Uncertainty and precaution in hunting wolves twice in a year

Adrian Treves*, Naomi X. Louchouarn

Nelson Institute for Environmental Studies, University of Wisconsin, Madison, Wisconsin, United States of America

* atreves@wisc.edu

Abstract

When humanity confronts the risk of extinction of species, many people invoke precautions, especially in the face of uncertainty. Although precautionary approaches are value judgments, the optimal design and effect of precautions or lack thereof are scientific questions. We investigated Wisconsin gray wolves *Canis lupus* facing a second wolf-hunt in November 2021 and use three legal thresholds as the societal value judgments about precautions: (1) the 1999 population goal, 350 wolves, (2) the threshold for statutory listing under the state threatened and endangered species act, 250 wolves; and (3) state extirpation <2 wolves. This allows us to explore the quantitative relationship between precaution and uncertainty. Working from estimates of the size wolf population in April 2021 and reproduction to November, we constructed a simple linear model with uninformative priors for the period April 2021-April 2022 including an uncertain wolf-hunt in November 2021. Our first result is that the state government under-counted wolf deaths in the year preceding both wolf-hunts. We recommend better scientific analysis be used when setting wolf-hunt quotas. We find official recommendations for a quota for the November 2021 wolf-hunt risk undesirable outcomes. Even a quota of zero has a 13% chance of crossing threshold 1. Therefore, a zero death toll would be precautionary. Proponents for high quotas bear the burden of proof that their estimates are accurate, precise, and reproducible. We discuss why our approach is transferable to non-wolves. We show how scientists have the tools and concepts for quantifying and explaining the probabilities of crossing thresholds set by laws or other social norms. We recommend that scientists grapple with data gaps by explaining what the uncertainty means for policy and the public including the consequences of being wrong.

Introduction

When humanity confronts threats to the planetary or local natural resources and biodiversity, many governments, critics, and commentators invoke precautions. For example, in 1992, United Nations authors endorsed a precautionary principle as follows,

"In order to protect the environment, the precautionary approach shall be widely applied by States according to their capabilities. Where there are threats of serious or irreversible
damage, lack of full scientific certainty shall not be used as a reason for postponing cost-effective measures to prevent environmental degradation.” (Principle 15 of [1]).

**Precaution**

The precautionary principle can be a double-edged sword. For many fields harm can arise from action or inaction, so the task of implementing precautions is not always obvious. For many practitioners debating whether to intervene in human poverty or illness, inaction can kill. Therefore, the harm and the precaution are not necessarily obvious. (For a full treatment of the precautionary principle or approach in fields from civil engineering to medicine, we recommend this article [2]). Where poverty or illness are the major killers, technological and medical interventions that alleviate these ills can save lives, and therefore, inaction can perpetuate harm. The precautionary principle seems to us more straightforward to apply when the potential harm is extinction.

There is no scientific uncertainty that human activities that directly kill organisms or degrade ecosystems have caused extinctions. The risk of extinction whether local or range-wide is higher for organisms that are few in number, or abundant ones that are narrowly endemic or genetically homogeneous [3]. For simplicity, we refer to the latter as listed hereafter. Precautions for imperiled species received affirmation by the 1978 USA Supreme Court decision on the snail darter threatened by Tellico Dam [4]: "The Supreme Court’s opinion in TVA v Hill is still good law, with Chief Justice Burger’s stentorian declaration repeatedly echoed in successive endangered species cases: ‘Congress has spoken in the plainest of words, making it abundantly clear that the balance has been struck in favor of affording endangered species the highest of priorities, thereby adopting a policy which it described as Institutionalized caution.’” p.305, emphasis added [5], citing majority opinion [4]; see also [6]. For example, under Endangered Species Act (ESA) protections and similar provisions of the E.U. Habitats Directive [7–9], permits for killing listed species are extremely restrictive.

Following efforts to reduce protections for gray wolves *Canis lupus* in the USA and E.U., much attention has been paid to proposed and enacted regulations and methods for public hunting, trapping, and hounding of wolves [10–20]. For wolves in the USA, a recently listed population reclassified from ESA endangered status in early January 2021, but whose reclassification is a matter of litigation as we write [21], similar institutionalized caution might still be appropriate. For example, in the wake of USA federal de-listing, the state of Wisconsin held a wolf-hunt in February 2021 during which permitted hunters killed at least 21% of the population in <72 hours [22]; another 98–105 wolves were estimated to have died (from poaching mainly) because of removal of federal protections between 3 November 2020–14 April 2021; and apparently at least a third of collared wolves went off the air without explanation [23,24]. A March 2021 proposal to hunt Wisconsin wolves again starting 6 November 2021 has raised public concerns and state wildlife agency cautions to decision-makers [25].

Here we present the second in a series examining the effects of wolf-hunting on Wisconsin’s wolf population [23] by forecasting the status of the population out to 14 April 2022, with and without permitted killing at various levels. To operationalize precaution without interposing our own values, we defined the result of wolf-hunting by the state of Wisconsin as eradication (<2 wolves), statutory listing under the state threatened and endangered species list (<251 wolves), and falling below the state population goal of 350 wolves [26]; all those values exclude wolves ranging across tribal reservations estimated at 42 wolves [27]. These three thresholds represent the value judgments made by society at one time or another, in principle, statute, and regulation respectively, about how cautious one should be about the status of the
state wolf population. We are not interposing our own value judgment about a desirable or undesirable number of wolves. Instead, we ask the scientific question of what death toll in Fall 2021 would cross undesirable thresholds set by existing regulatory mechanisms, so the public and decision-makers can judge caution and its absence.

Scrutiny of this case allows both a qualitative and a quantitative analysis of uncertainty in the presence or absence of institutionalized caution. Our interest in scrutinizing these plans is not ours alone. The federal legal mandate is 5 years of monitoring and possible emergency relisting under the ESA if the threats to wolves resurface strongly [28]. Given that the state wildlife agency expects serious federal scrutiny if the state population is reduced by 25% and recommended a lower quota of wolf-kills preceding both wolf-hunts than was set by the Natural Resource Board, NRB [25] and given co-sovereign tribes in the region have expressed strong concerns [29], scrutiny of the plans for a second wolf-hunt seems important to many actors. Relatedly, concerns have been expressed by scientists and managers about ‘political populations’ defined as wildlife whose population parameters are set by political pressures despite being biologically unrealistic [30]. Scientific work that can bridge between biological (or social scientific) observations on the one hand, and management or policy-making on the other hand, may help to minimize undue political pressure. Scientific scrutiny also presents a case study of the precautionary principle in the design of sustainable natural resource use.

### Uncertainty

The U.N. precautionary principle 15 above calls for reducing scientific uncertainty. Likewise, an early amendment to the USA ESA sought to base decisions solely on “the best available scientific and commercial data”, BAS [5]. Those principles identify scientific certainty and uncertainty as crucial fulcrums for decisions with more deliberation and less action the more uncertain we are.

When precautionary approaches are reduced to a question of certainty about harms, policy-makers face a dilemma well summed up in this quotation, “The very basis of the Precautionary Principle is to imagine the worst without supporting evidence . . . those with the darkest imaginations become the most influential.” emphasis added, [31]. To avoid that pitfall which afflicts extreme positions in the wolf-hunting debate, we do not imagine the darkest future but rather stick to peer-reviewed data and, where that is absent, restrict ourselves to the official state data, rely on peer-reviewed evidence when it conflicts with the state’s assertions of fact, and explain the limits to confidence with both.

The uncertainties in our case are not limited to scientific data or how to interpret those. The uncertainties extend to the political actors and decision-makers. Powerful actors differ on the ideal number of wolves dead or alive and competing views of what makes for the best available science. The socio-political context of the Wisconsin wolf debate includes multiple governmental entities, each one with a different worldview and each one able to act (subsequent to our writing) in ways we cannot anticipate. Given these actors differ in their institutionalized caution and in how individuals are given authority to use personal opinion about caution, our three above-mentioned thresholds (eradication, listing level, and population goal) serve as legal value judgments about precautions. Hence, the legal thresholds provide the basis we use to account for uncertainty.

