natural mortality numbers were low and close to equal before hunt, both trending on about constant level. The after-hunt period shows a distinct approximately tripling of human-caused mortality during the first hunt year, which was only gradually decreasing over the following years, and natural mortality notably dropping in the first hunt year, and gradually increasing over the following years, both altogether adding up to about doubling in overall wolf mortality over the years after initiation of hunting and trapping seasons.

Discussion

In this research, we applied linear regression analysis to ascertain the patterns of survival and mortality of wolves in Minnesota before and after initiation of wolf hunting seasons of 2012–2014 based on wolf radiotelemetry statistics collected by MN DNR for years 2004–2019. Our regression discontinuity analysis, regression weighting fit as compared with the high confidence extended period survival summaries, and the smallest residual standard errors of linear regression achieved when comparing 12 months periods starting on

November 1st of each year (see Appendix A.2 and Appendix A.3), all point to statistically significant trend discontinuity, timed with initiation of the first hunting season in November 2012.

We found that the period before wolf hunting seasons was characterized by close to constant wolf mortality averaging at 21.7% (see Table 1, with about equal proportions of mortality from human and natural causes (see Fig. 2b). After initiation of the wolf hunting seasons in 2012, the wolf mortality doubled to average of 43.4% and remained close to constant for the after-hunt period, with human-caused mortality becoming predominant, while the recorded natural mortality precipitously dropped during the wolf hunting seasons of 2012–2014. The human-caused mortality was highest during the hunting seasons, and while it started diminishing later, it remained notably higher than before the initiation of the hunting seasons throughout the year 2019. It is noteworthy that while overall mortality increased similarly for all wolf categories, human-caused mortality more than quadrupled for females and juveniles and at first their natural cause mortality almost vanished. For male wolves, while human-caused mortality less than doubled, the natural cause mortality also increased by 70%, which may be hypothesized to be caused by increased conflict and hunting difficulty due to pack disruption.

Let us discuss our study finding of the rapid jump in wolf mortality following the hunt initiation with the only other recent paper using the same data set by Chakrabarti et al. [12], who "did not observe evidence that survival was markedly reduced during years when a regulated hunting and trapping season was implemented for wolves (years 2012—2014)". Chakrabarti et al. [12] applied Bayesian analysis attempting to find which one out of five smooth regression models tested would best fit to the observed data (see Equations (1)–(6)[12]). Smooth continuous models are not well suited for detecting trend discontinuities, and the model information criteria – DIC, WAIC, LOOIC [14] – which are shown in Table 1[12] differed only slightly among these five models, showing that none of the models performed significantly better. In Chakrabarti et al. [12] defense, as we showed in Appendix A.3, running a smooth statistical model in calendar year 12 months statistical periods may have been additionally prone to mask the discontinuous behavior. We were aided by testing for trend cut-points and compared regression analysis trends for periods before and after introduction of the hunts, as was shown in Fig. 2. This also allowed us to discover finer changes in patterns of natural and human-caused wolf mortality.

Human-caused mortality includes hunting, trapping, problem wolves' elimination, roadkill, and other human causes [12]. It is not surprising that the level of human-caused mortality increased during hunting and trapping seasons, but it remaining high after hunts were discontinued may indicate human attitude becoming more negative toward wolves after their killing was legalized for a time.

It is remarkable that Fuller [15] reported similarly high levels of wolf mortality, in 1980-1985 radio-tracking study of 81 wolves, with even higher

human-caused mortality than we observed following 2012-2014 hunting and trapping seasons, even though wolf population was lower in 1980s. Fuller reported during the times when with "complete federal protection in 1974, controversy over wolves in Minnesota has abounded"[15].

In conclusion, we found that wolf mortality before initiation of the wolf hunting and trapping seasons of 2012–2014 was stable, with yearly wolf mortality at around 21.7%, combined of about equal proportions by natural and human causes, with natural causes being slightly higher. Something resembling a phase shift happened with initiation of the first hunting season, when wolf mortality doubled to 43.4%, became predominantly of human causes, and remained on such elevated level with only slight gradual decrease even during five years after the hunts were discontinued. On average, for period after the initiation of wolf hunting seasons, human causes kill 35.8% of the entire wolf population yearly, and natural mortality kills on average 7.6% of wolf population. This may reflect the reality that with such high yearly human-caused mortality not many wolves could reach the age when advancing age, diseases and injuries would become the main cause of death, as it appears was the situation before initiation of wolf hunting seasons in the years 2012–2014. We hope that this analysis will help better understanding of the trends associated with introduction of wolf trophy hunting and trapping seasons, and improve stewardship of the wolf populations in Minnesota and globally.

Methods

Description of the radiotelemetry data. The Minnesota DNR wolf telemetry data for the years 2004–2019 was received on our request, from the authors of Chakrabarti et al. [12], see Supplementary data file*MnWolfSurvivalMortalityAge.csv*.

