



# Predator control may not increase ungulate populations in the future: A formal meta-analysis

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## Abstract

1. Human-dominated landscapes are being recolonized by large carnivores, thereby increasing conflicts worldwide via predation of livestock and harvested wildlife such as ungulates. Recent meta-analyses have shown that predator control (hereafter, predator removal) has mixed success in reducing livestock predation. Yet, it is unknown how effective predator removal is in decreasing predation on ungulates due to a lack of quantitative synthesis, despite the long history of implementation in North America.
2. We quantified the demographic responses of ungulate survival and recruitment rates, abundance, and population growth to experimental predator removal and identified the ecological and experimental design factors affecting ungulate responses to predator removal. We conducted a literature review of management and natural experiments to increase ungulate demography finding 52 predator removal experiments and 10 natural experiments from 47 publications. We then conducted a meta-analysis to determine the overall effect size and factors which increased ungulate demography during predator removal. Lastly, we tested for evidence of publication bias and experimental rigour for these experiments.
3. We found that predator removal in both management and natural experiments increased ungulate demographic responses by 13% (95% CI = 4.1%–23%), yet prediction intervals overlapped with 0 (95% PI = –34% to 93%). Focusing just on management removals, ungulate demographic responses increased only by 7.8% (95% PI = –32% to 72%), indicating that future experiments could have negligible effects. Predator removal in both management and natural experiments was more successful in improving the demography of young (e.g. recruitment ES = 44%, 95% CI = 13%–83%) but equivocal in improving adult survival (ES = 5.4%, 95% CI = –18% to 36%) and ungulate abundance (ES = 13%, 95% CI = –17% to 31%). The low and variable effectiveness of predator removal for ungulate populations might be linked to ungulates' slow life history and the compensatory mortality of carnivores on ungulates, though effects were stronger on endangered prey.
4. We identified the experimental design factors that led to greater uncertainty in ungulate responses to predator removal, including lack of randomization, low replication and short temporal length. Lastly, we found evidence of publication bias, where experiments with poor rigour and negative effects (i.e. reduced ungulate demography following predator removal) were under-reported.

5. *Synthesis and Applications.* We recommend future predator removal experiments be conducted with a more rigorous experimental design to overcome these weaknesses, especially for endangered species where predator removal may work more effectively. We suggest that managers attempting to evaluate experimental practices to increase ungulate populations through predator removal could employ an open standards framework akin to the 'Open Standards for the Practice of Conservation' framework.

#### KEYWORDS

carnivore, harvest, human-wildlife conflict, meta-analysis, predator management, ungulates, wildlife management

## 1 | INTRODUCTION

Large carnivores and humans are expanding and encroaching on each other's ranges worldwide (Chapron et al., 2014; Larue et al., 2012; Mech, 1995; Wikramanayake et al., 2011; Woodroffe, 2011), thereby increasing human-carnivore conflicts (Treves & Karanth, 2003). Consequently, there is a growing call for large carnivore control (hereafter, predator removal) to mitigate these conflicts (e.g. Bottollier-Depois, 2019; Landers, 2019). Recent reviews have addressed the successes and limitations of predator removal for one component of human-carnivore conflict, livestock predation (Eklund et al., 2017; van Eeden et al., 2018). But there has been no comparable synthesis of predator removal to manage the other major component of conflict, predation on harvested wildlife species such as ungulates. Predator removal is often used as a tool in wildlife management, especially in North America, to ostensibly increase ungulate population size (Peek et al., 2012). Yet, there are many ecological and experimental reasons that predator removal might not work, and this lack of synthesis has limited the ability for managers to mitigate human-carnivore conflicts in the future.

One reason it is unclear if predator removal can increase ungulate populations is due to the complex nature of predator-prey interactions. Predation could be compensatory, that is, only surplus ungulate prey that were going to die anyway are predated (Errington, 1946). In this case, predator removal will not work as prey mortality would be the same with or without predation. Such compensatory mortality is to be expected when ungulate populations are close to food-based carrying capacity (Ballard et al., 2001; Errington, 1946). Ungulate populations could be limited by bottom-up factors like primary productivity, which can negatively interact with top-down factors like predation. For example, the effect of predators on roe deer *Capreolus capreolus* was stronger in poorly productive environments in Europe (Melis et al., 2009). Therefore, we hypothesize that predator removal could have a stronger effect in lower productivity environments. Lastly, as predator diversity increases, predation may lead to compensatory mortality in ungulates due to functional redundancy among the predator community (Griffin et al., 2011; Mech & Peterson, 2003). Predator removal of one predator in a community

may lead to release of other competing predators, thereby reducing the success of predator removal experiments of just one predator in diverse communities. Indeed, we can use predator removal experiments to test the ecological theory of predator-prey interactions.

Despite conflicting evidence on the nature of predation, predators have been historically removed to increase abundance of harvested ungulates, especially in North America (Reynolds & Tapper, 1996). Early observational studies corroborated historical predator removal, with predators shown to have strong effects on prey populations due to reports of irruptions of ungulates following predator removal in North America (Leopold et al., 1947). Later reviews, however, provided equivocal evidence of ungulate growth after removal (Caughley, 1970; Connolly, 1978). Early predator removal experiments (e.g. Gasaway et al., 1983) were used as evidence that maximizing harvestable ungulate population size may necessitate predator removal. Yet, many of these studies had experimental biases, such as a lack of experimental control or confounding variables, leading to uncertain support for predator removal as a management strategy (National Research Council, 1997). Furthermore, many predator removal experiments likely go unpublished (see Peek et al., 2012 for examples), and if these were 'unsuccessful' experiments, this could bias our understanding of predator-ungulate management practices. Conversely, natural predator recolonization or the opposite, natural declines (e.g. due to disease outbreaks) could also provide data on the effects of predator abundance on ungulate prey. Nevertheless, it is unclear when and under what conditions predator removal works, especially since recent robust experiments show varied results (e.g. Hayes et al., 2003; Hurley et al., 2011; Keech et al., 2011; Proffitt et al., 2020; White et al., 2010).