Uncertainty also characterizes the scientific literature on human-induced mortality patterns among wolves. We do not spend much effort to address sustainability for two simple reasons. First, concerns with sustainability are about future uses more than the risk of extirpation after a single use and we are concerned with crossing the above thresholds in the 2021–2022 wolf-hunting season. Second, the science of sustainable hunting of wolves is unsettled. Although
reviews of wolf population dynamics and sustainable levels of killing include many data points and seem to converge on a range of sustainable, annual human-caused mortality rates [32–36], the literature nonetheless concludes with three-fold differences in magnitude for estimates ranging from high teens to 48%. Although the prior literature would seem to guide decision-makers in Wisconsin to choose a Fall 2021 wolf-hunt quota that would not change the population, the wide variation in estimates above and the novelty of a second wolf-hunt in a single year produces new and greater uncertainties than the literature addresses. Also, in a series of papers on wolf science and policy in Wisconsin, we have shown how omissions of a history of methodological changes in censuses, censoring the information available in the disappearances of marked wolves, and a lack of alternative management scenarios altogether could both distort wolf policy and mire the science in uncertainties due to methods [23,33,37–46].

To support decision-making in the face of great uncertainty, we provide a step-by-step rationale for the uniform distributions we use and a simple linear model of births and deaths. The primary reason to take this simple approach is its practical advantage. We show how the state, tribes, public, and other interests can perform these estimates independently and reproduce our findings to explore their own scenarios for November death tolls. That is valuable given our inability to predict the eventual death toll and the reactions of the many interested governmental actors mentioned above. Thus, as we grapple with uncertainty at every step, we transparently present the bounds we consider plausible and why. Secondly, we use Bayesian concepts and terminology but not formal Bayesian algorithms, because many of our key input variables are uninformative and combine in simple linear fashion. To achieve our primary goal of clear communication and user-input, a formal Bayesian algorithm would be less accessible. We illustrate how any reader and user of our simple model can choose a death toll and calculate probabilities of crossing the legal thresholds. We offer this simple approach as a possible model for other scientists engaged in public policy debates whether or not contentious and uncertain, beyond wolves, and beyond North American hunting systems.

**Materials & methods**

Our study period is the wolf-year starting 15 April 2021 and ending 14 April 2022. We contend with three key scientific uncertainties in this study period. First, the effects of the 22–24 February wolf-hunt on wolf numbers, pack sizes, and reproductive potential are uncertain. Second, little information is available about reproduction for our study period. Wolf reproduction data is generally difficult to collect and the state census method used tends to confound pack size with past reproduction [46,47]. Third, we could not be confident about the legal quota when we analyzed data in Fall 2021 nor does anyone know the eventual death toll. Therefore, our forecasts for 14 April 2022 include estimates of all wolf mortalities even if the legal quota ends up unfilled. We describe the unprecedented methods of the February 2021 wolf-hunt first because it conditions the remaining uncertainties.

The February 2021 wolf hunt killed 218 wolves legally, took place during the mating and pregnancy season of the wolves, and included pursuit in deep snow by snowmobiles, nighttime hunting, hounds in packs of 6, and relays that allowed a team of hunters to substitute a fresh pack of hounds; >85% of kills were aided by the use of hounds according to hunter self-report [22]. Hunters overshot the legal quota by 99 wolves (82%), an event the DNR blamed on regulations that require 24 h notice to close zones and regulations that allowed hunters in open zones to delay reporting kills for 24 h even after the state quota was met. Also, the state sold permits for 13 hunters for every wolf that could be legally killed. These latter regulations increase the uncertainty about the eventual death toll of any legal quota [22,23,25,48].
Before we address the remaining uncertainties about population status in our study period, with a mix of qualitative and quantitative information, we explain the simple model we adopted for population change during the study period. Because of the preceding three scientific uncertainties and our desire to provide a method that others can use to plug in their own values or future data, we relied on a simple one-step model of population size change for our study period, as follows:

\[ N_{t+1} = N_t + R_t - M_t - H \]  

where \( N_t \) is the population size estimate on 15 April of year \( t \), \( t = 2021 \), \( R_t \) is the number of pups born in year \( t \) surviving to November when they are typically counted alongside adults using standard census methods [35, 49], \( H \) is the death toll in a wolf-hunt, and \( M_t \) is the number of dead wolves in year \( t \). We estimated \( R_t \) by Eq 2,

\[ R_t = B_t \cdot L \cdot S \]  

where \( B_t \) is the number of breeding packs, \( L \) is the litter size, and \( S \) is pup survival. We estimated \( M_t \) by Eq 3,

\[ M_t = D \cdot (N_t + R_t / 2) \]  

where \( D \) is the annual mortality rate estimate for a year without ESA protections and without a wolf-hunt as we describe further below in the section on deaths. Note that \( R \) from Eqs 1–3 represents pups surviving to November 2021. In Eq 3 these pups are exposed to one-half of a year of \( D \) from November-April.

Our simple model in Eq 1 assumes no net migration into or out of the state during the study period at a rate relative to deaths or births substantial enough to affect our results. Assuming no net migration is a precaution because it would be hopeful to imagine rescue from outside the state if legal thresholds were crossed in the state. Our assumption seems reasonable given long-distance migration leading to pack establishment has been rare [50]. Also, the assumption of no net migration has been used by others modeling this population [51, 52]. Also, Eqs 1–3 assume linear effects. We assumed no compensatory increases in birth or pup survival other than those encompassed by the range of values in [53]. We do not ignore Allee effects, compensation or negative density-dependence [54, 58, 59], but we do not model them because too many questions remain for Wisconsin wolves [3, 41, 43]. Nor do we model non-linear effects that would caution against high death tolls in a second wolf-hunt. For example, depensatory or super-additive effects as described by numerous studies of wolves including in the Wisconsin wolf population [33, 36, 45, 60, 61]. We defend the simplicity of our approach as follows: pending evidence that non-linear effects would play out detectably in the short period of our study and pending an analysis of net compensatory and depensatory effects, we simply assume the good conditions studied by [56] encompass any nonlinear effects for wolves in an environment with fewer competitors than before.

### Population size estimation

The second source of uncertainty described above was the point estimate and precision of that estimate of population size. The state government had implemented a new, unpublished method of census (hereafter new census method) which produces systematically higher estimates than the traditional census method [27, 54, 55]. However, the unprecedented February hunt described above, interrupted that census. Ending wolf census on 21 February has never been done. The resulting uncertainty about \( N_{2021} \) leaves us with two estimates using two methods.
The state estimated $N_{2020}$ by two methods, following [27]. The old census method yielded 1034–1057 (uninformative uniform distribution). Used since 1979 with a few changes over time, the traditional method attempted complete enumeration referred to as a minimum count [56], although efforts to validate that it did not double-count wolves are still lacking. The second, new census method yielded 1195 (957–1573, unknown distribution) and used an occupancy framework but the method has still not been published in a peer-reviewed, transparent manner [24]; S1 Fig 1. Although the two methods differ substantially in uncertainty, they don’t result in very different point estimates for $N_{2021}$.

The state and [23] estimated $N_{2021}$ in two ways. We estimated it from the old census method and estimates of population growth parameters and estimates of annual mortality rates [23] at 695–751 wolves, which we considered a maximum because of the likelihood of greater rates of illegal killing given the conditions of that hunt summarized above. The second estimate of $N_{2021}$ comes from the state government in summer 2021 and uses the new census method interrupted at 21 February 2021 [25].

The state’s justification for interrupting the new census method before 14 April 2021, when it would have been terminated as in previous years [27], was that the wolf-hunt of 22–24 February made accurate and precise data collection impossible. Therefore, the wolf population estimate derived from the new census method in 2021 lacked non-hunt mortality from 25 February to 14 April 2021, which is a season of high mortality from winter conditions and illegal killing historically [39,57–59]. We are not aware of any effort to correct the new census method estimate, therefore it seems to be a systematic over-estimate of $N_{2021}$. Furthermore, the state did not provide bounds on $N_{2021}$ but given the reported value (1195) of $N_{2021}$ equaled the central tendency of $N_{2020}$ (also 1195), we assume here the same bounds minus the 218 wolves killed legally in the February wolf-hunt, hence 977 (739–1355). That value minus some uncounted late winter mortality would bring the estimate closer to the prior estimate of 695–751. But the similarity of the two estimates for $N_{2021}$ is hard to evaluate so we use both throughout.

**Reproduction**

Eq 1 required the number of pups surviving to November, which in turn, requires Eq 2 to produce an estimate of $B$ for the number of breeding packs, $L$ for litter size in mid-summer, and $S$, pup survival to November. Because we face a nearly complete absence of information on wolf pack reproduction in summer 2021 [25,48], we used a mix of informative priors for $L$, $S$, and the proportion of potentially reproductive pairs that actually bred.

