

Quantifying the effects of delisting wolves after the first state began lethal management

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ABSTRACT

Predators and their protection are controversial worldwide. Gray wolves, *Canis lupus*, lost U.S. federal protection (delisting) and the State of Wisconsin began lethal management first among all states and tribes that regained authority over wolves. Here we evaluated the initial success of reaching the state's explicit objective, "...to allow for a sustainable harvest that neither increases nor decreases the state's wolf population..." We used official state figures for hunter-killed wolves, population estimates from April 2017–2020, and the latest peer-reviewed model of individual wolf survival to estimate additional deaths resulting from federal delisting. More than half of the additional deaths were predicted to be cryptic poaching under the assumption that this period resembled past periods of liberalized wolf-killing in Wisconsin. We used a precautionary approach to construct three conservative scenarios to predict the current status of this wolf population and a minimum estimate of population decline since April 2020. From our scenarios that vary in growth rates and additional mortality estimates, we expect a maximum of 695–751 wolves to be alive in Wisconsin by 15 April 2021, a minimum 27–33% decline in the preceding 12 months. This contradicts the state expectation of no change in the population size. We draw a conclusion about the adequacy of regulatory mechanisms under state control of wolves and discuss the particular governance conditions met in Wisconsin. We recommend greater rigor and independent review of the science used by agencies to plan wolf hunting quotas and methods. We recommend clearer division of duties between state wildlife agencies, legislatures, and courts. We recommend federal governments reconsider the practice of sudden deregulation of wolf management and instead recommend they consider protecting predators as non-game or transition more slowly to subnational authority, to avoid the need for emergency relisting.

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INTRODUCTION

Wolves and their protection are controversial worldwide and across the U.S. (*Bruskotter et al., 2018; Manfredo et al., 2020; Treves & Martin, 2011; Chapron et al., 2014; Dressel, Sandström & Ericsson, 2014*). The U.S. Endangered Species Act (ESA) aims to remove listed species (delist) from federal protection once recovered but contingent on adequate regulations in subnational jurisdictions to keep them off the federal list. Two U.S. Presidential Administrations have proposed the removal of federal protections for gray wolves (*Canis lupus*) nationwide but faced dissent by majorities (if not unanimity) of their official panels of scientists (*NCEAS, 2014; Atkins, 2019*). The Trump administration went ahead anyway and announced on 3 November 2020 it would transfer authority to states and tribes on 3 November 2020, declaring gray wolves recovered across most of the country under the Endangered Species Act, ESA (*USFWS, 2020*). That decision asserts that the species met the criteria of the five-factor analysis (ESA 16 USC § 1531 Sec. 4(a)) among others. The five factors necessary for delisting altogether ensure the delisted species remains secure for the foreseeable future. One of those criteria is the adequacy of state and tribal (subnational) regulatory mechanisms (*Zellmer, Panarella & Wood, 2020; Erickson, 2012*).

Whether delisted wolves are being managed with adequate regulatory mechanisms by subnational jurisdictions seems in part a scientific question (as opposed to a values-based question), because the adequacy of the mechanisms depends on their effectiveness in regulating factors that might reverse conditions and endanger wolves again. Chief among those factors for wolves has been human-caused mortality in five U.S. wolf populations, since modern monitoring (*Treves et al., 2017*), as in other regions (*Chapron et al., 2014; Boitani, 1995*). We present a data point to support scientific evaluations of the adequacy of regulatory mechanisms in subnational jurisdictions, for the first state to implement recreational hunting in the wake of federal wolf delisting announced on 3 November 2020.

The State of Wisconsin wolf policy and management between 2020–2021 offers an interesting case study for the following reasons. Wisconsin was the first subnational jurisdiction to resume lethal management of wolves after delisting. The State wildlife agency (Department of Natural Resources, DNR, Annapolis, MD, USA) was explicit about its goals for regulated wolf-hunting, “The quota’s objective is to allow for a sustainable harvest that neither increases nor decreases the state’s wolf population...” (<https://dnr.wisconsin.gov/topic/hunt/wolf/index.html>, accessed 14 April 2021) and similar statements to media before the wolf-hunt (*Anderson, 2021*). There are two phrases and two parts of that objective that can be evaluated scientifically, that of “a sustainable harvest” and “neither increases nor decreases the state’s wolf population”. This language mirrors recent reviews of the topic that have estimated the average expected, threshold rate of human-caused mortality predicted to result in stability of wolf populations (i.e., no increase or decrease).

The estimates of stabilizing levels of human-induced mortality that would be sustainable ranges from 28–29% (*Adams et al., 2008*) to 5–10% lower estimates by (*Fuller*

et al., 2003; Creel & Rotella, 2010; Vucetich, 2012). A higher estimate by Gude *et al.* (2012) has been questioned because of seeming errors in calculations (Vucetich, 2012), so their higher estimate needs replication or correction. We use the preceding meaning of sustainability, not the other meaning of sustain suggesting a wolf population can withstand 1 or 2 years of higher rates of mortality before extirpation. Our justification apart from the literature comes from the Wisconsin DNR itself, using the Adams *et al.* (2008) estimate in prior wolf-hunting plans (Natural Resources Board, 2012; Natural Resources Board, 2014), citation of those quota plans in 2021 (Natural Resources Board, 2021a), and explicit mention of using a 24% threshold on 15 February 2021 (Natural Resources Board, 2021b). Evaluating sustainability of natural resource uses demands long-term data, so here we only discuss the 1-year outcome in light of the objectives. Nevertheless, we can evaluate the state objective scientifically because we have official hunt statistics, official population estimates, and relevant, peer-reviewed scientific models. Namely, the wolves of Wisconsin were subject to two recent modeling efforts. First, models of population growth were built that took into account loosening of ESA protections as announced on 3 November 2020 (Chapron & Treves, 2016a; Chapron & Treves, 2016b; Chapron & Treves, 2017a; Chapron & Treves, 2017b); note we use 3 November from the Federal Register for consistency with prior studies (Chapron & Treves, 2016a; Santiago-Ávila, Chappell & Treves, 2020). Also, individual survival models used time-to-event analyses to estimate cryptic poaching in competing risk frameworks (Santiago-Ávila, Chappell & Treves, 2020). These allow us to estimate population change in a single year and increments in human-induced mortality following delisting and through the wolf-hunt period. The serendipitous combination of population estimates, hunter-killed totals, and models of the individual and population-level effects of reducing ESA protections make this case unique to our knowledge.

Another feature of the Wisconsin case that makes it relevant beyond that State are the subnational governance issues involved. The DNR was not alone in deciding or designing the state wolf hunt. A local court, the legislature, and the Natural Resource Board (NRB), which is a commission overseen by both the executive and the legislature, all had a say in the February 2021 wolf-hunt timing, methods, and quota (Material S1). Therefore, the Wisconsin case study may provide readers from other regions with insights into the checks and balances across three independent branches of a democratic government.

Here we evaluate whether the state attained its objective "...to allow for a sustainable harvest that neither increases nor decreases the state's wolf population...", by modeling population change after the State of Wisconsin issued 2,380 permits, intending to kill 119 wolves (<https://dnr.wisconsin.gov/newsroom/release/41071>, accessed 24 March 2021), but resulting in permitted kills of 218 wolves in <3 days (Wisconsin, 2021a).