The survival analysis was performed by first aggregating the radio-days for each tracked wolf, with cause of death date or sequestering date parsed and sorted with the help of C program *WolfDNR.exe* written for this purpose by the authors. Similarly to [12], the pups and yearlings were counted together as juveniles for the final statistics, as there were only 12 mortalities of juveniles altogether. The juveniles' radio-days were accounted so that April 15th of each year was considered a graduation day to the older age category [12, 15]. When crossing April 15th of a year at two years of age, these wolves' radio-days were thereafter counted as adults. Notably, there was one occasion in the source file when pup W05-2270 was registered on May 6, 2005, at which age it was unlikely to be radio-collared, thus it was most likely a yearling, and the adjustment to the program was made to account for such scenarios, although it was the only exceptional case. Thus, the pup W05-2270 was reclassified as an yearling; within less than a year it was sequestered while still yearling. The radiotelemetry data summaries parsed and arranged by our C program *WolfDNR.exe* (described further in this section) are visually explanatory,

unlike the raw input CSV file. See the summary of a standard calendar year view Table A1 and statistical year offset to November 1st each year in Table A2, with corresponding radio-days and mortality counts.

Imputation of wolf deaths from unknown causes. There were six wolves out of 59 in the dataset, whose mortality cause was not determined. Our preliminary analysis showed that mortalities within periods before hunt and after hunt were on a relatively constant level for each of these periods. We determined the ratio of human and natural mortalities separately for before and after the hunt periods, and imputed the missing mortality by assigning each of these mortalities' fractional values for human and natural causes. See the comparisons between Table 1 and corresponding Table A10 where unknown deaths were omitted. The patterns look qualitatively same between two representations, with 10% lower values across all numbers where the unknown deaths were omitted, showing the benefit of this imputation; see Appendix A.4.

Survival analysis. The yearly wolf radio-days were calculated in *WolfDNR.exe* using equation:

$$D(y) = \sum_{wolfId=0}^{wolfIdmax} \sum_{d=1}^{365} WolfDayArray[wolfId][365 * y + d], \tag{1}$$

thus summing all entries for each individual wolfID that were accumulated above in $WolfDayArray$ for the continuous count of days d of each year starting from 2004 denoted as y, resulting in the sum of D for each year. The deaths with their causes, wolf sexes and ages were added for each year in this same loop.

The average daily statistics were calculated using maximum likelihood estimator (MLE) [16, 17]. The periods were considered tracked every day, as described in [12], and wolf mortality dates considered well established, which led to all survival numbers for this simple case scenario matching the initial value of Trent & Rongstad [18] daily survival equation in the first MLE iteration:

$$S_d = (D - K)/D, \tag{2}$$

where D represents sum of radio-days for the time period, and K recorded mortality counts during this period.

The yearly survival was counted for standard 365 day years:

$$S_y = S_d^{365}, \tag{3}$$

where S_y is yearly survival. Yearly mortality M_y is a complementary to yearly survival:

$$M_y = 1.0 - S_y. \tag{4}$$

Weighted linear regression analysis. As the radio-day coverage was not even over the years, additionally statistics recording zero wolf mortality in the statistical year 2004, weighted linear regression was required to prevent bias by less representative data [19]. Two approaches are possible in this data set: weighting by yearly variance or weighting by yearly radio days squared. Both methods resulted in a remarkably close outcome, as discussed in Appendix A.2 (see comparisons in Table A3—Table A8). The weighting by yearly radio-days squared almost precisely matched the higher confidence summary survival data in Table 1, and thus was chosen for this study. See Appendix A.2 for the evaluation and choice of linear regression weighting.

Regression discontinuity analysis. The R script *WolfProc.R* iterated through each month of five consecutive years (2010–2014) and tested for the existence of regression discontinuity cut-points [13]. The only sharp trend discontinuity cut-point period was found spanning October, November and December 2012 with significant p-values of 0.022, 0.039 and 0.041 correspondingly, when the mortality trend jumped to a 22% higher than before level, and continued along this post-discontinuity trend line. Thus, the introduction of wolf hunting seasons in November 2012 timed with the statistically significant discontinuity in the wolf mortality trend. See in depth treatment in Appendix A.3.

Implementation of linear regression analysis. The linear regression with weighting was implemented using standard R libraries with the core regression model as follows:

$$wFit = lm(Y \sim X, data = df, weights = D^2), \tag{5}$$

where $wFit$ is weighted fit, Y are typically daily hazard values, X - years range, D - radio-days (measurements) in a year, K - recorded wolf deaths, df is an R data frame containing input loaded from the CSV data file. A simple linear regression is then used to trend the fraction of mortality by natural and human causes.