We used the only peer-reviewed, published study of reproductive success before November conducted among Wisconsin wolves [53], which provided estimates for the proportion of packs producing litters (0.55–0.89, mean 0.72), for $L$, litter size (3–6, mean 4.8), and for $S$, pup survival to 3–9 months 0.05–0.72 with a mean of 0.2, from three separate normal distributions centered on the means and bounded by the 95% CI around those means. For pup survival to 3–9 months, we noted the long right tail of the distribution in [53] and adjusted the normal distribution accordingly. Hence multiplying the three preceding parameters yielded an average of 0.69 (95% CI 0.15–4.32) pups surviving to November per pack. We estimate the number of breeding packs, $B$, to multiply it against in the following section.

The study in [53] was conducted during a period with ESA protections and a population recolonizing vacant range, i.e., reproductive performance in good years measured by [53]. We did not use another commonly cited summary [56] because it aggregated breeding data at the end of the wolf-year in April and we needed an estimate for November. Also, we have previously explained why winter estimates of pack size might be confounded with estimates of breeding at that time [47].
Number of breeding packs, B: The proportion of packs that produced pups in summer was estimated in [53] as a proportion of all packs studied. We had to estimate B from the packs present in the state multiplied by Thiel’s [53] estimate of the proportion producing a litter. For summer 2021, we assumed that the former was some subset of the total number of breeding females surviving the February 2021 wolf-hunt. For summer 2020, we used [53] estimates and a highly informative prior as follows.

In April 2020, the state contained 245 packs and tribal reservations held 11 packs [27]. An unknown number were eliminated in the February 2021 wolf-hunt. The state assumed no disruption to breeding after the February 2021 wolf-hunt [25]. Given the unprecedented nature of the wolf-hunt, the effects of the February 2021 wolf-hunt on R are uncertain. The number of packs that produced pups in summer 2021 might have been strongly affected by the February 2021 wolf hunt that took place during the breeding season and used methods (hounds, snow-mobiles, night-time tracking) that might have made breeders more vulnerable than in prior wolf hunts. Given the urine-marking habits of territorial alphas in snow, the possible olfactory conspicuousness of reproductively active alphas in February, the use of hounds, some but not all of our scenarios below treat breeding females as relatively more vulnerable than pack-mates and more vulnerable than in past years.

Reproductive success of wolf packs might drop when humans kill pack members, either directly through death of breeders or indirectly through stress, loss of adult wolf helpers, wounding, or other factors caused by people. Although there is high variability in the effect of breeder loss across studies and time of year [60–63], it is clear that breeders killed during the pregnancy or mating season almost invariably result in reproductive failure of the entire pack, especially when the alpha female dies. There is less evidence for the effect of removing other wolves, the effect of the novel methods used in the February 2021 wolf-hunt, or the effect of poaching on subsequent reproductive success of wolf packs. These data are almost absent for Wisconsin (but see [61]). Therefore, we estimated the number of breeding packs (B) in several ways.

We have five sources of information that help to parametrize B the variable of number of breeding packs in summer 2021. First, under beneficent conditions studied by [53], we know the mean (95% CI) for the proportion of packs that bred was 0.72 (0.55–0.89) during early to middle colonization under ESA protections during a less politically contentious phase of wolf policy. It seems inconceivable that a greater proportion of packs could have bred in summer 2021, so 218.05 (0.89 x 245 packs across the state) seems like an appropriate starting point to deduct packs that failed to breed because of the February 2021 wolf-hunt.

The minimum plausible deduction from 218.05 is 51 breeding packs which corresponds to approximately 0.23 pregnant females per wolf-kill. Below we explain why this is a minimum plausible deduction from 218.05. A preliminary report from a sample of 22 wolf carcasses volunteered by hunters from the February 2021 wolf-hunt was necropsied by the Great Lakes Indian Fish & Wildlife Commission [64]. They reported 65% of adult females and 50% of yearling females were pregnant in that small, nonrandom sample. Our minimum plausible proportion of 23% is much lower because a larger sample from a different hunt in Fall 2012 in neighboring Minnesota suggested 0.20–0.25 wolves were females with evidence of past breeding [65]. This hunt was very different (no hounds, no deep snow, no snowmobiles, no nighttime hunting, not during mating season, etc.). Given the average pack size in our region in late winter is approximately 4 wolves with a longer right tail (2–12), it would appear somewhat less than a quarter of pack members would be pregnant females if hunters killed them in proportion to their presence in the population. Thus deducting 51 wolf packs is one-quarter to one-sixth of the 218–323 extra deaths we described above. That leaves B = 167 as the maximum plausible upper bound.

The maximum plausible value of B described above seems a maximum for several reasons. For one, the Timber Wolf Alliance and Timber Wolf Information Network conducted summer
2021 howling surveys in portions of the state and estimated that fewer than half of the packs they encountered responded with pup vocalizations [64] citing court declaration by A.P. Wydev-en. Such howling surveys are somewhat accurate for the detection of pups in experimental, field tests but are not accurate for counting pack size or pup numbers in those same tests [66]. Although we cannot extrapolate to the whole state or assume that response to human howls would continue as in the past, their anecdotal data suggest a scenario with a lower estimate is also plausible. Also, there are reasons to expect breeding females would have been selected in greater proportions than their representation. Pregnant or mating female wolves deposit blood and different hormonal odors in their urine left to mark territorial boundaries. The large num-
ber of hounds used in the February 2021 wolf-hunt with deep snow might have made breeding females particularly conspicuous. Then we might use the higher value from Red Cliff instead to estimate that 144 wolf packs failed to reproduce in summer 2021, leaving B = 74 as a plausible lower bound. However, we suspect the real value lies between B = 74–167.

We also used an indirect source of information which came from spatial analysis of kill locations in February 2021 wolf-hunt to generate two additional scenarios. We assume that wolf packs that might have encountered hunters or hounds during the February 2021 wolf-hunt might be disrupted reproductively by stress or deaths of pack-mates. We assumed the maps of hunted areas and pack areas were accurate, every pack near to a hunted area would potentially be affected by hunting, and reservation packs and packs outside of hunted counties would be unaffected by hunting. If the spatial proximity of reported wolf-kills predicts the disruption of reproduction in the nearest pack, then the two scenarios in Fig 1 provide two more estimates of the number of breeding packs.

Note our unlikely lower bound of 12 breeding packs emerged from scrutiny of Fig 1 because only one pack lay mainly in a county without reported kills and 11 other packs lay mainly in tribal reservations where hunting was prohibited [64]. If hunters exert a suppressive effect on reproduction of wolf packs in a large area, the number of breeding packs would be estimated by B = 91. That is equivalent to 0.41 of our unlikely upper bound or the failure of 127 packs to breed. If hunters exert a suppressive effect in a much smaller area, the number of breeding packs would be estimated by B = 129.

In sum, we found four point estimates of the number of breeding packs that seem plausible (74, 91, 129, 167) without any additional information to choose between them. In Fig 2, we represent the uninformative uniform distribution between those four values and implausible, extreme values of 12 and 218.05.

Deaths

Eq 1 requires an estimate of $M_{2021}$, the number of dead wolves (composed of adults year-round and pups after November 2021), which relied on an estimate and variation in the annual mortality rate (D) as an input to Eq 3. We began by solving Eq 1 for M and R in year $t = 2020$. Because we knew N for $t$ and $t+1$, Eq 1 reduces to a change in population equals births minus deaths. Also, we had an informative prior $R_{2020}$ from [53] for a summer with ESA protections following a winter with no wolf-hunt. Hence, we solved for $M_{2020}$, which we used as an input to Eq 2 for D, the range of annual wolf mortality rates for years with those conditions. Note we did not use multiple prior years to estimate D because the last 5 years were under strict ESA protections year-round unlike 2020–2021, nor did we use the years with wolf-hunts 2012–2014 because these lacked one or both of the conditions in February 2021 (hunting with hounds or deep snow cover during the wolf mating season).

