PROCEEDINGS B

rspb.royalsocietypublishing.org

Invited reply

Check for updates

Cite this article: Chapron G, Treves A. 2017 Reply to comments by Olson *et al.* 2017 and Stien 2017. *Proc. R. Soc. B* **284**: 20171743.
http://dx.doi.org/10.1098/rspb.2017.1743

Received: 3 August 2017
Accepted: 20 October 2017

Subject Category:
Ecology

Subject Areas:
ecology

Authors for correspondence:
Guillaume Chapron
e-mail: guillaume.chapron@slu.se
Adrian Treves
e-mail: atreves@wisc.edu

† These authors contributed equally to this study.

The accompanying comments can be viewed at http://dx.doi.org/10.1098/rspb.2017.0273 and http://dx.doi.org/10.1098/rspb.2017.0267.

Electronic supplementary material is available online at https://dx.doi.org/10.6084/m9.figshare.c.3931933.

THE ROYAL SOCIETY
PUBLISHING

Reply to comments by Olson *et al.* 2017 and Stien 2017

Guillaume Chapron[1,†] and Adrian Treves[2,†]

[1]Grimsö Wildlife Research Station, Department of Ecology, Swedish University of Agricultural Sciences, 73091 Riddarhyttan, Sweden
[2]Nelson Institute for Environmental Studies, University of Wisconsin, 30A Science Hall, 550 North Park Street, Madison, WI 53706, USA

GC, 0000-0002-6727-1070

The management of large carnivores remains a contentious issue in many countries. Among the most contentious management options is 'tolerance hunting', or the killing of predators to increase tolerance among groups of people who do not accept the presence of these animals [1,2]. In [3,4], we used Bayesian state space models to evaluate the hypothesis that liberalizing culling of wolves changed wolf population dynamics from 1995 to 2012, and concluded it slowed growth, which we inferred was owing to increased poaching. Olson *et al.* [5] and Stien [6] re-visit our paper and we address their criticisms below.

First, we disagree with Olson *et al.*'s [5] and Stien's [6] assertions that our paper ignores the literature or reports it in a biased manner. We simply disagree about the interpretation of the literature as we explain below. While they can have a different interpretation of those papers, it does not mean that ours is incorrect and Stien's [6, p. 1] phrasing 'biased reporting of previously published results' almost suggests intent from us to mislead the reader. Both Olson *et al.* [5] and Stien [6] raised the issue of density dependence analysed by Stenglein *et al.* [7]. In that paper, the information on density dependence relevant to our paper is in figures 3, S2.4, S2.5 and S2.6 (we cannot find reported numerical estimates on how recruitment changed during the relevant period for our study in [7]). Stenglein *et al.* [7, p. 5] wrote that 'The evidence for a negative slope of the line for $t > 18$ was 69.0% (proportion of posterior that was <0)' but this concerns all years post-1998, which also include many years without culling. For the relevant period for our paper (when culling was allowed or wolf years 2004–2012), we need to interpret the figures ourselves. On figures 3, S2.4, S2.5 and S2.6 in [7], we find no obvious difference between the confidence intervals of annual recruitment estimates. In fact, the only significant drop in recruitment seems to happen much earlier, at the beginning of the $t > 18$ period (1998–2001 approximately) whereas the years with culling seem to show a stable recruitment regardless of the models used [7]. Because Stenglein *et al.* [7] clearly concluded that they found no density dependence on survival, we observed then and still interpret Stenglein *et al.* [7] to show no density dependence for the period relevant to our study. An additional sentence in our discussion in [3] explaining what we just explained above might have been welcome but seemed a digression. We also chose not to mention that Stenglein *et al.* [7, p. 5] appear to trust their model because '48.4% of the time, the estimated population sizes in Wisconsin from 1981 to 2011 were within the 95% posterior intervals of μ_t' implying that more than half the time their estimates failed this relatively undemanding test. Stenglein *et al.* [7] also did not, in our opinion, properly handle uncertainty by using the midpoint between minimum and maximum population size as their population count (while we allowed fluctuations between minimum and maximum in [3]). Both Olson *et al.* [5] and Stien [6] further insist that the decline in growth rate is owing to negative density dependence. Olson *et al.* [5] present a compilation of studies, but which also includes some unrelated to negative density dependence (see our electronic supplementary material). Neither of those papers present, in our opinion, empirical evidence to support a mechanism for density dependence in the population and period under discussion. Stien [6] argues that the quadratic relationship he found for area against population size is evidence of negative density dependence. However, as we wrote previously [8], one must first demonstrate a mechanism to assert negative density dependence. Indeed, the United States Fish and Wildlife Service reported that the Wisconsin wolf population grew from minima of 746 to 866 by April 2016 [9] after all wolf-killing including tolerance hunting was barred in December 2014, or a 1-year growth of 16%, which is larger than the annual median growth during our study period. This accelerating growth at the relevant population size demonstrates that there is still no evidence consistent with negative density dependence in the Wisconsin wolf population during the period of interest for our study.

