Uncertainty and precaution in hunting wolves twice in a year

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Short title: Uncertainty and precaution

Keywords: Canis lupus, endangered species, extinction, hunt, model, sustainability, policy

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 timing and effect of precautions or lack thereof are scientific questions. We investigated the 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 state wolf population in April 2021 and an estimate of 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. This emphasizes the need for greater precaution in 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 show how scientists have the tools and concepts for quantifying and explaining the probabilities of crossing thresholds set by laws or other social norms. Refusal by scientists to account for uncertainty opens the door to policy-making based on opinion, anecdote, and political rivalries. We recommend instead that

33 scientists grapple with data gaps by explaining what the uncertainty means for policy and the
34 public including the consequences of being wrong.

35 **Introduction**

36 When humanity confronts threats to the planetary or local natural resources and
37 biodiversity, many governments, critics, and commentators invoke precautions. For example, in
38 1992, United Nations authors endorsed a precautionary principle as follows,

39 "In order to protect the environment, the precautionary approach shall be widely
40 applied by States according to their capabilities. Where there are threats of serious or
41 irreversible damage, lack of full scientific certainty shall not be used as a reason for
42 postponing cost-effective measures to prevent environmental degradation." (Principle
43 15 of [1]).

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

53 There is no scientific uncertainty that human activities that directly kill organisms or
54 degrade ecosystems have caused extinctions. The risk of extinction whether local or range-wide

55 is higher for organisms that are few in number, or abundant ones that are narrowly endemic or
56 genetically homogeneous [3]. For simplicity, we refer to the latter as imperiled hereafter.
57 Precautions for imperiled species received affirmation by the 1978 USA Supreme Court decision
58 on the snail darter threatened by Tellico Dam [4]. “The Supreme Court's opinion in TVA v Hill is
59 still good law, with Chief Justice Burger's stentorian declaration repeatedly echoed in successive
60 endangered species cases: ‘Congress has spoken in the plainest of words, making it abundantly
61 clear that the balance has been struck in favor of affording endangered species the highest of
62 priorities, thereby adopting a policy which it described as Institutionalized caution.’ ” p.305 in
63 [5], citing majority opinion [4]. For example, under Endangered Species Act (ESA) protections
64 and similar provisions of the E.U. Habitats Directive [6-8], permits for killing listed species are
65 extremely restrictive.

66 Following efforts to reduce protections for gray wolves *Canis lupus* in the USA and E.U.
67 much attention has been paid to proposed and enacted regulations and methods for public
68 hunting, trapping, and hounding of wolves [9-19]. For the gray wolf in Wisconsin, USA, a
69 population reclassified from ESA endangered status in early January 2021, but whose
70 reclassification is a matter of litigation as we write, similar institutionalized caution might still
71 be appropriate in the wake of a February 2021 hunt during which permitted hunters killed 21%
72 of the population in <72 hours [20]. Another 98-105 wolves were estimated to have died
73 because of removal of federal protections between 3 November 2020-14 April 2021, and
74 apparently at least a third of collared wolves went off the air without explanation [21, 22]. The
75 proposal to hunt Wisconsin wolves again starting 6 November 2021 has raised public concerns
76 and state wildlife agency cautions to decision-makers [23]. Here we present the second in a

series examining the effect of wolf-hunting on Wisconsin's wolf population [21] by forecasting the status of the population out to 14 April 2022, with and without permitted killing at various levels. 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 [24]. 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 [23] and given co-sovereign tribes in the region have expressed strong concerns [25], scrutiny of the plans for a second wolf-hunt seems important to many actors. 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" [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, [26]. To avoid that pitfall

99 which afflicts extreme positions in the wolf-hunting debate, we do not imagine the darkest
100 future but rather stick to peer-reviewed data and, where that is absent, restrict ourselves to the
101 official state data, rely on peer-reviewed evidence when it conflicts with the state's assertions
102 of fact, and explain the limits to confidence with both.

103 The uncertainties and precautions in our case are not limited to scientific data or how to
104 interpret those. They extend to the political actors and decision-makers. Powerful actors differ
105 on the ideal number of wolves dead or alive and competing views of what makes for the best
106 available science. The socio-political context of the Wisconsin wolf debate includes multiple
107 governmental entities, each one with a different worldview and each one able to act
108 (subsequent to our writing) in ways we cannot anticipate. Given these actors differ in their
109 institutionalized caution and in how individuals are given authority to use personal opinion
110 about caution, we have chosen to define the most undesirable result of wolf-hunting by the
111 state of Wisconsin as eradication (<2 wolves), statutory listing under the state threatened and
112 endangered species list (<251 wolves), and falling below the state population goal of 350
113 wolves [27]; all those values represent wolves outside of tribal reservations last estimated at 42
114 [28]. These three thresholds represent the value judgments made by society at one time or
115 another, in principle, statute, and regulation respectively, about how cautious one should be
116 about the status of the state wolf population. We are not interposing our own value judgment
117 about a desirable or undesirable number of wolves. Instead, we ask the scientific question of
118 what death toll in Fall 2021 would cross undesirable thresholds so the public and decision-
119 makers can judge caution and its absence.

