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Gray wolf mortality patterns in Wisconsin from 1979 to 2012

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Starting in the 1970s, many populations of large-bodied mammalian carnivores began to recover from centuries of human-caused eradication and habitat destruction. The recovery of several such populations has since slowed or reversed due to mortality caused by humans. Illegal killing (poaching) is a primary cause of death in many carnivore populations. Law enforcement agencies face difficulties in preventing poaching and scientists face challenges in measuring it. Both challenges are exacerbated when evidence is concealed or ignored. We present data on deaths of 937 Wisconsin gray wolves (*Canis lupus*) from October 1979 to April 2012 during a period in which wolves were recolonizing historic range mainly under federal government protection. We found and partially remedied sampling and measurement biases in the source data by reexamining necropsy reports and reconstructing the numbers and causes of some wolf deaths that were never reported. From 431 deaths and disappearances of radiocollared wolves aged > 7.5 months, we estimated human causes accounted for two-thirds of reported and reconstructed deaths, including poaching in 39–45%, vehicle collisions in 13%, legal killing by state agents in 6%, and nonhuman causes in 36–42%. Our estimate of poaching remained an underestimate because of persistent sources of uncertainty and systematic underreporting. Unreported deaths accounted for over two-thirds of all mortality annually among wolves > 7.5 months old. One-half of all poached wolves went unreported, or > 80% of poached wolves not being monitored by radiotelemetry went unreported. The annual mortality rate averaged 18% ± 10% for monitored wolves but 47% ± 19% for unmonitored wolves. That difference appeared to be due largely to radiocollaring being concentrated in the core areas of wolf range, as well as higher rates of human-caused mortality in the periphery of wolf range. We detected an average 4% decline in wolf population growth in the last 5 years of the study. Because our estimates of poaching risk and overall mortality rate exceeded official estimates after 2012, we present all data for transparency and replication. More recent additions of public hunting quotas after 2012 appear unsustainable without effective curtailment of poaching. Effective antipoaching enforcement will require more accurate estimates of poaching rate, location, and timing than currently available. Independent scientific review of methods and data will improve antipoaching policies for large carnivore conservation, especially for controversial species facing high levels of human-induced mortality.

Key words: anthropogenic mortality, carnivore, conflict, illegal killing, poaching, sampling bias, take

Many societies value big cats, wolves (*Canis lupus*), or bears (*Ursus*) as sacred, symbolic, ecologically beneficial, intrinsically valuable, or as game (Knight 2000, 2003; Duffield et al. 2008; David 2009). Nevertheless, many people find these and other large carnivores difficult to live alongside and may report intolerance, animosity, or fear toward large carnivores (Flykt et al. 2013; Treves and Bruskotter 2014). Some individuals and organizations respond to these and other concerns by retaliating privately or pressuring governments to reduce the numbers of carnivores. Scientists often face challenges in measuring the relative magnitudes of the ensuing illegal and legal killing, as well as disentangling their interrelationships over time and space. Yet understanding these patterns is essential to evaluating whether humans will prevent conservation of carnivores. A better understanding of human-caused mortality may also reveal whether large carnivore populations will grow, stabilize, or decline as policies or human behaviors change.

For many populations of large carnivores, scientific debates about sustainable levels of human-caused mortality remain unsettled. It is widely accepted that more large carnivores are killed by humans than by any other cause, worldwide (Woodroffe and Ginsberg 1998). But it is less clear how much mortality large carnivore populations can sustain and remain stable or grow. Models using empirical data from wolves, tigers (*Panthera tigris*), leopards (*P. pardus*), and mountain lions (*Puma concolor*) suggest total mortality rates higher than 15–31% cannot be sustained (Adams et al. 2008; Chapron et al. 2008; Vucetich 2012). The models are supported by estimates from 8 populations, whose growths were slowed or reversed by mortality rates of 19–37% or human-caused mortality rates of 14–32% (Whitman et al. 2004; Woodroffe and Frank 2005; Goodrich et al. 2008; Creel and Rotella 2010; Smith et al. 2010; Liberg et al. 2012; Vucetich 2012; Artelle et al. 2013). Although population growth and decline is becoming better understood, scientific uncertainty persists about the indirect responses of individual carnivores and social groups to human-caused mortality. Local sinks (sites with very high levels of mortality) and superadditive mortality (direct killing that results in additional, indirect deaths due to breeding failure, infanticide, social group dissolution, etc.) may diminish large carnivore populations across broader regions than the localities around each death (Swenson et al. 1997; Andren et al. 2006; Loveridge et al. 2007; Adams et al. 2008; Brainerd et al. 2008; Person and Russell 2008; Borg et al. 2015). Furthermore, the common management tactic of setting future quotas according to past rates of legal human-caused mortality (Logan and Sweanor 2001) may amplify natural oscillations in the sizes of hunted populations and thereby raise the probability of a population crash (Fryxell et al. 2010). The many variables and nonlinear relationships we describe in this paragraph apply to situations in which mortality is observable. When humans kill carnivores and do not report the deaths, one finds the following additional challenges.

Poaching is difficult to detect and prevent, so it is often underestimated because of concealed evidence and other biases (Sanchez-Mercado et al. 2008; Gavin et al. 2010). For example, two-thirds of Swedish wolf-poaching was concealed and required extensive field investigation and statistical modeling to estimate (Liberg et al. 2012). Across various regions and large carnivore species, estimates of poaching range from 24% to 75% of overall mortality (Fuller et al. 2003; Andren et al. 2006; Chapron et al. 2008; Goodrich et al. 2008; Person and Russell 2008; Persson et al. 2009; Smith et al. 2010; Liberg et al. 2012). The latter estimates of relative risk only rank poaching relative to other causes of mortality. When one examines the percentage of individuals dying per unit time within a predator population (referred to as the hazard rate), poaching can push carnivore populations toward population crashes, at least in human-dominated landscapes. The poaching hazard rate was 34% for Amur tigers in 4 years with heavy poaching (Goodrich et al. 2008), and 11–30% for wolverines (*Gulo gulo*) in northern Scandinavia (Persson et al. 2009). By contrast, poaching accounted for a > 6% hazard rate in Northern Rocky Mountain wolves in and around strictly protected and wilderness areas (Smith et al. 2010). Evidence has accumulated that 6% was likely a systematic underestimate for the latter population (Treves et al. 2016). In the Swedish study of wolf mortality in a multiple-use landscape mentioned above, the poaching hazard rate was 15%, meaning that 15 in 100 wolves died from poaching (Liberg et al. 2012). Much of the activity of Swedish poachers went unreported, a phenomenon the latter authors referred to as cryptic poaching. Sweden conducts more intensive and extensive monitoring of its wolves than any country of which we are aware, including telemetry on at least 1 individual from every wolf pack, genetic analysis to build pedigrees whenever samples are collected, and extensive, annual snow-track surveys to find every wolf pack (Liberg et al. 2012). Nevertheless, more than two-thirds of the poaching was cryptic. Therefore, reliable estimates of poaching will demand novel analytical techniques and meticulous use of every piece of information available, especially for poorer governments that cannot afford to monitor so intensively and extensively as Sweden did.

The standard method for estimating mortality rates has been to use telemetry to follow marked animals over time and record life-history traits such as the hazard rate. However, researchers following marked animals until they die depend on unbiased sampling and unbiased measurement of different causes of death, which are often difficult to accomplish at regional scales for large samples. The difficulty is compounded when poachers destroy evidence.

We investigated the challenges posed by cryptic poaching and biases in sampling and measurement of mortality causes among gray wolves in the state of Wisconsin from 1979 to 2012. We identified sampling biases in selecting wolves for radiocollaring and measurement biases in the data and analyses of death records. We developed methods to correct some of the biases, which took into account evidence from necropsies performed by veterinarians and the behavioral ecology of humans and wolves that may influence detection and reporting biases. We identify inaccuracies and imprecision in official estimates of wolf mortality and recommend ways data should be collected and reported by government agencies for independent scientific review before enacting policy.

Materials and Methods

Study area and history of wolf recolonization.—Wisconsin extends over 138,644 km^2 with human population density approximating 41/km^2 and 19 housing units/km^2 (United States Census Bureau 2010). Many private lands and > 75% of public lands are open to hunting for at least 1 season annually, including the November hunt for white-tailed deer (*Odocoileus virginianus*) that involves ~500,000 hunters. Wolf range in Wisconsin contained no vast wilderness and few areas under strict preservation (Mladenoff et al. 2009; Thiel et al. 2009; Treves et al. 2009; Wydeven et al. 2009b). Wolf packs and individual wolves use areas of the state with relatively less agriculture and human use than expected by chance (Mladenoff et al. 2009; Treves et al. 2009).