Olson *et al*. [5] also argue that their previous study [10] demonstrated that illegal killing decreases with increasing availability of lethal management. However, this study [10] was, in our opinion and that of an anonymous reviewer, not quantitatively rigorous. One reviewer of our paper [3] indeed agreed and wrote that our 'paper is also important because the results are at least somewhat contradictory to a recent paper Olson *et al.* [10]. That recent paper had some important shortcoming for which this paper seems to "fix"'. We admit we might have explained the below shortcomings in our original paper [3] but did not wish to appear confrontational. Olson *et al*. [10] assumed that observed poaching correlated tightly to unobserved poaching (even for radio-collared wolves). Embracing this assumption leads to the faulty conclusion that observed poaching is an unbiased sample of all poaching and can be used as the response variable for a correlation with temporal changes in policy. Treves *et al*. [11] did not find support for that assumption. In a separate study in Scandinavia, Liberg *et al*. [12] found that two thirds of poaching was not observed. For Wisconsin wolves, Treves *et al*. [11] estimated that same observation error to be half of all poached wolves. Olson *et al*. [10] also used the number of recovered radio-collared wolves inferred to have died from poaching as their response variable, without considering errors in inferring poaching as a cause of death. Systematic errors in attributing poaching to Wisconsin wolf carcasses ranged from 6–37% depending on which subsample one examined, as reported by veterinary pathologists contributing to Treves *et al*. [13]. Both Olson *et al*. [10] and Treves *et al*. [11,13] agree that a high proportion of radio-collared wolves disappeared without trace (unknown fate), which must be addressed in some way in any analysis of poaching [11]. Most importantly, Olson *et al*. [10] ignored exposure time of radio-collared wolves. We do not understand why they did not use a survival (time to event) model with the proportion of the year with culling as an explanatory variable. However, even using a time to event model would require a proper treatment of unknown fates. Finally, Olson *et al.* [10] did not seem to consider that marked animals (radio-collared wolves) may not suffer the same mortality pattern as the unmarked population. This has been shown specifically in two recent studies of wolves, which have undermined the assumption of identical mortality patterns [14,15].

Olson *et al*. [5] and Stien [6] raise other points which we address in detail in our electronic supplementary material. Briefly, Stien [6] claims that there is a strong link between probability of reproduction and proportion of the year with legal culling. However, we believe other models in Stien [6] supplementary code do not support this conclusion, which, if they would, would still not warrant a change of our conclusions (see electronic supplementary material). We explain Olson *et al*. [5]'s assertion—that our hypothesis is not parsimonious—is built on a misunderstanding of the cause-and-effect relationships between cognition and behaviour. Moreover, Olson *et al*. [5]'s hypothesis of density dependence is not supported by evidence (see above), so its simplicity does not give it strength. We also argue that there is no support for the frustration hypothesis proposed by Olson *et al*. [5] because previous research demonstrates that tolerance for wolves declined, and inclination to poach rose, in the years following culling authority. Here and elsewhere, the reasoning in Olson *et al*. [5] leaves the impression of cherry-picking the literature while accusing us inaccurately of ignoring or misrepresenting it. Olson *et al*. [5] insinuate that we chose to start our analysis in 1995 because it somehow supported our hypothesis. Our choice is justified by two of Olson *et al*.'s [5] co-authors writing how monitoring substantially improved after 1995 [16]. The papers they cite [7,17,18] that begin analyses earlier do not seem to account for that change in census methods, which may affect their results. Finally, Olson *et al*. [5] criticize us for calling our study 'quasi experimental' and write that it is instead a 'worst case design' despite having published on the exact same study system [10]. We do not follow the logic by which a system can suddenly become the worst when other different authors write about it. Overall, the pattern emerging from analyses in Olson *et al*. [5,10] is one of a stream of unrigorous assertions which together portray a picture of the Wisconsin wolf population that is inaccurate. When management policies are built on such weak assertions, these policies cannot have a scientific basis, as has been shown for wolf hunting in the United States [19]. In addition, Olson *et al*. [5] seem, in our opinion, inclined to divert from a collegial discussion and adopt the language and style of advocacy. While there may be many reasons to pledge allegiance to management agencies, we believe that scholarly debates are not compatible with ad-hominem attacks and misleading soundbites.