Code and executables. The data preparation and sorting were done with help of a C program *WolfDNR.exe*, which outputs CSV files with radio-days, mortality counts and corresponding daily hazard - overall and by mortality cause, yearly survival and mortality data points, using approach described above. The majority of the processing was performed by R script *WolfProc.R*, which takes as an input the raw yearly summaries aggregated by *WolfDNR.exe*, performs linear regression and regression discontinuity analysis, extracts the relevant statistics and outputs the figures and tables in PDF and Latex form, as used in the manuscript. Two additional R scripts, *WolfSummaryTableBeforeAfter.R* and *WolfTableByYear.R*, output the remaining tables used in the manuscript. All the above programs and code are available in the Supplementary Data, along with the batch files that allow to perform all the processing, starting with the MN DNR data set CSV file, and

outputting the data tables and graphs used in this manuscript. This code was intended for this MN DNR data set, but it can be easily adjusted for processing different datasets.

Statistics and Reproducibility

The survival analysis was performed on radiotelemetry data originally sourced from MN DNR, and obtained on request from Chakrabarti et al. [12]. The linear regression fit and discontinuity analysis were performed using standard R libraries. The reported tables and figures include the 95% confidence intervals. The regression discontinuity analysis used p-value significance of ≤ 0.05.

Data Availability

The input data, source code, executable, batch files necessary to perform analysis are available in Supplementary Data .ZIP file.

Author Contributions

R.O. conceived the project, performed statistical analysis and wrote the manuscript.

Competing interests

The authors declare no competing interests.

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Appendix A

A.1 MN DNR radiotelemetry data summary for years 2004 – 2019

Table A1: Radiotelemetry summaries for standard calendar years starting **January 1st**.

		Deaths			Daily hazard	
Year	**R-days**	**all**	**human**	**natural**	**unit**	**variance**
2004	469	0	0.000	0.000	0e+00	0e+00
2005	1668	0	0.000	0.000	0e+00	0e+00
2006	2946	2	1.000	1.000	6.79e-04	2.3e-07
2007	4645	4	3.545	0.455	8.61e-04	1.85e-07
2008	2716	3	1.000	2.000	1.1e-03	4.06e-07
2009	1839	0	0.000	0.000	0e+00	0e+00
2010	3030	2	0.545	1.455	6.6e-04	2.18e-07
2011	2175	2	1.000	1.000	9.2e-04	4.22e-07
2012	4412	5	3.000	2.000	1.13e-03	2.57e-07
2013	2889	6	5.786	0.214	2.08e-03	7.17e-07
2014	4617	6	6.000	0.000	1.3e-03	2.81e-07
2015	4424	5	4.000	1.000	1.13e-03	2.55e-07
2016	4487	8	5.786	2.214	1.78e-03	3.97e-07
2017	3316	2	2.000	0.000	6.03e-04	1.82e-07
2018	4716	9	6.571	2.429	1.91e-03	4.04e-07
2019	2388	5	3.000	2.000	2.09e-03	8.75e-07

R-days column title stands for radiotelemetry days. Fractional wolf death counts are the result of six wolf deaths that were of unknown causes, imputed proportionately to the known mortality causes for each period.

Table A2: Radiotelemetry summaries for first day of the year offset to **November 1st**, the month of the commencement of wolf hunting seasons.

		Deaths			Daily hazard	
Year	**R-days**	**all**	**human**	**natural**	**unit**	**variance**
2004	1424	0	0.000	0.000	0e+00	0e+00
2005	2672	1	0.000	1.000	3.74e-04	1.4e-07
2006	4262	3	2.462	0.538	7.04e-04	1.65e-07
2007	3533	4	2.000	2.000	1.13e-03	3.2e-07
2008	1200	1	1.000	0.000	8.33e-04	6.94e-07
2009	3143	2	0.462	1.538	6.36e-04	2.02e-07
2010	2541	2	1.000	1.000	7.87e-04	3.1e-07
2011	3598	2	0.000	2.000	5.56e-04	1.54e-07
2012	3431	6	6.000	0.000	1.75e-03	5.09e-07
2013	4375	7	6.825	0.175	1.6e-03	3.65e-07
2014	4694	7	6.000	1.000	1.49e-03	3.17e-07
2015	4720	6	4.825	1.175	1.27e-03	2.69e-07
2016	2941	3	2.000	1.000	1.02e-03	3.46e-07
2017	4825	7	5.650	1.350	1.45e-03	3e-07
2018	2948	7	4.000	3.000	2.37e-03	8.04e-07
2019	299	1	1.000	0.000	3.34e-03	1.11e-05

Wolf hunting seasons always commenced in November of wolf hunting seasons 2012–2014, therefore all statistics are offset to start each year on November 1st. This data arrangement was used as the basis for the regression analysis in this study. R-days column title stands for radiotelemetry days. Fractional wolf death counts are the result of six wolf deaths that were of unknown causes, imputed proportionately to the known mortality causes for each period.