Humans extirpated wolves from Wisconsin in ~1957, and then wolves recolonized the state by 1978 without direct human intervention (Wisconsin Department of Natural Resources [WDNR] 2015). The population grew to > 814 by 15 April 2012 (Table 1). From 1979 to 2003, wolves in Wisconsin were federally classified as "endangered" (Refsnider 2009). On 1 April 2003, the federal government temporarily reclassified wolves as "threatened," which gave the State of Wisconsin new legal authority under the Endangered Species Act Rule 4(d) to kill wolves implicated in either verified damage to livestock or concerns for human safety. In the ensuing years, federal courts and the federal government changed wolf classification or state authority to use lethal control permits 11 additional times. Throughout the study period, state agents killed small numbers of wolves following threats to human safety or accidents in livetrapping (Ruid et al. 2009), without regard to whether the wolves were radiocollared or not ("Results" and Supplementary Data SD1A for the corresponding wolf deaths classified as "legal").

Wolf sampling.—From 1979 to 2012, WDNR or federal agents livetrapped, chemically immobilized, and fitted 486 wolves with VHF radiocollars primarily (Wydeven et al. 2009b; WDNR 2015). We refer to these wolves as radiocollared hereafter but also subdivide this class into 2 subsets described below. The collaring date and fate of radiocollared wolves are presented in Supplementary Data SD2. Annually, the WDNR monitored radiocollared wolves representing 8–37% of the wolf population, declining over time to a mean of 13% after wolf-year 2002 (Table 1; Wydeven et al. 2009b). We define a wolf-year to begin 15 April of year $t - 1$ and end on 14 April of year t.

Radiocollared wolves were not a random sample of the population because collaring effort was not distributed randomly across the wolf range (Wydeven et al. 2004; Mladenoff et al. 2009; Ruid et al. 2009; Thiel et al. 2009; Wydeven et al. 2009b). This occurred for 3 reasons. State agents usually livetrapped wolves near the estimated territories of known wolf packs and placed traps on public lands with low road densities

Table 1.—Numbers of Wisconsin gray wolves, *Canis lupus*, packs, and individuals aged > 7.5 months, from wolf-year 1980 to 2012, indicating subsets of dead wolves, as described in text.

Wolf-year[a]	Packs	Individual wolves alive			Wolves reported dead, by subset[b]			Wolves missing, by subset[b]	
	n	Minimum	Maximum	Radiocollared	Actively monitored	Unmonitored but collared	Non-radiocollared	Unmonitored but collared	Non-radiocollared
1980	5	25	28	3	2	0	0	1	2.1–2.1
1981	5	20	24	5	1	1	0	0	2.5–2.5
1982	4	23	27	10	2	0	0	4	3.0–3.0
1983	5	19	20	9	3	0	0	4	3.6–3.6
1984	4	18	19	7	1	0	1	5	4.3–4.3
1985	4	14	16	6	2	0	1	1	5.1–5.1
1986	5	15	15	7	1	1	0	0	6.1–6.1
1987	5	18	20	9	0	0	2	2	7.2–7.2
1988	6	26	27	9	0	0	1	0	8.6–8.6
1989	7	31	31	10	1	1	1	0	10.2–10.3
1990	10	34	34	13	1	0	0	3	12.2–12.2
1991	12	39	41	10	2	0	0	2	14.5–14.5
1992	13	45	52	15	3	3	0	1	17.2–17.2
1993	12	40	42	16	4	0	2	1	20.4–20.4
1994	16	54	61	19	0	0	3	2	24.1–24.1
1995	20	83	86	27	3	2	4	4	28.4–28.5
1996	31	99	105	32	4	1	2	7	33.5–33.6
1997	35	148	151	30	2	0	4	7	39.3–39.4
1998	47	178	184	39	7	2	7	6	46.0–46.2
1999	57	205	211	38	4	1	9	6	53.7–53.8
2000	65	248	259	45	4	2	10	2	62.4–62.6
2001	70	257	259	49	9	4	9	4	72.1–72.4
2002[b]	83	327	343	51	13	5	21	4	83.0–83.3
2003	94	335	353	80	16	4	33	14	94.9–95.3
2004	108	373	410	67	12	6	37	13	107.9–108.4
2005	113	435	465	65	12	5	47	10	121.9–122.5
2006	116	467	504	55	10	3	63	8	136.6–137.4
2007	141	540	577	64	11	5	52	16	152.0–152.9
2008	143	537	564	57	17	1	74	8	167.8–168.9
2009	168	626	662	61	13	2	82	9	183.8–185.1
2010	181	690	733	69	14	2	63	10	199.7–201.3
2011	202	782	824	79	16	2	56	8	215.3–217.1
2012	213	815	880	69	19	3	58	11	230.4–232.3

[a]A wolf-year t spans 15 April year $t - 1$ to 14 April year t.

[b]Reconstruction of missing data described in "Materials and Methods" and in Supplementary Data SD3.

because these areas were estimated to contain more wolves, and trapping in such locations might reduce the risk of trapping nontarget species (e.g., dogs). That method also reduced the probability of collaring wolves in peripheral areas of the wolf range or periphery of a territory, when a wolf might be preparing to disperse out of the state (WDNR 2015). Public lands and areas with lower road densities generally had higher densities of wolves (Mladenoff et al. 2009). The WDNR also did not collar many pups in order to avoid injury by constriction as the wolf grew but the collar did not expand. Therefore, pups, loners, dispersers, and wolves beyond known ranges of packs would be underrepresented in the radiocollared sample (Fuller and Snow 1988; Fuller 1989; Fuller et al. 2003). Some wolves were collared after unintentional capture by private trappers or intentional trapping by a government agent following a verified threat to domestic animals or perceived threat to human safety. All the preceding factors might be associated with different risks of different mortality causes (Coffey et al. 2006; Schmidt et al. 2015).

Reported wolf deaths.—We used a number of steps in accessing sources on wolf deaths and in analyzing the data (Fig. 1). The WDNR used 3 sources to find dead wolves: a mortality signal emitted by the VHF transmitter on a radiocollar; instances of government killing as described above for legal causes; or private citizens reporting a dead wolf (Fig. 1, Step 1). The WDNR stopped monitoring if pilots failed to detect a radiocollar during several months of search by telemetry during midaltitude aerial search (Wydeven et al. 2004; Wydeven et al. 2009b). The data in the WDNR mortality records were later supplemented or refined by other agencies. Here, we used information from several sources because no single source contained all mortality records or all the necessary information for each dead wolf. We analyzed records from the following sources: the WDNR wolf mortality database (Supplementary Data SD1), WDNR annual reports (WDNR 2015), unpublished data collected by R. P. Thiel, retired WDNR (Supplementary Data SD1C), the state of Michigan carcass tracking database (Supplementary Data SD2) accessed by the Little River Band of Ottawa Indians through a federal Consent Decree, necropsy records of the WDNR Wildlife Health Program (Supplementary Data SD4A and B), and necropsy information from the National Wildlife Health Center of the United States Geological Survey (Supplementary Data SD5). The WDNR mortality database was the largest data set but it was missing information that could sometimes be recovered from the other sources (Supplementary Data SD1 includes a column identifying which records we reconciled when discrepancies arose between the source data sets).

The pathology databases provided excerpts of transcripts from necropsy, radiographic data summaries for metal remains, and results of laboratory investigations. We examined partial or complete pathology reports from 342 necropsies (36.5%) and 256 radiographs (27.3%) from the complete set of 937 mortality records (Fig. 1, Step 2). We could not access all or complete necropsy reports for all wolves because many were not available in digital form and our participating staff had limited time. Furthermore, the WDNR did not send all carcasses for necropsy. We focused on poaching, thus the pathology reports that we reviewed were not a random subset of all pathology reports; this precludes extrapolation of our pathology conclusions to the entire population.