We appreciate the scrutiny that our analysis and our writing have sparked. Science progresses through invalidation of hypotheses and presentation of new evidence, therefore we welcome scrutiny of our work and collegial discussions. However, we also feel obligated to point out that statements supporting the tolerance hunting hypothesis, either from scientists or governments, seem to be taken for granted and evade scrutiny. A recent illustration is a paper about wolves in Norway bluntly claiming that 'it is not an unreasonable expectation that allowing legal harvest might prevent some of the illegal killing' [20, p. 135]. In our opinion, the careful wording of nuances in the above sentence only signals a value-based statement intended to influence policy regardless of evidence. While our model has faced substantial and legitimate scrutiny, scientists have remained silent about flaws or lack of evidence supporting the tolerance hunting hypothesis. In other words, killing predators appears immune to evidence-based scrutiny, while not killing predators must be justified by the highest level of evidence. One possible reason is that killing predators may simply be viewed as not worthy of justification unless one is driven by emotions [21], an attitude revealing contempt for changing public attitudes about the value of wildlife [22] and a refusal to serve the broad public interest [23]. Another possible reason may be that killing predators is a goal by itself regardless of its effectiveness in reducing poaching because it provides political services [24]. As a consequence, tolerance hunting is today a widespread management intervention for large carnivores [2] (see our electronic supplementary material for updated context), perhaps because it has the potential to justify large scale killing and is extremely difficult to evaluate scientifically. We believe that double standards in evaluating evidence are hazardous. The double standard that we observe runs contrary to the precautionary principle and the level of scrutiny should not be lower or plainly absent for writings supporting tolerance hunting than for results invalidating it. We conclude by hoping that the debate our paper triggered will encourage further research on this controversial topic.

Data accessibility. This article has no additional data.

Competing interests. We declare we have no competing interests.

Funding. This work benefited from support from the Swedish Environmental Protection Agency, the National Socio-Environmental Synthesis Center (SESYNC)-NSF award DBI-1052875, the US and Swedish Fulbright Commissions, University of Wisconsin-Madison, and the Little River Band of Ottawa Indians.