120 We also do not spend much effort to address sustainability for two simple reasons. First,
121 concerns with sustainability are about future uses more than the risk of extirpation after a
122 single use and we are concerned with crossing the above thresholds in a single use in Fall 2021.
123 Second, the science of sustainable hunting of wolves is unsettled. Although reviews of wolf
124 population dynamics and sustainable levels of killing include many data points and seem to
125 converge on a range of sustainable, annual human-caused mortality rates [29-33], the literature
126 nonetheless concludes with three-fold differences in magnitude for estimates ranging from
127 high teens to 48%. Although the prior literature would seem to guide decision-makers in
128 Wisconsin to choose a Fall 2021 wolf-hunt quota that would not change the population, the
129 wide variation in estimates above and the novelty of a second wolf-hunt in a single year
130 produces new and greater uncertainties than the literature addresses. Also, in a series of
131 papers on wolf science and policy in Wisconsin, we have shown how omissions of changes in
132 census methods, ignoring the information available in the disappearances of marked wolves,
133 and a lack of alternative management scenarios could both distort wolf policy and mire the
134 science in uncertainties due to methods [21, 30, 34-43].
135 To support decision-making in the face of great uncertainty, we provide a step-by-step
136 rationale for the uniform distributions we use and a simple linear model of births and deaths.
137 The primary reason to take this simple approach is its practical advantage. We show how the
138 state, tribes, public, and other interests can perform these estimates independently and
139 reproduce our findings to explore their own scenarios for November death tolls. That is
140 valuable given our inability to predict the eventual death toll and the reactions of the many
141 interested governmental actors mentioned above. Thus, as we grapple with uncertainty at

142 every step, we transparently present the bounds we consider plausible and why. Secondly, we
143 use Bayesian concepts and terminology but not formal Bayesian algorithms, because many of
144 our key input variables are uninformative and combine in simple linear fashion. To achieve our
145 primary goal of clear communication and user-input, a formal Bayesian algorithm would be less
146 accessible. We illustrate how any reader and user of our simple model can choose a death toll
147 and calculate probabilities of crossing the legal thresholds. We offer this as a possible model for
148 other scientists engaged in public policy debates that are contentious and uncertain.
149

150 **Materials & Methods**

151 Our study period is the wolf-year starting 15 April 2021 and ending 14 April 2022. We
152 contended with three key scientific uncertainties in this study period. First, the effects of the
153 22-24 February wolf-hunt on wolf numbers, pack sizes, and reproductive potential are
154 uncertain. Second, little information is available about reproduction for our study period. Wolf
155 reproduction data is generally difficult to collect and the state census method used tends to
156 confound pack size with past reproduction [43, 61]. Third, the wolf policy in 2021 is so
157 contentious as of writing that we cannot be confident about the legal quota or the eventual
158 death toll. We describe the unprecedented methods of the February 2021 wolf-hunt first
159 because it conditions the remaining uncertainties.

160 The February 2021 wolf hunt killed 218 wolves legally, took place during the mating and
161 pregnancy season of the wolves, and included pursuit in deep snow by snowmobiles, night-time
162 hunting, hounds in packs of 6, and relays that allowed a team of hunters to substitute a fresh
163 pack of hounds; >85% of kills were aided by the use of hounds according to hunter self-report

164 [20]. Hunters overshot the legal quota by 99 wolves (82%), an event the DNR blamed on
165 regulations that require 24 h notice to close zones and regulations that allowed hunters in open
166 zones to delay reporting kills for 24 h even after the state quota was met. Also, the state sold
167 permits for 13 hunters for every wolf that could be legally killed. These latter regulations
168 increase the uncertainty about the eventual death toll of any legal quota [20, 21, 23, 62].

169 Before we address the remaining uncertainties about population status in our study
170 period, with a mix of qualitative and quantitative information, we explain the simple model we
171 adopted for population change during the study period. Because of the preceding three
172 scientific uncertainties and our desire to provide a method that others can use to plug in their
173 own values or future data, we relied on a simple one-step model of population size change for
174 our study period, as follows:

175 Eq. 1: $N_{t+1} = N_t + R_t - M_t - H$,

176 where N_t is the population size estimate on 15 April of year t, t=2021, Rt is the number of pups
177 born in year t surviving to November when they are typically counted alongside adults using
178 standard census methods [32, 63], H is the death toll in a wolf-hunt, and M_t is the number of
179 dead wolves in year t. We estimated R_t by equation 2,

180 Eq. 2: $R_t = B_t * L * S$

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

183 Eq. 3: $M_t = D \bullet (N_t + R_t / 2)$

184 where D is the annual mortality rate estimate for a year without ESA protections and without a
185 wolf-hunt as we describe further below in the section on deaths. Note that R from Eq.1-3

186 represents pups surviving to November 2021. In Eq. 3 these pups are exposed to one-half of a
187 year of D from November-April.

