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

†Both authors contributed equally to this study.

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Reply to comment by Pepin *et al*. 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

We commend Pepin *et al*. [1] for initiating a conversation about the role of science in policy generally and a specific discussion of our recent findings published earlier in the pages of this journal [2]. Our study assessed whether liberalizing culling of wolves changed wolf population dynamics from 1995 to 2012 through a decrease of illegal killing or poaching. The US Fish and Wildlife Service (USFWS) claimed that lethal control of endangered wolves (*Canis lupus*) was necessary for the 'propagation or survival of the affected species' in Wisconsin and Michigan, USA [3]. The USFWS argued that 'the ability of the states to take problem wolves will likely decrease the illegal take of wolves', that 'the mortality authorized by the Wisconsin permit is not likely to slow the recovery of the species' and that 'the purpose of depredation control is to increase the social carrying capacity for wolves' [4]. This claim has repeatedly been asserted by other governments and management authorities [5,6]. Its veracity has often been attributed to common sense or pragmatic knowledge [7]. In our study, we took advantage of repeated policy changes in the recovering wolf populations of Wisconsin and Michigan to evaluate whether the policy signal to allow wolf culling would decrease or increase population growth, irrespective of the number of wolves culled. Our paper found that allowing wolf culling was substantially more likely to slow population growth than to raise population growth. We inferred the slow-down was due to increased poaching by examining alternative hypotheses related to reproductive decreases or emigration increases. The alternatives to poaching seemed unsupported. Although our main result that culling did not work as the government claimed does not change, Pepin *et al*. [1] offered to re-examine our study and reported several issues with our conclusions, which we would like to discuss hereafter.

First, Pepin *et al*. [1] wrote that the magnitude of the policy effect we reported is biologically weak. They argued that the policy effect is not biologically meaningful because there were not substantially fewer wolves in the model that included the policy effect relative to a model that did not. We did not claim in our study that the slower growth of the wolf populations induced by a policy signal threatened the persistence of these wolf populations. In fact, we reported in [2] that growth rate with year-long culling would be $r = 0.12$ (in Wisconsin) and $r = 0.10$ (in Michigan). Governments claim that allowing culling will help conserve carnivore populations and decrease poaching, but we find on the contrary that population growth slowed independent of the number of wolves culled, and that increased poaching was the likely explanation for the slow-down. Even if the increase of poaching is not large enough to trigger a substantial population reduction, a slow-down in population growth is not the expected benefit of reduced poaching, which was the justification behind the policy to allow killing of a protected species.

Second, Pepin *et al*. [1] argued that an 83% chance of a negative effect of culling policy (and thus a 17% chance that it is positive) is not a substantial policy effect because there is still a one in five chance the policy effect is positive. We re-examined our analyses thanks to the collegial scientific discussion Pepin *et al*. [1] initiated while writing their reply and found a minor error described in [8], which has the effect of strengthening our results. Corrected results indicate that with a year-long culling policy signal, a decline of growth rate was 12 times more likely than an increase [8]. We nevertheless do not think a policy with a probability of success lower than 1 in 5 or 1 in 12 is strong evidence in support of that policy. The relevant approach here is to compare the relative likely outcomes of policies (including the option of doing nothing), an approach at the core of decision theory [9]. The alternative approach of using low, fixed significance levels to make environmental management decisions may lead to costly mistakes [10]. Taking an epidemiological analogy, we do not believe experts would recommend policies where increasing the prevalence of a disease is five times more likely than reducing it, simply because success might conceivably still happen. Selecting management actions is an important question in applied ecology and an approach based on calculating ratios of Bayesian posterior densities has been recommended; see [11] for managing brucellosis (*Brucella abortus*) in the Yellowstone bison (*Bison bison*) population and [12] for controlling fertility of overabundant ungulates. This approach proposes statements expressed in terms of likelihood of achieving a goal and not in significant effects. Our paper did not make any claim about the statistical significance of the effect we reported. We did not attempt to explain whether a policy signal was a statistically significant factor in growth rates, but instead whether this policy signal was more likely to increase or decrease growth rate. In our case, not sending the policy signal had a higher probability of success than sending it. Therefore, Pepin *et al.*'s [1] assessment does not change our conclusion that culling endangered species to improve population status or to reduce poaching has not been shown to succeed. There may also be more than two options (send the policy signal or do not), such as enforcing anti-poaching laws strictly [13]. This precautionary approach in making decisions about endangered species was endorsed by the Supreme Court of the US in the snail darter (*Percina tanasi*) case with the majority opinion explaining that, 'Congress has spoken in the plainest of words, making it abundantly clear that the balance has been struck in favor of affording endangered species the highest of priorities, thereby adopting a policy which it described as "institutionalized caution"' (*Tennessee Valley Authority v. Hill*, 437 US 153, 194 (1978)).