References

1. Epstein Y. 2017 Killing wolves to save them? Legal responses to 'tolerance hunting' in the European Union and United States. *Rev. Eur. Comp. Int. Environ. Law* **26**, 19–29. (doi:10.1111/reel.12188)
2. Treves A. 2009 Hunting for large carnivore conservation. *J. Appl. Ecol.* **46**, 1350–1356. (doi:10.1111/j.1365-2664.2009.01729.x)
3. Chapron G, Treves A. 2016 Blood does not buy goodwill: allowing culling increases poaching of a large carnivore. *Proc. R. Soc. B* **283**, 20152939. (doi:10.1098/rspb.2015.2939)
4. Chapron G, Treves A. 2016 Correction to 'blood does not buy goodwill: allowing culling increases poaching of a large carnivore'. *Proc. R. Soc. B* **283**, 20162577. (doi:10.1098/rspb.2016.2577)
5. Olson ER, Crimmins SM, Beyer DE, MacNulty DR, Patterson BR, Rudolph BA, Wydeven AP, Van Deelen TR. 2017 Flawed analysis and unconvincing interpretation: a comment on Chapron and Treves. *Proc. R. Soc. B* **284**, 20170273. (doi:10.1098/rspb.2017.0273)
6. Stien A. 2017 Blood may buy goodwill: no evidence for a positive relationship between legal culling and poaching in Wisconsin. *Proc. R. Soc. B* **284**, 20170267. (doi:10.1098/rspb.2017.0267)
7. Stenglein JL, Zhu J, Clayton MK, Van Deelen TR. 2015 Are the numbers adding up? Exploiting discrepancies among complementary population models. *Ecol. Evol.* **5**, 368–376. (doi:10.1002/ece3.1365)
8. Chapron G, Treves A. 2017 Reply to comment by Pepin *et al.* 2017. *Proc. R. Soc. B* **284**, 20162571. (doi:10.1098/rspb.2016.2571)
9. USFWS 2016 Gray wolf numbers in Minnesota, Wisconsin, and Michigan (excluding Isle Royale). See https://www.fws.gov/midwest/wolf/aboutwolves/pdf/MN-WI-MI-table.pdf.
10. Olson ER, Stenglein JL, Shelley V, Rissman AR, Browne-Nuñez C, Voyles Z, Wydeven AP, Van Deelen T. 2015 Pendulum swings in wolf management led to conflict, illegal kills, and a legislated wolf hunt. *Conserv. Lett.* **8**, 351–360. (doi:10.1111/conl.12141)
11. Treves A, Artelle KA, Darimont CT, Parsons DR. 2017 Mismeasured mortality: correcting estimates of wolf poaching in the United States. *J. Mammal.* **98**, 1256–1264. (doi:10.1093/jmammal/gyx052)
12. Liberg O, Chapron G, Wabakken P, Pedersen HC, Thompson Hobbs N, Sand H. 2012 Shoot, shovel and shut up: cryptic poaching slows restoration of a large carnivore in Europe. *Proc. R. Soc. B* **270**, 91–98. (doi:10.1098/rspb.2011.1275)
13. Treves A, Langenberg JA, López-Bao JV, Rabenhorst MF. 2017 Gray wolf mortality patterns in Wisconsin from 1979 to 2012. *J. Mammal.* **98**, 17–32. (doi:10.1093/jmammal/gyw145)
14. Borg BL, Arthur SM, Bromen NA, Cassidy KA, McIntyre R, Smith DW, Prugh LR. 2016 Implications of harvest on the boundaries of protected areas for large carnivore viewing opportunities. *PLoS ONE* **11**, e0153808. (doi:10.1371/journal.pone.0153808)
15. Schmidt JH, Johnson DS, Lindberg MS, Adams LG. 2015 Estimating demographic parameters using a combination of known-fate and open N-mixture models. *Ecology* **96**, 2583–2589. (doi:10.1890/15-0385.1)
16. Wydeven AP, Wiedenhoeft JE, Schultz RN, Thiel RP, Jurewicz RL, Kohn BE, Van Deelen TR. 2009 History, population growth, and management of wolves in Wisconsin. In *Recovery of gray wolves in the great lakes region of the United States* (eds AP Wydeven, TR Van Deelen, EJ Heske), pp. 87–105. Berlin, Germany: Springer.
17. Stenglein JL, Van Deelen TR. 2016 Demographic and component Allee effects in southern Lake Superior gray wolves. *PLoS ONE* **11**, e0150535. (doi:10.1371/journal.pone.0150535)
18. Van Deelen TR. 2009 Growth characteristics of a recovering wolf population in the Great Lakes region. In *Recovery of gray wolves in the Great Lakes Region of the United States: an endangered species success story* (eds AP Wydeven, TR Van Deelen, EJ Heske), pp. 139–153. New York, NY: Berlin, Germany: Springer.
19. Creel S *et al.* 2015 Questionable policy for large carnivore hunting. *Science* **350**, 1473–1475. (doi:10.1126/science.aac4768)
20. Linnell JDC, Trouwborst A, Fleurke FM. 2017 When is it acceptable to kill a strictly protected carnivore? Exploring the legal constraints on wildlife management within Europe's Bern convention. *Nat. Conserv.* **21**, 129–157. (doi:10.3897/natureconservation.21.12836)
21. Nelson MP, Bruskotter JT, Vucetich JA, Chapron G. 2016 Emotions and the ethics of consequence in conservation decisions: lessons from Cecil the Lion. *Conserv. Lett.* **9**, 302–306. (doi:10.1111/conl.12232)
22. van Eeden LM, Dickman CR, Ritchie EG, Newsome TM. 2017 Shifting public values and what they mean for increasing democracy in wildlife management decisions. *Biodivers. Conserv.* **26**, 2759–2763. (doi:10.1007/s10531-017-1378-9)
23. Treves A, Chapron G, López-Bao JV, Shoemaker C, Goeckner AR, Bruskotter JT. 2017 Predators and the public trust. *Biol. Rev.* **92**, 248–270. (doi:10.1111/brv.12227)
24. Chapron G, López-Bao JV. 2014 Conserving carnivores: politics in play. *Science* **343**, 1199–1200. (doi:10.1126/science.343.6176.1199-b)