Here, we conducted a meta-analysis of ungulate populations in response to predator removal experiments, which we define as management-induced reductions of predator abundances to increase ungulate prey, or natural experimental changes in predator abundances. While we focus on North America, where many predator removal management experiments occurred, we also considered natural experimental changes in predator abundances from Europe and Africa. In doing so, we first aimed to quantify the demographic response of ungulate populations to management-induced

experimental predator reduction. Here, we define ungulate demographic responses as survival and recruitment rates, abundance and population growth rates. Next, we tested for the ecological factors that increase the likelihood of successful outcomes for management goals (e.g. increase ungulate abundance), such as additive mortality or low primary productivity. Defining success is challenging and indeed, controversial in such predator removals, but here we defined success as ultimately if survival and recruitment rates, abundance or population growth rates of ungulates increased. Finally, we identified the tenets of experimental design and rigour which increased the likelihood of successful predator removal and used these results to suggest an improved set of recommendations for future predator removal management experiments.

## 2 | MATERIALS AND METHODS

### 2.1 | Data collection

We conducted a literature review to collate published studies, graduate theses, wildlife management reports, etc., of management-induced or nature-induced (e.g. due to disease outbreaks) experimental predator removal (hereafter, management experiments) to increase ungulate populations. We also included 'natural' experimental predator removal combined with, and separated from predator removal experiments. We searched for relevant articles online using Web of Science, with combinations of the following keywords: predator, predation, control, removal, manipulation and ungulate. We also used bibliographies of earlier reviews to find experiments (Ballard et al., 2001; Connolly, 1978; National Research Council, 1997; Peek et al., 2012; Salo et al., 2010). Finally, we considered used expert knowledge to find reports of experiments.

#### 2.1.1 | Data extraction

We recorded information on each experiment, such as location, duration, the manipulated predator species and the target prey species. We collected any demographic (e.g. survival rates) or population-level variable of prey (e.g. abundance, population growth rate) recorded within the experimental or control group from either the manuscript text or extracted from figures using Web Plot Digitizer (Rohatgi, 2012). We recorded two types of predictor variables: (a) ecological variables, which we hypothesize will modify the effect of predators on prey, and therefore the intensity of predator removal and (b) experimental variables, which we hypothesized could confound the intensity of predator removal experiments.

#### 2.1.2 | Ecological variables

We hypothesized that management experiments will have the strongest effects on the ungulate response parameters (e.g. survival

of young) that the population growth rate is least sensitive to (hereafter, 'sensitive'), and the weakest effects on the most sensitive parameters like adult survival and abundance (Gaillard et al., 2000). Prey response was the demographic or population-level variable of prey which was recorded (e.g. abundance, calf survival). We hypothesized that predators will have a larger impact on smaller-bodied prey (Sinclair et al., 2003), which we tested using the ratio of predator to prey biomass. We hypothesized that there may be species-level variability on the impact of predator removal. We tested this using prey and predator average biomass as a proxy. We hypothesized that experiments with greater predator-prey diversity may have weaker results due to competition amongst predators or alternative prey being released following removal of one predator (Mech & Peterson, 2003). Lastly, we considered the effect of primary productivity on predator removal efficiency, which we hypothesized that predator removal experiments will be more impactful in areas with low primary productivity (Melis et al., 2009). We calculated a proxy for primary productivity using composite dynamic habitat indices (DHIs) from gross primary productivity (Hobi et al., 2017). DHIs encompass the phenological productivity of species over each year and can be used to describe habitats of different species (Hobi et al., 2017).

#### 2.1.3 | Experimental design variables

We hypothesized that as experimental design improved, the estimated predator removal effect size would decrease due to improved experimental rigour following evidence of similar patterns across the medical meta-analysis literature (Guyatt et al., 2011). This is because poorly designed studies, such as before and after comparisons, often have uncontrolled, confounding variables which often explain some of the ungulate response. We included as experimental type: before-and-after design (BA), to simultaneous experiment and control (SEC) and to before-after-control-impact design (BACI), a combination of both SEC and BA experiments.

We categorized type of treatment into an ordinal scale of increasing intensity of predator removal: (a) harvest and translocations; (b) ground shooting and trapping; (c) aerial shooting; (d) poisoning (National Research Council, 1997). We hypothesized that effectiveness of removal would increase as type of treatment became more intense in terms of the % of the predator population removed. We also hypothesized that increased predator removal would result in stronger effects on ungulate prey; therefore, we recorded verbal or statistical evidence that the predator was successfully manipulated. If possible, we recorded the estimated percent change in predator density. We recorded if multiple predator species were removed, as this can non-additively increase predator removal success (Salo et al., 2010). We hypothesized that studies which were too spatially small to encompass the home range of the manipulated predator will experience smaller effects due to immigration from nearby conspecifics (Salo et al., 2010). We hypothesized that studies which were too temporally short will be unable to assess demographic responses of ungulates to predator

removal due to time needed to confirm that a stable state is reached (Connell & Sousa, 1983). Therefore, we recorded the spatial (in km<sup>2</sup>) and temporal (in months) scales of the experiment.

To account for the confounding effects of experimental rigour in our ecological analysis, we created a composite score for rigour using variables from our experimental analysis based on the three prominent sources of systematic bias in wildlife management: selection, performance and measurement/assessment bias (Pullin & Stewart, 2006). Other useful approximate measurements of experimental design have been recently proposed—including ‘gold’ to ‘bronze’ standards based on the influence of design on experimental inference (Louchouart et al., 2020; Treves et al., 2019), and the Grading of Recommendations Assessment, Development, and Evaluation (GRADE) guidance in medicine and epidemiology (Guyatt et al., 2011). To assess selection bias, we scored the design of study (BA = 0, SEC = 1, BACI = 2). We recorded if the study was natural (if so = 0, if not = 1). To assess performance bias, we scored +1 if the size of the treatment was larger than the predator's maximum home range, +1 if length of treatment was longer than the prey's generation time, and +1 if the effectiveness of predator removal was greater than a 50% decline. To assess assessment bias, we scored +2 if studies were replicated and scored the type of ungulate response measured (calf–cow ratio, recruitment, calf survival = 0, adult survival = 1, population growth rate, abundance, density = 2), based on previous knowledge of the importance of demographic rates in determining the population growth rate (Gaillard et al., 1998, 2000). Overall, the composite rigour score ranges from a minimum score of 0 to a maximum score of 10.