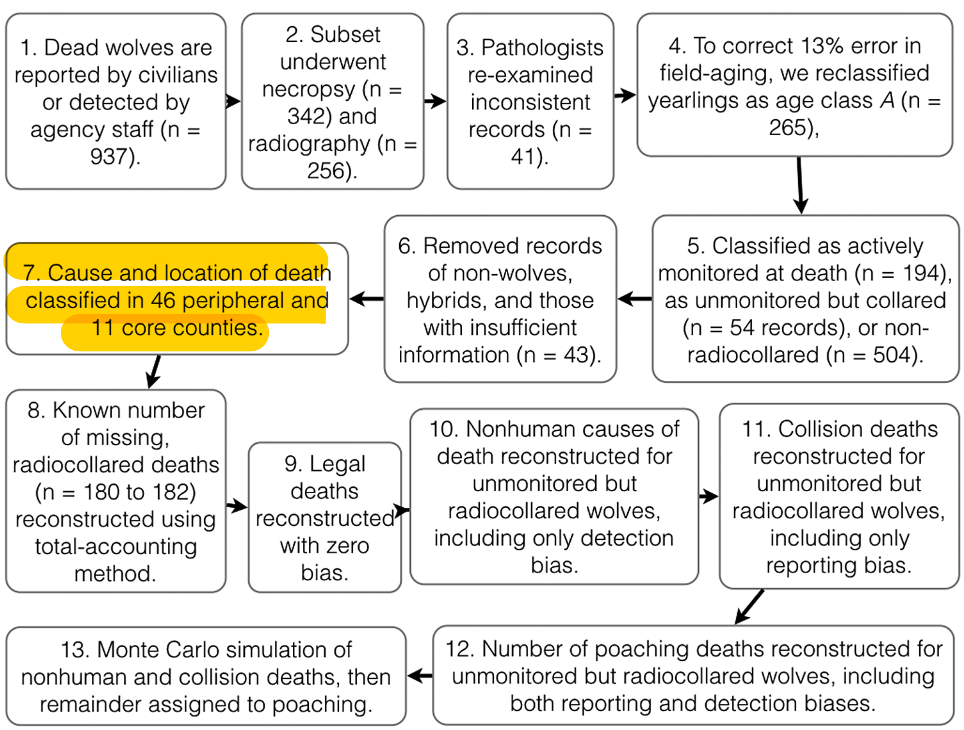

Fig. 1.—Steps for assessing mortality patterns in gray wolves, *Canis lupus*, in Wisconsin, beginning at upper left and proceeding to bottom row, following the arrows. Steps are described in the text and data sources in Supplementary Data SD1–SD5.

We consulted a number of sources because we found ambiguities or missing information (age class, sex, date, cause of death) in 144 (15%) records in the WDNR mortality database. We reconciled these by examining summaries of necropsy records from the National Wildlife Health Center ($n = 56$) and from the WDNR laboratory ($n = 88$). Of those 144 records, 41 were reexamined in detail by one of us (JAL) or other colleagues (Fig. 1, Step 3; "Acknowledgments" and Supplementary Data SD4 and SD5). Another of us (AT) selected those for reexamination based on any 1 of 2 criteria: inconsistencies between sources described above, or if the radiograph revealed metal but cause of death was not attributed to gunshot. Ultimately, the pathologists and veterinarians reinterpreted 19.5 of the 41 (48%) records. When discrepancies remained, we coded a record as 0.5 for each of the possibilities (e.g., because the cause of death was equally likely to have been poaching or vehicle collisions; Supplementary Data SD4A). Gunshot wounds in a carcass were not always visible from field inspection. When collision injury was extensive and severe and metal fragments had also been detected in the tissues, it was difficult to assess any tissue changes associated with the metal fragments that might help determine whether the gunshot happened perimortem or whether it had happened well before the collision. We also are aware that gunshot wounds might have hastened death by starvation, disease, or collision.

Collaring records and some necropsies provided estimates of ages in years for 21 dead wolves that had been radiocollared as pups < 1 year old; other records appeared to classify age in the field as adult, yearling, or pup. WDNR methods for age classifications in the field were not documented and apparently conducted by many individuals independently over years. Veterinarians who performed necropsies classified age based on tooth eruption and wear, body size, and parity. When we compared age classifications of 147 records that were in both the WDNR database and necropsy reports, we found differences in 19 (13%; Supplementary Data SD1A). In virtually every case, the differences were for individuals classified in the field as pups or yearlings but classified in necropsies as older animals, probably because state agents tended to use body size to classify wolf carcasses in the field (Treves et al. 2010). The yearling age class was particularly problematic, so we dichotomized age class at death by time of year as follows: *A* for all those found dead 1 December–14 April or those classified as adults in the field or *P* for small individuals classified as pups in the field and found dead 15 April–30 November (Fig. 1, Step 4). Our approach is consistent with prior work on Northern Rocky Mountain wolves in which causes of death for adults and yearlings were statistically indistinguishable (Murray et al. 2010) and made our estimates compatible with estimates of pup survival to winter (Fuller 1989; Fuller et al. 2003). Ultimately, we reclassified 265 dead wolves as age class *A* based on the criteria above (i.e., wolves aged > 7.5 months). We make no claim for reproductive maturity or social role of wolves classified as *A*.

We classified records into 3 subsets based on radiocollar and monitoring status of the dead wolf as follows: "actively monitored" referred to the subset that was being monitored by radiocollar at the time of death; "unmonitored but collared" for the subset with radiocollars that were not being monitored; and "non-radiocollared" for the subset without radiocollars (Fig. 1, Step 5). Supplementary Data SD2 presents the histories of radiocollared wolves in both the actively monitored and unmonitored but collared subsets. The unmonitored but collared subset included both wolves whose collars had ceased transmitting and those wolves the WDNR stopped monitoring because they could not be detected by aerial or ground telemetry. Mechanical or battery failure is rare in VHF technology generally (Coffey et al. 2006) and specifically in the WDNR reports (WDNR 2015). Dead wolves in the unmonitored but collared subset were occasionally recovered later. But these were found by means similar to non-radiocollared wolves (i.e., visual detection, not radiotelemetry). Thus, a wolf that began "actively monitored" could switch subsets to "unmonitored but collared" but never the reverse. That step improved on traditional methods of "censoring" lost animals because their eventual fate was later determined. That step proved fundamental to our total-accounting method as explained further below.

We discarded records for individuals that were not wolves, such as coyotes (*C. latrans*), dogs, and most wolf-dog hybrids (Fig. 1, Step 6). State agents suspected 57 dead individuals to be hybrids based on field inspection of carcasses during 2003–2012. Of these 57, the WDNR reported conclusions from genetic tests that 14 (25%) were "genetically confirmed" hybrids, 38 (67%) were "genetically confirmed" wolves, and 5 (8%) were "indeterminate genetically"; thus, identifications of hybrids in the field were confirmed genetically to be wolves in two-thirds of cases. We adopted the following rules for suspected hybrids. We retained the record of a death of a suspected or confirmed hybrid, if it was classified *A* age class and believed by field agents to be associated with a wolf pack as noted on the WDNR mortality database. We assumed a canid associating with a wild wolf pack would shed light on mortality causes more than 1 living alone. In sum, we discarded 43 records by the above criteria or because too little information could be found in any database, and we retained 14 (Supplementary Data SD1D).

Cause of death and location.—For every record, we classified the cause of death mutually exclusively as "legal" (lethal control of wolves as described previously), "nonhuman" (disease, other wolves, or accidents that did not seem to involve people), "collision" (massive blunt force trauma by vehicles), "poached" (any other human-caused killing without a permit), or "unknown" (Fig. 1, Step 7). The categories of poached and collision do not necessarily imply human intention. If 2 categories were implicated in 1 record, we assigned the more certain cause (i.e., deleting "unknown"). Unknown causes remained in the data set because not all carcasses underwent necropsy or decomposition precluded definitive diagnosis during necropsy. If we discarded the unknown causes, we would overrepresent known causes (e.g., legal) and undercount the causes that were more difficult to discern in necropsy (e.g., disease, poaching).

Almost all mortality records were accompanied by spatial information (Fig. 2), but precise locations were redacted here to protect wolves and people, by agreement with the WDNR. We assumed a death reported in a county occurred in that county.

When > 1 county was listed, we randomly assigned one of the counties. We defined 46 counties as "peripheral" if they provided fewer records than the median of 29 and 11 counties as "core" that had more records than the median. The median was determined by sorting counties by the number of radiocollared deaths and summing all deaths until 467 (midpoint of the total) was reached. We designated the 1 record with no location recorded and the 30 out-of-state records as peripheral.