Supplementary Material

Density-dependence in the Wisconsin wolf population

Olson et al. [5] compile studies that they report as having documented negative density dependence, but we find that their list includes a study that documented positive density dependence (Allee effect) in Wisconsin [17] and another study of Michigan and Wisconsin describing an individual based model and not including the term "density dependence" [25]. Moreover, the studies they list are North American focused and ignore relevant studies from other regions of the world. For example, wolves in Western Poland have grown exponentially with no sign of density dependence [26]. In addition, their list includes populations such as the tiny Isle Royale National Park and the vast protected areas of Yellowstone National Park, neither of which seems a reasonable comparison to the Wisconsin and Michigan wolf populations in their heavily human dominated landscapes without large protected areas. All of these observations raise concerns about the criteria Olson et al. [5] used to build their list. As we wrote previously [8], fitting a logistic growth model alone cannot demonstrate density dependence as was done in [18]. Specifically, a mechanism must be found to support a claim of density dependence. This applies also to Stien [6]'s writing that the quadratic relationship he found for area against population size is evidence of negative density- dependence. It is not (see section: Relationship for area against population size in this supplement). Many of the studies Olson et al. [5] report (in their Table S1) do not present evidence for a mechanism. Still, when Olson et al. [5] report mechanisms for density dependence, these are not found for the Wisconsin wolf population: they propose litter size would decrease [27], but Stenglein et al. [7] shows no negative density-dependence on recruitment during the period of our study (see main text), they propose reproduction would decrease [27], we find it increases, they propose survival would decrease [28], Stenglein et al. [7] shows it remained constant. Finally, we present evidence in the main text about continued population growth above the median annual rate at the same time as the wolf population apparently exceeded the densities we studied.

Chain of inference and parsimonious hypotheses

Olson et al. [5] argue that our hypothesis is not parsimonious because it requires a longer chain of inference. They do so by presenting their own interpretation of three different hypotheses and their respective chains of inference. Our hypothesis is presented with the longest chain, while density dependence has the shortest one (one link only). We find this misleading. For one, they misunderstand the cause-and-effect relationships between cognition and behavior [29]. For both the frustration hypothesis and our hypothesis – that the policy signal of legalizing culling motivated poachers – there can be a single cognitive step and a single behavioral step. For the former, the cognitive step is that would-be poachers are motivated by frustration with continued protection of wolves, whereas our hypothesis proposed would-be poachers are motivated by lessening protections. The causal chains are the same length. In addition, Olson et al. [5] should also increase the chain for density dependence by presenting at least one falsifiable, detailed biological mechanism, because density dependence is not as simple as "*density dependence in component of growth → reduced growth at high density*". Finally, a hypothesis that is not supported by evidence does not gain strength by being simpler.

Frustration hypothesis

Olson et al. [5] assert that "*there is no evidence that devaluation of wolves was exclusive to the period after implementation of LDM [2003]*". First, we never said this was exclusive, rather we substantiated a decrease in tolerance for wolves, during the period 2001–2013. Second, AT and his colleagues have meticulously measured changes in human attitudes in the same individual residents of Wisconsin's wolf range since 2001. Their measures in four separate surveys include the years 2001, 2004, 2009, and 2013 as well as a focus group approach with repeated measures from 2010-2012. Four publications [30-33] demonstrate that tolerance for wolves declined following culling authority and three measured inclination to poach, which also rose in those years. Indeed, Hogberg et al. [31] document that frustration continued to increase after wolf-killing was further liberalized to include public hunting and trapping. The non peer-reviewed report [34] on attitudes that Olson et al. [5] cite cannot address the topic of change in attitudes because it is a measure at one time point. Likewise, the Michigan state agency report [35] cited by Olson et al. [5] was not a measure of change in attitudes either. We still find no evidence in support of the frustration hypothesis in [5] and emphasize that the highest tolerance for wolves was measured in 2001 [32] and ever since it has declined in Wisconsin, when we compared the same individuals' responses to the same questions years later [33]. The focus group study [30] seems to directly invalidate the frustration hypothesis.