## 2.2 | Meta-analysis

To understand the effect of predator removal on ungulate demographic responses, we calculated the log-response ratio (RR), which is an effect size measurement defined as follows:

$$RR = \ln\left(\frac{\bar{X}_E}{\bar{X}_C}\right), \quad (1)$$

where  $\bar{X}_E$  and  $\bar{X}_C$  are the mean treatment and control responses, respectively (Koricheva et al., 2013). Effect sizes  $RR > 0$  indicate that predator removal had a positive effect on the prey species,  $RR \approx 0$  indicate no response, and  $RR < 0$  indicate a negative effect (Koricheva et al., 2013). The variance of the log-response ratio,  $\text{Var}(RR)$  was approximated using the delta method, assuming independence between  $\bar{X}_E$  and  $\bar{X}_C$ :

$$\text{Var}(RR) = \frac{SE(\bar{X}_E)^2}{\bar{X}_E^2} + \frac{SE(\bar{X}_C)^2}{\bar{X}_C^2}, \quad (2)$$

where  $SE(\bar{X})$  represents the standard error of either the experimental or control group. To understand the effect of predator removal on the variance of ungulate demographic responses, we calculated the

coefficient of variation ratio (CVR; Nakagawa et al., 2015), defined as follows:

$$CVR = \ln\left(\frac{CV_E}{CV_C}\right), \quad (3)$$

where  $CV_{E/C}$  is the coefficient of variation,  $SE(\bar{X}) / \bar{X}$ , for the experimental or control groups. The variance of the coefficient of variation ratio,  $\text{Var}(CVR)$  was defined as follows:

$$\begin{aligned} \text{Var}(CVR) = & \left(\frac{SE(\bar{X}_E)}{\bar{X}_E}\right)^2 - 2\rho_{\ln\bar{X}_E, \ln SE(\bar{X}_E)} \frac{SE(\bar{X}_E)}{\bar{X}_E} \\ & + \left(\frac{SE(\bar{X}_C)}{\bar{X}_C}\right)^2 - 2\rho_{\ln\bar{X}_C, \ln SE(\bar{X}_C)} \frac{SE(\bar{X}_C)}{\bar{X}_C}, \end{aligned} \quad (4)$$

where  $\rho_{\ln\bar{X}, \ln SE(\bar{X})}$  are the correlations between the means and standard error in the experimental or control groups on the log scale across studies (Nakagawa et al., 2015). We report both the 95% confidence interval on the effect size and effect size of covariates but also consider effect sizes in terms of future prediction intervals to evaluate effects of future predator removal studies. Prediction intervals represent the variation in treatment effects across all possible settings, including what is expected in future experiments (IntHout et al., 2016). However, because the studies we use were not selected randomly, the prediction intervals we report are potentially underestimated.

## 2.3 | Statistical analysis

We accounted for heterogeneity between studies using weighted generalized linear mixed-effects models in the R package ‘METAFOR’ (Viechtbauer, 2010). We included the nested random effect of year within study to account for similarities in studies that conducted multiple experiments and/or conducted them over many years. We weighted studies by the inverse of their sampling variances. For studies which did not record standard errors or variances (49% of overall studies), we imputed variances using the means of treatment and control responses and the ecological and experimental predictor variables with predictive mean matching in the R package ‘MICE’ (van Buuren & Groothuis-Oudshoorn, 2011). Predictive mean matching is a semi-parametric imputation approach that fills missing data randomly with observed donor values whose regression-predicted values are closest to the regression-predicted value for the missing data point (van Buuren & Groothuis-Oudshoorn, 2011). We conducted separate statistical analyses with these imputed data to determine if their inclusion changed our results.

We conducted two statistical analyses to explain variation in the effect size (RR), one for ecological predictor variables and one for experimental predictor variables, given the large degrees of freedom that it would take to adequately analyse these variables

together. The ecological analysis included the following variables: biodiversity, calculated by adding together predator and prey diversity; predator and prey biomass; predator–prey ratio; primary productivity, type of response; and as nuisance variables, the experimental rigour score and the categorical variable 'natural'. The experimental analysis included the following variables: type of study; natural; size and length of experimental treatment; % change in predator numbers due to removal; multiple predators, a categorical variable denoting whether many predators were experimentally removed; replication, if studies were replicated or not; and treatment score, our ordinal variable for the intensity of predator removal treatment. For both analyses, we conducted backwards stepwise selection until we reached the lowest AIC (Burnham & Anderson, 2003). We also reported effect sizes with both predator removal and natural experiments combined and separated, despite small sample sizes of the latter, to isolate potential differences between management and natural experimental interventions. We repeated the above analyses with the imputed datasets to determine if there were any statistical differences in our results. We combined the variables from the top ecological and top experimental models in one single model to test if accounting for confounding variables would change our model selection results, which it did not.

## 2.4 | Publication bias

It is also possible that there may be publication bias in predator removal experiments. Similar to the medical field (Schulz et al., 1995), we suspected that unsuccessful predator removal experiments will be less likely to be published. We assessed publication bias using funnel plots (Koricheva et al., 2013) where we graphed the precision ( $1/SE$ ) of the experiments versus their effect size. If there is no publication bias, we would expect a 'funnel' shape around the true effect size mean, where studies with smaller precision will have the largest variation in effect size, and as precision increases, we would expect a narrowing of the funnel to smaller effect sizes (Koricheva et al., 2013). Any deviation from this shape may indicate publication bias. We used these data to conduct a statistical test for funnel plot asymmetry which would reveal potential biases of unpublished studies (Viechtbauer, 2010).