188 Our simple model in Eq. 1 assumes no net migration into or out of the state during the
189 study period at a rate relative to deaths or births substantial enough to affect our results.
190 Assuming no net migration is a precaution because it would be hopeful to imagine rescue from
191 outside the state if legal thresholds were crossed in the state. Our assumption seems
192 reasonable given long-distance migration leading to pack establishment has been rare [64].
193 Also, the assumption of no net migration has been used by others modeling this population [65,
194 66]. Also, Eqs. 1-3 assume linear effects. We assumed no compensatory increases in birth or
195 pup survival other than those encompassed by the range of values in [44]. We do not ignore
196 Allee effects, compensation or negative density-dependence [54, 58, 59], but we do not model
197 them because too many questions remain for Wisconsin wolves [3, 41,
198 43](http://faculty.nelson.wisc.edu/treves/archive_BAS/Treves%20public%20comment%20NRB
199 %203%20Aug%202021.pdf). Assuming compensatory effects would be incautious. Nor do we
200 model non-linear effects that would caution against high death tolls in a second wolf-hunt. For
201 example, depensatory or super-additive effects as described by numerous studies of wolves
202 including in the Wisconsin wolf population [33, 36, 45, 60, 61]. We defend the simplicity of our
203 approach as follows: pending evidence that non-linear effects would play out detectably in the
204 short period of our study and pending an analysis of net compensatory and depensatory
205 effects, we simply assume the good conditions studied by [56] encompass any nonlinear effects
206 for wolves in an environment with fewer competitors than before.

207 **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 [28, 67, 68]. 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 [28]. 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 [69], 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 [22]. Although the two methods differ substantially in uncertainty, they don't result in very different point estimates for N_{2021}.

The state and [21] 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 [21] 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 [23].

The state's justification for interrupting the new census method before 14 April 2021, when it would have been terminated as in previous years [28], 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 [36, 45, 70]; Santiago-Ávila in review. We are not aware of any effort to correct the new census method estimate therefore it is 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 unaccounted 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 [23, 62], 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 [44] , 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 [44] and adjusted the normal distribution accordingly. Hence multiplying the three preceding parameters yielded an average of 0.69 (95% CI 0.15-4.32) per pack. We estimate the number of breeding packs, B, to multiply it against in the following section.

The study in [44] was conducted during a period with ESA protections and a population recolonizing vacant range, i.e., reproductive performance in good years measured by [44]. We did not use another commonly cited summary [69] 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 [61].

Number of breeding packs, B: The proportion of packs that produced pups in summer was estimated in [44] as a proportion of all packs studied. We had to estimate B from the packs present in the state multiplied by Thiel's 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 [44] estimates and a highly informative prior as follows.

In April 2020, the state contained 245 packs and tribal reservations held 11 packs [28]. An unknown number were eliminated in the February 2021 wolf-hunt. The state assumed no disruption to breeding after the February 2021 wolf-hunt, an incautious assumption [23].

Given the unprecedented nature of the wolf-hunt, the effects of the February 2021 wolf-hunt on R are uncertain. The statewide 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, snowmobiles, 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 [71-74], 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 [72]). Therefore, we estimated the number of breeding packs (B) in several ways.

We have five sources of information that help to parametrize the variable of number of breeding packs in summer 2021. First, under beneficent conditions studied by [44], 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 (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 is 51 breeding packs which corresponds to approximately 0.23 pregnant females per wolf-kill. 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, Red cliff et al. [51]. They reported 65% of adult females and 50% of yearling females were pregnant in that small, nonrandom sample. 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 [75]. This hunt was very different (no hounds, no deep snow, no snowmobiles, no nighttime hunting, outside of 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 or B = 167 as a plausible upper bound.

The above seems incautious. For example, 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 [51] citing declaration by A.P. Wydeven. 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 [76]. 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.

However, from a different viewpoint 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 number 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.