MATERIALS AND METHODS

We used official population estimates since April 2017 as the population grew from 925–1,034 minimum counts (Material S1) to estimate the population in April 2021. We began with population estimates and dynamics since April 2017, which represents the

most recent 4 years of wolf population growth after the last wolf-hunt in December 2015 ([Wisconsin, 2021b](#)). Therefore, we assume similar population dynamics, such as density-dependence, as observed in 2017–2020. We also assume the effects of that prior wolf-hunt had worked themselves out of the population dynamics preceding the wolf-hunt of February 2021. Some readers may be interested in seeing a 1-year population change model that allows for density-dependence or compensatory effects on mortality, reproduction, recruitment, or migration. In [Material S2](#), we explain why a population model without such non-linear effects is the more conservative model.

We used three conservative scenarios for estimating population change. Our precautionary approach is to begin with the minimum bound of the April 2020 estimate by the State in its wolf population census. Our approach is precautionary because loners and transients contribute little to population growth or the total size of the population and few if any packs have been missed in previous years. Also, the minimum count of 1,034 wolves in 256 packs is consistent with long-term average pack sizes of approximately four wolves ([Wydeven et al., 2009](#)). Moreover, the state used 1034–1057 (SM1 Figure 2) and analogies to previous wolf-hunts that used the same wolf census method when the state recommended its quota for February 2021 ([Wisconsin, 2021c](#)).

The first scenario, which we label HIGH, uses the average growth estimated by the state during periods of strict ESA protection 2017–2020 ($(N_{t+1} - N_t)/N_t = +3.8\%$), and accounts for mortality additional to background levels found during those years to account for the delisting period from 3 November 2020 to 14 April 2021. Specifically, we deduct additional deaths expected during periods without ESA protection from a recent peer-reviewed model of individual survival as policies changed.

Recent quantitative models predict that cryptic poaching—illegal killing in which perpetrators conceal evidence ([Liberg et al., 2012](#))—rises significantly for endangered wolves when wolf-killing or removal from the wild, mostly by government agents, is legally permitted ([Santiago-Ávila, Chappell & Treves, 2020](#); [Louchouart et al., 2021](#)). The latter two recent models used independent datasets to estimate mortality and disappearance of marked wolves from the date of collaring (mainly VHF radio transmitters) until death or disappearance, using individual-level, time-to-event analyses to compare periods of strict ESA protection to periods of reduced protection during which time wolf-killing or removal of wild wolves to captivity was liberalized ([Santiago-Ávila, Chappell & Treves, 2020](#); [Louchouart et al., 2021](#)). The rationale for assigning most additional disappearances of radio-collared wolves to cryptic poaching follows discussions in those papers and others ([Treves et al., 2017](#); [Agan, Treves & Willey, 2020](#); [Treves et al., 2017](#)), which we summarized in [Material S2](#), after describing compensatory mortality. The latter works improved upon earlier efforts ([Olson et al., 2015](#); [Stenglein et al., 2015](#)), as did ([Stenglein, Wydeven & Deelen, 2018](#)), but those we use here also improved by explicitly accounting for radio-collared wolves that disappeared as a function of the length of time wolves were exposed to policy periods that reduced ESA protections ([Santiago-Ávila, Chappell & Treves, 2020](#)). Unregulated and often undocumented illegal killing (poaching) exceeded legal, reported wolf-killing in every population studied thus far ([Treves et al., 2017](#); [Adams et al., 2008](#); [Liberg et al., 2012](#); [Agan, Treves & Willey, 2020](#)). Therefore, it is

essential to accurate monitoring and quota-setting that prudent managers consider these additional deaths and count all mortality, or at least all anthropogenic mortality, when planning and communicating public hunting seasons.

The second scenario, which we label MODERATE, uses the minimum growth estimated by the state in those years $(N_{t+1} - N_t)/N_t = -2.2\%$. Using the minimum population growth observed in the past 4 years is consistent with a precautionary approach, the findings for a population-level model of all wolves in Wisconsin and Michigan from 1995–2012 (*Chapron & Treves, 2016a; Chapron & Treves, 2016b*). Those studies report that periods of liberalized wolf-killing were associated with an unidentified and unreported source of mortality that slowed population growth, independent of legal killing, by 4–6% annually. These studies resisted quantitative and qualitative challenges without published support for alternative hypotheses of density-dependence on mortality (*Chapron & Treves, 2017a; Chapron & Treves, 2017b; Stien, 2017; Pepin, Kay & Davis, 2017; Olson et al., 2017*). Furthermore, social scientific data corroborated the population-level findings with independent datasets (*Browne-Nuñez et al., 2015; Hogberg et al., 2015*) and the authors' own findings (*Treves, Naughton-Treves & Shelley, 2013; Treves & Bruskotter, 2014*). This scenario also deducted additional wolf deaths as in the HIGH scenario.

Finally, for the third, LOW scenario, we took the minimum population growth observed in years of full ESA protection (-2.2%) and subtract another 5%, for a final decrement of -7.2% . The LOW scenario, adjusts the observed minimum growth downward by 5% ($(N_{t+1} - N_t)/N_t = -7.2\%$), but does not add the additional mortality because that might double-count the effect of reduced protections after delisting on 3 November 2020.

Assumptions

Our estimates contain a set of assumptions, all of which we aimed to make conservatively, so our outputs are minimum estimates of deaths and maximum estimates of population size.

We report only the increment in deaths and disappearances after delisting, i.e., those that we estimate would have survived had delisting not proceeded. We use these as increments in mortality for the HIGH and MODERATE scenarios only. The lower estimate for additional deaths and disappearances comes from wolves in Wisconsin from 1980–2012 (*Santiago-Ávila, Chappell & Treves, 2020*). The higher estimate for Mexican gray wolves, in New Mexico and Arizona, is more certain because of more intensive monitoring of a greater proportion of the population (*Louchouart et al., 2021*). Therefore, the Wisconsin estimates are conservative among available estimates of cryptic poaching increments.

As summarized in [Material S2](#), when we estimate additional wolf deaths and disappearances after delisting, we assume those wolves are lost to the Wisconsin population. Studies in at least four populations found that the vast majority of radio-collared wolf disappearances are earlier than would be expected from battery or mechanical failure (*Treves et al., 2017; Santiago-Ávila, Chappell & Treves, 2020; Liberg et al., 2012; Louchouart et al., 2021; Agan, Treves & Willey, 2020; Treves et al., 2017*). We are aware of no evidence of a mechanism by which mechanical failure rates would

increase in association with a liberalized killing period. Further, the Scandinavian studies that first described cryptic poaching used genetics to confirm the disappearance of known wolves, and later associated those rates to policies, concluding that missing wolves no longer moved on the landscape, as opposed to eluding monitoring ([Liberg et al., 2012](#); [Liberg et al., 2020](#)), but see our qualms about their inferences about policy effects ([Treves, Louchouart & Santiago-Ávila, 2020](#)). Indeed, migration into, rather than out of, regions that experienced high rates of legal and illegal wolf-killing seems more likely. In the Alaskan gray wolf study widely used to identify a sustainability threshold for wolf-killing ([Adams et al., 2008](#)), the authors reported >75% of human-caused mortality was caused by intentional, unregulated hunting, and that the off-take was unsustainable without large amounts of immigration.