A.2 Fit of weighting methods used in linear regression

The DNR radiotelemetry data was characterized by years with varying numbers of cumulative radio-days and varying wolf mortality numbers (as can be seen in Table A1 and Table A2). The common approach to limit bias by less representative data samples and outliers is to apply linear regression with weighting [19]. In statistical sampling an inverse of variance is often used. However, in our data, years 2004, 2005, and 2009 in Table A1 have 0 wolf deaths, and thus no variance calculated. Similarly year 2004 in Table A2 has no variance, and quite low number of radio-days with one wolf death, producing an outlier in the year 2019. The outliers are handled well by the variance weighting, but the zero variance requires additional estimation of possible variance, perhaps from the nearby valid entries. Additionally, with high granularity radiotelemetry as used in MN DNR data collection, the higher variance for the years with higher wolf mortality may create it's own bias. A second weighting approach is using radio-days. This is because of a simple correspondence, derived as:

$$V = \frac{p(1-p)}{D} = \frac{\frac{K}{D}\frac{D-K}{D}}{D} \approx \frac{K}{D^2} \sim \frac{1}{D^2}, \tag{A1}$$

where V is variance, p and $(1-p)$ is data fraction, D - number of radio-days (measurements), and K the count of wolf deaths in the radio-days period. With large D and small K, $(D-K)/D \approx 1$, and $K/D^2 \sim 1/D^2$. The last step shows the use of the unbiased by number of recorded deaths weight by radio-days; thus when weighting can be performed as $1/V$ it needs to be performed alternatively as R^2. The advantage of this second weighting approach is its consistency, and it does not require inventing special treatment for the years with no recorded wolf mortality. The following comparisons shows that this weighting method also allows a more precise match of the regression to the summary analysis in Table 1.

Finally, the R models for these two weights are implemented as follows:

$$wFit1 = lm(Y \sim X, data = df, weights = 1/V), \tag{A2}$$

and

$$wFit2 = lm(Y \sim X, data = df, weights = D^2), \tag{A3}$$

where wFit1 and wFit2 are the corresponding weighted fits scenarios for the linear regression, Y are typically daily hazard values or survival, X - years range, D - radio-days (measurements) in a year, K - recorded wolf deaths, df is an R data frame with loaded CSV input. See also Sheather [19].

On the following three pages, the tables are grouped in comparison pairs for weighting using inverse variance and R^2 (see Table A3–Table A4, Table A5–Table A6, and Table A7–Table A8). These tables for completeness show the linear regressions parameters with year offset to first day of each month of the year. The most important columns are stdError - the standard

error of regression, r^2 - the goodness-of-fit, and the mean survival, which is customarily calculated as:

$$SurvM = (\prod_{t=Y_{min}}^{Y_{max}} S[t])^{1/T}, \tag{A4}$$

where $(SurvM)$ is mean survival over the subsequent number of years T in the regression interval Y_{min} to Y_{max}. As can be seen below, stdErr is the comparatively lowest for years offset to start as of November 1st in all tables except Table A4 where it is close second. The regression parameter r^2 is a goodness-of-fit of the trend. In Table A3–Table A6 r^2 is low, representing a close to constant level of survival and mortality. We also performed analysis for the entire dataset duration in this case, as expected there is a trend, and the best regression is also happens with November 1st time frame offset - right before the hunt.

The second equally important consideration for the weighting method is how well the mean survivals in these tables match the summaries in Table 1. Here the summaries from sections in Table 1 compared with radio-days squared weighting in the regression analysis as follows (Equation A3 scenario): for time period 2004-2011 as 0.783 vs 0.775, 2012-2019 as 0.566 vs 0.573 , and also for the all years time interval as 0.653 vs 0.658 — an almost exact match. While inverse variance weighting (Equation A2 scenario) was further apart from the summary values in Table 1, showing correspondingly — 0.783 vs 0.804, 0.566 vs 0.582 , and also for the all years time interval as 0.653 vs 0.685 — in each case exaggerating the summary survival by a few percent.

Consequently, the regression analysis when using inverse variance weighting resulted in almost identical but slightly underestimated mortality trend values. Thus, we used the weighting by the radio-days squared in our reported analysis.

Table A3: The linear regression fit parameters by assigned first month of year for **years 2004–2011, inverse variance weighting**.