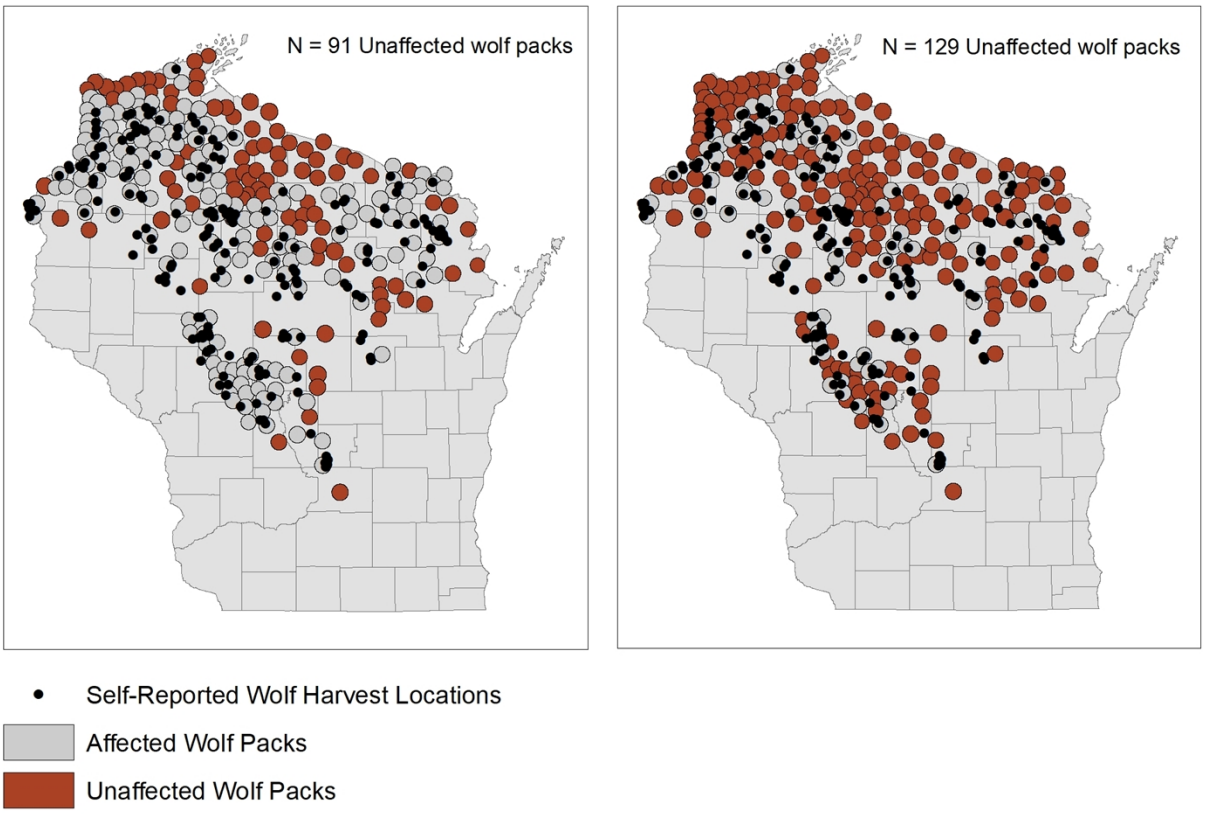
We also used an indirect source of information which came from spatial analysis of kill locations in February 2021 wolf-hunt to generate additional scenarios. We assume that wolf packs that might have encountered hunters or hounds during the February 2021 wolf-hunt might be disrupted reproductively by 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 the hunt, and reservation packs and packs outside of hunted counties would be unaffected by the hunt. These assumptions of spatial patterns are depicted graphically in Figure 1.

If the spatial proximity of reported wolf-kills predicts the disruption of reproduction in the nearest pack, then the two scenarios in Figure 1 provide two more estimates of the number of breeding packs. Note our unlikely lower bound of 12 breeding packs emerged from scrutiny of Figure 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. If hunters exert a

suppressive effect on reproduction of wolf packs in a large area, the number of breeding packs 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 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 Figure 2, we represented the uninformative uniform distribution between those four values and implausible, extreme values of 12 and 218.

Figure 1. (A) 91 breeding packs scenario: Any wolf kill location self-reported by hunters was extended by the average wolf territory size and if it overlapped a wolf territory, those wolf packs were assumed not to have reproduced successfully. (B) 129 breeding packs scenario: Any hunter-reported wolf-kill location inside a wolf pack territory was assumed to have prevented that pack from reproducing successfully. To estimate the number of breeding wolf packs for these two scenarios, we used ArcGIS Desktop 10.7.1 to convert the map of 2020 Wisconsin wolf pack locations reported in [20] and the February 2021 self-reported wolf harvest location map from [28] into shapefiles. We then used spatial overlay and geo-rectification to find overlap in territories and self-reported kill locations



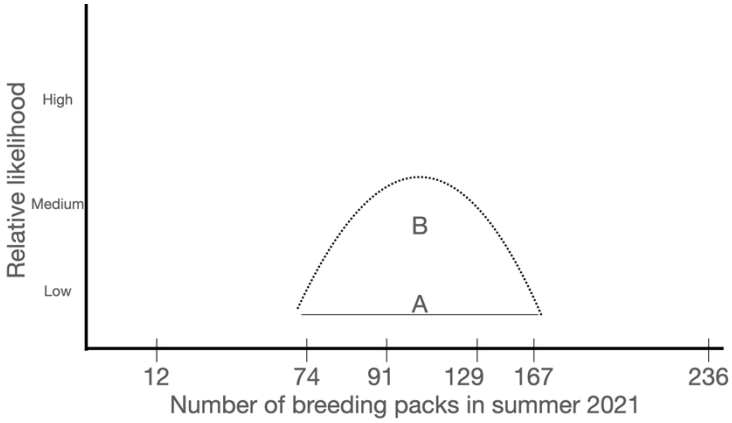


Figure 2 presents two ways to depict the uncertainty about the number of breeding packs in the state. We selected the uniform distribution (A) because we had no evidence to support the

normal distribution (B). Also the uniform, uninformative distribution allows the data to influence the result rather than our preconceived notions of what is typical in biological distributions.

Deaths

Eq. 1 requires an estimate of M_{2021}, the number of dead wolves (adults year-round and pups after November) 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 - deaths. Also, we had an informative prior R_{2020} from [44] 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 how could we validate these? 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 [36-38, 77-79] and particularly incomplete after 14 April 2012 [22, 23, 62, 67, 68, 80, 81].