We present the estimates of D in Results but validating these may not be obvious. There is little scientific consensus on annual mortality rates among Wisconsin wolves. The DNR
provided incomplete and unclear data on deaths of wolves after 31 December 2011 [39–41,67–69] and particularly incomplete after 14 April 2012 [24,25,48,54,55,70,71]; S1 Fig 2. To validate the estimate of D, we had separate published estimates using different methods for adult wolves from 1979–2012. For collared wolves only, the cumulative incidence of all endpoints (deaths or disappearances) for collared wolves 365 days after collaring was 0.42–0.52 depending on ESA listing status [39]. That study used time-to-event analyses in a competing risks framework. By contrast, a cruder estimate using a weighted average of collared and uncollared adult wolves dead as a proportion of the population size at the start of each wolf-year, which did not take into account time-to-event but considered uncollared wolves, estimated the rate at 0.18 for radio-collared wolves and 0.47 (SD 0.19 annually) for uncollared wolves [40]. Similarly, [72] reported higher mortality rates for uncollared Alaskan gray wolves. See also [73] for another large carnivore in which GPS collars are
associated with higher survival. In 2020, approximately 5% of the wolf population was collared, so the weighted average annual mortality rate would be 0.46. The third peer-reviewed estimate of mortality covered the years 1979–2013 which included a wolf-hunt in Fall 2012. However that estimate it provided of 23.5% annual mortality for radio-collared adults in a time-to-event analysis [58] seems low. For instance, that study failed to account for several confounding variables and took unjustified steps in analyses. The unjustified steps were to include a variable for a change in slope in the year 2004 which is distinguishable only by the methods of analysis of census data [44,46]. And there were similar changes in census methods and methods of analysis in 1995, 2001–2003, and 2012, which [58] did not consider. We do not understand why 2004 was special and they did not explain why. Also, the authors lumped nonhuman causes of death with unknown causes of death, a step that several analyses have shown to be unjustified because time-to-event analyses show very different timing in the hazard of nonhuman and unknown causes [39–41,59]. Moreover, [58] did not acknowledge that uncollared wolves may have faced higher rates of mortality, or the multiple, corroborating lines of evidence showing that wolf survival and wolf population growth declined when ESA protections were lifted 7 times from 2003–2013 [12,39–41,51,74,75]. Finally, [58] did not account for the changes in incidence of wolf mortality with hound-training seasons, deer-hunting seasons, and bear-hunting seasons, especially elevated during months of snow cover [59]. Therefore, h [58] is certainly too low given the conditions between 3 November 2020 and 13 April 2021.

In sum, we had three published estimates of annual mortality rate from prior years ranging from 0.235–0.52 using three different methods on similar datasets, with which we could validate our estimate of D, at least qualitatively. We used a uniform distribution analogous to Fig 2 for D.
Scenarios for wolf-hunt death tolls (H) and order of operations in our model

The last step in our analysis was to subtract H for the death toll from the uncertain wolf-hunt scheduled for November 2021. These death tolls assume zero sub-lethal injuries unreported as legal kills, and assuming zero additional cryptic poaching beyond that already captured in annual mortality rates during periods without ESA protections [23,39].

Uncertainty about the death toll reflects different permutations of the quota set by the DNR (130 wolves) and that quota voted by the NRB on 11 August 2021 (300 wolves) in addition to the following factors that might raise or lower the eventual death toll: over-kill in February 2021 of 99 or 82% might repeat itself; or the tribal treaty right to reserve 43% of the declared state quota (leaving a death toll of 74 if the DNR quota of 130 were to be implemented). Therefore, we modeled H as a continuous, normal distribution with a mean of 300 ranging from 0–600. H was our perfectly measured x variable on which to regress the population estimate using ordinary least squares algorithms. In Results and Discussion, we focus on three x values (0, 130, and 300) representing the preferred, legal death tolls for the plaintiffs [64,76], DNR, and NRB respectively. We also discuss a fourth death toll (74), which was the DNR’s 130 death toll minus the tribal treaty right reserved 43%.

Because annual mortality rate is a proportion of living wolves, the order in which we deduct non-hunt deaths may be important. Subtracting the November wolf-hunt first would over-count deaths from other causes because these are calculated as a proportion using the annual mortality rate described above. However, half the year passes before the wolf-hunt and a smaller number of wolves (adults only) are present to die of such causes, so the number of deaths would be under-counted, if we deduct the non-hunt mortality first. Ideally, one would subtract the adult summer mortality, add pups surviving to November, subtract the wolf-hunt and then subtract adults and pups dying from other causes in the winter. However, we believe uncertainty about the other parameters described previously is far greater than the slight difference this more realistic algorithm would create. Therefore, to keep the calculations simple, we deducted all the annual mortality before the wolf-hunt, which treats the wolf-hunt as purely additive. The bias we introduce by estimating a higher number of non-hunt deaths is offset by the bias we have already introduced by dismissing unreported deaths and excess illegal killing. For example, the most rigorous study of cryptic poaching to date on the endangered Mexican wolf estimated that disappearances of collared wolves in this closely monitored population went up 121% when the wolf was not listed under the ESA, compared to periods of strict ESA protection [38]. However, we took the conservative step of not using this estimate or the higher mortality rate of collared wolves estimated in [39].

Finally, before evaluating legal thresholds, we subtracted 42 wolves living entirely or mostly on tribal reservations [27], because these are managed by the co-sovereign tribes whose governments declared wolves protected from public hunts [77].

Randomizing: Our modeling procedure used random generation of values for every parameter in Eqs 1 and 2 in 1200 iterations repeated once for each census method (traditional and new). We tripled that for the final estimates of $N_{2021}$, to 3600 iterations to boot-strap the distribution around the means. S1 Table provides the randomization outcomes and the distributions for each parameter. S2 Table provides the code.

Results

Table 1 presents the estimate of annual rate of mortality, D, which ranged from 0.38–0.56 when we used the traditional census method or a range from 0.17–0.58, with the most likely values 0.38–0.48, when we used the new census method. Note these two methods have
different distributions. The former is uniform and the latter is unknown but extremely unlikely to be uniform. Given the new method has very wide bounds and hence great uncertainty and lacks peer reviewed validation as of writing, we have elected to view it qualitatively as consistent with the traditional method because its bounds entirely contain the bounds of the traditional method, Also, the latter is consistent with recent, peer-reviewed published estimates of annual mortality rates (see Methods). Therefore, in the next step we take D to be 0.38–0.56 with a uniform distribution.

State wolf population \( N_{2022} \)

Figs 3 and 4 depict the probabilities of crossing legal thresholds for the Wisconsin wolf population. The slope of Fig 3A suggests that any death toll above 16 creates a better than average possibility of crossing the threshold of 350 wolves (state population goal). For the new census method (Fig 3B), that threshold is met at a death toll of 88 but the uncertainty is three times greater and the risk of crossing lower thresholds also increases. The probability of crossing the second threshold (state listing) exceeded 50% at death tolls of 113 and 189 wolves, for the traditional and new census methods respectively. The traditional census method had a reliable slope judged by its \( r \)-squared value, twice as reliable as the new census method (Fig 3A and 3B).

Even a death toll of zero might lead to the wolf population declining below the 1999 population goal of 350 (Fig 4). If the new census method were used, the distributions would be flatter raising the probability of undesirable thresholds.

The DNR asserted the tribal treaty right to 43% would be respected and the co-sovereign tribes that signed those treaties had asserted they would not hunt those wolves. Therefore, we examine the resulting death toll of 74 next. Using the traditional census method, \( N_{2022} \) would average 329 (SD 44) wolves with a 1% probability of crossing the listing threshold of 251 and a 65% probability of crossing the state population goal of 350 (orange and yellow lines respectively in Figs 3 and 4). Using the broader, flatter distribution from the new census method, \( N_{2022} \) would average 402 (SD 132) wolves with a 13% probability of crossing the listing threshold.
threshold of 251 and a 36% probability of crossing the state population goal of 350 (orange and yellow lines respectively in Figs 3 and 4). The above averages and probabilities assume no over-kill or illegal kills beyond that estimated by our background mortality rate.