	Daily hazard fit				Survival		
First month	**stdError**	r^2	**Slope**	**Intercept**	**mean**	**begin**	**end**
Jan	0.000068	0.1207	0.000062	-0.1	0.796	0.861	0.735
Feb	0.000072	0.1469	0.000073	-0.1	0.799	0.877	0.727
Mar	0.000065	0.0418	-0.000034	0.07	0.802	0.768	0.837
Apr	0.000075	0.0130	-0.000021	0.04	0.792	0.771	0.814
May	0.000075	0.0083	-0.000017	0.03	0.795	0.778	0.812
Jun	0.000075	0.0067	-0.000015	0.03	0.799	0.784	0.814
Jul	0.000075	0.0058	-0.000014	0.03	0.804	0.790	0.818
Aug	0.000060	0.0030	0.000008	-0.02	0.802	0.811	0.794
Sep	0.000060	0.0162	-0.000019	0.04	0.796	0.777	0.816
Oct	0.000045	0.0031	-0.0000061	0.01	0.818	0.812	0.825
Nov	0.000042	0.1530	0.000043	-0.09	0.804	0.850	0.761
Dec	0.000047	0.0070	-0.0000097	0.02	0.792	0.782	0.802

Statistics for years: 2004 - 2011, linear regression weighted by inverse variance. 'stdError' is standard error, 'r^2', 'slope' and 'intercept' of the linear regression fit. Survival 'begin' and 'end' are survivals in the first and last year of the period.

Table A4: The linear regression fit parameters by assigned first month of year for **years 2004–2011, radio-days squared weighting**.

	Daily hazard fit				Survival		
First month	**stdError**	r^2	**Slope**	**Intercept**	**mean**	**begin**	**end**
Jan	0.000071	0.0182	0.000024	-0.05	0.764	0.788	0.742
Feb	0.000081	0.0261	0.000033	-0.06	0.772	0.804	0.740
Mar	0.000075	0.1014	-0.000062	0.1	0.756	0.698	0.818
Apr	0.000077	0.0538	-0.000045	0.09	0.754	0.712	0.799
May	0.000078	0.0392	-0.000039	0.08	0.757	0.720	0.795
Jun	0.000079	0.0430	-0.000041	0.08	0.760	0.721	0.801
Jul	0.000080	0.0525	-0.000046	0.09	0.764	0.721	0.811
Aug	0.000070	0.0061	-0.000013	0.03	0.760	0.747	0.773
Sep	0.000065	0.0344	-0.00003	0.06	0.766	0.737	0.797
Oct	0.000050	0.0495	-0.000028	0.06	0.779	0.752	0.807
Nov	0.000047	0.0027	0.0000061	-0.01	0.775	0.781	0.769
Dec	0.000043	0.0924	-0.000033	0.07	0.770	0.738	0.804

Statistics for years: 2004 - 2011, linear regression weighted by radio-days squared. 'stdError' is standard error, 'r^2', 'slope' and 'intercept' of the linear regression fit. Survival 'begin' and 'end' are survivals in the first and last year of the period.

Table A5: The linear regression fit parameters by assigned first month of year for **years 2012–2019, inverse variance weighting**.

	Daily hazard fit				Survival		
First month	**stdError**	r^2	**Slope**	**Intercept**	**mean**	**begin**	**end**
Jan	0.000096	0.0041	0.000015	-0.03	0.625	0.638	0.613
Feb	0.000113	0.0069	-0.000023	0.05	0.638	0.620	0.658
Mar	0.000139	0.0101	0.000034	-0.07	0.657	0.686	0.629
Apr	0.000104	0.0019	0.000011	-0.02	0.625	0.634	0.616
May	0.000109	0.0018	0.000011	-0.02	0.628	0.637	0.619
Jun	0.000113	0.0012	-0.0000098	0.02	0.626	0.618	0.634
Jul	0.000090	0.0005	-0.0000049	0.01	0.601	0.597	0.604
Aug	0.000088	0.0054	0.000016	-0.03	0.601	0.614	0.589
Sep	0.000092	0.0028	0.000012	-0.02	0.597	0.606	0.588
Oct	0.000087	0.0007	-0.0000058	0.01	0.587	0.583	0.592
Nov	0.000079	0.0003	0.0000034	-0.005	0.582	0.585	0.580
Dec	0.000119	0.0017	-0.000012	0.03	0.593	0.584	0.603

Statistics for years: 2012 - 2019, linear regression weighted by inverse variance. 'stdError' is standard error, 'r^2', 'slope' and 'intercept' of the linear regression fit. Survival 'begin' and 'end' are survivals in the first and last year of the period.

Table A6: The linear regression fit parameters by assigned first month of year for **years 2012–2019, radio-days squared weighting**.