Relationship for area against population size

Stien [6] argues that our log linear model is not appropriate to detect density dependence and that a quadratic relationship for area against population size is needed. Stien [6] writes that the quadratic relationship he found is evidence of negative density-dependence. We are not convinced and we reassert that one must also show that a life history parameter affecting birth or death exists before claiming density-dependent population growth. The lack of empirical evidence for a decline in demographic parameters with increasing population size is the crux of the matter here. If as Stien [6] argues, weak evidence of density dependence in total area used by the entire wolf population implies density-dependence in wolf population growth, then Stien [6] must also show that the decrease resulted from density effects on life history itself rather than other factors independent of density. For example, the area used by the entire wolf population does not necessarily bear a direct, causal relationship to pressures acting on individual wolf packs. In addition, the data on area used by the entire wolf population does not have an observation error which means that it is unclear whether the small, reported 0.0016 wolf / km^2 increase from 2000–2011 is evidence of increasing density. Stien [6] has not presented a single such density-related biological change, nor explained how density changed if at all. We are not persuaded by the argument in Stien [6] for density-dependence based on the total area used by the wolf population because without associated changes in survival or reproduction, it is unclear then how this assumed density-dependence can account for a decline in growth rate that we reported. There may be changes in behavior but if those changes do not translate into changes in demographic parameters, it is difficult to understand how they can change growth rate. Finally, we point out that Figure 1 in Stien [6] is strongly influenced by the last data point when the area grew less but the population still grew 13% which is the median growth in the time series.

Probability of reproduction as a function of proportion of the year with legal culling

Stien [6] models the probability of reproduction as a function of proportion of the year with legal culling (see associated Figure 2 in Stien [6]). Specifically, Stien [6] mentions one model "*slope = -0.89, SE = 0.41, P = 0.03, binomial GLMM with logit link function and year fitted as random effect*". However, there are also other models that have very close AIC values where the proportion of the year with legal culling is not significant or is absent (see models lme.breed.H and lme.breed.DH in Stien [6] supplementary material) but that Stien [6] did not discuss. Stien [6] writes in his conclusion that "*My analysis highlights the responsibility that researchers have to expose models to alternative hypotheses that are refined and biologically* *plausible*". We agree and add that models explored in Stien's R code [6] merit further consideration. When these models are considered, it is much less certain that the negative correlation between reproductive rates and legal culling is so important. In our opinion, after assessing the model including both variables and the model-averaged coefficients, neither the proportion of the year with legal culling nor the number of wolves culled are significant predictors of probability of reproduction. Both independent variables together show low multicollinearity after testing a variance inflation factor (VIF = 1.76), so it is statistically correct to include both variables in the model to explain the change in probability of reproduction. Indeed, we may lose valuable statistical and biological information by focusing only on proportion of the year with legal culling while ignoring the number of wolves culled or ignoring the alternative models. In addition, even if Stien's [6] claim of a strong link between probability of reproduction and proportion of the year with legal culling were right, this would not change our message [3, 4]. Reproductions might decrease if culling and poaching killed pack members that bred or supported reproduction. So in our opinion, Figure 2 and Stien's [6] assertion that "*reproductive rates have to be accounted for in the analysis of population growth rates*" do not invalidate our conclusion and might on the contrary suggest a mechanism through which the policy signal operates. Our original paper [3] ended with an implicit hypothesis from our inference that poaching rose; it is possible that poaching of breeding adults in particular rose or that poaching of pups pre-census rose. Similarly, Stien [6] concluded from his extension of our Bayesian model that "*there was a strong positive relationship between probability of reproduction in year t and the population growth rate from year t-1 to t*" [6], which is not relevant for our analysis. It only shows that a population grows more when it breeds more, but does not evaluate the role of the policy signal (the proportion of the year with legal culling) in changing growth over time.

Updated context on tolerance hunting

To provide more updated context, the issue of hunting large carnivores to increase people's tolerance has become white hot in many countries. In the USA, the FWS final rule to delist the grizzly bear [36] states that "*removals promote conservation of the GYE grizzly bear population by minimizing illegal killing of bears*" without providing evidence and adds that "*based on recent experiences with wolves in Idaho and Montana, social tolerance for wolves improved as both States implemented an adaptive management approach to managing conflict during the post-delisting monitoring period"*, apparently confusing tolerance for wolves and tolerance for authorities managing wolves and mischaracterizing the research as revealing changes in tolerance – if they are citing the only such study of which we are aware [37]. In Norway, the government faced a political controversy in winter 2016–2017 after the environment minister decided there was no valid reason to kill 47 wolves out of a population of 68 wolves and scaled down the hunting quota to 15 [38, 39]. In Finland, after two years of such tolerance hunting intended to reduce poaching, the wolf population has collapsed (by 25% in 2017, down to 150–180 animals) [40, 41] while a recent analysis of the dynamic of wolf poaching in Finland concluded that "*tolerance for carnivores cannot be promoted by legal hunting alone*" [42]. These controversies are likely to continue if governments and scientists continue to advocate for tolerance hunting without evidence.