Conclusions

We modeled a population of wolves recently removed from the USA list of endangered species, subjected to an unprecedented hunting season in February 2021, and proposed for another hunt in the winter of 2021–2022. We present this case, among other reasons, to illustrate the use of legal thresholds to define the probabilities that policy will result in undesirable effects. Societal value judgments have produced legal thresholds that decide what is precautionary and what is not, relieving scientists of the appearance of making personal value judgments when evaluating policy effects. We quantified the probabilities of crossing three legal thresholds with simple models and Bayesian concepts to account for uncertainty. We demonstrated constructive approaches to using a mix of qualitative and quantitative information to reduce uncertainty to manageable levels with uninformative, uniformly distributed prior information. The precautions we studied were set by legal thresholds so we could operationalize precautionary approaches without interposing our own values. For organisms at risk of extinction like in our case, precautions are relatively clear because hunting can only harm the targets, assumptions about resilience should be viewed as risky, and the sustainability of human actions should be viewed skeptically.
Several new results emerged for Wisconsin’s wolves. We report high probabilities that a second wolf-hunt in winter 2021–2022 would drive the Wisconsin wolf population to undesirably low levels, judged by legal thresholds and the current quotas recommended or set by the state. Moreover, a repetition of the over-kill of the February 2021 wolf-hunt (by 99 wolves or 182% of the legal quota) risks extirpation of the state population leaving only wolves in tribal reservations. Even a well-regulated wolf-hunt at the quota level recommended by the state wildlife agency (130) is more likely than not to require statutory listing on the state endangered and threatened species list. We found any wolf-hunt in November 2021 poses a measurable risk of an undesirable outcome and any quota >16 wolves is more likely than not to lead to an April 2022 wolf population below the threshold of the 1999 population goal [43]. Therefore, no wolf-hunt is safe when viewed from a precautionary viewpoint. We also present the first estimates for annual mortality rate between 15 April 2020 and 14 April 2021. That rate per year was 0.38–0.56 adults and young of the year that survived to November. If we add the February 2021 wolf-hunt to the latter rate, the total annual mortality rate in 2021 would rise by \(0.18\) (218 / 1195). The sum of those two rates seems unsustainable, even if we accept a nonhuman-caused rate of mortality of 0.09 [45]. The resulting one-year mortality rate of 0.56–0.74 in Table 1 is too high to be sustainable by any of the credible estimates in the literature reviewed by [31]. Also, Table 1 annual mortality rates are substantially higher than the DNR “consensus” estimate of 13% [23] plus approximately 9% nonhuman-caused. Therefore, we reject the DNR’s consensus method for estimating mortality as unscientific and highly inaccurate. Furthermore, the range of annual mortality rates in Table 1 was almost never so low as estimated by [45]. Their estimate of 23.5% is only plausible for 2020 if one accepts a drastic rise in

---

**Fig 4.** Distributions of predicted population estimates for Wisconsin’s wolves on 14 April 2022. Frequency distributions assume death tolls of 300 (green), 130 (gray), and 0 (blue) relative to reference lines of extirpation (red), listing (orange), and population goal (yellow). We ran 3600 iterations to generate smoother probability distributions as “shadow grams” made in JMP® 15.0, 2021, for each value of \(H\). These distributions rely on the traditional census method (Fig 3A) and average and SD follow: (green) 61 SD 44 with a 9% chance of extirpation and 100% chance of dropping below the state listing threshold, (gray) 231 SD 45 with a >99.5% chance of dropping below the state population goal and a 64% chance of dropping below the state listing threshold, (blue) 361 SD 44 with a 13% chance of falling below the state population goal.

https://doi.org/10.1371/journal.pone.0259604.g004
population size from 2020 to 2021, which no authority has claimed. As predicted by [36], the February 2021 wolf-hunt seems to have led to an increase in wolf-killing in response to alleged predation on domestic animals. Also as predicted by [36], reducing protections for wolves increases calls for legal killing; see also [46]. Reducing protections leads to lower survival for wolves when all causes of death are considered [36]. Therefore, we recommend the state halt lethal management of wolves in years it plans wolf-hunts because we see no method or regulation in place to deduct state lethal control totals from legal quotas. We also recommend the state revise its estimate of mortality and in so doing also publish all mortality data in a scientific manner including distinguishing between radio-collared wolves and others with time on the air for the former. For all governments reporting wolf mortality, we recommend more care in estimating poaching and the use of forecasting methods that take into account a spike in legal mortality after governments lower protections for imperiled species [38]. Also we recommend wolf managers focus on poaching enforcement when seasons for hunting other (non-wolf) large mammals are open [59]. These recommendations probably apply as well to other controversial wildlife.

Bridging science and policy when both are controversial

Our topic is controversial in wildlife management science and in public policy. Below we discuss how values in wolf policy affect the handling of precautions and how controversies in science affect handling of uncertainty. The foundations of the controversies are diverse values toward wolves in the USA [78,79], mirrored elsewhere [20,80]. These publics do not simply diverge quantitatively in their support of wolves but qualitatively, differing in mutualism values that favor non-lethal coexistence [81]. Naturally, such public debates affect government agencies charged with managing wildlife.

In the USA, wildlife agencies are typically allied to hunters [82,83]. Regardless of its origins, the status quo in all but a few states (California and Colorado currently) that host gray wolves is towards liberalizing wolf-killing. States such as Wisconsin repeatedly moved towards public, regulated hunting, trapping, and hounding for the past 23 years [46]. Those values embraced by the agency push against the above-mentioned shift in public values. State wildlife policies also clash with scientific evaluations.

Several governments’ legal wolf-killing quotas exceed levels deemed sustainable by scientists who cite the agencies for non-transparent handling of uncertainty or data [23,33,37,46]. High quotas for killing large carnivores such as wolves, bears, big cats, have sometimes been associated with undue political pressures on the agencies. One manifestation of such political pressures is the tendency for agencies to report unrealistic biological parameters that appear to the uninformed to support claims that killing is ‘sustainable’ or ‘safe’. Such “political populations” [30] seem designed to satisfy political demands by inflating population parameters of the carnivores targeted for killing. A recent review of 666 North American wildlife hunting plans found a large majority of the plans lacked hallmarks of scientific process such as setting clear objectives, independent review, and transparency about data or methods [84,85]. Regrettably, the Wisconsin wildlife agency got high marks for past management in the latter review. Our work suggests those high marks were not merited then or now [23,46]. We report here that the state of Wisconsin created a political population, by the above definition, when it set quotas for a second wolf-hunt in one year without data on reproduction or poaching in the 11 months prior. Such inflation or other distortions of sound science-informed management seem to surface when agencies are not required by law to use best available science defined by third parties, but rather can pick and choose the evidence they wish to use based on their personal or organizational values [10,12,46,86–88].
The politics that led to the current situation in Wisconsin are complex and go beyond a pro-wolf and anti-wolf dichotomy. In brief, a state wildlife agency (DNR) under the executive branch led by the governor appears to be clashing with the commission (NRB) whose members are appointed by governors but confirmed by the legislative branch. Those two bodies clashed publicly over wolf policy in August 2021 (https://www.wpr.org/listen/1836191, accessed 17 August 2021;[25]). Besides that intra-governmental clash there is a long-standing intergovernmental dispute between the state and the co-sovereign tribes of the region who have federal treaty rights to half of almost all natural resource extraction. The state and tribes have co-managed a subset of resources relatively amicably under federal treaties, but walleye fish and wolves have been a point of friction for over a decade [77,89,90]. The Red Cliff tribal government and other tribal governments that signed those treaties filed a federal lawsuit on 19 September 2021 alleging treaty rights violations during 2021 wolf-hunt rule-making [64]. Besides being pro-wolf, tribes in our region are also pro-hunting for subsistence, spiritual, and traditional uses, which represents a distinct set of values in the broader public. Consistent with the controversial nature of our topic, the Wisconsin wolf-hunt under consideration here is the subject of lawsuits instate court [76] and federal court [64].

The state case led to a temporary injunction barring the sale of permits to hunt wolves based on the judge’s decision that the state wildlife agency acted unconstitutionally [91]. Although legal decisions generally reflect only a court’s interpretation of the law, the ongoing state court case also raises issues of science that concern us here. The state court agreed with plaintiffs on the need to delay the case [92], when the plaintiffs brought to the court’s attention that the state had filed an incomplete administrative record [93]. A complete record of all comments and other materials submitted to the agency by the public is required by law, following the Wisconsin Supreme Court decision of Lake Beulah Management District. The Supreme Court advised the public to “submit evidence to the agency decision makers while they are deciding what action to take” p.7, [94], so that they can “ensure that information will be considered by an agency in its decision making and will be included in the record on review . . .” p.355, [94]. The plaintiffs identified 59 instances where comments from scientists and the public were missing from the administrative record under review by the state court [93]. The plaintiffs’ implied that the administrative record was preferentially full of gaps that had been submitted by scientists and scholars critical of the proposed wolf-hunt (p.5 [93]. In sum, the state wildlife agency in this case has in part created a political population of wolves by ignoring contradictory scientific evidence and commentary. In our context, the above elements of controversy about Wisconsin’s wolves underline another point about uncertainty and precaution.

When public comments opposing killing policies or otherwise encouraging caution are dismissed or omitted from the administrative record, the government creates an illusion that its plans are supported by the public and an illusion that is plans are cautious, because dissenting voices were silenced. Furthermore, dismissal or omission of scientific evidence that undermines the government’s assertions of fact seem to treat scientific uncertainty as something that can be willed away through political might. Scientists should speak out against such handling of scientific information by governments. The above-referenced controversies among publics, within the scientific management community, and between managers and decision-makers highlight that neither science of uncertainty nor values towards precautionary approaches alone are at play.