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

383 0.42-0.52 depending on ESA listing status [36]. That study used time-to-event analyses in a
384 competing risks framework. By contrast, a cruder estimate using a weighted average of collared
385 and uncollared adult wolves dead as a proportion of the population size at the start of each
386 wolf-year, which did not take into account time-to-event but considered uncollared wolves,
387 estimated the rate at 0.18 for radio-collared wolves and 0.47 (SD 0.19 annually) for uncollared
388 wolves [37]. Similarly, [82] reported higher mortality rates for uncollared Alaskan gray wolves.
389 See also [83] for another large carnivore in which GPS collars are associated with higher
390 survival. In 2020, approximately 5% of the wolf population was collared, so the weighted
391 average annual mortality rate would be 0.46. The third peer-reviewed estimate of mortality
392 covered the years 1979-2013 which included a wolf-hunt in Fall 2012. However that estimate it
393 provided of 23.5% annual mortality for radio-collared adults in a time-to-event analysis [45]
394 seems low. Also, that study failed to account for several confounding variables and took
395 unjustified steps in analyses. The unjustified steps were to include a variable for a change in
396 slope in the year 2004 which is distinguishable only by methods of analysis of census data we
397 have shown [41, 43]. And there were similar changes in census methods and methods of
398 analysis in 1995, 2001-2003, and 2012, which [45] did not consider. We do not understand why
399 2004 was special and they did not explain why. Also, the authors lumped nonhuman causes of
400 death with unknown causes of death, a step that several analyses have shown to be unjustified
401 because time-to-event analyses show very different timing in the hazard of nonhuman and
402 unknown causes [36-38]. Moreover, the authors did not acknowledge that uncollared wolves
403 may have faced higher rates of mortality. Finally, the authors did not acknowledge the multiple,
404 corroborating lines of evidence showing that wolf survival and wolf population growth declined

405 when ESA protections were lifted 7 times from 2003-2013 [11, 36-38, 65, 84, 85]. In sum, we
406 had three published estimates of annual mortality rate from prior years ranging from 0.235-
407 0.52 using three different methods on similar datasets, with which we could validate our
408 estimate of D, at least qualitatively.

409 **Scenarios for wolf-hunt death toll and the order of operations in our model**

410 The last step in our analysis was to subtract H for the death toll from the uncertain wolf-
411 hunt scheduled for November 2021. These death tolls assume zero sub-lethal injuries
412 unreported as legal kills, and assuming zero additional cryptic poaching beyond that already
413 captured in annual mortality rates during periods without ESA protections [21, 36].

414 Uncertainty about the death toll reflects different permutations of the quota set by the
415 DNR (130) and that quota voted by the NRB on 11 August 2021 (300) in addition to the
416 following factors that might raise or lower the eventual death toll: over-kill in February 2021 of
417 99 or 82% might repeat itself; or the tribal treaty right to reserve 43% of the declared state
418 quota (leaving a death toll of 74 if the DNR quota of 130 were to be implemented). Therefore,
419 we modeled H as a continuous, normal distribution with a mean of 300 ranging from 0-600. H
420 was our perfectly measured x variable on which to regress the population estimate using
421 ordinary least squares. In Results and Discussion, we focus on three x values (0, 130, and 300)
422 representing the preferred, legal death tolls for the plaintiffs, DNR, and NRB respectively. We
423 also discuss a fourth death toll (74), which was the DNR's 130 death toll minus the tribal treaty
424 right reserved 43% because that was the legal quota at the time of writing.

425 Because annual mortality rate is a proportion of living wolves, the order in which we
426 deduct non-hunt deaths may be important. Subtracting the November wolf-hunt first would

427 over-count deaths from other causes because these are calculated as a proportion using the
428 annual mortality rate described above. However, half the year passes before the wolf-hunt and
429 a smaller number of wolves (adults only) are present to die of such causes, so the number of
430 deaths would be under-counted, if we deduct the non-hunt mortality first. Ideally, one would
431 subtract the adult summer mortality, add pups surviving to November, subtract the wolf-hunt
432 and then subtract adults and pups dying from other causes in the winter. However, we believe
433 uncertainty about the other parameters described previously is far greater than the slight
434 difference this more realistic algorithm would create. Therefore, to keep the calculations
435 simple, we deducted all the annual mortality before the wolf-hunt, which treats the wolf-hunt
436 as purely additive. The bias we introduce by estimating a higher number of non-hunt deaths is
437 offset by the bias we have already introduced by dismissing unreported deaths and excess
438 illegal killing. For example, the most rigorous study of cryptic poaching to date on the
439 endangered Mexican wolf estimated that disappearances of collared wolves in this closely
440 monitored population went up 121% when the wolf was not listed under the ESA, compared to
441 periods of strict ESA protection [35]. However, we took the conservative step of not using this
442 estimate or the higher mortality rate of collared wolves estimated in [36].

443 Finally, before evaluating legal thresholds, we subtracted 42 wolves living entirely or
444 mostly on tribal reservations [28], because these are managed by the co-sovereign tribes whose
445 governments declared wolves protected from public hunts [50].