Also, we assumed no super-additive mortality per capita of legal kills, as reported or inferred for exploited wolf populations ([Creel & Rotella, 2010](#); [Vucetich, 2012](#)), because we assume our estimates of cryptic poaching model some super-additivity. This is conservative because failed pregnancies, litter loss, and unreported deaths of uncollared wolves that might accompany and follow the hunting and poaching would not have been captured in the individual models that used marked adult wolves only. Non-radio-collared wolves succumbed to all deaths at higher rates than radio-collared wolves in Alaska ([Schmidt et al., 2015](#)), and in Wisconsin ([Treves et al., 2017](#)). Possibly some poachers are deterred by the threat of prosecution if they kill a collared animal ([Persson, Rauset & Chapron, 2017](#)). In sum, estimates of incremental deaths and disappearances in the HIGH and MODERATE scenarios are likely to under-estimate deaths.

Next we assumed permitted wolf-killing will have similar effects on the wolf population and on would-be wolf-poachers as that estimated from 2003–2012, during which time government agents were primarily responsible for wolf-killing and no public hunts were held. This is conservative given the 2021 wolf-hunt killed more wolves than in past periods ([Chapron & Treves, 2016a](#); [Wisconsin, 2021b](#)), and did so with unprecedented methods (e.g., snowmobile chase, night-time, hounds, traps) in a very rapid timeframe. It would be plausible to assume rapid, efficient poaching also, but we do not.

Also, we assume all growth occurs prior to delisting because pups recruited into the population in November are treated as adults for purposes of census ([Fuller, 1989](#)). Relatedly, we assume that wolves alive on 15 April 2020 began their exposure to hazards at that time, rather than considering their full time alive as adults, for which we have no data. This is conservative because (1) the cumulative incidence (rather than the instantaneous hazard) of mortality increases with monitoring time naturally, and (2) the difference between the cumulative incidence functions for each protection period ([Fig. 1](#)) increases with monitoring time beyond our study period ($t = 365$) ([Santiago-Ávila, Chappell & Treves, 2020](#)).

Finally, we did not use unpublished, preliminary, unverified estimates provided by the DNR in April 2021 that 17 out of 50 collared wolves disappeared prior to or during the 2021 wolf-hunt and another 7 were killed by hunters ([Materials S1, Fig. 1](#)). Had we uncritically used those figures for deaths and disappearances of the entire wolf population, our estimate of wolf mortality would have been 48% and the associated wolf population

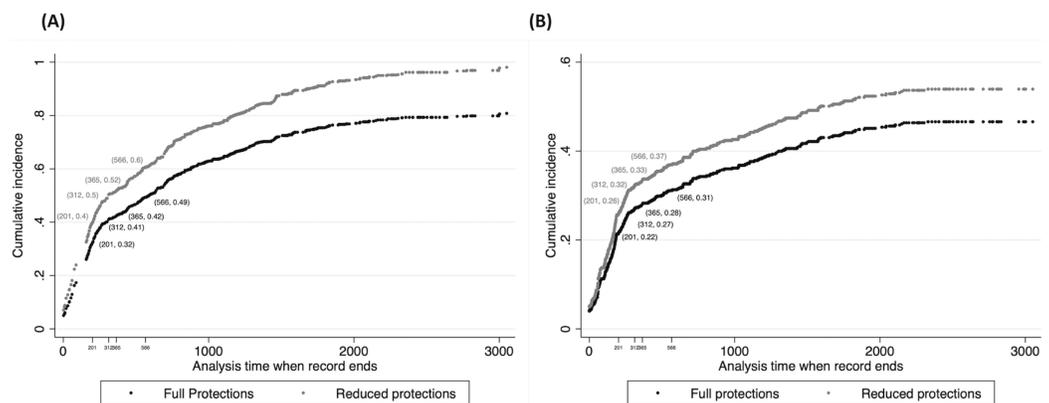


Figure 1 Cumulative Incidence of endpoints by protection period. Cumulative incidence functions (CIFs) for 499 monitored, adult wolves in Wisconsin during two policy periods (gray: reduced ESA protections; black: full ESA protections) for all deaths and disappearances (Panel A: $n = 499$), and disappearances only (Panel B: $n = 243$) from 1979–2012. Coordinates (x, y) represent the cumulative incidence or proportion of monitored wolves experiencing an endpoint (y-axis); showing all deaths in (A) or all disappearances in (B), over time (x-axis) in days. Time zero is set to 16 April 2020, a conservative step because death or disappearance increases with time, by definition. CIFs modeled with semi-parametric Fine-Gray models (Santiago-Ávila, Chappell & Treves, 2020). The first period of 201 days runs from 15 April 2020 to 3 November 2020 when delisting was announced in the Federal Register (USFWS, 2020) and the period of reduced ESA protection began. Day 312 marks the start of the Wisconsin wolf-hunt on 22 Feb 2021, and day 365 marks the end of the wolf-year on 14 April 2021. Finally, day 566 marks the approximate start date of the putative, next wolf-hunt, to illustrate further increases in the CIFs of mortalities and disappearances. We used the increment between the period of full ESA protection (black markers) to the corresponding value on the upper curve of reduced ESA protection (gray markers) to estimate the additional wolves deducted from the population by any endpoint (A) or LTF (B) which we predict would have survived if delisting had not occurred. [Full-size](#) DOI: 10.7717/peerj.11666/fig-1

decline would have been much greater. But those data are unverified currently and, as noted above, collared wolves suffer different mortality hazard than uncollared ones in Wisconsin and elsewhere.

The formula we use for all three scenarios is Eq. (1)

$$N_{2021} = (N_{2020} \cdot r) - 218 - E \quad (1)$$

where $N_{2020} = 1,034$, r varies by scenario as +0.038 (HIGH), -0.022 (MODERATE), or -0.072 (LOW) respectively, and ‘E’ refers to additional wolves dead due to reduced ESA protections, calculated using the cumulative incidence functions (CIFs, Fig. 1A) for all endpoints during a period of liberalized wolf-killing from (Santiago-Ávila, Chappell & Treves, 2020), but set to zero for the LOW scenario. CIFs by policy periods for all endpoints and LTF (Figs. 1A, 1B) were calculated using semi-parametric Fine-Gray models, with data from 513 monitored, adult wolves (1979–2012) (Santiago-Ávila, Chappell & Treves, 2020).

We also estimate the proportion of all additional mortalities due to cryptic poaching, using the difference in CIFs for Radio-collared wolves lost to follow-up, in the two types of policy periods (Fig. 1B), divided by the same difference in the CIFs of all endpoints (Fig. 1A) at day 365 (15 April 2021).

Table 1 Population and extra mortality estimation in scenario HIGH that assumes annual growth +3.8% by Apr 2021.