Third, Pepin *et al.* [1] compared our model with a null model (exponential growth without policy effect) and found that the deviance information criterion (DIC) values between the models were not substantially different. We followed [14] and considered that insights could be gained from our model without relying on model selection statistics (see also [15]): the null model proposed by Pepin *et al.* [1] is equivalent to having the posterior of our parameter β_1 centred on zero, which was not the case. Pepin *et al.* [1] also explored alternative models, some of which included density-dependent population growth (logistic model), and reported that the models with the policy effect were not substantially different from models with logistic growth. We agree that density dependence must be considered a hypothesis to explain the logistic growth; however, it cannot be asserted just by statistical support for a logistic growth model. Empirical evidence of density dependence also needs to be documented and should not be assumed. The alternative hypothesis to density dependence is that mortality factors with no relationship to density appeared in the later years and these slowed the growth of the population. Therefore, we believe that only three factors could have caused the slow-down in population growth we observed in both US states: (i) decline in births (for which we found the opposite evidence in reproductive performance of wolf packs); (ii) emigration (but there is no known or hypothesized mechanism by which emigration out of state would respond to a policy signal independent of the number of wolves culled); and (iii) a new source of mortality that is influenced by the policy signal. Our finding is consistent with [16], which reported no density-dependent effect on survival and hinted at a new factor needed to explain the Wisconsin wolf population slow-down we observed. Pepin *et al.* [1] wrote there were no data on poaching rates for testing the poaching hypothesis, but we disagree. Longitudinal surveys of inclination to poach and tolerance to wolves have been conducted in Wisconsin since 2001 [17], and have found an increase of inclination to poach [18,19] and a decrease of tolerance for wolves when wolf culling and other legal killing was liberalized [18–20]. This evidence of poaching from social sciences and lack of evidence of density dependence from ecological data [2] allowed us to infer the decline of growth rate could be attributed to poaching. Finally, Pepin *et al.* [1] wrote that we tested the null hypothesis—'a policy that allows wolf culling by the government causes no effects on wolf population growth rate beyond the number of wolves removed from policy actions'—and did not reject it. The hypothesis we evaluated is not that one but instead whether liberalizing culling of wolves changed wolf population dynamics from 1995 to 2012 [2]. We found that growth slowed independent of the number of wolves culled, and therefore found no support to the government claim that culling had conserved the wolf population by reducing poaching. We also inferred that the opposite effect—an increase of poaching—was more likely to happen, although we agree this is an inductive inference which might hold less if alternative mechanisms proposed by Pepin *et al.* [1] would receive more evidential support.

We agree with Pepin *et al.* [1] that management decisions should be based on rigorous science with clear interpretation of uncertainty. Our study reported uncertainty—a probability of 83% the policy effect would be negative—which allowed Pepin *et al.* [1] to assess our claim. We view both our study and their response as a contribution in that direction and want to reiterate our appreciation of their prompting this debate. However, we believe that an overlooked aspect in the broad context of carnivore conservation and management relates to the burden of proof. Should a policy be implemented until proven harmful or held until proven harmless? Should burden of proof be different according to the hypothesis tested? We are criticized for supporting a hypothesis that has a 17% probability of being wrong. However, evaluating the hypothesis that culling reduces poaching indicates it has an 83% probability of being wrong. We think that rejecting our conclusion must in turn imply rejecting the latter conclusion even more forcefully.

With poaching accounting for a substantial amount of mortality in large carnivore populations [21,22], we conclude by stressing the importance to devote more research attention to this unobserved source of mortality and how it responds to policy changes. We hope that our paper and the discussion started by Pepin *et al.* [1] will encourage additional studies in different systems.

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