446 Randomizing: Our modeling procedure used random generation of values for every
447 parameter in Eqs. 1 and 2 in 1200 iterations repeated once for each census method (traditional
448 and new). We tripled that for the final estimates of N_{2021} to 3600 iterations to boot-strap the

distribution around the means. Data in Supporting information provides the randomizations and the distribution for each parameter.

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.

Table 1. Estimates of the annual mortality rate (D_{2020}) of Wisconsin wolves between 15 April 2020 and 14 April 2021 using two census methods to estimate N_{2020} and N_{2021} and reproductive parameter R (mean, lower and upper bounds of the 95% CI from [44] for 256 wolf packs. D is estimated as (N_{2021}-N_{2020}) divided by (0.5 * R_{2020} + N_{2020}) following Eq. 3. We assumed the mean value for N_{2021} because the state did so for setting policy.

	Traditional census method (uniform distribution) estimating D_{2020}		New census method (unknown non-uniform distribution) estimating D_{2020}		
Estimates of D_{2020}* **	**A***	**B***	**C****	**D****	**E****
Mean	0.41	0.45	0.51	0.36	0.22
Minimum bound	0.38	0.43	0.50	0.34	0.17
Maximum bound	0.53	0.56	0.58	0.48	0.38

* For the traditional census method the minimum bound in 2020 (1034) - the maximum bound in 2021 (751+218) provides the values in column A and the maximum bound in 2020 (057) - the minimum bound in 2021 (695+218) provides the values in column B.

** For the traditional census method, the state set policy used the mean in 2021 (1195 - 218), so we calculated variation by using the upper bound (1355) in column C, the mean (11995) in column D, and the lower bound (739) in column E.

*** The mean, minimum bound, and maximum bound reflect the mean and CI of R (see Methods).

468

469

470 **State wolf population N_{2022}**

Figures 3 and 4 depict the probabilities of crossing legal thresholds for the Wisconsin wolf population. The slope of Figure 3A suggests that any death toll above 16 creates a better than average possibility of crossing threshold 1 (350 wolves). 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 threshold 2 (state listing) exceeded 50% at death tolls of 113 and 189 wolves, for the traditional and new census methods respectively. The probability of crossing threshold 3 (state extirpation) exceeded 50% at death tolls of 359 and 443 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 (Figs. 3A, B).

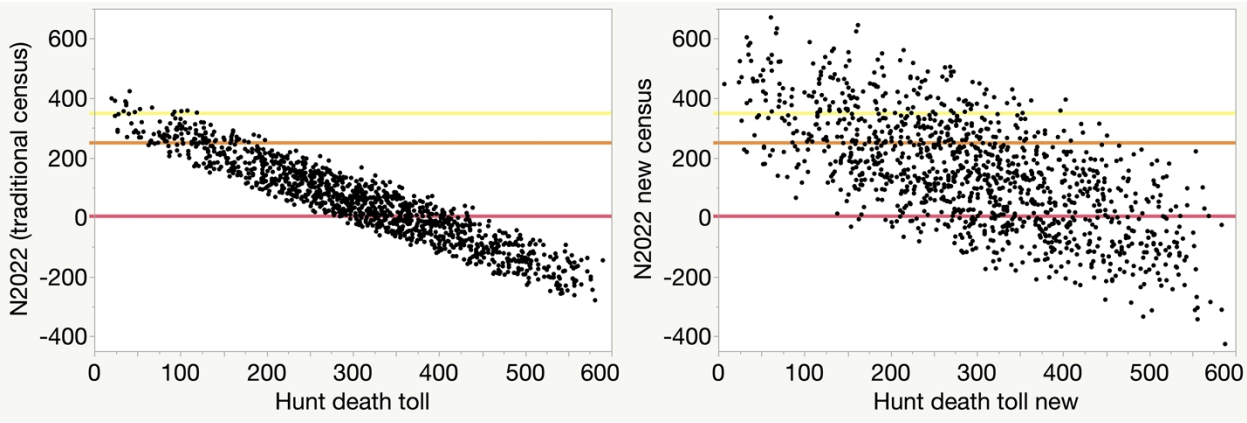
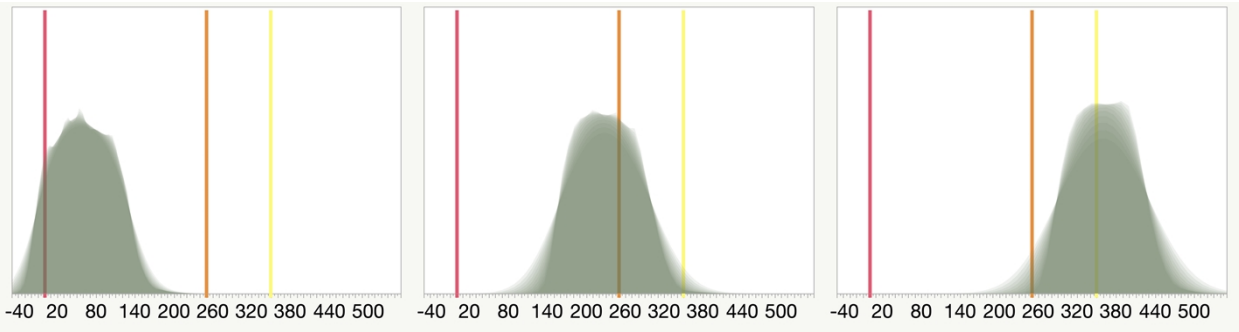