Timeline of wolf population changes	N	Individuals dead and disappeared	
		Additional, due to reduced ESA protections*	Notes
15 April 2020 in 256 packs, Day 0	1,034		We assume wolves begin monitoring on this date
Expected by 2 Nov 2020, Day 201- <i>REDUCED PROTECTION PERIOD BEGINS ON 3 NOV 2020</i>	1,073	97	Nov 3-Feb 21 (Days 202–312, 111 day interval): Liberalized wolf-killing period cumulative incidence as a relative increment of +0.09 for all endpoints relative to baseline of strict ESA protection
Expected by 24 Feb 2021, Day 315- <i>END OF WOLF-HUNT</i>	759	218	Legal kills during wolf-hunt Feb 22–24 (3 days)
Expected by 15 Apr 2021, Day 365	751	8	Feb 22-Apr 14 (Days 313–365, 51 day interval): Liberalized wolf-killing period cumulative incidence as a relative increment of +0.01 for all endpoints relative to baseline of strict ESA protection

Note:

* Source for all cumulative incidences is *Santiago-Ávila, Chappell & Treves (2020)*.

Table 2 Population and extra mortality estimation in scenario MODERATE that assumes annual change –2.2% by Apr 2021.

Timeline of wolf population changes	N	Individuals dead and disappeared	
		Additional, due to reduced ESA protections*	Notes
15 April 2020 in 256 packs, Day 0	1,034		We assume wolves begin monitoring on this date
Expected by 2 Nov 2020, Day 201- <i>REDUCED PROTECTION PERIOD BEGINS ON 3 NOV 2020</i>	1,011	91	Nov 3-Feb 21 (Days 202–312, 111 day interval): Liberalized wolf-killing period cumulative incidence as a relative increment of +0.09 for all endpoints relative to baseline of strict ESA protection
Expected by 24 Feb 2021, Day 315- <i>END OF WOLF-HUNT</i>	702	218	Legal kills during wolf-hunt Feb 22–24 (3 days)
Expected by 15 Apr 2021, Day 365	695	7	Feb 22-Apr 14 (Days 313–365, 51 day interval): Liberalized wolf-killing period cumulative incidence as a relative increment of +0.01 for all endpoints relative to baseline of strict ESA protection

Note:

* Source for all cumulative incidences is *Santiago-Ávila, Chappell & Treves (2020)*.

We do not attempt to model population change from 15 April 2021–November 2021 when the next wolf-hunt is putatively planned because there are too many uncertainties about reproduction, legality, and planning processes. A lack of transparency about state wolf data from 2013–2015 prevents independent scientific scrutiny of past regulated hunting (*Santiago-Ávila, Chappell & Treves, 2020; Treves et al., 2017*).

RESULTS

We predict the state population by 15 April 2021 will stand at a maximum possible number of wolves of 695–751 wolves (scenarios: LOW 742, MODERATE 695, HIGH 751) (*Tables 1, 2*). This represents a minimum of a 27–33% decrease in 1 year. We emphasize

that is a minimum and the population size is a maximum because of the many conservative methods we used.

We estimate that in addition to the 218 wolves reported killed during the wolf-hunt, 98–105 wolves died since 3 November 2020 that would have been alive had delisting not occurred. Of these 56–63% (55–58 wolves) at a minimum would have been killed through cryptic poaching. Therefore, the addition of cryptic poaching and wolf-hunting in Wisconsin after 3 November 2020 seems to have augmented human-caused mortality by approximately 30% (320 of 1,034–1,071) over pre-delisting levels.

DISCUSSION

We report the expected additional wolf mortality and population reduction in the aftermath of U.S. federal removal of endangered species protections followed by one state's swift adoption of a policy for liberalized wolf-killing, including permitted, public hunting, trapping, hounding, and snow-mobile pursuit by day and night. We estimate the incremental addition of at least 98–105 wolf deaths prompted by removing protections, of which cryptic poaching would comprise the majority, in addition to the hunting deaths.

We estimate a population reduction of at least 27–33% in 1 year, which contradicts the expectation by the state wildlife agency that there would be no reduction in the wolf population. Moreover, our estimates are strict minima for actual reductions in the population, so our population estimate is a maximum conceivable under the most conservative assumptions. The reality is probably a greater reduction and a lower population count as of writing.

If the second planned wolf-hunt in November 2021 ([Material S1](#)) were cancelled, we predict the state wolf population could rebound in 1–2 years. However, there are preliminary indications from the state Natural Resource Board that another wolf-hunt with a similar or higher quota will be advocated by some on the board ([Material S1](#)). Proponents for such point to the 1999 population goal for wolves of 350 individuals in late winter. We have shown that number is a value judgment by a few individuals not a scientifically sound target ([Treves et al., 2021](#)). Therefore, the adequacy of state regulatory mechanisms seems fragile, for reasons detailed in SM1 for those interested in policy background. The frailty of regulatory mechanisms can be summarized as follows:

1. The intervention of numerous branches of the state government ([Material S1](#))
2. A Wisconsin statute which mandates a hunt in the event of federal delisting, rather than granting discretion to the DNR ([Material S1](#))
3. Various disparate estimates of the population size, the hunter take, poaching, and resilience that have been espoused by officials and the public ([Material S1](#))

In sum, the state wildlife agency (DNR) did not meet its explicit objectives of no change in the wolf population, still being advocated by that agency as of writing (<https://dnr.wisconsin.gov/topic/hunt/wolf/index.html>, accessed 16 April 2021). The facts of hunters over-shooting the quota by 83% before the DNR could close zones, of the Natural Resource Board over-ruling the DNR's more cautious permit number, the legislature mandating

a hunt, a county court ordering a hunt on very short notice, and an appeals court declining to review that decision ([Material S1](#)), all speak to problems with different branches intervening to reduce the discretion of the wildlife agency. That loss of discretion by the ostensible expert managers itself raises serious questions about the adequacy of regulatory mechanisms to prevent wolves becoming endangered again. It also leads us to recommend reform of trustee duties in the state and perhaps others with unclear responsibilities and unclear divisions between decision-making and implementation functions.

CONCLUSIONS

For jurisdictions elsewhere, we caution that science may play little role in wolf politics where the animal has become a symbol for political rhetoric and a symbol of cultural divisions ([Nie, 2003](#)). However, science only reveals past, present or future conditions, not what we humans ought to do.

Proponents of wolf-killing argued that the state population goal of 350 wolves demands such swift reductions ([Material S1](#)), but evidence suggests that goal is a value judgment by a few individuals that was treated as if it were an output of a scientific model ([Treves et al., 2021](#)). Moreover, the model used suffers from scientific flaws, so its assumptions and predictions are dubious ([Treves et al., 2021](#)). Nevertheless, the goal was reaffirmed in February 2021 ([Material S1](#)). Furthermore, the state did not collect wolf carcasses for aging or detection of alpha females by placental scars, as is fairly standard for scientific studies, e.g., ([Stark & Erb, 2012](#))—see [Material S1](#) for tribal involvement in such analyses. This type of scientific information is indispensable for science-based management. Without it, illegal wolf-killing is more difficult to detect, the age and reproductive class of hunter-killed wolves is likely imprecise ([Treves et al., 2017](#)), and the breeding status and hence reproductive performance for the following year cannot be estimated accurately.