**Recommendations for scientific management**

We recommend scientists account transparently for uncertainty so that decision-makers can apply precautionary approaches to public policy. Scientific uncertainty often hinders
precautionary approaches. Yet policymakers are often forced to decide anyway. If scientists turn away from public policy debates characterized by wide gaps in data or great uncertainty, then decision-makers may decide based on opinion, anecdote, or political pressures. We aimed to bolster scientists’ confidence in their ability to grapple with uncertainty in a way useful to public policy. We recommend that scientists practice analysis and communication that improves their ability to explain what the uncertainty means for policy and the public.

A common thread running through our work is that the more uninformative the prior data, the more scenarios one should present and the more transparent the assumptions about inputs should be. This recommendation aligns with our inclination to use a simple model so that non-specialist members of the public and decision-makers can easily explore and adjust inputs. Any reader can follow our lead and estimate the outcomes for any death toll they prefer. Also, we avoided the critique of precautionary approaches articulated by Curtis (see Introduction) by sticking to peer-reviewed evidence wherever available, evaluating that evidence transparently, and when unavailable we used uninformative, uniform distributions on priors to account for gaps in important data. Our results speak to how precaution can be operationalized even with high uncertainty about data.

The 82% over-kill seen in <3 days during the February 2021 wolf-hunt has raised national debate about the security of state wolf populations. That hunt and our calculations here suggest hunters and poachers can extirpate a relatively small wolf population, in short order and without poison, which contradicts an unsubstantiated assumption that poison would be needed to eradicate wolf populations [95]. We expect proponents of that assumption will claim that the Wisconsin wolf population would persist in tribal reservations, that it would be rescued by neighboring states, or claim that we were too pessimistic. However, such arguments miss the point. Anyone who steps away from the precautionary approach must present stronger evidence for their more optimistic view. The uncertainty grows when one takes optimistic views because the more extreme higher values produce greater intervals between minimum and maximum bounds (because we were bounded by zero in this small population of wolves). Therefore, the burden of proof and demands for data is heavier for those who advocate for killing.

Supporting information

S1 Fig. Unpublished figures by WDNR staff on 8 April 2021 during a public presentation to the Wolf Harvest Planning Committee. Fig 1 shows unpublished results of the new census method. Fig 2 shows how mortality data for April 2020-April 2021 were presented. (PDF)

S1 Table. Outputs of randomization for each variable in Eqs 1–3. Table headers describe the distributions used in randomization. Yellow cells are not user-defined but rather outputs of randomization or outputs of equations. White cells are user-defined so a user can enter different death tolls (H). These are provided for the purposes of exact replication of our results. See S2 Table for algorithms. Yellow fields are generated randomly, white fields are input by the user, and gray fields are outputs of algorithms associated with the white input fields. The attached example is of H = 74 input by the user. (PDF)

S2 Table. Algorithms used in randomization and modeling scenarios, showing formulae in Apple Numbers 2021 v11.2. Note that the formulae should follow the insertion of ‘=’ to become active and then should be pasted into all cells within a sheet. Yellow sheets contain outputs of randomization, whereas white or gray sheets are user input fields. S2 Table presents the outputs of these algorithms in a single iteration used in the Results (1200 values) whereas
results in Fig 4 represent three such iterations (3600 values).

Acknowledgments
We thank F. J. Santiago-Ávila for comments on the revision.

Author Contributions
Conceptualization: Adrian Treves.
Data curation: Adrian Treves.
Formal analysis: Adrian Treves.
Funding acquisition: Adrian Treves, Naomi X. Louchouarn.
Investigation: Adrian Treves.
Methodology: Adrian Treves.
Project administration: Adrian Treves.
Resources: Adrian Treves.
Validation: Adrian Treves.
Visualization: Adrian Treves.
Writing – original draft: Adrian Treves, Naomi X. Louchouarn.
Writing – review & editing: Adrian Treves, Naomi X. Louchouarn.

References
1. The United Nations Conference on Environment and Development. Rio declaration on environment and development. United Nations; 1992.
2. Wikipedia. Precautionary principle. Wikipedia [Internet]. Accessed 29 January 2022. Archived: /web/20220129155106/https://en.wikipedia.org/wiki/Precautionary_principle.
3. Groom MJ, Melfe GK, Carroll T. Principles of conservation biology, 3rd edition. Sunderland, MA: Sinauer Associates; 2007. https://doi.org/10.1111/j.1523-1739.2006.00627.x PMID: 17391180
4. Tennesee Valley Authority v Hill. 1978, U.S. Supreme Court 437 U.S. 153.
5. Plater ZJB. Endangered species act lessons over 30 years, and the legacy of the snail darter, a small fish in a pork barrel. Environmental Law. 2004; 34(2):289–308.
6. Sullivan PJ, Acheson J, Angermeier PL, Faast T, Flemm J, Jones CM, et al. Defining and implementing best available science for fisheries and environmental science, policy, and management. Fisheries. 2006; 31(9):460–5.
7. Darpo J. The last say? Comment on cjeus judgement in the tapiola case (c-674/17). Journal for European Environmental & Planning Law. 2020; 17(1):117–30.
8. Epstein Y. Governing ecologies: Species protection in overlapping and contiguous legal regimes: Acta Universitatis Upsaliensis_91, Faculty of Sciences, Uppsala; 2013.
9. Epstein Y, Chapron G. The hunting of strictly protected species: The tapiola case and the limits of derogation under article 16 of the habitats directive. European Energy and Environmental Law Review 2018; June:78–87.
10. Chapron G, López Bao JV, Kjellander P, Karlsson J. Misuse of scientific data in wolf policy. Science. 2013; 339:1521. https://doi.org/10.1126/science.339.6127.1521-a PMID: 23539578
11. Chapron G, Kaczynsky P, Linnell JDC, von Arx M, Huber D, Andrén H, et al. Recovery of large carnivores in europe’s modern human-dominated landscapes. Science. 2014; 346(6216):1517. https://doi.org/10.1126/science.1257553 PMID: 25525247
12. Chapron G, Treves A. Reply to comments by olson et al. 2017 and stien 2017. Proceedings of the Royal Society B. 2017; 284(1867):20171743. https://doi.org/10.1098/rspb.2017.1743 PMID: 29167362
13. Epstein Y. Killing wolves to save them? Legal responses to ‘tolerance hunting’ in the European Union and United States. RECIEL. 2017; 26(1):19–29.

14. Epstein Y, Lopez-Bao J, Trouwborst A, Chapron G. Eu court: Science must justify future hunting. Science. 2019; 366(6468):961. https://doi.org/10.1126/science.aaz8424 PMID: 31753989

15. Treves A, Bruskotter JT. Gray wolf conservation at a crossroads. Bioscience. 2011; 61(8):584–5.

16. Treves A, Bruskotter JT. Tolerance for predatory wildlife. Science. 2014; 344(6183):476–7. https://doi.org/10.1126/science.1252690 PMID: 24786065

17. Treves A, Bruskotter JT, Toman E, Enzler SA, Schmid RH. Gray wolves not out of the woods yet. Science. 2010; 327:30.

18. Bruskotter JT, Enzler S, Treves A. Rescuing wolves from politics: Wildlife as a public trust resource. Science. 2011; 333(6051):1828–9. https://doi.org/10.1126/science.1207803 PMID: 21960614

19. Bruskotter JT, Enzler S, Treves A. Response to mech and johns. Science. 2012; 335(17):795.

20. Bruskotter JT, Vucetich JA, Enzler S, Treves A, Nelson MP. Removing protections for wolves and the future of the U.S. Endangered species act (1973) Conservation Letters. 2013; 7:401–7.

21. Defenders of wildlife, et al. v Haaland. United States District Court for the Northern District Of California 3:21-Cv-344; 2021.

22. Johnson RR, Schneider A. Wisconsin wolf season report february 2021. Madison, Wisconsin 2021.

23. Treves A, Santiago-Ávila FJ, Putrevu K. Quantifying the effects of delisting wolves after the first state began lethal management. PeerJ. 2021; 9: e11666. https://doi.org/10.7717/peerj.11666 PMID: 34268009

24. WDNR. Presentation by j. Price tack to wolf harvest committee 8 april 2021. Madison, WI 2021.

25. Natural Resources Board. Request approval of the fall 2021 wolf season harvest quota. Madison, WI: Wisconsin Department of Natural Resources; 80628C59-435D-488C-841A100DD2CD3C2021.