Fig. 3. The relationship between wolf-hunt death tolls in Fall 2021 (x-axis) and predicted wolf population status in Wisconsin on 14 April 2022 (y axis). Ordinary least squares regression of N_{2022} against H for the traditional census method (A, regression line not shown adjusted r^2=0.89, N2022 = 366 - 1.016*H, SE slope = 0.010) and new census method (B, regression line not shown adjusted r^2=0.45, N2022 = 437 - 0.983*H, slope SE = 0.032). We ran 3600 iterations for each panel, in which we randomly selected 1200 values for each parameter in Eqs. 1 and 2.

488 Three reference lines represent the legal thresholds of 1 (extirpation, red), 250 (state listing,
489 orange), and 350 (state population goal, yellow).
490

491 

492 Fig. 4. Distribution of predicted population estimates for Wisconsin's wolves on 14 April 2022
493 assuming death tolls of 300 (A), 130 (B), and 0 (C), including reference lines as in Figure 3. For
494 these histograms, we ran 3600 iterations to generate smoother probability distributions as
495 "shadow grams" made in JMP® 15.0, 2021, for each value of H (see Methods). These
496 distributions rely on the traditional census method (Fig. 3A) and average and SD follow: (A) 61
497 SD 44 with a 9% chance of extirpation and 100% chance of dropping below the state listing
498 threshold, (B) 231 SD 45 with a >99.5% chance of dropping below the state population goal, a
499 64% chance of dropping below the state listing threshold, (C) 361 SFD 44 with a 13% chance of
500 falling below the state population goal.
501

502 Even a death toll of zero might lead to the wolf population declining below the 1999
503 population goal of 350. If the new census method were used in Figure 3A-C, the distributions
504 would be flattened raising the probability of undesirable thresholds.

At the time of writing, the legal quota was set at 130 (Fig. 4b) but 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 Figures 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 of 251 and a 36% probability of crossing the state population goal of 350 (orange and yellow lines respectively in Figures 3 and 4). The above averages and probabilities assume no over-kill or illegal kills beyond that estimated by our background mortality rate.

Discussion

We addressed how scientists should 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 use a case study of a recently delisted endangered species subjected to hunting 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

527 is precautionary and what is not, relieving scientists of the appearance of making personal
528 value judgments when evaluating policy effects. We addressed the probabilities of crossing
529 three legal thresholds with simple models and Bayesian concepts to account for uncertainty.
530 We demonstrated constructive approaches to using a mix of qualitative and quantitative
531 information to reduce uncertainty to manageable levels with uninformative, uniformly
532 distributed priors.

533 We recommend that scientists practice analysis and communication that improves their
534 ability to explain what the uncertainty means for policy and the public. For scientists, a
535 common thread might be that the more uninformative the prior data, the more scenarios one
536 should present and the more transparent the assumptions about inputs should be. This
537 recommendation aligns with our inclination in the above methods to use a simple model so
538 that non-specialist members of the public and decision-makers can easily explore and adjust
539 inputs. We did so in the final paragraph of Results by assuming the quota set by the DNR and
540 the treaty reserved rights were the most likely outcomes of the November 2021 wolf-hunt. Any
541 reader can follow our lead and estimate the outcomes for any death toll they prefer.

542 Also, we avoided the critique of precautionary approaches articulated by Curtis (see
543 introduction) by sticking to peer-reviewed evidence wherever available, evaluating that
544 evidence transparently, and when unavailable we used uninformative, uniform distributions on
545 priors to account for gaps in important data.

546 **Wisconsin wolves**

547 We addressed the global question of precaution and uncertainty with a case study of
548 the Wisconsin gray wolf population recently delisted from the U.S. Endangered Species Act. For

organisms at risk of extinction like in our case, precaution is obvious at each step 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.

Our results speak to how precaution can be operationalized even with high uncertainty about data. We report high probabilities that a second wolf-hunt in 2021 will 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 (over-kill 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 outdated and unscientific population goal first articulated in 1999 [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 not including the hunt. 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 (or 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