Likewise, state plans for another hunt raise questions about sustainability. Although one subnational jurisdiction may not predict another, doubts about sustainable wolf-killing and misuse of scientific information have been raised previously for several other governments (see [Creel et al. \(2015\)](#) and [Chapron et al. \(2013\)](#), respectively). Therefore, we find our case is not unique, and provides insights for other jurisdictions. Similar wolf-killing might be replicated elsewhere when subnational jurisdictions in the USA and EU regain authority for controversial predators. Federal governments in both regions should recognize that loosening protections for predators, and perhaps other controversial species, opens the door for antagonists ([Treves & Martin, 2011](#); [Brown & Samuels, 2021](#)) to kill large numbers in short periods, legally and illegally. The history of political scapegoating of wolves ([Chapron et al., 2013](#); [Chapron & Lopez-Bao, 2014](#)) may repeat itself. Elsewhere, we have shown that the response should not be to allow more wolf-killing under the misguided concept of blood buys goodwill or ‘tolerance killing’ ([Chapron & Treves, 2017b](#); [Santiago-Ávila, Chappell & Treves, 2020](#); [Louchouart et al., 2021](#); [Treves & Bruskotter, 2014](#)).

Federal decision-makers might consider different classifications that make predators protected non-game, or states should prove themselves capable of reducing poaching to a stringent minimum for a 5-year post-delisting monitoring period. Alternately, federal governments might address upgrades to federal laws regardless of species classifications. Given the importance of predators in restoring ecosystem health and function (*Estes et al., 2011*) and of non-anthropocentric wildlife trusteeship (*Treves, Santiago-Ávila & Lynn, 2018; Santiago-Ávila, Lynn & Treves, 2018; Santiago-Ávila, Treves & Lynn, 2020*), we also recommend instead that transparent legal standards of trusteeship be used to manage wildlife (*Bruskotter, Enzler & Treves, 2011; Treves et al., 2018*), not the vagaries of opaque electoral politics and interest group lobbying (*Treves et al., 2017*). Moreover, our recommendation conforms to global goals for the preservation of nature.

ADDITIONAL INFORMATION AND DECLARATIONS

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The authors declare that they have no competing interests.

Author Contributions

- Adrian Treves conceived and designed the experiments, performed the experiments, analyzed the data, prepared figures and/or tables, authored or reviewed drafts of the paper, and approved the final draft.
- Francisco J. Santiago-Ávila conceived and designed the experiments, performed the experiments, analyzed the data, prepared figures and/or tables, authored or reviewed drafts of the paper, and approved the final draft.
- Karann Putrevu analyzed the data, authored or reviewed drafts of the paper, and approved the final draft.

Data Availability

The following information was supplied regarding data availability:
The data are available in the [Supplemental Files](#).

Supplemental Information

Supplemental information for this article can be found online at <http://dx.doi.org/10.7717/peerj.11666#supplemental-information>.

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1 **Supplementary Material 1: the public and governmental context of the Wisconsin wolf-hunt**

2
3 The case we described in main text includes court action, legislative action, executive branch
4 action, and public comment.

5 6 **Judicial branch**

7 In mid-February 2021, a circuit court in Jefferson County issued a writ of mandamus ordering
8 the state wildlife agency to hold the hunt as soon as legally feasible in February 2021. The state
9 appealed to a higher court which declined jurisdiction because the circuit court had not
10 formally closed the case.

11 12 **Legislative branch**

13 In 2012, the Wisconsin legislature passed Act 169 designating gray wolves as game, mandating
14 an annual wolf-hunt to begin in the first week of November each year the wolf is not under
15 federal protection. The unusual statutory mandate to hold a hunt took some authority away
16 from the executive branch in deciding when or if such a hunt should be held. That legislative
17 action informed the subsequent judicial action in 2021 mentioned above.

18 19 **The Natural Resources Board (NRB)**

20 The NRB is overseen by both the legislative and executive branches.

21
22 After initially voting against authorizing a wolf-hunt on 22 January 2021
23 (<https://dnrmedia.wi.gov/main/Play/731c92f70bb84be69b8f69ef1ccbb99c1d> accessed 27 April
24 2021), the NRB responded to the above court action by approving a wolf-hunt beginning 22
25 February 2021 with a quota of 200 non-reservation wolves, availability of 20 times that number
26 of permits, and the zonal quotas summing to 200 [1]. In the video-recording of the latter NRB
27 meeting, three topics relevant to our present context were also discussed [2]. All quotations
28 below derive from the latter meeting and the video-recording at that link.

29
30 The chair, F. Prehn, added to the official record regarding the judicial proceeding described
31 above. He reported that neither he nor the NRB had been consulted on filing the appeal [2].

32
33 NRB members reaffirmed the state population goal and declared that the NRB was not aiming
34 to stabilize the population but rather “Move population toward population goal.” And “The
35 current population is almost four times higher.” [2], which referred to 350 wolves [3-5].

36
37 Following a question about science behind the quota of 200, DNR’s D. MacFarland stated,
38 “[DNR] started with the population estimate and there are two published studies by Fuller et al.
39 2003; Adams et al. 2008...one identifies a stabilization point at 22% mortality, the other at 29%
40 mortality...we used non-harvest mortality of 14% and combined it with the harvest rate
41 estimate by the quota to get the stabilization rate... in a nutshell [that’s] how we get from the
42 quota to a stabilization level.” Here, the authors note there are two to three additional
43 published estimates as reviewed in the main text [2].

44

45 Following the above quotation, an NRB member asked about the two different estimates (1034
46 and 1195) of the wolf population in April 2020, which we review in main text and below in SM 1
47 Figure 2 legend. The DNR favored the higher estimate in response. The NRB member who
48 posed the question (G. Kazmierski) indicated a personal preference for a higher quota but
49 moved to approve the quota as follows [2].

50

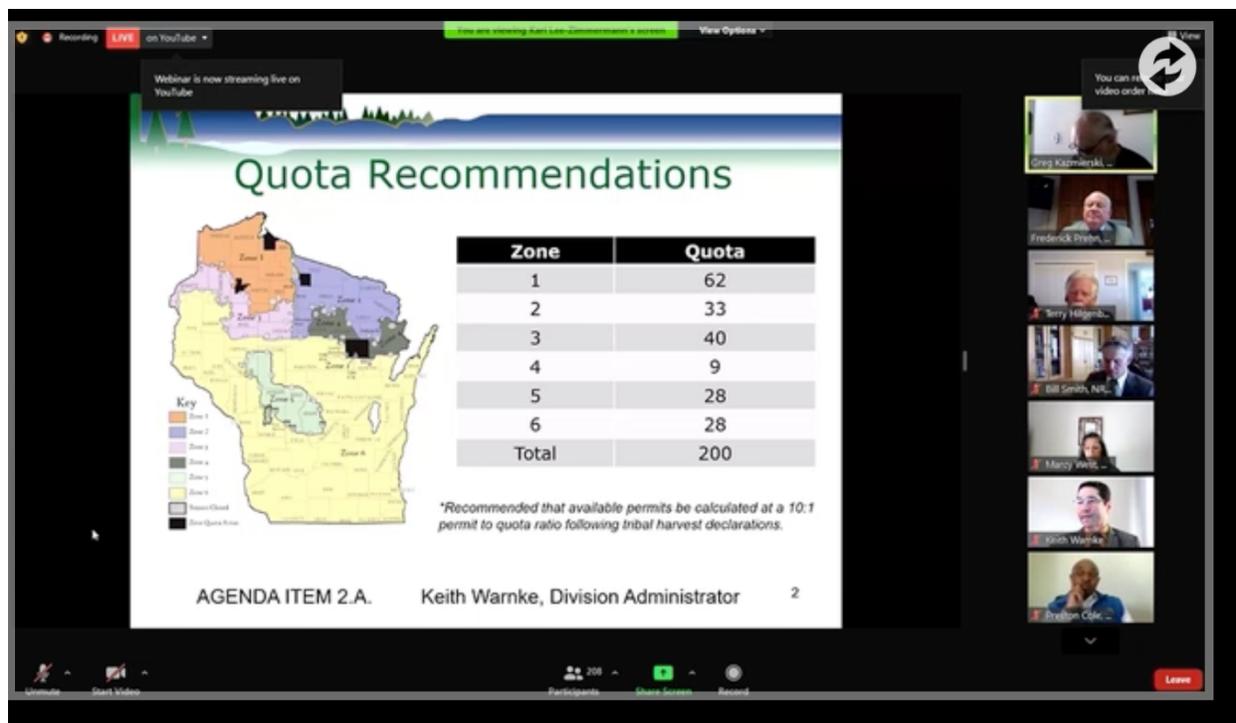
51 G. Kazmierski moved, "... the NRB approve a quota of 200 non-reservation wolves and a permit
52 number of 20 times the quota with a directive to the Department that no zone will be closed
53 prior to the end of the season on February 28th unless the full amount of harvest for that zone
54 has been reached." That motion passed unanimously. The above directive seems to constrain
55 the DNR's discretion in the matter. Also, the NRB over-ruled the DNR request for ten times the
56 permits and instead doubled the number of permits made available to hunters. When the NRB
57 member who brought the motion, G. Kazmierski, justified doubling the permit availability, he
58 stated "We have a very short window to reach those harvest goals and objectives... because
59 there is such a short window to accomplish this harvest by the end of February, by upping the
60 number of hunters in the field, it will give us a better shot at filling that quota." [2]