Reconstructing missing deaths of unmonitored but collared wolves.—Because we found spatial, temporal, and age-class differences between subsets, we could not uncritically estimate patterns of mortality from any 1 subset, from all records, or from a random selection of records. Had we estimated mortality patterns solely from the deaths of actively monitored wolves, as is traditional, our estimates would have been biased by livetrapping particular age classes in a nonrandom subset of wolf range as described above (Schmidt et al. 2015). To correct the biases within subsets, we reconstructed the missing, unmonitored but collared wolves using a total-accounting method (Supplementary Data SD3).

Although some unmonitored but collared wolves were recovered later when found by means other than monitoring, a sizeable proportion of radiocollared wolves were never recovered. To correct that bias, we had to reconstruct the missing deaths (Fig. 1, Step 8). We began with the total number of radiocollared wolves that had ever been collared in Wisconsin (Supplementary Data SD2) and removed the numbers of living, monitored radiocollared wolves and reported dead radiocollared wolves from that total. We also had to estimate the number of radiocollared wolves that might still be alive but were unmonitored at the time of writing (Supplementary Data SD3). With the remainder composed of the estimated number of missing radiocollared deaths, we reconstructed the causes of those deaths (Fig. 1, Step 9).

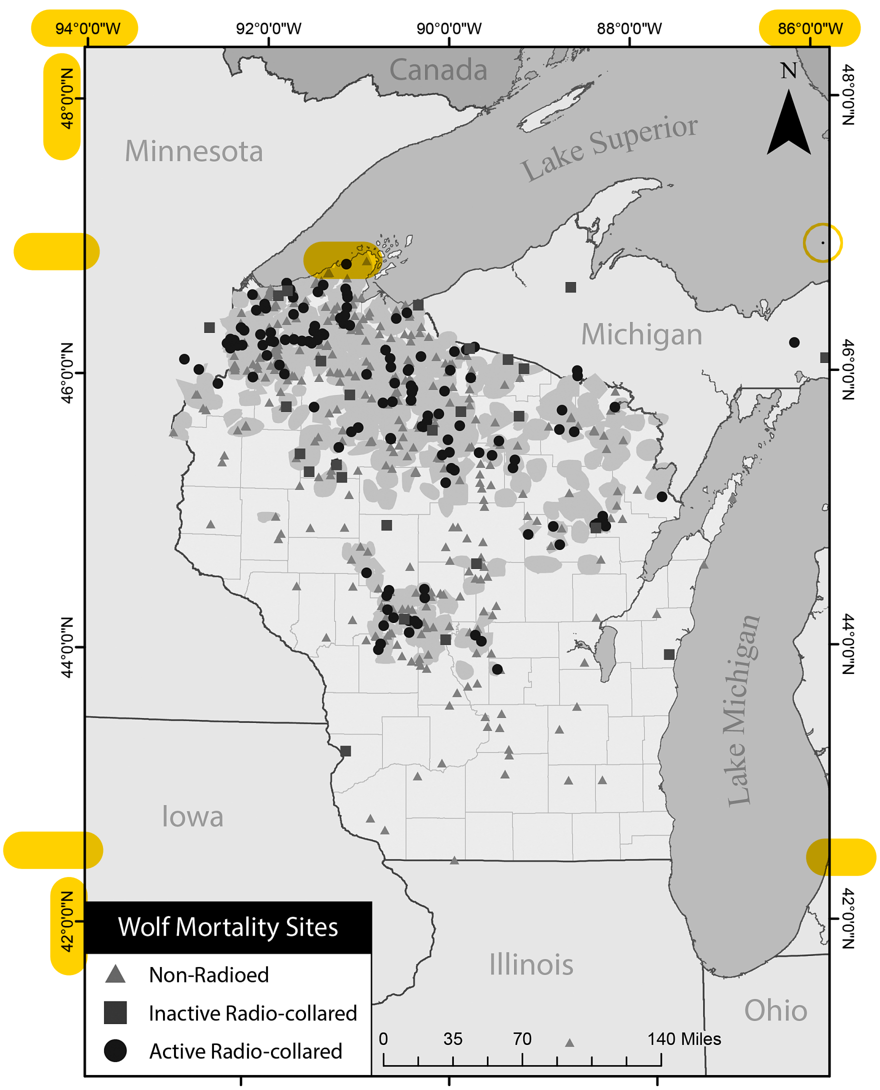

Fig. 2.—Gray wolf, *Canis lupus*, death sites (n = 653) reported in 3 subsets across Wisconsin for wolf-years 2000–2012. We excluded records without GPS locations, most of which preceded wolf-year 2000. Counties are shown with gray boundaries within Wisconsin. Gray polygons are estimated wolf pack territories (WDNR 2015). Subsets include age class *P* and were actively monitored (active), unmonitored but collared (inactive), or non-radiocollared deaths.

Total accounting for unreported deaths and the roles of detection and reporting biases.—We assumed state governments reported all legal causes of wolf death in Wisconsin and its neighboring states of Michigan and Minnesota during the study period (Fig. 1, Step 10). That assumption is consistent with the legal procedures involved (Refsnider 2009), and it is supported by several other procedures in the region, namely that field staff reported legal deaths to central authorities, and radiocollars had state identifiers, so neighboring states reported to Wisconsin when a radiocollared wolf was killed legally (WDNR 2015); interstate communications were well established (Wydeven et al. 2009a), and all states worked with the same federal agency to implement most wolf-killing (Ruid et al. 2009). Unlike legal causes, other causes of death were not recorded perfectly.

Detection bias or reporting bias both introduced uncertainty into the mortality data because deaths of unmonitored wolves might go undetected and some causes (such as poaching) were unlikely to be reported. Also, poaching might change a wolf from actively monitored to unmonitored if the VHF transmitter was removed or damaged. Obviously, the WDNR monitored wolves to improve detection and reporting. We assumed that wolves in the actively monitored subset would experience no detection or reporting bias—although that subset experienced the sampling biases and the age-class and other biases in measurement described previously. When monitoring ended for wolves, detection bias began. For non-radiocollared wolves, detection bias began at birth of course. By contrast, when a radiocollared wolf disappeared and changed subset from actively monitored to unmonitored but collared, both detection and reporting biases might then apply to its death. For example, a poacher might report a dead wolf or not; passersby might detect a carcass or not. However, the actively monitored subset by itself produced biased estimates of mortality patterns because of missing deaths of the unmonitored but collared wolves, which was not random with regard to cause of death (e.g., legal causes being perfectly reported and poaching having a low likelihood of reporting).

In summary, we assumed detection and reporting biases were zero for the actively monitored subset for every cause of death because they were either monitored and found or unmonitored and the wolf became part of the unmonitored but collared subset. Only the unmonitored but collared and non-radiocollared subsets contained detection bias. Furthermore, some deaths due to poaching and collisions might also be missed due to reporting bias. Our separation of the 2 components of bias allowed us to reconstruct unreported deaths with greater certainty as we explain below.

Cause-specific bias in mortality records.—We assumed that humans had not tampered with radiocollars of wolves that died of a nonhuman cause because people were not involved in such deaths. We also assumed wolves dying of nonhuman causes almost never died in such a way as to inactivate their radiocollars. Further, we assumed radiocollared wolves died of nonhuman causes at the same rates whether monitored or unmonitored, an assumption of virtually all telemetry studies (Coffey et al. 2006). We did not assume nonhuman causes affected radiocollared and non-radiocollared wolves equally, because this assumption was recently shown to be false in an Alaskan population (Schmidt et al. 2015). Nevertheless, the latter assumption is more fragile than the first 2 because monitoring might end when a wolf dispersed. However, departures from that assumption for nonhuman causes of mortality specifically would tend in the direction of higher human-caused mortality, especially poaching (Liberg et al. 2012), rather than higher nonhuman causes. That is because the unmonitored but collared subset of dead wolves was found more often in peripheral counties where human-caused mortality predominated (Wydeven et al. 2001; “Results”). Therefore, our assumption was conservative because it assumed higher rates of nonhuman causes of mortality in unmonitored wolves and lower rates of human-caused mortality in unmonitored wolves. With the preceding 3 assumptions we could reconstruct a credible range of values for nonhuman causes of death for the missing, unmonitored but collared wolves (Fig. 1, Step 10; Supplementary Data SD3 for the mathematical calculations). Note we did not attempt to reconstruct cause of death for non-radiocollared wolves—although the same logic applies—because of the original sampling bias in the radiocollared subset that precludes firm extrapolation to non-radiocollared wolves.