## 3 | RESULTS

### 3.1 | Summary statistics and overall experimental impact

We found 62 experiments from 47 publications ( $n = 373$  experimental years) which met our search criteria. These included 14 replicated experiments, defined as those with at least two control and two treatment plots or a before-and-after design where the treatment was reversed between plots (Salo et al., 2010), and 48 un-replicated

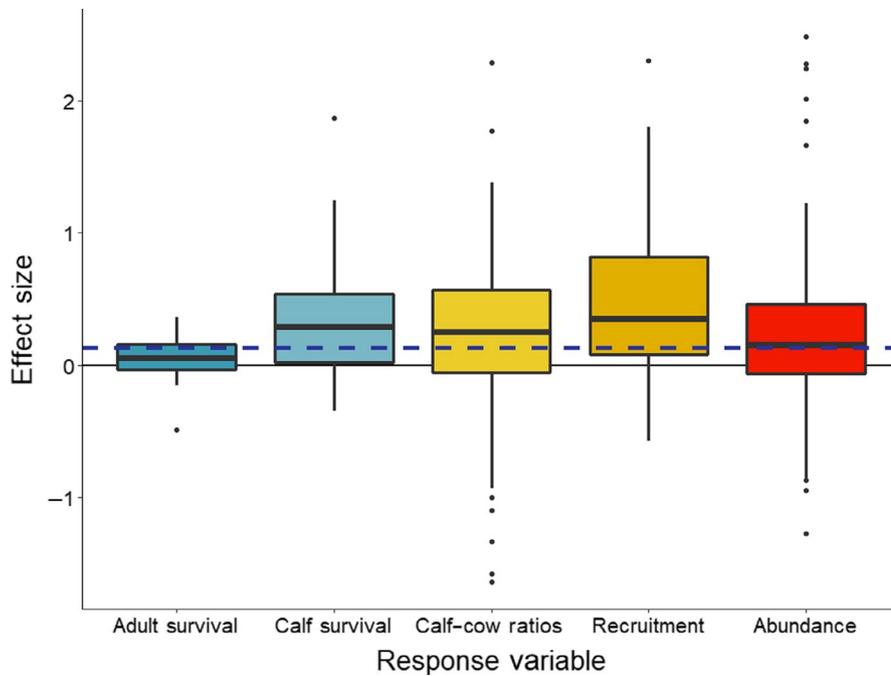
experiments. In all, 32 experiments ( $n = 148$  experimental years) reported variance of ungulate demographic measurements, 30 did not. Ten of the experiments were naturally carried out (e.g. resulting from disease outbreaks). Most studies were conducted in North America ( $n = 43$ ), with a few natural experiments in Africa ( $n = 3$ ), and Europe ( $n = 1$ ; Figure S1).

Predator removal management experiments were largely carried out to increase North American harvested ungulate populations, such as moose *Alces alces* (19.4% of experiments), white-tailed deer *Odocoileus virginianus* (17.7%), mule deer *O. hemionus* (14.5%) and elk *Cervus canadensis* (11.3%). Other predator removal experiments were carried out on species like caribou *Rangifer tarandus* (12.9% of experiments), where management goals were either to increase abundance or recover threatened populations. Most predator experiments removed large carnivores, dominated by canids (e.g. grey wolves *Canis lupus*, 37.1%; coyotes *C. latrans*, 24.2%), felids (e.g. mountain lions *Puma concolor*, 12.9%) and ursids (e.g. black bears *Ursus americanus*, 12.9%; brown bears *U. arctos*, 6.5%).

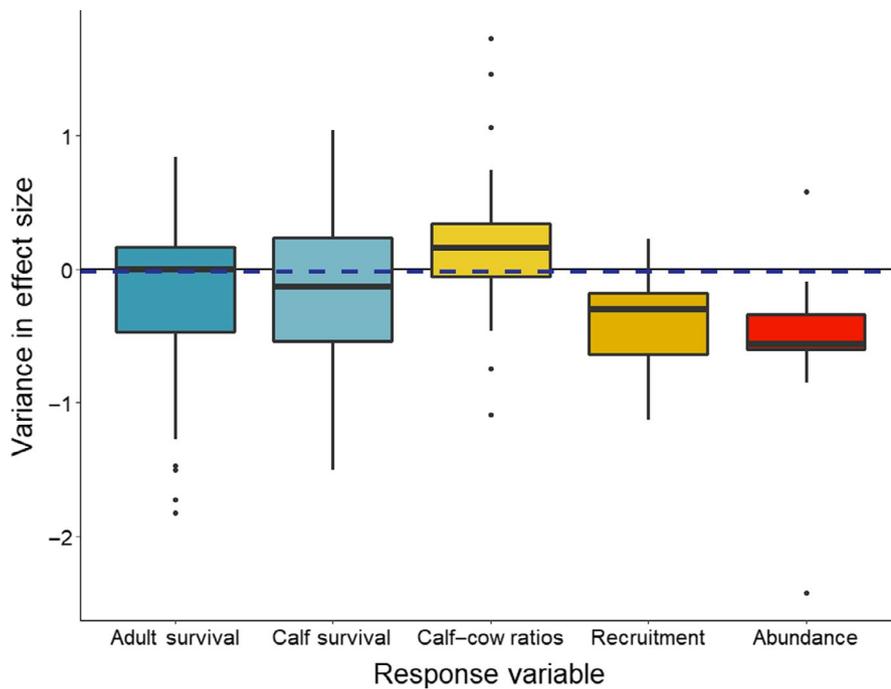
Almost all studies qualitatively self-reported that predator removal was 'high' and therefore successful (83.9% of experiments), with a median 53.5% (95% CI in removal = 20.5%–90.7%) decline in predators across non-natural experiments. Yet, many (38.7%) experiments did not quantitatively measure or report the magnitude of change in predator populations after removal. The majority (64.5%) of management experiments were carried out in areas larger than the manipulated predator's maximum home range. However, only six experiments carried out predator removal experiments longer than the target prey's generation time. Most experiments (67.7%) continued human harvest of target ungulate species during predator removal; however, a small minority did reduce ungulate harvest by humans during these experimental periods (e.g. Hayes et al., 2003). Very few of the experiments reported changes in hunter success post-predator removal (e.g. Proffitt et al., 2020).