61

62 Following a question about timing and process, the DNR staff Warnke opined they "We would
63 have been more confident and more comfortable had we taken more time." [2]

64

65 The NRB chair asked about tribal declaration under federal tribal treaty rights (see section on
66 Ojibwe tribal governments below). The DNR administrator K. Warnke clarified that "The tribes
67 have not made a declaration yet. So those quotas typically ...always by law... will be adjusted
68 when we account for tribal declaration by treaty rights." Then Chair Prehn asked for expansion
69 on that issue, stating "Zone 1 has a harvest objective of 62.....no matter what negotiations do
70 with the tribe... that zone will not be closed until the quota is met?". Then a new speaker from
71 DNR agreed with the chair's question. It remains unclear if the tribal declaration reserving 82
72 wolves reduced the zonal quotas which summed to 200 during the above meeting (SM 1 Fig 1)
73 or if the NRB directed the DNR to permit 200 wolves to be killed "no matter what negotiations
74 do with the tribes" [2].

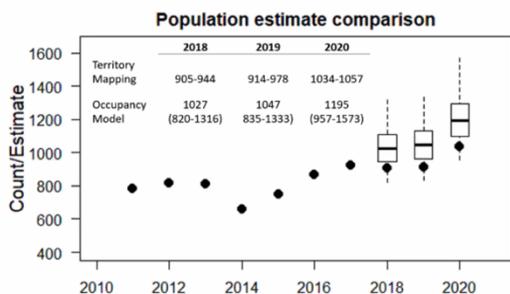


75
76 **SM 1 Figure 1.** Slide shown during the 15 February 2021 NRB meeting to vote on the DNR's
77 recommended quota, permit availability, and zonal quotas [2]

78
79 An NRB member asked about carcass collection for scientific purposes. The DNR responded
80 they would not collect carcasses given the short time frame. "Typically the wolves that are
81 harvested are not generally of breeding age, they are generally younger than breeding age
82 wolves." The present authors are not aware of the science used to support that statement. We
83 cited Stark [6] in the main text that seems inconsistent with the statement. Also see below for
84 tribal report on carcass collection [2].

85
86 **Executive branch**

87 The DNR's objectives for the February 2021 wolf-hunt were, "The quota's objective is to allow
88 for a sustainable harvest that neither increases nor decreases the state's wolf population...The
89 DNR is actively working to prepare for a fall 2021 wolf harvest season through a transparent
90 and science-based process." (<https://dnr.wisconsin.gov/topic/hunt/wolf/index.html> accessed
91 15 April 2021). We use the latest wolf kill total from 8 April 2021 [7] (SM 1 Figure 2).



Feb 2021 Wolf Season Report

Table 2. Harvest and zone summary for the February 2021 wolf season.

Wolf Harvest Zone	Total Quota	State-licensed Quota	State-licensed Harvest	Zone closure date and time*
1	62	31	53	Feb 24 3pm
2	33	18	43	Feb 24 10am
3	40	20	42	Feb 24 3pm
4	9	6	4	Feb 24 3pm
5	28	27	31	Feb 24 10am
6	28	17	45	Feb 24 10am
Total	200	119	218	



Table 3. Method of take summary for wolves harvested during the February 2021 wolf season.

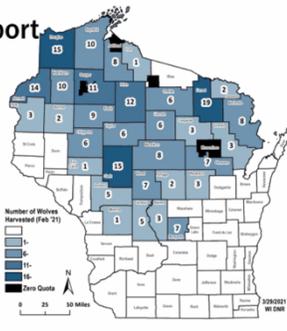
Method	Number	%
Aid of Dogs*	188	86%
Hunting/Predator Call	16	7%
Foothold Trap	7	3%
Cable Restraint	3	2%
Stand/Still Hunting	4	2%
Total	218	100%

*wolves harvested by gunshot with the aid of trailing hounds.

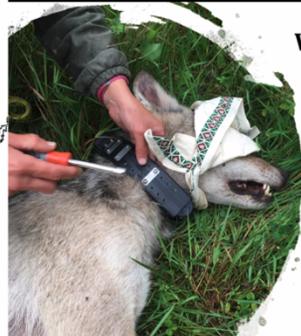
Feb 2021 Wolf Season Report

Table 4. Sex and estimated age of wolves harvested during Feb. 2021 wolf season.

	Male	Female	Combined Total	% of Total by Age
Young of the year (<1 yr.)	10	10	20	9%
Subadults (1-1.5 yr.)	57	53	110	51%
Adults (≥2.5 yr. or older)	47	38	85	39%
No Age Data	2	1	3	1%
	116	102	218	
% of Total by Sex	53%	47%		



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Wolf Processing

Information Collected

- Measurements
- Weight and Length (nose to tip of tail)
- Neck and head diameter
- For collar size and cable restraint size purposes
- Toe pads & paws, shoulder to pad, eye to nose

Currently collared wolves

- 43 currently collared
- 16 functioning correctly
- 4 transmitting intermittently
- 17 missing - collars stopped transmitting for unknown reasons
- 6 are VHF collars
- 7 harvested during season