For wolves that died by collision or poaching, we expected a reporting bias (Fig. 1, Step 11). We assumed that virtually all humans would detect a death or life-threatening injury when their vehicle collided with a wolf even if they did not realize it was a wolf. Therefore, we assumed detection bias was negligible for collisions. We predicted that reporting bias for vehicle collisions would be lower than detection bias for nonhuman causes in unmonitored wolves and lower than the combination of detection bias and reporting bias for poached wolves. We make that prediction for 3 reasons that shed light on the distinctions between the 2 types of bias. Drivers might report a collision with a wolf because there were no legal repercussions for doing so, unlike those for poaching. If a driver did not report a collision death, then common travel paths increased the probability of reports by subsequent passersby. Finally, most Wisconsin counties contracted citizens or wildlife agents to remove roadkill (McCaffery 1973). In sum, we treated detection bias as zero for collisions that killed wolves and missing deaths were attributable to reporting bias (Fig. 1, Step 11; Supplementary Data SD3 for the mathematical calculation of missing collision deaths among unmonitored but collared wolves).

Both reporting bias and detection bias would apply to many incidents of poaching. As above, we predicted poaching would have higher reporting bias than vehicle collisions because perpetrators might fear legal repercussions. After incidents of poaching, subsequent detection bias by other people would be lower than for collisions or nonhuman causes of death, because poachers might conceal evidence and poach in less-traveled locations. We expected some self-reporting of poached wolves because accidental killing might occur in the course of trapper bycatch, or mistaking wolves for coyotes or free-running dogs, both of which can be legally shot in many circumstances in Wisconsin. Voluntary admission of such errors never resulted in prosecution during our study period (Refsnider 2009; WDNR 2015). Our analytical task for reconstructing missing poaching deaths was simplified by the prior steps that took into account all other causes of death. We could therefore assign the remainder of missing, unmonitored but collared wolf deaths to poaching (Fig. 1, Step 12; Supplementary Data SD3 for the mathematical calculation of missing poaching deaths and estimation of detection and reporting biases for each cause of death).

In summary, we had 2 reliably estimated parameters for mortality patterns (legal causes in the radiocollared subset and nonhuman causes in the actively monitored subset), which allowed us to reconstruct missing deaths of unmonitored but collared wolves that consisted of undetected nonhuman deaths, unreported collision deaths, and poaching that entailed both undetected and unreported deaths.

We then conducted a Monte Carlo simulation to estimate the number of missing deaths by each of the 3 causes in sequential steps (Fig. 1, Step 13). That simulation addressed the uncertainty in the exact number of missing, dead, unmonitored but collared wolves and the uncertainty created by the unknown causes of death in the actively monitored subset (Table 2). Our procedure was also robust to the uncertainty about migration of wolves.

Migration.—Wolves radiocollared in Wisconsin occasionally crossed state boundaries and some of these died out-of-state. Eight radiocollared Wisconsin wolves died in Michigan out of a total of 264 with known fates (3%; Supplementary Data SD1B and SD2). Also, 26 radiocollared Michigan wolves died in Wisconsin out of a total of 191 with known fates (13%) from that state's mortality data. So the net immigration of 18 radiocollared wolves from the 2-state total with known fates represented net immigration of 4% into Wisconsin from Michigan.

Another 19 radiocollared Wisconsin wolves died in Minnesota (7% calculated as above) and 2 collared Minnesota wolves died in Wisconsin. The pattern of migration between Wisconsin and Minnesota could reflect either net emigration or that radiocollared, Minnesota wolves lived comparatively farther from the border with Wisconsin than did radiocollared Wisconsin wolves. We could not resolve these alternatives, but the latter seems more likely, given the wolf population in Minnesota was at least twice as large as that in Wisconsin throughout the study period (USFWS 2015) and recolonization from Minnesota is supported by more evidence (Thiel 1993).

We compared the relative risks (percentage of all reported mortality attributable to each of the 5 causes of death) among radiocollared migrants to and from Wisconsin to the relative risks faced by radiocollared wolves that died in-state, so as to evaluate if our total-accounting method was robust to the uncertainty caused by wolf migration.

Statistics and compliance.—We present measures of variability as ± *SD* throughout. We used median tests to compare central tendencies and distributions, and chi-square tests for comparisons of proportions between categorical variables. We used proportional hazards analysis to examine time-to-death or disappearance or date of death events within a year. In proportional hazards models, we included cause of death, sex, subset, state lethal control authority (binary variable indicating whether the state could kill wolves for perceived threat to property or future human safety), and county (central or peripheral); unknown causes were treated as censored, $n = 42$. All tests were conducted in JMP (SAS Institute 2013).

This study conforms to the guidelines of the American Society of Mammalogists (Sikes et al. 2011) as well as to

Table 2.—Numbers and causes of deaths reported and reconstructed for Wisconsin gray wolves, *Canis lupus*, aged > 7.5 months, from wolf-year 1980 to 2012[a].

Wolves	Actively monitored	Unmonitored but collared[b]	Unmonitored but collared[b]	Non-radiocollared
Alive by 15 April 2012 (L)	38	3	2	774–776
Sum of reported deaths (O)	194	56	56	504
Reported, legal cause	25	2	2	156
Reported, nonhuman cause	59	10	10	27
Reported, collision cause	21	14	14	192
Reported, poaching cause	70	20	20	107
Reported, unknown cause	19	10	10	22
Sum of missing deaths to reconstruct (M)	0	180.4	181.5	1,986.0
Reconstructed, legal cause	0	0	0	?
Reconstructed, nonhuman cause	0	55.5[b]	84.1[b]	?
Reconstructed, collision cause	0	19.4	19.5	?
Reconstructed, poaching cause	0	105.5	77.9	?
Detection bias, nonhuman cause[c]	0	85%	81%	?
Reporting bias, collision cause[c]	0	58%	58%	?
Detection + reporting biases, poaching cause[c]	?	84%	80%	?

[a]Wolf-years begin 15 April year $t - 1$ and end 14 April year t; reported deaths from Supplementary Data SD1A–D; reconstructions from Supplementary Data SD3.
[b]Left column treated unknown causes of death separately, whereas the right column treated unknown causes as nonhuman causes, which is a clear overestimate (see "Discussion").
[c]Biases are expressed as a % of all radiocollared mortalities (reported + reconstructed).

relevant institutional requirements. Neither live animals nor human subjects were studied.

Results

Between 12 October 1979 and 14 April 2012, 907 wolf deaths were reported in Wisconsin and 30 Wisconsin wolves died out-of-state (Supplementary Data SD1A–C). Of the 937, we assigned 150 to age class *P*, 783 to age class *A*, and 4 to unknown age class. Age class *A* included 357 females, 399 males, and 27 unsexed due to decomposed carcasses or inadequate records. Every wolf-year, reported deaths represented 3–21% (mean 11% ± 4%) of the minimum population estimate (Table 1). Legal causes were not biased by whether a wolf was collared because radiocollared wolves comprised 13% (n = 183) of legal causes and also averaged 13% of the population in the years with legal causes (wolf-year 2002 onward; Table 1).

Among the 754 in-state deaths reported for age class *A*, we analyzed 250 that were radiocollared, including 194 actively monitored, 56 unmonitored but collared, and 504 non-radiocollared (Supplementary Data SD1A and SD2). The reported deaths in the radiocollared subsets had higher percentage *A* than the non-radiocollared subset (94% and 79%, respectively; Fisher's exact P < 0.0001). Sex did not differ between radiocollared deaths and non-radiocollared subset (52% and 53% females, respectively; P = 0.91), but sex differed within age-class *A* (53% radiocollared females compared to 47% non-radiocollared females $d.f.$ = 1, χ^2 = 8.8, P = 0.009). Among the 21 deaths of known age wolves in age class *A*, we found our 5 categories of cause did not vary by age in years (Supplementary Data SD2; median test 1-way, $d.f.$ = 1, χ^2 = 3.6, P = 0.45; legal causes n = 2, median age 4 years, nonhuman causes n = 9, median age 4 years, collision n = 3, median age 6 years, poached n = 4, median age 3 years, unknown n = 3, median age 3 years). Therefore, our technique for pooling wolves > 7.5 months of age did not appear to bias our analyses.