### 3.2 | Meta-analysis of effect size and variation

Overall, across all ungulate demographic responses in studies which included measurements of variance, log-response ratios (RRs) of predator removal experimental groups were 13.1% higher than control groups (95% CI = 4.1%–23.0%), yet prediction intervals overlapped with 0 (95% PI = –33.7% to 92.9%) and high heterogeneity between effect sizes was present ( $I^2 = 82.6%$ ; Figure 1). Separated out, management experiments had an average 7.8% increase (95% CI = 0.1%–16.1%, 95% PI = –32.4% to 71.9%), compared to natural experiments, which had an average 41.5% increase (95% CI = 6.1%–88.8%, 95% PI = –34.0% to 303%; Figure S2). When imputed measurements of variance were included for those studies that were missing them, predator removal experimental groups were 38.3% higher than control groups (95% CI = 24.4%–53.8%), but again prediction intervals overlapped with 0 (95% PI = –47.4% to 264%). Overall, across variation in ungulate demographic responses, the CV of predator removal experimental



**FIGURE 1** Effect size of predator removal experiments by ungulate response variable measured. Effect size was calculated as the log-response ratio of the experimental over control group. Effect size  $>0$  indicates that predator removal has a positive effect on ungulate prey,  $<0$  indicates a negative effect, and  $\approx 0$  indicates a negligible effect. 'Abundance' represents experiments which measured abundance, density or population growth rate. Dashed blue line represents the overall mean of the effect size of predator removal experiments in our meta-analysis



**FIGURE 2** Variance in the effect size of predator removal experiments by ungulate response variable measured. Variance in effect size was measured using the coefficient of variation ratio, calculated as the natural log of the coefficient of variation of the experimental group over the coefficient of variation of the control group. Variance in effect size  $>0$  indicates that predator removal increases the variance in ungulate prey responses,  $<0$  indicates a reduction in variance, and  $\approx 0$  indicates a negligible effect on variance. 'Abundance' represents experiments which measured abundance, density or population growth rate. Dashed blue line represents the overall mean of the variance of the effect size of predator removal experiments in our meta-analysis

groups was 1.9% lower than the CV of control groups (95% CI =  $-16.6\%$  to  $15.4\%$ , 95% PI =  $-57.4\%$  to  $126\%$ ) (Figure 2). When imputed measurements of variance were included for those studies that were missing them, the CV of predator removal experimental groups were 5.5% lower than the CV of control groups (95% CI =  $-18.3\%$  to  $9.4\%$ , 95% PI =  $-58.8\%$  to  $117\%$ ).

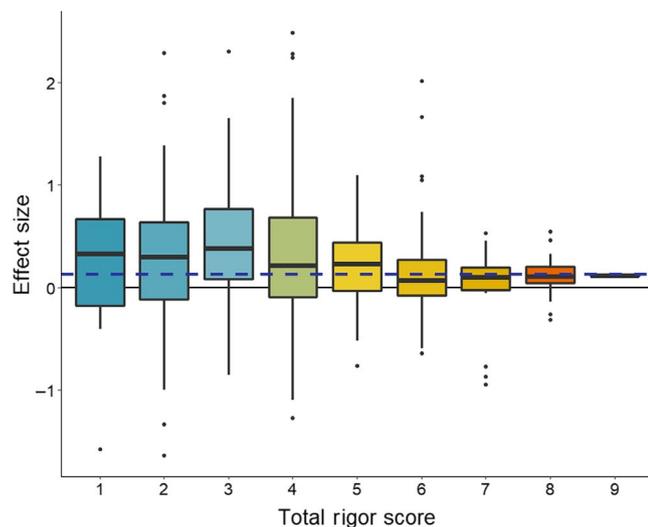
### 3.3 | Ecological and experimental variables

Our final model with ecological variables (Table S1) retained the categorical variable, type of demographic response (e.g. survival rates,

abundance, etc.). Overall, effect sizes were much stronger for demographic rates known to have weak effects on population growth rate, and effect size diminished for demographic rates known to have stronger effects on population growth rate. For example, effects of predator removal experiments on the demography of young were slightly positive: calf-cow ratios increased by 19.5% (95% CI =  $-7.6\%$  to  $54.5\%$ ), calf survival by 26.1% (95% CI =  $-8.6\%$  to  $74.0\%$ ) and recruitment by 44% (95% CI =  $13.4\%$ – $82.9\%$ ; Table 1; Figure 1; Figure S2). Yet, predator removal experiments increased adult survival by a smaller margin of 5.35% and confidence intervals highly overlapped with 0 (95% CI =  $-18.3\%$  to  $35.8\%$ ; Table 1; Figure 1). Population-level metrics of abundance increased by 13.4% (pooled

**TABLE 1** Final ecological model parameters for the effect size of predator removal experiments to increase ungulate demography. Model selection was run using non-imputed data. Final model was chosen by ranking  $\Delta$ AIC. Coefficients and SEs are shown in log-odds ratios

| Intercept       | Coefficient | SE    | p value |
|-----------------|-------------|-------|---------|
| Intercept       | 0.127       | 0.074 | 0.110   |
| Adult survival  | -0.074      | 0.056 | 0.082   |
| Calf-Cow ratios | 0.052       | 0.057 | 0.320   |
| Calf survival   | 0.106       | 0.091 | 0.170   |
| Recruitment     | 0.238       | 0.048 | <0.001  |
| Pred mass       | -0.001      | 0.001 | <0.001  |
| Natural         | 0.268       | 0.108 | 0.010   |