	Daily hazard fit				Survival		
First month	**stdError**	r^2	**Slope**	**Intercept**	**mean**	**begin**	**end**
Jan	0.000079	0.1374	0.000077	-0.2	0.584	0.644	0.529
Feb	0.000098	0.0330	0.000044	-0.09	0.574	0.608	0.543
Mar	0.000107	0.0038	0.000016	-0.03	0.581	0.593	0.569
Apr	0.000097	0.0171	0.000031	-0.06	0.573	0.597	0.551
May	0.000106	0.0092	0.000025	-0.05	0.573	0.592	0.555
Jun	0.000106	0.0054	0.000019	-0.04	0.582	0.596	0.568
Jul	0.000088	0.0010	0.0000067	-0.01	0.582	0.587	0.577
Aug	0.000084	0.0092	0.00002	-0.04	0.587	0.602	0.573
Sep	0.000084	0.0003	0.0000038	-0.006	0.584	0.587	0.581
Oct	0.000080	0.0081	-0.000018	0.04	0.584	0.571	0.597
Nov	0.000069	0.0055	0.000013	-0.02	0.573	0.582	0.564
Dec	0.000117	0.0040	-0.000018	0.04	0.569	0.556	0.583

Statistics for years: 2012 - 2019, linear regression weighted by radio-days squared. 'stdError' is standard error, 'r^2', 'slope' and 'intercept' of the linear regression fit. Survival 'begin' and 'end' are survivals in the first and last year of the period.

Table A7: The linear regression fit parameters by assigned first month of year for **years 2004–2019, inverse variance weighting**

	Daily hazard fit				Survival		
First month	**stdError**	r^2	**Slope**	**Intercept**	**mean**	**begin**	**end**
Jan	0.000027	0.3511	0.000074	-0.1	0.704	0.862	0.575
Feb	0.000030	0.2679	0.000067	-0.1	0.712	0.856	0.593
Mar	0.000035	0.1838	0.000063	-0.1	0.737	0.874	0.621
Apr	0.000031	0.2591	0.000069	-0.1	0.707	0.853	0.586
May	0.000032	0.2480	0.000068	-0.1	0.708	0.854	0.587
Jun	0.000032	0.2432	0.000069	-0.1	0.709	0.855	0.587
Jul	0.000030	0.3481	0.000082	-0.2	0.698	0.873	0.557
Aug	0.000028	0.3981	0.000084	-0.2	0.701	0.883	0.556
Sep	0.000030	0.3567	0.000084	-0.2	0.702	0.884	0.558
Oct	0.000027	0.4305	0.000087	-0.2	0.705	0.896	0.555
Nov	0.000021	0.5959	0.000095	-0.2	0.685	0.889	0.528
Dec	0.000030	0.3397	0.000079	-0.2	0.693	0.861	0.558

Statistics for years: 2004 - 2019, linear regression weighted by inverse variance. 'stdError' is standard error, 'r^2', 'slope' and 'intercept' of the linear regression fit. Survival 'begin' and 'end' are survivals in the first and last year of the period. .

Table A8: The linear regression fit parameters by assigned first month of year for **years 2012–2019, radio-days squared weighting**.

	Daily hazard fit				Survival		
First month	**stdError**	r^2	**Slope**	**Intercept**	**mean**	**begin**	**end**
Jan	0.000026	0.4570	0.000088	-0.2	0.667	0.849	0.525
Feb	0.000032	0.3626	0.000089	-0.2	0.660	0.843	0.517
Mar	0.000035	0.2356	0.000073	-0.1	0.654	0.798	0.536
Apr	0.000032	0.2998	0.000079	-0.2	0.649	0.805	0.523
May	0.000035	0.2722	0.000079	-0.2	0.649	0.806	0.522
Jun	0.000034	0.2565	0.000076	-0.2	0.655	0.806	0.532
Jul	0.000031	0.3060	0.000076	-0.2	0.656	0.808	0.532
Aug	0.000028	0.3471	0.000076	-0.2	0.660	0.811	0.536
Sep	0.000028	0.3526	0.000078	-0.2	0.659	0.815	0.533
Oct	0.000027	0.3907	0.000081	-0.2	0.662	0.826	0.530
Nov	0.000023	0.5217	0.000089	-0.2	0.658	0.840	0.515
Dec	0.000033	0.3148	0.000084	-0.2	0.652	0.821	0.518

Statistics for years: 2004 - 2019, linear regression weighted by radio-days squared. 'stdError' is standard error, 'r^2', 'slope' and 'intercept' of the linear regression fit. Survival 'begin' and 'end' are survivals in the first and last year of the period.

A.3 Pinpointing the trend change timing with regression discontinuity analysis

Regression discontinuity analysis was performed to find whether there was a cut-point where the trend may have become discontinuous [13], as would happen if before and after a specific date or event the trends may significantly change magnitude and slope. It was implemented in R script *WolfProc.R* as a varying slope regression discontinuity analysis [20–22].

Table A9: Regression discontinuity analysis finds significant trend cut-point in October, November and December 2012.