Dead wolves of both age classes were reported in 57 Wisconsin counties (radiocollared subsets in 63% of the counties and the non-radiocollared subset in 95%, $d.f.$ = 1, χ^2 = 9, P < 0.01; Fig. 2). Overall, 601 (65%) deaths occurred in 11 core counties, whereas the remainder occurred in 46 peripheral counties or out-of-state. In the actively monitored subset, 78% of deaths occurred in the 11 core counties compared to 38% in the unmonitored but collared subset ($d.f.$ = 1, χ^2 = 25, P < 0.0001; Fig. 2). When we combined the actively monitored and the unmonitored but collared subsets, we found no difference between the occurrences of radiocollared and non-radiocollared deaths in core counties (65% and 64.5%, respectively). Therefore, pooling the radiocollared subsets would seem to correct partially the geographic sampling bias caused by radiocollaring, but not the detection, sex, and age biases we identified.

Pathology reports.—Subsets differed significantly in the proportions of carcasses that underwent necropsy: 160 of 295 (54%) radiocollared compared to 163 of 638 (26%) non-radiocollared ($d.f.$ = 1, χ^2 = 62, P < 0.0001). In 256 radiographic records, 31 showed metal but the wolf died of legal cause (i.e., state agent shot a livetrapped wolf) and 6 showed metal that was likely within the gastrointestinal tract suggestive of ingestion (Supplementary Data SD4 and SD5). In the remaining 219 radiographic records, veterinarians identified healed gunshot wounds in 8 wolves (4%)—evidenced by bone remodeling or closed wounds around metal fragments—but the wolves died later from other causes. Including those eight, 21 wolves died of causes other than gunshot but bore evidence of noningested metal (nonhuman n = 2, collision n = 19; Supplementary Data SD1). The absence of metal in radiographs was also revealing. In 74 of 256 radiographs (29%) veterinarians did not find metal: 3 legal (9% of legal deaths that were radiographed), 29 nonhuman (94%), 32 collision (63%), 3 poached (2%), and 7 unknown (100%; Supplementary Data SD1). Therefore, the vast majority of poaching was by gunshot and more than one-third of collisions were associated with some old or recent gunshot, which might have been perimortem. The latter suggest vehicles might have been used as weapons. Possibly, 6% of nonhuman deaths actually did involve people, given the radiographic evidence.

The veterinarians' reexaminations of 41 necropsy reports revealed 14.5 (35%) that required reclassification of cause of death. Veterinarians were conservative about assigning a definitive cause of death, so half of the reclassifications simply changed the category from nonhuman to unknown. However, 7 wolves were reclassified as having died from gunshot after a different attribution by the WDNR, and 1 wolf death appeared incorrectly attributed to gunshot (Supplementary Data SD4A and SD5). The net underreporting of 6 (15%) poached in these 41 cases should not be extrapolated because we focused on discrepant records or gunshot evidence. Interpretation of gunshot trauma was often complex. For example, the database included a wolf whose ultimate cause of death was ruled to be sarcoptic mange by the WDNR, but the examining pathologist noted,

> It seems likely that 2 kinds of previous trauma debilitated this wolf [WI-2007-077] (as seen by its emaciated state) and predisposed it to developing severe mange: chronic severe injury to the foot, associated with being trapped 6 months before death, and resolving, but significant injury around the lumbar vertebral column, apparently associated with being shot. (Supplementary Data SD4A)

JAL estimated the above injury, which included a chip fracture to a vertebra, was weeks old. We reclassified the wolf as poached because it was debilitated by illegal trapping and gunshot (Supplementary Data SD4A).

Causes of death and total accounting.—In Table 2, we present cause of death for wolves in age class *A*. We estimated that deaths of 180–182 unmonitored but collared wolves went unreported or 42% of dead radiocollared wolves (Supplementary Data SD3). Among all radiocollared wolves, legal causes of death posed a relative risk of 6.3% (Table 3). We estimated the relative risk of nonhuman causes in all radiocollared wolves (reported + missing) at 29–42% (Table 3), where we reconstructed the missing using Monte Carlo simulation (Supplementary Data SD3). We expect the upper bound is an overestimate, because, in reality, not all unknown causes would be nonhuman causes. We estimated the relative risk of collisions at 13% in all radiocollared wolves (reported + missing). We estimated the relative risk of poaching at 39–45% in all radiocollared wolves (reported + missing; Table 3; Supplementary Data SD3). The maximum of that range (45%) is also a likely underestimate for the reasons described above relating to necropsy and radiography revealing net underestimates of poaching exceeding 6%.

Migration.—For the 30 known migrants, all but one of which had a radiocollar (Supplementary Data SD1B), we estimated the relative risks of mortality as follows: legal 10%, nonhuman 24%, collision 16%, poaching 40%, and unknown 10%. We found no difference between those estimates and the relative risks reported for the monitored subset that died in-state (13%, 30%, 10%, 37%, 10%, respectively, *d.f.* = 4, $\chi^2 = 2.0$, $P = 0.73$; Table 2). Therefore, it appeared that we could reconstruct missing radiocollared wolves as if they had died in Wisconsin even though some might have died out-of-state. That suggests our total-accounting method was robust to uncertainty caused by migration.

We estimated detection bias for the reported + missing dead wolves. For nonhuman causes of death among unmonitored but collared wolves, detection bias was 81–85% (Table 2; Supplementary Data SD3). For collisions involving the unmonitored but collared wolves, reporting bias was 58%, which was lower than the detection bias for nonhuman causes, as predicted. For poached wolves among the unmonitored but collared wolves, reporting bias was 80–84% (Table 2). Pooling all radiocollared dead wolves, whether monitored or not and reported + missing, we estimated that radiotelemetry and other reports of wolf deaths reduced the reporting bias for poached wolves to 46–54%.

Timing of death.—We found no evidence that the percentage of reported deaths correlated to the percentage of unreported deaths annually (Table 1; Supplementary Data SD3). We estimated the average annual mortality rate (hazard rate) over the study period at 18% ± 10% for actively monitored wolves and a minimum estimate of 47% ± 19% for all unmonitored wolves (Table 1; Supplementary Data SD3). The distributions of mortality hazard rates for actively monitored and for unmonitored wolves do not overlap, demonstrating significantly different hazard rates for non-radiocollared wolves in Wisconsin. We estimated a weighted mean for the 2 estimates for a total annual mean hazard rate of 38–41% (*SD* 10%). During the study period, the wolf population grew at an annual mean rate of 1.13 ± 0.18 (N_{t+1}/N_t), which declined over time to 1.09 ± 0.07 in the last 5 years (Table 1).

Excluding unknown causes of death, we found the monthly distributions of reported deaths differed by cause ($n = 705$, *d.f.* = 33, $\chi^2 = 306$, $P < 0.0001$; Table 4). Namely, 70% of poached wolves were recorded November–April (*d.f.* = 33, $\chi^2 = 29$, $P = 0.002$), with November alone accounting for 27%. Also, the radiocollared records differed in monthly distribution of deaths from the non-radiocollared subset ($n = 705$, *d.f.* = 11, $\chi^2 = 66$, $P < 0.0001$; Table 4), where the winter months of November–April revealed more non-radiocollared wolf carcasses (sum of monthly *d.f.* = 11, $\chi^2 = 56.4$). Poaching explained these monthly differences between subsets ($n = 221$, *d.f.* = 11, $\chi^2 = 19$, $P = 0.035$), but not legal causes (*d.f.* = 11, $\chi^2 = 14$, $P = 0.17$), nonhuman (*d.f.* = 11, $\chi^2 = 16$, $P = 0.15$), nor collisions (*d.f.* = 11, $\chi^2 = 12$, $P = 0.37$). Comparing the timing

Table 3.—Relative risk of mortality for reported deaths plus reconstructed deaths of all Wisconsin radiocollared gray wolves from wolf-year 1980 to 2012 from Table 2.

Cause of death	Relative risk as % of mortalities[a]	Relative risk as % of mortalities[a]
Legal cause	6%	6%
Nonhuman cause	29%	42%
Collision cause	13%	13%
Poaching cause	45%	39%
Unknown cause	7%	0

[a]The left column treated unknown causes of death separately, whereas the right column treated unknown causes as nonhuman causes of death, which is an overestimate (see "Discussion").

Table 4.—Monthly numbers of deaths of Wisconsin gray wolves, *Canis lupus*, aged > 7.5 months, from wolf-years 1980 to 2012 in 3 subsets (active = actively monitored; inactive = unmonitored but collared; non-radioed = non-radiocollared)[a].