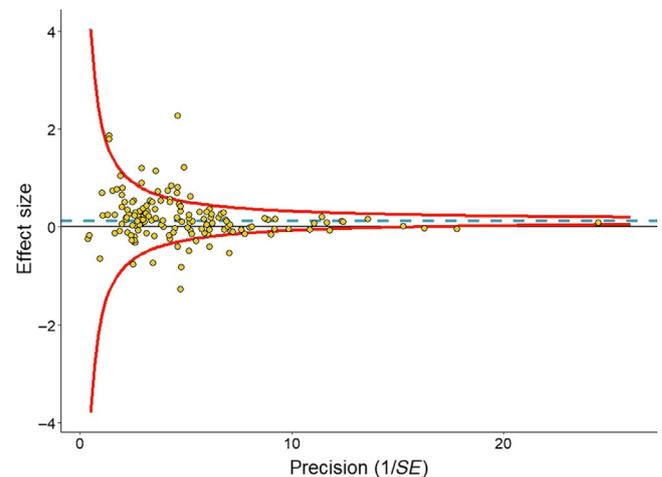
**FIGURE 3** Effect size of predator removal experiments on ungulate demography by total rigour score. Effect size was calculated as the log-response ratio of the experimental over control group. Total rigour score was calculated as a qualitative composite score of the amount of assessment, selection and performance bias in experiments from 0 to 10, 0 indicating very low rigour, and 10 indicating very high rigour. Dashed blue line represents the overall mean of the effect size of predator removal experiments in our meta-analysis

between natural and management studies) and were similar but overlapped 0 (95% CI = -17.4% to 31.2%), compared to our overall effect size of 13.1%. Predator mass had a slightly negative relationship (slope = -0.2%, 95% CI = -0.3% to 0.0%; Table 1). Experimental design variables were retained in our top model (Table S1; Figure 3). Repeated analyses with imputed data did not change our model selection results.

Our final model with experimental variables retained experimental type, treatment type, % change of predators and temporal length (Table S2). Experiment type was negatively related with effect size as rigour increased from before-after to simultaneous control-experiment to BACI design (Table 2). The effect size decreased as experimental

**TABLE 2** Final experimental model parameters for the effect size of predator removal experiments to increase ungulate demography. Model selection was run using non-imputed data. Final model was chosen by ranking  $\Delta$ AIC. Coefficients and SEs are shown in log-odds ratios

| Intercept             | Coefficient | SE    | p value |
|-----------------------|-------------|-------|---------|
| Intercept             | 0.110       | 0.147 | 0.105   |
| Experiment type: BACI | -0.145      | 0.119 | 0.782   |
| Experiment type: SEC  | -0.340      | 0.100 | 0.163   |
| Treatment score: 2    | -0.015      | 0.234 | 0.390   |
| Treatment score: 3    | -0.013      | 0.086 | 0.348   |
| Treatment score: 4    | -0.198      | 0.165 | 0.007   |
| % Change pred         | -0.002      | 0.003 | 0.001   |
| Temporal length       | 0.005       | 0.004 | 0.038   |



**FIGURE 4** Funnel plot for the effect size of predator removal experiments on ungulate demography to test publication bias. Effect size was calculated as the log-response ratio of the experimental over control group. Yellow dots represent individual observations in experiments. Red lines represent 95% confidence intervals at respective standard errors. Dashed blue line represents the overall mean of the effect size of predator removal experiments in our meta-analysis

treatment intensity (harvest < ground shooting < aerial shooting < poisoning) increased (Table 2). As the temporal length of experiments increased, effect size slightly increased (slope = 0.47%, 95% CI = -0.7% to 1.5%; Table 2). As the % change of predators removed increased, effect size slightly decreased (slope = -0.2%, 95% CI = -1.1% to 0.06%; Table 2). Repeated analyses with imputed data retained all above variables and the categorical variable for 'natural' experiments, which was positively related with effect size. Experimental rigour was moderately low, with a median composite score of 4 (range = 1-9; Figure 3). Visual inspection of the funnel plot and statistical evidence using Egger's regression test showed a possible bias against publishing non-significant results ( $z = 2.52$ ,  $p = 0.011$ ; Figure 4).

## 4 | DISCUSSION

We found that predator removal experiments (management and natural) caused an overall ~13% increase in ungulate population abundance, growth rates, or survival and recruitment rates averaged across all responses. Focusing only on management removal experiments, however, indicated a weaker ~8% ungulate population response. Due to high between-study heterogeneity, 95% prediction intervals for the effect sizes overlapped with 0. Thus, while responses were positive, and sometimes led to biologically meaningful demographic responses (e.g. a 7.8% increase in management experiments), the large variation across studies reduced certainty in future outcomes. It is therefore essential for wildlife managers to utilize prediction intervals to truly anticipate the success of future predator removal experiments. Our results indicate that it is uncertain if future predator removal experiments would have the desired positive effect on ungulate prey, especially population abundance. Furthermore, our understanding of predator removal as a management strategy will continue to be uncertain if future experiments are carried out with similarly low rigour (median = 4; e.g. weak experimental design without replication, no randomization, etc.) as some of those in our meta-analysis.

Our results confirm that predator removals can positively impact ungulates like past reviews of predator removals for other vertebrates (Coté & Sutherland, 1997; Salo et al., 2010). For example, in harvested ungulate populations, an 8%–13% increase in population abundance in a population of 10,000 could translate to an additional ~800 to 1,300 harvestable animals. This may be important for specific socioeconomic settings, or in the case of Indigenous or subsistence hunting, such as in Alaska where such harvest is a policy mandate (National Research Council, 1997). Nevertheless, it is important to place the magnitude of predator removal (top-down) on abundance in context with the magnitude of bottom-up management strategies to increase ungulate population abundance. For example, Raithel et al. (2007) used life-stage simulation analysis to compare the effects of bottom-up versus top-down factors in a synthesis of elk populations. Supplemental feeding of elk increased population growth rates by 5%, compared to reduced vehicular access (and lower exposure to hunting) during hunting seasons, which increased growth rates by ~6% to 7%. In contrast, following the large-scale fires in the Greater Yellowstone Ecosystem in 1988, elk population growth rates increased by 15%–20% (Raithel et al., 2007), confirmed independently by time-series population modelling (Barber-Meyer et al., 2008; Taper & Gogan, 2002). These comparisons illustrate that the changes we report in ungulate demography via predator control are similar to changes induced by other management actions. Thus, while statistically uncertain, and admittedly controversial, the magnitude of top-down effects is consistent with these other, bottom-up drivers of ungulate populations.