Cut-point	**Year**				
Month	**2010**	**2011**	**2012**	**2013**	**2014**
Jan	0.990 (0%)	0.530 (9%)	0.520 (9%)	0.652 (5%)	0.481 (-7%)
Feb	0.736 (8%)	0.414 (15%)	0.470 (13%)	0.350 (-12%)	0.443 (-10%)
Mar	0.822 (-5%)	0.346 (19%)	0.240 (23%)	0.656 (-7%)	0.731 (-5%)
Apr	0.861 (-4%)	0.646 (8%)	0.223 (21%)	0.736 (-4%)	0.827 (-3%)
May	0.855 (-4%)	0.671 (8%)	0.241 (21%)	0.828 (-3%)	0.955 (-1%)
Jun	0.825 (-5%)	0.728 (6%)	0.205 (22%)	0.751 (-4%)	0.426 (-10%)
Jul	0.774 (-5%)	0.746 (5%)	0.105 (24%)	0.766 (-4%)	0.257 (-13%)
Aug	0.731 (-6%)	0.745 (5%)	0.193 (17%)	0.834 (-2%)	0.284 (-11%)
Sep	0.971 (-1%)	0.637 (7%)	0.095 (21%)	1.000 (0%)	0.523 (-7%)
Oct	0.999 (0%)	0.684 (6%)	0.022* (25%)	0.834 (2%)	0.356 (-9%)
Nov	0.907 (-2%)	0.813 (3%)	0.039* (19%)	0.684 (4%)	0.460 (-6%)
Dec	0.790 (4%)	0.721 (6%)	0.041* (24%)	0.757 (-4%)	0.511 (-7%)

The R script tested for the existence of discontinuity cut-points in each month of five consecutive years. The table cells show p-value significance of discontinuity, followed in parentheses by overall wolf mortality percentage change at the discontinuity time. * mark p-values ≤ 0.05.

The R script iterated through each month of five consecutive years and tested for the existence of discontinuity cut-points, see Table A9. The only sharp trend discontinuity cut-point [13] was found spanning October, November and December 2012 with significant p-values of 0.022, 0.039 and 0.041 correspondingly, when the mortality trend jumped to a new 22% higher level (an average of these three months). This timing coincided with the initiation of first wolf hunting and trapping season of 2012. It can be seen that there are no candidates for any other timing of cut-points, as the p-values become increasingly less significant for earlier months of 2012, and all columns for years 2010, 2011, 2013 and 2014 have large p-values.

The January row in Table A9 shows that statistics aligned with standard calendar years starting on January 1st are particularly unsuitable for noticing a sharp discontinuity. Only part of mortality from 2012-2013 hunting season happened in November and December 2012, thus producing a smooth transition when counting statistics in calendar years.

Fig. A1 graphically illustrates the numerical p-values in Table A9. Testing for the cut-points on November 1st of years 2011 and 2013 showed low likelihood of such cut point, at p-values of 0.813 and 0.684 correspondingly, leading to the appearance of Fig. A1a and Fig. A1c. On the other hand, p-value

equal 0.039 for November 2012 corresponds to a sharp break of the trend on Fig. A1b.

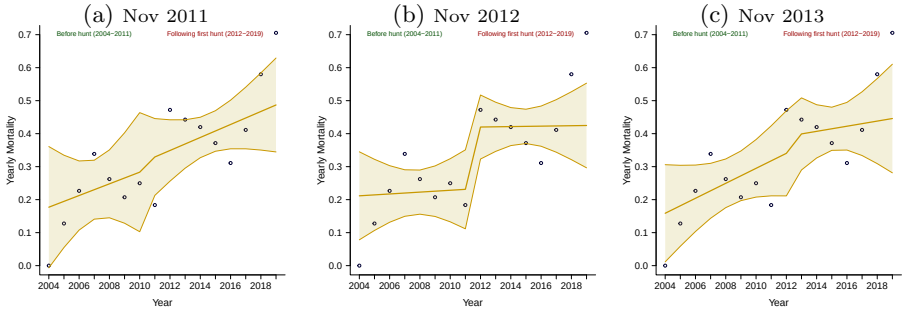

Fig. A1: **Graphical illustration of the regression discontinuity test results.** (a) Trend cut-point November 1, 2011. (b) Trend cut-point November 1, 2012. (c) Trend cut-point November 1, 2013. With statistical beginning of year offset to November 1st, there are large p-values produced by discontinuity test in 2011 and 2013 as reflected in the lack of discontinuity in plots (a) and (c). Plot (b) corresponds to significant low p-value = 0.039 produced by the test for year starting at the hunting season initiation month November 2012 (see all values in Table A9). The beige solid line shows the mean value of the discontinuous regression, shaded areas show 95% confidence intervals.

Thus, November 1st of year 2012, being the timing of initiation of the 2012–2014 wolf hunting seasons coincides well with the middle of the trend discontinuity cut-point in October–December 2012. A choice of October 2012, with the lowest discontinuity p-value=0.022, would result in a similar trend, with even higher jump in mortality at the trend cut-point (see in Fig. A2).