92

93 **SM 1 Figure 2.** Wisconsin DNR presented data to the Wolf Harvest Committee and the public on
 94 8 April 2021, showing (upper left) wolf population estimates, (upper right) hunter take by
 95 method, (lower left) hunter take by age and zone, (lower right) marked wolf fates. These are
 96 presented to substantiate population estimate and hunter take and not any other data because
 97 other potentially relevant data are unverified and ambiguous. There are three scientific reasons
 98 not to use the higher estimate of 1195 for the April 2020 wolf population as summarized in the
 99 main text: (1) The lower bound of the occupancy model lies below the estimate we use of 1034,
 100 yet it is presented graphically and in text without explaining if it is a 95% confidence interval or
 101 some other measure of uncertainty so the 1034 estimate is conservative; (2) the occupancy
 102 model has not undergone peer review as of writing; (3) the official state report on wolf
 103 population monitoring includes methods additional to the occupancy sample and appears to
 104 integrate multiple sources of information; and (4) the DNR justified its recommended quota and
 105 design based in part on the 1034-1057 estimate in this figure (upper left) and in part on the
 106 2012-2014 wolf-hunts for which the newer occupancy model was unavailable [2, 8]. The public
 107 meeting and presentation of slides was made during the following meeting:
 108 <https://dnr.wisconsin.gov/calendar/meeting/42691#:~:text=Time%3A%201%3A30%20a.m.%20%2D%20%3A30%20p.m.&text=The%202021%20Harvest%20Committee%20Meeting,providin%20Wolf%20Monitoring%20Program%20updates>,
 109 accessed 27 April 2021.
 110

111 Regarding the assertion of science-based process, we summarize methods and timing of the
 112 hunt. A combination of environmental and anthropogenic factors, most notably the use of
 113 hounds and unprecedented issuance of permits relative to stated quotas, undermined the
 114 WDNR objective in its own words. For example, the Minneapolis Star Tribune reported,

115 “Fresh snowfall on Monday and Tuesday made wolf tracks easy to spot and
 116 captured their scent for trailing hounds to follow, said Randy Johnson, large

117 carnivore specialist for the Wisconsin DNR. ‘This season was fairly
118 unprecedented,’ Johnson said. ‘The use of dogs is a very efficient method of
119 harvest.’ The Wisconsin DNR, which originally fought opening a season so soon
120 after the animals were delisted, issued twice as many hunting permits than it
121 had before for wolf hunts. It gave out 20 permits for every wolf it wanted
122 harvested, rather than the more typical 10 per wolf. That’s a decision that will be
123 revisited, said Eric Lobner, director of the Wisconsin DNR’s wildlife management
124 program. ‘It’s important for us to get more in line with what we normally issue
125 for permits per quota,’ he said. The Wisconsin DNR planned for the hunt to last a
126 week, but started shutting it down Tuesday afternoon [Feb 23, 2021] when
127 hunters had reported enough kills to nearly fill the entire quota. Lobner and
128 Johnson reiterated that the Upper Midwest’s wolf population is robust and
129 resilient. Before the hunt, the population was estimated to be around 1,200
130 wolves. The quota was set with the goal of keeping the population stable, Lobner
131 said” [9], accessed 27 March 2021.

132 Also see the quotation from Warnke in the section on NRB above.

133
134 The state’s claim of no reduction in wolf population might merit consideration if sufficient pups
135 were born after the wolf-hunting and poaching periods we studied. However, the timing of the
136 wolf-hunt during the wolf mating season casts doubt on the relative success of wolf
137 reproduction in 2021 because of the unprecedented February wolf-hunt. For example, a
138 landscape with long-distance visibility enhanced by snow cover (27.5 cm in wolf range in
139 Rhinelander, Wisconsin, a record-breaking snowfall in February 2021
140 <https://waow.com/2021/02/05/snow-reports-from-february-4th/>, accessed 27 March 2021)
141 would have increased the risk to breeders posed by hunters, snowmobiles, and hounds
142 pursuing wolves. Breeding alpha males and females would have been particularly conspicuous
143 due to their territorial marking and courtship behaviors that lead them to urinate in tandem on
144 snow and show conspicuous patterns of behavior and ranging during mating [10]. Also, the DNR
145 reported that >85% of wolves were killed by hunters who used hounds, yet several efforts to
146 measure this population of hunters back in 2001 and 2005 found them few in number and
147 above average in age relative to likely wolf-hunters [11-13]. These data and the report (above)
148 that 86% of wolves were killed by hunters using hounds raise questions about the role of
149 hounds in killing wolves, which is illegal (p.6 in [https://widnr.widen.net/s/g9mtwx6vzw/2021-
150 wolf-regulations](https://widnr.widen.net/s/g9mtwx6vzw/2021-wolf-regulations), accessed 29 March 2021). Therefore, our estimates in the main text are
151 conservative because we used model parameters from periods in Wisconsin when wolf-killing
152 was primarily done by government agents in response to real or perceived livestock threats
153 rather than public hunting seasons with novel methods. Few such ‘agency kills’ occurred in
154 February [14]. Our estimates are also conservative because our model parameters for cryptic
155 poaching come from Wisconsin’s historical patterns rather than more recent, much higher
156 estimates of cryptic poaching in Mexican gray wolves, which also have higher certainty [15].

157
158 Finally, the repeated claims above for a scientific basis for the wolf-hunt are inconsistent with
159 recent evidence. We have shown previously that the 1999 population goal of 350 wolves could
160 not be based on science and the state population model from 1999–2018 omitted crucial

161 information [16]/. Furthermore, the state systematically under-estimated mortality rates during
 162 its wolf-hunt planning [14, 17, 18]. It did so again on 15 February 2021 when it estimated
 163 nonharvest mortality at 14%
 164 ([https://dnrmedia.wi.gov/main/Play/ccb5cf0361c5471e9cbc7c7a898cfc741d?catalog=9da0bb4](https://dnrmedia.wi.gov/main/Play/ccb5cf0361c5471e9cbc7c7a898cfc741d?catalog=9da0bb432fd448a69d86756192a62f1721)
 165 [32fd448a69d86756192a62f1721](https://dnrmedia.wi.gov/main/Play/ccb5cf0361c5471e9cbc7c7a898cfc741d?catalog=9da0bb432fd448a69d86756192a62f1721) accessed 27 April 2021, see testimony by D. MacFarland).
 166 Deficits in science seem to be the rule rather than the exception for North American wildlife
 167 management agencies, given a review of 667 wildlife hunting management plans across North
 168 America found the majority of cases made scientific claims about population estimates, quotas,
 169 or sustainability of hunting without providing evidence [19, 20].

170

171 **Public**

172 As of 27 March 2021, we found 173 articles or opinions since 1 January 2021 using Google
 173 News search for “Wisconsin” and “wolf” and removing an unrelated homicide case. In opinion
 174 articles and other venues, members of the public have accused the state of several missteps in
 175 management. Yet, very few media reports make claims that can be evaluated scientifically.
 176 However, one such claim is that the high rate of wolf killing reflected a state under-estimate of
 177 the wolf population ([http://www.onwisconsinoutdoors.com/WisconsinBlog/Wolf-Hunt-Meets-](http://www.onwisconsinoutdoors.com/WisconsinBlog/Wolf-Hunt-Meets-Harvest-Goal)
 178 [Harvest-Goal](http://www.onwisconsinoutdoors.com/WisconsinBlog/Wolf-Hunt-Meets-Harvest-Goal) accessed 27 March 2021). That is a scientific claim we can address.