Month[a]	Legal cause of death			Nonhuman cause of death			Collision cause of death			Poaching cause of death		
	Active	Inactive	Non-radioed	Active	Inactive	Non-radioed	Active	Inactive	Non-radioed	Active	Inactive	Non-radioed
1	0	0	0	16	3	6	2	1	16	8	1	9
2	0	0	1	7	1	2	2	3	23	7	6	8
3	0	0	7	5	0	4	2	1	17	2	1	14
4	3	0	18	2	1	6	0	1	27	5	0	17
5	2	1	36	2	0	3	1	1	17	4	3	5
6	4	0	13	1	0	0	1	0	10	0	0	0
7	5	0	23	2	0	1	2	0	16	2	1	5
8	3	1	30	3	0	1	2	3	13	0	1	2
9	1	0	15	3	0	0	5	1	10	3	2	3
10	5	0	11	1	0	0	2	1	21	6	0	10
11	1	0	2	6	1	2	1	1	13	24	3	29
12	1	0	0	11	4	2	1	1	11	9	2	5

[a]Wolf-years start 15 April year $t - 1$ to 14 April year t; 1 = January, 2 = February, etc.

of poaching in the actively monitored and unmonitored but collared subsets, we found no differences in monthly distributions (n = 221, $d.f.$ = 11, χ^2 = 16.6, P = 0.12). Either poachers killed radiocollared and non-radiocollared wolves at different times of year or reporting bias differed across the year.

We calculated the number of days until death after the start of each wolf-year (means for legal causes 118 ± 143 days or 7 August; nonhuman 228 ± 142 days or 26 November; collision 179 ± 275 days or 7 October; and poaching 207 ± 236 days or 5 November). Proportional hazards analysis revealed 2 significant predictors of the number of days until death (cause of death $d.f.$ = 4, χ^2 = 118, P < 0.0001 and whether the state had lethal control authority or not: $d.f.$ = 1, χ^2 = 17, P < 0.0001; whole model $d.f.$ = 9, χ^2 = 135, P < 0.0001). We also calculated the number of days between radiocollaring and known fate (means for legal causes 461 ± 612 days, nonhuman 685 ± 723, collisions 778 ± 832, poached 558 ± 539, and disappearances 529 ± 762).

Discussion

Humans caused at least two-thirds of the deaths of radiocollared gray wolves in Wisconsin from 1979 to 2012. Poaching predominated at a minimum, relative risk of 39–45% of all deaths, which was an underestimate as we explain below. Our best estimate for mean per capita mortality rate for wolves across the 33-year study period was an annual 38% and possibly 41% (SD 10%) with unmonitored wolves experiencing more than 20% higher mortality rates than monitored wolves. Our mean values are higher than official estimates after 2012.

Comparison with prior research.—Our estimate of mortality rate overlaps the state estimate given in 2012 of 32–47% for a similar time period (Natural Resources Board 2012). However, subsequent state estimates declined 8–19% when one compares human-caused mortality rates before and after the 2012 and 2013 hunting and trapping seasons. The decline was not explained and was reported without data on reproduction (Natural Resources Board 2012, 2014).

Our estimate of the relative risk of poaching compared to other causes of death exceeded the official estimate in 2012. The state reported relative risks of 34% for poaching (5–11% lower than our estimate which we documented to be a minimum), 12% for legal, lethal control (6% higher than our estimate), 9% for vehicle collisions (4% lower than our estimate), and 45% "natural" and "other and unknown causes" which were not defined (Natural Resources Board 2012). The latter value was 3–9% higher than our estimate for the relative risk of nonhuman and unknown causes summed (Table 3). We find the WDNR decision to pool nonhuman and other causes dubious because it created a category with the plurality of causes of death but presented no evidence the causes were similar to each other. Furthermore, we find their estimates contained a number of important biases.

The 1st bias arose because the WDNR did not correct for sampling biases in radiocollaring, which we identified here. In the mortality data, the radiocollared wolves were disproportionately female and older residents that died in core wolf range compared to the majority, non-radiocollared wolves. That sampling bias overestimated survival. Second, the WDNR wolf mortality database had the following measurement biases: 15% of the records had missing or ambiguous data fields, 13% misclassified age, and a notable proportion did not account for necropsy or radiography data properly. For an example of the latter, our nonrandom subset of necropsies and radiographs indicated that 6% of nonhuman deaths and 37% of collision deaths included perimortem or premortem gunshot that was not a result of legal killing, and 16% of the cases we reevaluated in detail were found to be unreported poaching. We cannot extrapolate to the entire sample; however, fewer non-radiocollared wolf carcasses underwent necropsy than radiocollared carcasses, therefore, poaching rates are likely to be higher. Relating to age misclassifications, WDNR estimates from 2012 to 2014 (Natural Resources Board 2012, 2013, 2014) relied on an unpublished Ph.D. dissertation that did not account for age discrepancies adequately (Stenglein 2014). Namely, Stenglein (2014) concluded that poachers took "yearlings" disproportionately but did not define "yearling" or detect the 13% discrepancy in age classification we found. We surmise those "yearlings" referred to wolves aged 7.5–19.5 months. Many of these animals might have been reproductive (Stark and Erb 2013). Thus, we cannot agree with Stenglein's (2014, 2015) conclusion that poaching was removing animals that would not contribute much to population growth. Because we estimated > 2,167 wolves aged > 7.5 months had died unreported over our 33-year study period and the majority of those were poached (Tables 2 and 3), we infer the size of the wolf population was reduced primarily by poaching. Indeed, from 2008 to 2012, population growth slowed by 4% on average despite 4% net immigration from Michigan.

Our conclusion is also consistent with the Swedish wolf study by Liberg et al. (2012). Indeed, our (under)estimate of the relative risk of poaching resembled the Swedish estimate of 51% of all mortality causes (Liberg et al. 2012). By contrast, Strenglein and colleagues from the WDNR (2015) pooled data from radiocollared wolves in Wisconsin regardless of whether they had been monitored or not, which neglects the lessons of Liberg et al. (2012) about cryptic poaching and the important distinction between detection and reporting biases that we report here and discuss below.

Cryptic poaching.—Poaching was the single largest category of cause of death for wolves in our study and unreported poaching dominated that cause (Tables 2 and 3). Unreported wolf mortality is not new. Adams et al. (2008) reported 73% of "harvested" wolves were not reported to the state authorities. Both reported poaching and unreported poaching merit deeper scrutiny because we found no correlation between annual rates of the 2. Therefore, estimating poaching rates from only the reported cases seems incorrect, contra Olson et al. (2014). We also found reported poaching peaked in the winter months primarily because non-radiocollared wolves were reported poached more often in those months. It remains unclear if that seasonal pattern would hold for unreported poaching because we did not attempt to reconstruct month of death for missing, radiocollared wolves. Regardless, we recommend against isolating data for each winter and correlating it with the events preceding or following it as Olson et al. (2014) did. By definition, winter months with more reported poaching both follow and precede summers, the time in which wolf-culling by the state was more likely in Wisconsin. Therefore, their conclusion that culling reduced poaching is just as likely as poaching reduced culling, and neither can be supported without statistical control over the time series underlying wolf population dynamics and human wolf-killing patterns. We did so in a separate analysis that indicated that legal wolf-culling did not reduce illegal wolf-poaching (Chapron and Treves 2016). Finally, until the majority category of unreported poaching is better understood, evaluating interventions will be impossible.

Our study adds to our understanding of unreported poaching. Liberg et al. (2012) estimated that two-thirds of Swedish wolf-poaching was cryptic (undetected by government monitors and unreported by the public) based on disappearances of wolves subject to intensive and extensive monitoring (previously discussed in the Introduction). We estimated that 80–84% of poached, unmonitored but collared wolves went undetected and unreported (Table 2). This seems higher than in Sweden but the difference may reflect less frequent monitoring of wolves in Wisconsin. Reporting bias may also reflect legal differences between the regions. Some unreported poaching in Wisconsin may be unintentional, because in many areas much of the year, one could legally kill the similar-appearing coyote without reporting deaths. Thus, poaching without reporting may be more likely in Wisconsin. Yet we can extract added information from the mix of monitored and unmonitored wolves and their reported and unreported deaths.