Nevertheless, the overall average increase (8%–13%) following predator removals were much lower than other studies. For example, Salo et al. (2010) found an overall 70% increase in terrestrial vertebrates following predator removal. Yet, Salo et al. (2010)'s

review was mostly comprised of faster life-history species (e.g. rodents = 30% of experiments, birds = 39%) with relatively high intrinsic rates of growth compared to ungulates (which were only 10% of studies in Salo et al., 2010). Therefore, the lowered effectiveness of predator removal for ungulates may be linked to their relatively slow life history and delayed response to temporally short predator removal experiments. The common paradigm in ungulate population dynamics is that adult survival has low variability and high elasticity, whereas calf survival has high variability but low elasticity (Gaillard et al., 2000; Raithel et al., 2007). Our results support the classic paradigm in ungulates, where the effects of predator removal on calf survival were much higher and variable than adult survival, which was much lower and static (Figure 1). These marked increases in calf survival following predator removal did not translate to large increases in population rates (Figure 1). We suggest that differences in the canalization of demographic rates to variability (Gaillard & Yoccoz, 2003) could drive the low success of predator removal for ungulates. Predator removal may increase calf survival and decrease its variability (Figures 1 and 2), but this parameter has low elasticity and may not translate to increases in populations unless variability is quite high (sensu Raithel et al., 2007). Ultimately, predator removal studies should strive to measure the ultimate population success metric, ungulate abundance (65% of studies), and not just responses of demographic rates that have limited effect on population abundance. Even this overlooks that often the goal in what are coupled human–natural systems is to enhance hunter harvest, which very few studies here addressed directly.

The average effect of predator removal for an endangered ungulate, the woodland caribou (*R. t. caribou*) was slightly higher (RR = 14.0%) and more likely to have a positive effect in the future (95% PI = 5.6%–23.0%). The proximate cause of their decline is apparent competition via predation by wolves which is ultimately driven by unsustainable rates of habitat loss and alteration (Johnson et al., 2020; Wittmer et al., 2005). We were unable to directly test for the effects of predator removal on endangered ungulates due to small sample size ( $n = 2$  studies). Yet, predation can be more impactful, and therefore removal more beneficial, for an endangered species because the predation rate (% of prey killed) is likely greater and more destabilizing than for a typical stable harvested species (Sinclair et al., 1998). For example, an estimated predation rate of wolf-killed woodland caribou is ~23% (Serrouya et al., 2020), in comparison to a predation rate of ~5% for wolf-killed non-endangered elk in Yellowstone (Vucetich et al., 2011). Moreover, caribou are known to exhibit a slower life history, with delayed age at reproduction, which would render them more vulnerable to predation (DeCesare et al., 2012). These lines of evidence suggest that removal of predators, in addition to other treatments, can lead to increases in population growth for woodland caribou (Hervieux et al., 2014; Serrouya et al., 2019), and possibly other endangered species (e.g. Johnson et al., 2013).

Our results also support the notion that predation might be partially compensatory in some ungulates. Predator removals were self-assessed in the original studies as highly successful with

an average 54% decline in predators, yet ungulate demographic responses only increased by 13%. This disparity suggests partial compensation, likely driven by multiple mechanisms. First, overwinter calf survival can be compensatory, as predators predate late-born, low-weight calves that would have starved otherwise. For example, Barber-Meyer et al. (2008) estimated that approximately 87% of elk calf deaths caused by predation in Yellowstone could be compensatory with starvation, disease or accidents. Second, predator–prey dynamics are often nonlinear. Most wolf–ungulate interactions are found to approach an asymptote at high predator densities (Vucetich et al., 2011). This suggests that predator removals may not lead to a linear increase in ungulate prey. Lastly, compensatory mortality may be driven by functional redundancy and interspecific competition between predators. If wolves are removed, bears, mountain lions or other predators could predate the prey that would have been predated by wolves. For example, Griffin et al. (2011) found that predator diversity affected neonate elk mortality in a compensatory manner, facilitated via interspecific interference and exploitative competition between predators (e.g. Caro & Stoner, 2003; Tallian et al., 2016). Certainly, other factors, such as habitat productivity and abundance of prey relative to carrying capacity could be compensatory mechanisms; however, we did not find statistical evidence for the former and few studies quantified the latter. Nonetheless, the weak responses of ungulates to predator removal across taxa lends support for the compensatory mortality hypothesis.

Indeed, we found that natural experiments were much stronger (42% increase) than non-natural experiments (7.8% increase). Natural experiments almost always led to a complete removal of all predators, often due to disease, poisoning, or poaching (e.g. Sinclair et al., 2003), or recovery, in the case of carnivore recolonization (e.g. Hebblewhite et al., 2005). This magnitude of predator removal could not be greater (e.g. 0%–100%), and therefore shows the effects of predators on ungulate prey under the most extreme treatment intensity. Yet, management experiments achieved on average only a 54% reduction in predators, indicating a possible upper limit to predator treatment intensity (Bischof et al., 2012). However, the magnitude of treatment intensity could be positively biased, since  $\sim 1/3$  of studies did not report the magnitude of change in predator numbers following removal. This is a weakness in most studies, that few explicitly tested for the effects of predator removal on predator demography (e.g. Proffitt et al., 2020). Furthermore, studies with high rigour and effort only achieved moderate reductions in predators. For example, Hervieux et al. (2014) removed wolves using high-effort aerial shooting and poisoning and only achieved a reduction of  $\sim 45\%$ , which may be below the mortality needed to sustain population reductions given wolf population growth rates (Adams et al., 2008; Gude et al., 2012). Therefore, predator removal experiments could be limited by the ability to effectively remove high numbers of predators given predator demography over a large spatial and temporal scale (e.g. Bischof et al., 2012). This is especially possible because of compensatory immigration of large carnivores that can swamp short-scale predator removals (Robinson et al., 2008).