179

180 The efficiency of legal wolf-killing (kills per unit time) should reflect a combination of encounter
 181 rate, hunter effort as a product of numbers and time spent searching, successful kills per
 182 attempted kill, and wolf detection as a product of wolf numbers and probability of detection.
 183 Any increment in hunter search effort even preceding the wolf-hunt, or conspicuousness of
 184 wolves might change the expectation for legal wolf-killing efficiency without the need for a
 185 gross inaccuracy in wolf population estimates. Therefore, we find no evidence has been
 186 presented to doubt the state estimate of the wolf population, especially given its consistency to
 187 historical pack sizes (1034 wolves in 256 packs mirrors the 40-year average pack size in the
 188 state) [21].

189

190 **Co-sovereigns of the State: Tribal governments**

191 By federal treaty, most of Wisconsin’s wolf range is co-managed by co-sovereign tribal
 192 governments and the State of Wisconsin [22]. Ojibwe tribes of the region revere and protect
 193 the wolf as brother or companion in their creation story and for ecological reasons such as
 194 maintaining the health of white-tailed deer populations and the health of medicinal plants on
 195 which the tribes depend [23-25]. Therefore, the tribes have opposed wolf-hunting in the past
 196 and continue to do so [26].

197

198 "Midway through the hunt, when the tribal government co-sovereign jurisdictions requested
 199 wolf carcasses, the state asked hunters to volunteer carcasses and 20 were turned in. “ (P.
 200 David, Great Lakes Indian Fish & Wildlife Commission, email to the lead author on 21 April
 201 2021). As of writing, those carcasses and two subsequent ones have been necropsied by P.
 202 David, A. Fergus, and tribal staff but the results have not been made public. Therefore, data on
 203 the number of breeding wolves killed or data on illegal methods, such as hound bites, will never
 204 be available to the public or independent scientific scrutiny for more than 8% of the legally

205 killed wolves. Although hunters reported age estimates and sex of legally killed wolves, we have
 206 no way to verify those data.

207
 208 P. David also reported “I discovered, and DNR confirmed, that they erroneously set the quota
 209 28 wolves higher than the Adams model they were using would have indicated. Not earth
 210 shaking by itself, but another contributing factor to likely pop decline arising from the
 211 hunt.”(email to the lead author on 20 April 2021).

212

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- 284

Supplementary Material 2: Why a population model without nonlinear effects is conservative

Non-linear responses such as density-dependence and compensatory mechanisms acting on population dynamics have sometimes been identified for some wolf populations in some periods. However, using a more complex model is not justified for several reasons.

The general population ecology literature predicts when density-dependence will not be observed and Wisconsin's wolves met three of the criteria: Fowler [1] long ago reviewed many mammal populations, wherein a majority -- but not all -- of wildlife populations show density-dependence. Similarly, Brook and Bradshaw [2] added to our understanding with modeling of 1198 populations and explained why many conditions would prevent or obscure a density-dependent population dynamic for long periods or forever. We now cite our work published this month that documents three of those conditions to explain why Wisconsin wolves did not show negative density-dependence from 1980-2012 [3]. Indeed, it seems unsurprising that the Wisconsin wolves did not show negative density-dependence given pack territoriality, minimal changes in density over time, and the change in census methods 2 times between 1980-2012 and another 2 times between 2013 and the present.

Secondly, Stenglein et al. [4] and Chapron & Treves [5] agree there was no detectable negative density-dependence on mortality (which is our main focus). Although there is no consensus on density-dependence on reproduction, the only study finding such [4] found negative density-dependence which would tend to decrease the survival of juveniles to November 2020, increasing the percent reduction in the population reported. Our omission of such is therefore conservative. Furthermore, we find the evidence for negative density-dependence on recruitment is unsubstantiated [6, 7]. Therefore, inclusion of negative density-dependence is not justified and would only add to our estimate of percent reduction.

Some readers might wonder if there were compensatory effects on vital rates that might have arisen during our study period and might have led to an increase in the population or its rate of growth beyond the 3.8% average rate we began to model with. During our study period April 2020-April 2021, compensatory effects might surface as fewer deaths from other causes because hunters killed wolves, more immigration because of vacancies created by hunting, or more births or higher recruitment rates because of space or resources freed up by the death of

adults during the hunt. However the hunt occurred at the end of February 2021, so compensatory effects of the hunt, if any, would emerge afterwards. Our modeling concerns April 2020-April 2021. Claims about compensatory effects that might recover lost population have to show evidence for such effects AFTER the hunt.

Therefore, our simple population model, based on average growth rates of previous years, already incorporates potential structural non-linear effects to predict the population by November 2020 and then we begin deducting the additional human-caused deaths that began with federal delisting. The cumulative incidence functions we describe below already incorporate non-linear effects on mortality but research has proven those effects are depensatory not compensatory [8, 9], which is consistent with population-level analyses showing super-additive mortality [10] and depensatory population decline [5, 6, 11-13].

Regarding the inferences we made about depensatory effects, below we explain how the inferences about cryptic poaching were made with confidence.

We used time-to-event analyses on radio-collared wolves in two populations (and two independent datasets) to evaluate the changes in survival of wolves over time as policies changed. The policies in question were reductions in ESA protections interspersed with periods of stricter protection. We showed that disappearances of radio-collared wolves increased substantially during periods with reduced ESA protections, estimated at 19% in Wisconsin's less intensively monitored population [8] and 121% in the Mexican gray wolf population monitored five-ten times more intensively by several measures [9]. But it is not only the association with 6 changes in policy that allow us to estimate cryptic poaching.

We also examined mechanical failures of collars and migration. There are only three known outcomes for wolves with radio-collars that are lost to monitoring by radio-telemetry. First the transmitter may undergo mechanical or battery failure. Second, the collared animal may migrate out of range of telemetry. Third, the animal may die and its transmitter be destroyed by people.

There is no known mechanism by which policy change can cause mechanical or battery failure but moreover, disappearances of radio-collared wolves occur several hundred to 1000s of days

earlier than expected for the life of radio-collars judging from the average life of collars in wolves that die from natural deaths, as we have shown for a number of populations of wolves [14-16].

As for migration, a radio-collared wolf must leave the state not simply shift range to be lost to monitoring. For Mexican gray wolves, the intensive monitoring once per week or twice per week and assiduous search for missing wolves did not reveal more than perhaps one case in >400 of a wolf with radio-collar migrating so far and being lost to contact, i.e., even migrants are often recovered [9]. A red wolf study with >500 radio-collared wolves reported the same pattern [14]. Although Wisconsin wolves were not monitored as intensively then or now, our prior work showed migration was seven times more frequent into Wisconsin from Michigan than the converse [15], and moreover we used the more conservative cumulative incidence curves from Wisconsin rather than the much more dramatic 121% increase in LTF from Mexican gray wolves. Note emigrants are nonetheless lost to Wisconsin's wolf population making emigration an unsatisfactory rebuttal of our estimate of population decline.

We consider it vanishingly rare that a radio-collared wolf died of a non—poaching cause in a medium or substrate (e.g., salt water or underground) that destroyed the transmitter soon after death, although a case of poaching and dumping in saltwater is known [14].

The only remaining possible cause of disappearance of a monitored wolf is human manipulation. A great deal of social scientific data also support the willingness and intention to poach wolves in Wisconsin and beyond [17-21]. That evidence was summarized in Science [22].

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