The percentage of all radiocollared wolves (monitored or not) estimated to have been poached but never reported was 50% (Table 2). We infer that radiotelemetry or other forms of reporting revealed half of the poached, radiocollared wolves. This value of 50% and that of 82% above bracket the Swedish estimate of 67% and suggest that 32% of unreported poaching would have been detected had monitoring continued for the missing, radiocollared wolves. More broadly, most governments cannot afford to monitor their carnivores as intensively as Sweden did for its wolves. Therefore, the role of unreported poaching is likely to be a concern for most governments attempting to conserve large carnivores. Furthermore, the absolute magnitude of underestimation of poaching should be a significant concern for many governments as we explain below.

Over our study period, 54% of all radiocollared wolves in Wisconsin died unmonitored (Table 2), so not only was unreported poaching the major cause of death among our 5 categories, it was also the major source of uncertainty in the radiocollared sample, which is the basis for all published population dynamic studies in Wisconsin since 1995 (Wydeven et al. 1995). It may take years to evaluate if wolf population dynamics in Wisconsin were estimated accurately.

Underestimated poaching.—We believe we underestimated poaching in this study because of evidence from migration, unreported poaching, and unmonitored wolves. It is believed that more wolves immigrated into Wisconsin than emigrated to Minnesota since 1978 (Thiel 1993). We showed that substantially more wolves immigrated into Wisconsin from Michigan than emigrated to Michigan from Wisconsin. The resulting net immigration into Wisconsin during our study might have resulted in additional dead wolves that were not radiocollared, so adding to the real hazard rate for non-radiocollared wolves. Second, we found unaccounted poaching when reviewing a nonrandom subset of necropsies. There was abundant evidence of attempted poaching in the form of sublethal gunshot wounds. For example, over one-third of vehicular collisions included perimortem or premortem evidence consistent with poaching. Overall, 20% of wolves had evidence of gunshots that did not kill the wolves (n = 52 of 256 radiographed). For comparison, Liberg et al. (2012) reported 12 of 87 (14%) Swedish wolves had old, healed gunshot wounds. Third, the mean interval between radiocollaring and disappearance of missing wolves was closer to the mean interval between collaring and poaching (29 days) than it was to the mean interval between collaring and collision or nonhuman causes (202 days, using the median of the 2 mean durations). Finally, our total-accounting method included an assumption that would underestimate poaching in missing wolf deaths by overestimating nonhuman causes (Supplementary Data SD3). We treated disappearances of radiocollared wolves as if monitoring had ceased *before* death had occurred. We then assigned cause of death for nonhuman causes first, then collision, and finally only poached wolves remained by definition. However, some disappearances of radiocollared wolves might have been caused by poachers, which would be underestimated by our method.

We also believe we underestimated mortality hazard rates for non-radiocollared wolves (Table 1; Supplementary Data SD3). The nonoverlapping distributions of mortality hazard rates for radiocollared and non-radiocollared wolves probably reflect differential hazard rates in core and peripheral counties because monitored wolves were disproportionately found dead in core counties (Fig. 2). People killed wolves at higher rates in the periphery of their range in our study and in others (Murray et al. 2010). In sum, we have several reasons to expect poaching to have been higher than we reported and much higher than official estimates. Therefore, our findings raise 2 concerns. The first is a concern about Wisconsin wolf policy implemented subsequent to April 2012 because wolf-hunting quotas were not set at sustainable levels. Second, and more generally, wolf-hunting quotas and liberalized culling appear risky wherever one lacks reliable estimates of poaching.

Why estimating poaching accurately and precisely is important.—In numerous countries, including the United States, wolves are a public trust asset, which means the government is accountable to the broad public interest to preserve and regulate the exploitation of wolves, as a trust for the benefit of current and future generations not narrow interests (Sax 1970; Blumm and Guthrie 2012; Treves et al. 2015). That trustee obligation recognized since 1842 by the United States Supreme Court carries with it normative imperatives for all branches of governments, as well as wildlife managers, scientists, and the diverse beneficiaries of wildlife assets. Government trustees, including the lead author and other publicly funded scientists, have a duty to account transparently for legal and illegal uses of public assets (Smith 2011; Treves et al. 2015). That accounting duty should include sophisticated and careful measures of uses of the asset (Sax 1970; Sagarin and Turnipseed 2012). Without estimates of mortality and births that are unbiased, precise, and accurate (approximating the true values with high certainty), policies that promote the killing of wildlife will risk unsustainable mortality and raise the probability of a population crash. The current government of the state of Wisconsin risked that crash when it issued high wolf-hunting quotas and when it liberalized culling from 2012 to 2014, both done without presenting careful, transparent accounting of mortality and births (Natural Resources Board 2012, 2013, 2014). From a late-winter wolf population estimated at 779 adults outside of Native American reservations in April 2012, private hunters and government trappers legally killed ~119 or 15% of the wolf population aged > 7.5 months—approximate because pups were reportedly killed as well (Macfarland and Wiedenhoeft 2013). In 2013, the state increased the quota without presenting evidence for reproduction or poaching after the first hunt, and did so with inadequate accuracy (this study) and analysis of mortality patterns that did not conform to standards of the best available science (Treves et al. 2014). The following year, the state permitted killing of ~160 additional wolves aged > 7.5 months or 21% of the ~775 wolves outside tribal reservations in April 2013 (Macfarland and Wiedenhoeft 2013). Clearly, these policies did not preserve the principal of the trust asset which was > 814 wolves in April 2012 after the federal government relinquished authority to the state of Wisconsin. Yet at present, it is impossible to evaluate the outcomes of these wolf-killing policies because the state became less transparent over time (Treves et al. 2015). Therefore, we presented the raw data to promote public debate and accountability based on peer-reviewed evidence.

Recommendations beyond Wisconsin and beyond wolves.—For an adequate representation of the patterns of mortality in large carnivores, one needs information from recovery of unmarked carcasses as well as those marked and monitored. Our total-accounting method is 1 approach but has limitations because it demanded 2 data streams that may not always be available. First, one needs a moderate sample of marked animals that die of nonhuman causes, and second, a component of the mortality spectrum that is perfectly reported. Reporting bias will remain a confounding factor though. We recommend that governments record how carnivore carcasses were reported and by whom.

We also recommend more scientific investigation of poachers and incidents of poaching. These steps will likely require collaboration between law enforcement, managers, social scientists, and the interest groups in which people with an intention to poach are found (Browne-Nuñez et al. 2015). Regarding the treatment of carnivore carcasses, we recommend governments take the following steps. Veterinarians are essential to rigorous estimation of causes of death. High rates of error in estimation of age and cause of death should be expected without such review, particularly for inconspicuous poaching (vehicular, nonmetal, cryptic, premortem). We recommend that evidence of premortem gunshot be considered attempted poaching and governments report that estimate separately from confirmed poaching. We suggest submitting a random sample of carcasses for necropsy rather than a selected sample, if the agency cannot afford to submit all. We recommend managers report radiocollar disappearances and more detailed descriptions of sampling methods for radiocollared animals (Treves et al. 2016). Most commonly used statistical techniques assume that disappearance is random with regard to cause of death and marked animals die of similar causes as unmarked ones. Those assumptions were not robust for Wisconsin's wolves and probably not for other wolves (Treves et al. 2016).

Ultimately, carnivore management agencies should submit their data and methods for independent review by scientists with academic freedom who are insulated from financial and political conflicts of interest. Such a step would begin to fulfill legal mandates for use of the best available scientific data in endangered species policy.

Supplementary Data

Supplementary Data SD1A.—Reported deaths of gray wolves, *Canis lupus*, inside Wisconsin from wolf-year 1980 to 2012.
Supplementary Data SD1B.—Reported deaths of gray wolves, *Canis lupus*, collared by the State of Wisconsin that died outside the state.
Supplementary Data SD1C.—R. P. Thiel, retired WDNR, data on dead or missing gray wolves, *Canis lupus*, for calendar years 1980–1989.
Supplementary Data SD1D.—Records discarded as described in "Materials and Methods."
Supplementary Data SD2.—Gray wolves, *Canis lupus*, collared by the State of Wisconsin from wolf-year 1980 to 2012.
Supplementary Data SD3.—Total-accounting method for reconstructing missing deaths of gray wolves, *Canis lupus*, in Wisconsin from wolf-year 1980 to 2012.
Supplementary Data SD4A.—Review of 11 WDNR gray wolf, *Canis lupus*, necropsy cases … by J. A. Langenberg.
Supplementary Data SD4B.—Necropsy and radiography information from WDNR.
Supplementary Data SD5.—United States Geological Survey National Wildlife Health Center review of a selected sample of gray wolf, *Canis lupus*, necropsies.

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