571 are substantially higher than the DNR "consensus" estimate of 13% [23] plus approximately 9%
572 nonhuman-caused. Therefore, we reject the DNR's consensus method as wishful thinking.
573 Furthermore, the range of annual mortality rates in Table 1 was almost never so low as
574 estimated by [45]. That estimate probably erred by extrapolating to the population from a non-
575 random sample of radio-collared animals. Their estimate of 23.5% is only plausible for 2020 if
576 one accepts a drastic rise in population size from 2020 to 2021, which no authority has claimed.
577 We recommend those estimating mortality during periods without ESA protection should use a
578 high rate of mortality than in periods with ESA protection, because the state and federal
579 agencies responded to a high rate of complaints of wolf attack on farm animals, which led the
580 USDA and private permittees to kill 34 wolves in summer 2021 (D. Ruid, unpublished data
581 presented to [23]). As predicted by [36], the February 2021 wolf-hunt seems to have led to an
582 increase in wolf-killing in response to alleged predation on domestic animals. Also as predicted
583 by [36], reducing protections for wolves increases calls for legal killing; see also [46]. Reducing
584 protections also leads to lower survival for wolves when all causes of death are considered [36].
585 Therefore, we recommend the state halt lethal management of wolves in years it plans wolf-
586 hunts because we see no method or regulation in place to deduct state lethal control totals
587 from legal quotas. We also recommend the state revise its estimate of mortality and in so doing
588 also publish all mortality data in a scientific manner including distinguishing between radio-
589 collared wolves and others with time on the air for the former.
590 The 82% over-kill seen in <3 days during the February 2021 wolf-hunt has raised
591 national debate about the security of state wolf populations. That hunt and our calculations
592 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 [47]. 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 we have taken 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 are bounded by zero in this small population of wolves). Therefore, the burden of proof is heavier for those who advocate for higher death tolls. To this we add another insight from the current study. If the state wildlife agency wishes to continue to invest little in monitoring reproductive success of wolves, it must set precautionary lower expectations for wolf-hunts and enforce against over-shooting the quota. Without data on reproduction and signs of success in reproduction, all quotas are unsafe, and unscientific in the coming year.

Politics of precautions and the role of science

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 over wolf policy in August 2021 (https://www.wpr.org/listen/1836191, accessed 17 August 2021;[23]) which was followed by an ongoing lawsuit by the executive branch against the chair of the NRB. Besides that intra-governmental clash there is a long-standing intergovernmental

615 dispute between the DNR and the co-sovereign tribes of the region who have federal treaty
616 rights to half of almost all natural resource extraction. The state and tribes have co-managed a
617 subset of resources amicably under federal treaties, but walleye fish and wolves have been a
618 point of friction for over a decade [48-50]. The Red Cliff tribal government and other tribal
619 governments that signed those treaties filed a federal lawsuit on 19 September 2021 alleging
620 treaty rights violations [51]. Besides being pro-wolf, tribes in our region are also pro-hunting for
621 subsistence, spiritual, and traditional uses, which creates a different dynamic than anti-hunting
622 or anti-wolf-hunting interests in the broader public. Three other lawsuits filed to protect wolves
623 in state and federal courts are also pending from groups opposed to wolf-hunting policies.
624 Finally, a small, vocal minority expresses anti-tribal
625 (https://dnr.wisconsin.gov/calendar/meeting/46286), anti-wolf views, and has espoused a wolf
626 population target <81 [52]. In sum, the public policy debate is riven by more than two fault
627 lines.

628 Many actors in the above public policy clashes want to claim scientific evidence is on
629 their side. Testifying to this, observe how many speakers from the public, the DNR, or the NRB
630 offered facts or made assertions of fact in the policy process [23]. Comments by the majority in
631 the 7-person NRB showed that rather than considering the peer-reviewed science or the agency
632 recommendation, the majority in the NRB over-ruled the recommendation in favor of anecdote
633 and personal beliefs about wolves, to set a higher quota. Such procedures are the opposite of
634 precautionary and treat uncertainty as if it could be overcome by conviction in one's beliefs.
635 Unsubstantiated fact claims or using power to overcome uncertainty are not restricted to
636 Wisconsin or wolf policy, e.g., [53], nor restricted to wildlife public policy debates we expect.

637 However, in our opinion, none of the actors in Wisconsin's wolf policy debate wish to undergo
638 the rigor of independent review by anonymous peer experts. This too is common as the
639 preceding citation attests. Therefore, we feel it important to remind readers of how science is
640 and is not judged.

641 Science is not judged by whether one likes or dislikes the findings. It is judged by its
642 methods. Nor is science judged by who conducts it, but by the transparency and reproducibility
643 of methods and inferences. That is why it is so important to subject observations and
644 measurements of the natural world to independent scrutiny and tests of replication. Despite
645 weaknesses in the peer review process [54-58], the alternatives have many of the same
646 weaknesses only worse. Namely, when authors select their own peer reviewers, the biases,
647 competing interests, and omissions by the authors may be shared by their reviewers. When the
648 outcome of analyses is selected before the methods are evaluated or when the methods are
649 shaped by desired outcomes, the lack of independent peer review may allow massive
650 inaccuracies, imprecisions, or fabrications to persist in the public record. This has plagued
651 Wisconsin wolf policy then and now [43]. Also, competing interests are a pervasive concern in
652 U.S. wildlife management as shown by the copious review of policy documents by [59]. Those
653 authors showed how wildlife agencies have been captured by hunting interests. Favoring or
654 showing affinity to special interests is a competing interest in scientific work. The claim that
655 such an agency's management is "science-based" cannot be credited. Such concerns might be
656 alleviated by transparent adherence to recommendations in the peer-reviewed literature and
657 USA federal government recommendations (citations above and [60] on fostering scientific
658 integrity). We offer the preceding analyses and discussions as a path for scientists to play a

more appropriate and important role in public policy debates that confront substantial uncertainty about evidence.

Acknowledgements

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

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