26. WDNR. Wisconsin wolf management plan. Madison, WI: Wisconsin Department of Natural Resources; 1999.

27. Wiedenhoeft JE, Walter S, Gross M, Kluge N, McNamara S, Stauffer G, et al. Wisconsin gray wolf monitoring report 15 april 2019 through 14 april 2020. In: MANAGEMENT BOW, editor. Madison, Wisconsin: Wisconsin Department of Natural Resources; 2020.

28. USFWS. Post-delisting monitoring plan for the western great lakes distinct population segment of the gray wolf. Bloomington, MN and Ft. Snelling, MN: U.S. Fish and Wildlife Service, Twin Cities Field Office and Midwest Region, 2008.

29. Affiliated Tribes of Northwest Indians, Association on American Indian Affairs, Great Plains Tribal Chairmen’s Association, Inter Tribal Council of Arizona, Native Justice Coalition, Navajo Nation, et al. Letter to secretary d. Haaland et al. Dated 14 september 2021. 2021.

30. Curtis A. The power of nightmares. BBC; 2004.

31. Adams LG, Stephenson RO, Dale BW, Ahgook RT, Demma DJ. Population dynamics and harvest characteristics of wolves in the central Brooks range, Alaska Wildlife Monographs. 2008; 170:1–25.

32. Creel S, Rotella JJ. Meta-analysis of relationships between human offtake, total mortality and population dynamics of gray wolves (Canis lupus). PLoS ONE. 2010; 5(9):1–7.

33. Vucetich JA. Appendix: The influence of anthropogenic mortality on wolf population dynamics with special reference to creel and rotella (2010) and gude et al. (2011) in the final peer review of four documents amending and clarifying the wyoming gray wolf management plan. Federal Register. 2012; 50:78–95.

34. Fuller TK, Mech LD, Cochrane JF. Wolf population dynamics. In: Mech LD, Boitani L, editors. Wolves: Behavior, ecology, and conservation. Chicago: University of Chicago Press; 2003. p. 161–91.

35. Gude JA, Mitchell MS, Russell RE, Sime CA, Bangs EE, Mech LD, et al. Wolf population dynamics in the U.S. Northern Rocky Mountains are affected by recruitment and human-caused mortality. J Wild Manage. 2012; 76(1):108–18.

36. Creel S, Becker M, Christianson D, Dröge E, Hammerschlag N, Hayward MW, et al. Questionable policy for large carnivore hunting. Science. 2015; 350(6267):1473–5. https://doi.org/10.1126/science.aac4768 PMID: 26680181

37. Louchoaurm NX, Santiago-Ávila FJ, Parsons DR, Treves A. Evaluating how lethal management affects poaching of mexican wolves Open Science. 2021; 8 (registered report):200330. https://doi.org/10.1098/rsos.200330 PMID: 33959305

38. Santiago-Ávila FJ, Chappell RJ, Treves A. Liberalizing the killing of endangered wolves was associated with more disappearances of collared individuals in Wisconsin, USA. Scientific Reports. 2020; 10:13881. https://doi.org/10.1038/s41598-020-70837-x PMID: 32807840
40. Treves A, Langenberg JA, López-Bao JV, Rabenhorst MF. Gray wolf mortality patterns in Wisconsin from 1979 to 2012. J Mammal. 2017; 98(1):17–32. https://doi.org/10.1093/jmammal/gyw145 PMID: 29674782
41. Treves A, Artelle KA, Darimont CT, Parsons DR. Mismeasured mortality: Correcting estimates of wolf poaching in the United States. J Mammal. 2017; 98(5):1256–64. https://doi.org/10.1093/jmammal/gyx052 PMID: 30135609
42. Treves A, Artelle KA, Paquet PC. Differentiating between regulation and hunting as conservation interventions. Conservation Biology 2018; 33(2):472–5. https://doi.org/10.1111/cobi.13211 PMID: 30152178
43. Treves A, Krofel M, Ohrens O, Van Eeden LM. Predator control needs a standard of unbiased random-ized experiments with cross-over design. Frontiers in Ecology and Evolution. 2019; 7:402–13.
44. Treves A. Peer review of the proposed rule and draft biological report for nationwide wolf delisting. In: Fuller TK. Population dynamics of wolves in North Central Minnesota. Wildlife Monographs. 1989; 105:3–41.
45. Treves A, Louchouarn NX, Santiago-Avila F. Modelling concerns confound evaluations of legal wolf-killing. Biol Conserv. 2020; https://doi.org/10.1016/j.biocon.2020.108643.
46. Treves A, Paquet PC, Artelle KA, Comman AM, Krofel M, Darimont CT. Transparency about values and assertions of fact in natural resource management. Frontiers in Wildlife Dynamics. 2021; 2:e631998.
47. Wydeven AP, Treves A, Brost B, Wiedenhoft JE. Characteristics of wolf packs in Wisconsin: Identification of traits influencing depredation. In: Fascione N, Delach A, Smith ME, editors. People and predators: From conflict to coexistence. Washington, D.C.: Island Press; 2004. p. 28–50.
48. Natural Resources Board. Meeting to set fall 2021 wolf hunting quota, 11 August 2021 agenda item 4h. 2021 https://dnr.wisconsin.gov/About/NRB/2021/10-August archived at /web/20220130192152/https://dnr.wisconsin.gov/About/NRB/2021/10-August.
49. Fuller TK. Population dynamics of wolves in North Central Minnesota. Wildlife Monographs. 1989; 105:3–41.
50. Treves A, Martin KA, Wiedenhoft JE, Wydeven AP. Dispersal of gray wolves in the great lakes region. In: Wydeven AP, Van Deelen TR, Hesse EJ, editors. Recovery of gray wolves in the Great Lakes region of the United States: An endangered species success story. New York: Springer; 2009. p. 191–204.
51. Chapron G, Treves A. Blood does not buy goodwill: Allowing culling increases poaching of a large carnivore. Proceedings of the Royal Society B. 2016; 283(1830):20152939. https://doi.org/10.1098/rspb.2015.2939 PMID: 27170719
52. Stenglein JL, Zhu J, Clayton MK, Van Deelen TR. Are the numbers adding up? Exploiting discrepancies among complementary population models. Ecology and Evolution. 2015; 5(2):368–76. https://doi.org/10.1002/ece3.1365 PMID: 25691964
53. Thiel RP, Hall W, Heilhecker E, Wydeven AP. A disjunct gray wolf population in Central Wisconsin. In: Wydeven AP, Van Deelen TR, Hesse EJ, editors. Recovery of gray wolves in the Great Lakes region of the United States: An endangered species success story. New York: Springer; 2009. p. 107–18.
54. Natural Resources Board. Request that the board take action to consider approval of a quota for a February 2021 wolf hunt in accordance with the circuit court order issued on February 11, 2021 in Hunter Nation et al. v Wisconsin DNR et al., 2021cv000031 Document 96 Jefferson County. Madison, Wisconsin Department of Natural Resources, 15 February 2021. Report No.: 3DC01AE6-681A-457C-AD29-0CC96F975FDE. https://widnr.widen.net/view/pdf/sbtdbr1v2w/2021-02-2A-Special-meeting-wolf-quota.pdf?l.download=true&u=ulxqjn
55. Natural Resources Board. 15 February 2021 special meeting. 2021. 37 min, transcript of video available at /web/20220130184720/https://dnrmedia.wi.gov/main/Play/ccb5cf0361c5471e9cbb7c7a898cf741d?catalog=9da0bb432dd448a69d86756192a62f1721 archived at /web/20220130184720/https://dnrmedia.wi.gov/main/Play/ccb5cf0361c5471e9cbb7c7a898cf741d?catalog=9da0bb432dd448a69d86756192a62f1721
56. Wydeven AP, Wiedenhoft J, Schultz RN, Thiel RP, Jurwicz RR, Kohn B, et al. History, population growth and management of wolves in Wisconsin. In: Wydeven AP, Van Deelen TR, Hesse EJ, editors. Recovery of gray wolves in the great Lakes region of the United States: An endangered species success story. New York: Springer; 2009. p. 87–106. https://doi.org/10.1097/01.NMC.0000360424.52228.dc PMID: 19713800
57. Stenglein JL, Van Deelen TR, Wydeven AP, Mladenoff DJ, Wiedenhoft J, Langenberg JA, et al. Mortality patterns and detection bias from carcass data: An example from wolf recovery in Wisconsin. J Wildl Manage. 2015; 7:1173–84.
58. Stenglein JL, Wydeven AP, Van Deelen TR. Compensatory mortality in a recovering top carnivore: Wolves in Wisconsin, USA (1979–2013). Oecologia. 2018; 187(1):99–111. https://doi.org/10.1007/s00442-018-4132-4 PMID: 29627957
59. Santiago-Ávila FJ, Treves A. Poaching of protected wolves fluctuated seasonally and with non-wolf hunting. Scientific Reports. 2022. https://doi.org/10.1038/s41598-022-05679-w PMID: 35110599

60. Borg BL, Brainard SM, Meier TJ, Prugh LR. Impacts of breeder loss on social structure, reproduction and population growth in a social canid. Journal of Animal Ecology 2015; 84(1):177–87.