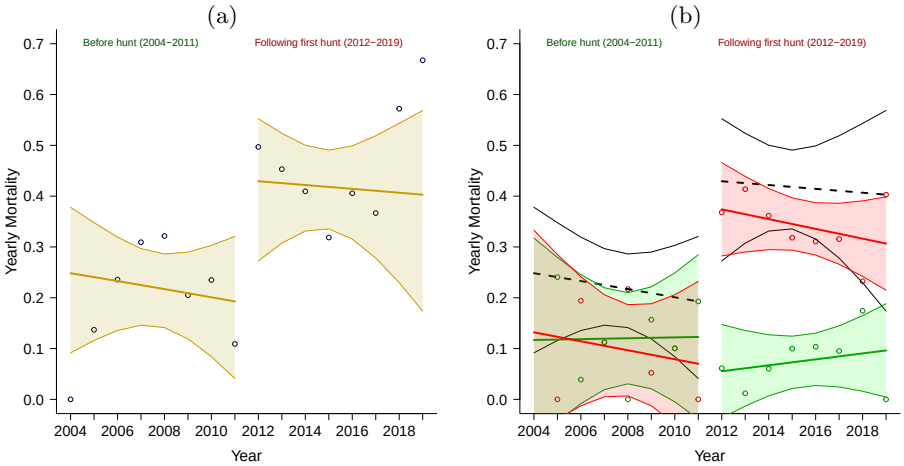

Fig. A2: **Wolf mortality for period before and following the first hunt using October 1st, 2012 as trend cut-point.** (a) All cause mortality before and following hunting seasons. Beige line – trend, before and after hunt indicated near the top of the figure. (b) Same as (a), with mortality share by natural and human causes. Green lines and data points – mortality trend by natural causes, red lines and data points - mortality trend by human causes. Black dashed line – trend and confidence interval outline sum of all cause mortality. All corresponding shaded areas – 95% confidence intervals. For comparison with Fig. 2.

A.4 Confirming the consistency of regression when wolf deaths by unknown causes are excluded

Table A10 shows the regression analysis performed discounting the six wolf mortalities out of 59 due to unknown causes, rather than imputing them as fractional shares of mortalities. Imputing the unknown cause mortality allows to account for all wolf deaths in the data, rather than underestimating wolf mortality, without a noticeable bias in the regression outcome.

Table A10: Wolf survival and mortality summary **excluding** imputation of wolf deaths by unknown causes.

		Yearly mortality				Wolf deaths by cause	
Period	**Survival**	**all**	**human**	**natural**	**R-days**	**human**	**natural**
			All wolves				
Before	0.809 (0.72-0.91)	19.1%	8.8%	10.3%	22373	6.00	7.00
After	0.596 (0.51-0.70)	40.4%	33.3%	7.1%	28233	33.00	7.00
All	0.682 (0.62-0.76)	31.8%	23.4%	8.4%	50606	39.00	14.00
			Adult				
Before	0.789 (0.69-0.90)	21.1%	10.6%	10.6%	18440	6.00	6.00
After	0.602 (0.50-0.72)	39.8%	30.8%	9.0%	22341	24.00	7.00
All	0.680 (0.61-0.76)	32.0%	22.3%	9.7%	40781	30.00	13.00
			Male				
Before	0.754 (0.61-0.93)	24.6%	14.1%	10.6%	9035	4.00	3.00
After	0.624 (0.49-0.80)	37.6%	21.5%	16.1%	10841	8.00	6.00
All	0.680 (0.58-0.80)	32.0%	18.3%	13.7%	19876	12.00	9.00
			Female				
Before	0.824 (0.69-0.98)	17.6%	7.1%	10.6%	9405	2.00	3.00
After	0.583 (0.45-0.75)	41.7%	39.3%	2.5%	11500	16.00	1.00
All	0.681 (0.58-0.80)	31.9%	26.1%	5.8%	20905	18.00	4.00
			Juvenile				
Before	0.911 (0.76-1.09)	8.9%	0.0%	8.9%	3933	0.00	1.00
After	0.572 (0.40-0.82)	42.8%	42.8%	0.0%	5892	9.00	0.00
All	0.690 (0.55-0.87)	31.0%	27.9%	3.1%	9825	9.00	1.00

Wolf hunting seasons always commenced in November of wolf hunting seasons 2012–2014, therefore all statistics are offset to start each year on November 1st. Periods before include 2004 to October 31, 2012, after – November 1st 2012 to the end of 2019, all years calculated for the entire data time span combining before and after periods. The range in braces following 'Survival' is 95% confidence interval range. R-days stands for radiotelemetry days for each time interval. Fractional wolf death counts are the result of six wolf deaths that were of unknown causes, imputed proportionately to the known mortality causes for each period.

See the comparisons between Table A10 and corresponding Table 1 where imputation was performed, which shows that the patterns look qualitatively same between two representations, with 10% lower values across all numbers where the unknown deaths were omitted, showing the benefit of this imputation.