#### 4.1 | Rigour of predator removal experiments

Most predator removal experiments we reviewed had relatively low experimental rigour. In just a few cases, predator removals were held over a large scale with multiple replicates and robust experimental design (e.g. Hurley et al., 2011; Proffitt et al., 2020). For example, Hurley et al. (2011) monitored demographic and population-level responses of mule deer under coyote and/or mountain lion removal with a  $2 \times 2$  randomized factorial design over 6 years. Over this longer period, they found a weak to negligible effect of predator removal, partially because of high annual variation induced by weather. Weak experimental rigour through poor experimental design, such as non-randomized application of treatments, before–after designs, lack of replication, etc., also increased uncertainty about effect sizes. Moreover, there was no evidence that experimental rigour is improving in modern predator management; many recent coyote–white-tailed deer predator removal studies were conducted on shorter temporal scales without rigorous experimental design (e.g. Gulsby et al., 2015; Kilgo et al., 2014; Watine & Giuliano, 2016). As rigour increased, effect size and its variance decreased until it approached the mean in the highest rigour experiments (Figure 3). This relationship is mirrored in experimental design, where we found that more robust designs like BACI experiments had lower effect sizes approaching the mean than un-replicated BA experiments (Table 2). These conclusions are expected based on previous meta-analytic literature (e.g. medical studies; Guyatt et al., 2011), and emphasize the crucial importance of improving experimental rigour. Considering these results, we recommend that experimentally randomized, replicated, long-term studies should become the ‘gold standard’ for predator removal experiments (Treves et al., 2019).

We also found evidence of publication bias in the literature on predator removal. Publication bias followed the same pattern found in medical literature (Schulz et al., 1995), that is, studies were under-reported when they had negative effect sizes. We suspect that this bias in the literature could confound some of our results, and because of that, there could be contrasting effects of ecological/experimental drivers and publication bias/experimental rigour on the effect size of predator removal experiments. To illustrate this, we found that increasing the % of predators removed slightly decreased effect size, contrary to our hypotheses (National Research Council, 1997). This may be because experiments that removed more predators had higher rigour; therefore, the effect of rigour outweighed the effect of % predator removal in our analysis. Similarly, predator removal with more effective treatments (e.g. poisoning) had slightly lower effect sizes, indicating again that rigour was a stronger driver of effect size than effective treatments. Despite these issues with publication bias, we found similar results between our dataset without experiments that did not record standard error (a sign of poor experimental practice) and fully imputed datasets. Our meta-analysis provides insight into the potential ecological and experimental drivers of successful predator removal for ungulate populations.

## 5 | CONCLUSIONS

We found a slight positive effect of predator removal on ungulate population metrics, from 8% to 13%, depending on whether predator removal was due to management or both management and natural experiments combined, respectively. Yet, due to variation in predator–ungulate ecology and experimental design, future experiments could find ambiguous or even negative results. For example, the National Research Council (1997) recommended that predator removal should have a more research-based and experimental approach that included public and economic evaluations. Yet in the more than two decades since, while there have been improvements, there is still controversy over predator management and whether these recommendations have been adequately adopted (see Boertje et al., 2010; Miller et al., 2011). In the meantime, many predator removal experiments in North America are still carried out with experimental design weaknesses. Few studies have explicitly integrated sociological or economic data into evaluating ‘success’ in predator removals. One example, Hurley et al. (2011) found that the maximum effect, minimum-cost scenario of coyote removal to increase mule deer populations would cost \$17,127 per harvestable trophy deer over 10 years. Yet, without a social science study of the economic costs and ecological effects in this instance, it is difficult to truly evaluate management ‘success’ even in stronger predator removal studies. This study is nearly unique in attempting to address the ultimate response variable, ungulate harvest. If predator removal is rationalized in terms of increasing ungulate harvest, managers need to rigorously include assessment of harvest in future efforts. Therefore, we maintain that the tenets of science-based management necessitate a higher experimental standard for predator removal experiments than current efforts.

There is currently no framework for mitigating predator-harvested ungulate conflicts beyond recommendations given decades ago when large predators were mostly extirpated and conflict was relatively marginal (e.g. Connolly, 1978; National Research Council, 1997; Theberge & Gauthier, 1985). We believe that there are great challenges in managing predators given these conflicts and argue that robust science-based management cannot be achieved without adequate guidelines and decision-making frameworks. We therefore propose the need for an ‘Open Standards for Predator Management’ akin to the Open Standards for the Practice of Conservation framework developed by the Conservation Measures Partnership (2013). This conservation framework plans and prioritizes conservation actions based on priorities, likelihood of success, cost, etc., and has been implemented globally with successful results (Schwartz et al., 2012). Wildlife management as a profession needs to develop a similar framework when testing and assessing predator removal experiments and their effectiveness to reduce human–wildlife conflicts globally, given the lack of experimental rigour in many studies in our meta-analysis. Until then, it is unclear if predator removal to mitigate this conflict is ecologically, economically and ethically sustainable.

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## AUTHORS' CONTRIBUTIONS

T.J.C. and M.H. conceived the ideas and designed methodology; T.J.C. collected the data; T.J.C. analysed the data; T.J.C. and M.H. led the writing of the manuscript. Both authors contributed critically to the drafts and gave final approval for publication.

## DATA AVAILABILITY STATEMENT

Code and data needed to reproduce the analysis available via can be found on Github <https://doi.org/10.5281/zenodo.4279580> (Clark, 2020).

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## SUPPORTING INFORMATION

Additional supporting information may be found online in the Supporting Information section.

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