Supplementary references

25. Stenglein, J.L., et al., *An individual-based model for southern Lake Superior wolves: A tool to explore the effect of human-caused mortality on a landscape of risk.* Ecological Modelling, 2015. **302**: p. 13-24.
26. Nowak, S. and R.W. Mysłajek, *Wolf recovery and population dynamics in Western Poland, 2001–2012.* Mammal Research, 2016: p. 1-16.
27. Stahler, D.R., et al., *The adaptive value of morphological, behavioural and life-history traits in reproductive female wolves.* Journal of Animal Ecology, 2013. **82**(1): p. 222-234.
28. Cubaynes, S., et al., *Density-dependent intraspecific aggression regulates survival in northern Yellowstone wolves (Canis lupus).* Journal of Animal Ecology, 2014. **83**(6): p. 1344-1356.
29. Ajzen, I., *The theory of planned behavior.* Organizational behavior and human decision processes, 1991. **50**(2): p. 179-211.
30. Browne-Nuñez, C., et al., *Evaluating the potential for legalized lethal control of wolves to reduce illegal take: A mixed-methods examination of attitudes and behavioral inclinations.* Biological Conservation, 2015. http://dx.doi.org/10.1016/j.biocon.2014.12.016.
31. Hogberg, J., et al., *Changes in attitudes toward wolves before and after an inaugural public hunting and trapping season: early evidence from Wisconsin's wolf range.* Environmental Conservation, 2015. **FirstView**: p. 1-11.
32. Naughton-Treves, L., R. Grossberg, and A. Treves, *Paying for tolerance: the impact of livestock depredation and compensation payments on rural citizens' attitudes toward wolves.* Conservation Biology, 2003. **17**(6): p. 1500-11.
33. Treves, A., L. Naughton-Treves, and V. Shelley, *Longitudinal Analysis of Attitudes Toward Wolves.* Conservation Biology, 2013. **27**(2): p. 315-323.
34. Holsman, R., N. Kaner, and J. Petchenik, *Public attitudes towards wolves and wolf management in Wisconsin.* 2014, Wisconsin Department of Natural Resources Madison, WI.
35. Beyer, D., et al., *Review of social and biological science relevant to wolf management in Michigan.* Michigan Department of Natural Resources, Lansing, Michigan, USA, 2006.

36. USFWS, *Removing the Greater Yellowstone Ecosystem Population of Grizzly Bears From the Federal List of Endangered and Threatened Wildlife.* Federal Register, 2017. **82 FR 30502**.
37. Lewis, M.S., et al., *Selected results from four separate surveys of resident Montanans regarding Montana's wolf hunt.* HD Unit Research Summary, 2012(33).
38. Harvey, F., *Norway plans to cull more than two-thirds of its wolf population.* The Guardian, 2016. https://www.theguardian.com/environment/2016/sep/16/norway-wolf-cull-government-wwf-friends-earth-environment-protest.
39. Sutterud, T. and E. Ulven, *Norway reprieves 32 of 47 wolves earmarked for cull.* The Guardian, 2016. https://www.theguardian.com/environment/2016/dec/20/norway-reprieves-32-of-47-wolves-earmarked-for-cull.
40. AFP, *Finland approves wolf hunt in trial cull.* The Guardian, 2016. https://www.theguardian.com/world/2016/jan/21/finland-approves-wolf-hunt-trial-cull-illegal-poaching.
41. Harvey, F., *Finland has far fewer wild wolves than previously thought, census shows.* The Guardian, 2017. https://www.theguardian.com/world/2017/jun/26/finland-has-far-fewer-wild-wolves-than-previously-thought-census-shows.
42. Suutarinen, J. and I. Kojola, *Poaching regulates the legally hunted wolf population in Finland.* Biological Conservation, 2017. **215**: p. 11-18.