61. Brainard SM, Andrén Henrik, Bangs Edward E., Bradley Elizabeth H., Fontaine Joseph A., Hall Wayne, et al. The effects of breeder loss on wolves. Journal of Wildlife Management. 2008; 72(1):89–98.

62. Bassing SB, Ausband DE, Mitchell MS, Schwartz MK, Nowak JJ, Hale GC, et al. Immigration does not offset harvest mortality in groups of a cooperatively breeding carnivore. Anim Conserv. 2020; 23(6):750–61.

63. Ausband DE. Gray wolf harvest in idaho. Wildl Soc Bull. 2016; 40(3):500–5.

64. Red Cliff et al. v Cole et al.: U.S. District Court Western District Wisconsin 3:21-cv-00597; 2021.

65. Stark D, Erb J. 2012 minnesota wolf season report. Grand Rapids, MN: Minnesota Department of Natural Resources, 2013 5 July 2013. Report No.

66. Palacios V, Font E, García EJ, Svensson L, Llaneza L, Frank J, et al. Reliability of human estimates of the presence of pups and the number of wolves vocalizing in chorus howls: Implications for decision-making processes. European Journal of Wildlife Research. 2017; 63:59–66.

67. Treves A, Chapman CA. Conspecific threat, predation avoidance and resource defense: Implications for grouping in langurs. Behav Ecol Sociobiol. 1996; 39:43–53.

68. Treves A, Bergstrom BJ, Parsons D, Paquet PC, Thiel RP. Letter to the usfws describing concerns about use of the best available science in the state of wisconsin’s post-delisting monitoring report on gray wolves. http://faculty.nelson.wisc.edu/treves/archived at/web/20220130193312/http://faculty.nelson.wisc.edu/treves/reports/Letter%20to%20USFWS/2014_Letters-to-USFWS.zip 15 August 2014. Report No.

69. Treves A, Chapron G, López-Bao JV, Shoemaker C, Goeckner A, Bruskotter JT, Predators and the public trust. Biological Reviews. 2017; 92:248–70. https://doi.org/10.1111/brv.12227 PMID: 26526656

70. WDNR. NRB wolf information request: Agenda item 2a –january 22, 2021 special meeting. In: Resources DoN, editor. Madison, WI 2021 https://widnr.widen.net/s/vh58xn81fr/2021-01-2a-addition al-information archived at /web/20220130184852/https://widnr.widen.net/s/vh58xn81fr/2021-01-2a-additional-information.

71. WDNR. Request from legislators to immediately implement a wolf hunting season in jan-feb 2021, with set quotas, application dates, and set number of tags to be issued. In: Resources WDNR, editor. Madison, WI document 6B6765FA-4A43-4106-8140-012A95659D7 2021.

72. Schmidt JH, Johnson DS, Lindberg MS, Adams LG. Estimating demographic parameters using a combination of known-fate and open n-mixture models. Ecology. 2015; 56(10):2583–9. https://doi.org/10.1890/15-0385.1 PMID: 26649379

73.illeret C, Bischof R, Dupont P, Breseth H, Odden J, Mattisson J. Gps collars have an apparent positive effect on the survival of a large carnivore. Biol Lett. 2021; 17(0000).

74. Chapron G, Treves A. Correction to ‘blood does not buy goodwill: Allowing culling increases poaching of a large carnivore’. Proceedings of the Royal Society B. 2016; Volume 283(1845):20162577. https://doi.org/10.1098/rspb.2016.2577 PMID: 28003458

75. Chapron G, Treves A. Reply to comment by pepin et al. 2017. Proceedings of the Royal Society B. 2017; 2016257(1851):20162571. https://doi.org/10.1098/rspb.2016.2571 PMID: 28330925

76. Great Lakes Wildlife Alliance et al. v Wisconsin DNR and Cole. Circuit Court Dane County, Wisconsin Case 2021CV002103 Document 5; 2021.

77. Sanders JD. Wolves, lone and pack: Ojibwe treaty rights and the wisconsin wolf hunt. Wisconsin Law Review. 2013; 2013:1263–94.

78. Manfredo MJ, Teel TL, Berl RE, Bruskotter JT, Kitayama S. Social value shift in favor of biodiversity conservation in the united states. Nature Sustainability. 2021; 4:323–30.

79. Bruskotter JT, Vucetich JA, Slagle KM, Berardo R, Singh AS, Wilson RS. Support for the U.S. Endangered species act over time and space: Controversial species do not weaken public support for protective legislation. Conservation Letters. 2018; e12595:1–7.

80. Dressel S, Sandström C, Ericsson G. A meta-analysis of studies on attitudes toward bears and wolves across europe 1976–2012. Conserv Biol. 2014; 29(2):568–74. https://doi.org/10.1111/cobi.12420 PMID: 25412113

81. Manfredo MJ, Teel TL, Don Carlos AW, Sullivan L, Bright AD, Dietsch AM, et al. The changing sociocultural context of wildlife conservation. Conserv Biol. 2020. https://doi.org/10.1111/cobi.13493 PMID: 32128885

82. Gill RB. The wildlife professional subculture: The case of the crazy aunt. Human Dimensions of Wildlife. 1996; 1(1):60–9.
83. Clark SG, Milloy C. The north american model of wildlife conservation: An analysis of challenges and adaptive options. In: Clark SG, Rutherford MB, editors. Large carnivore conservation: Integrating science and policy in the north american west. Chicago: The University of Chicago Press; 2014. p. 289–324.

84. Artelle KA, Reynolds JD, A. T, Walsh JC, Paquet PC, Darimont CT. Hallmarks of science missing from North American wildlife management. Science Advances 2018; 4(3):eaa0167.

85. Artelle KA, Reynolds JD, A. T, Walsh JC, C. P, Darimont CT. Distinguishing science from “fact by assertion” in natural resource management. Science Advances (eLetter), 2018; 4(3):eaa0167.

86. Artelle KA, Anderson SC, Cooper AB, Paquet PC, Reynolds JD, Darimont CT. Confronting uncertainty in wildlife management: Performance of grizzly bear management. PLoS ONE. 2013; 8(11):1–9. https://doi.org/10.1371/journal.pone.0078041 PMID: 24223134

87. Artelle KA, Reynolds JC, Paquet PC, Darimont CT. When science-based management isn't. Science. 2014; 343:1311. https://doi.org/10.1126/science.343.6176.1311-a PMID: 24653018

88. Chapron G, Lopez-Bao J. Conserving carnivores: Politics in play. Science. 2014; 343(14):1199–200. https://doi.org/10.1126/science.343.6176.1199-b PMID: 24626913

89. David P. Ma‘iingan and the ojibwe. In: Wydeven AP, Van Deelen TR, Heske EJ, editors. Recovery of gray wolves in the great lakes region of the united states: An endangered species success story. New York: Springer; 2009. p. 267–78.

90. Shelley VS, Treves A, Naughton-Treves L. Attitudes to wolves and wolf policy among ojibwe tribal members and non-tribal residents of wisconsin’s wolf range. Human Dimensions of Wildlife. 2011; 16:397–413.

91. Great Lakes Wildlife Alliance et al. v Wisconsin DNR and Cole: Order granting petitioners’ motion for temporary injunction. Circuit Court Dane County, Wisconsin Case 2021CV002103 Document 114; 2021.

92. Great Lakes Wildlife Alliance et al. v Wisconsin DNR and Cole: Petitioners’ brief in support of motion to modify briefing schedule. Circuit Court Dane County, Wisconsin Case 2021CV002103 Document 177; 2022.

93. Great Lakes Wildlife Alliance et al. v Wisconsin DNR and Cole: Order granting petitioners’ motion for temporary injunction. Circuit Court Dane County, Wisconsin Case 2021CV002103 Document 186; 2022.

94. Lake Beulah Management District v Wisconsin DNR. Wisconsin Supreme Court 54 Wis. 2d 47, 799 N. W.2d 73; 2011.

95. Mech LD. Considerations for developing wolf harvesting regulations in the contiguous united states J Wildl Manage. 2010; 74(7):1421–4.