REVIEWS

Predator manipulation experiments: impacts on populations of terrestrial vertebrate prey

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Abstract. Quantifying the relative impacts of top-down vs. bottom-up control of ecosystems remains a controversial issue, with debate often focusing on the perennial question of how predators affect prey densities. To assess predator impacts, we performed a worldwide meta-analysis of field experiments in which the densities of terrestrial vertebrate predators were manipulated and the responses of their terrestrial vertebrate prey were measured. Our results show that predation indeed limits prey populations, as prey densities change substantially after predator manipulations. The main determinant of the result of an experiment was the efficiency of predator manipulation. Positive impacts of predator manipulation appeared to increase with duration of the experiment for non-cyclic prey, while the opposite was true for cyclic prey. In addition, predator manipulation showed a large positive impact on cyclic prey at low prey densities, but had no obvious impact at peak prey densities. As prey population densities generally respond predictably to predator manipulations, we suggest that control of introduced vertebrate predators can be used to effectively conserve and manage native wildlife. However, care should be taken when controlling native predators, especially apex species, owing to their importance as strong interactors and the biodiversity value of their habitats. We discuss gaps in our knowledge of predator–prey relationships and methodological issues related to manipulation experiments. An important guideline for future studies is that adequate monitoring of predator numbers before and during the experiment is the only way to ensure that observed responses in prey populations are actually caused by changes in predation impacts.

Key words: meta-analysis; population limitation; predator–prey dynamics; predator removal; species interactions; wildlife management.

INTRODUCTION

The act of predation, whereby one animal kills and consumes another, is often dramatic and obvious, but the effects of predators on prey population dynamics are usually more subtle and complicated. An intuitive and commonly held view is that predators reduce the availability of prey to humans (Reynolds and Tapper 1996, Berger 2006); in consequence, predator control has been used since ancient times to protect livestock and to enhance prey populations for human harvest (Myrberget 1990, Reynolds and Tapper 1996). However, some early ecological research suggested that predators did not always have large detrimental effects on prey populations (Elton 1927). Other early studies indicated that predators often have coexisted with their prey for long periods and may kill only non-reproductive or surplus individuals that were destined to die in any case (the doomed-surplus hypothesis; Errington 1956). In this view, predator-induced mortality is compensatory and rates of prey mortality would be the same whether predators are present or not. Such observations are often associated with the bottom-up view of population limitation which suggests that population abundances at higher trophic levels are limited from below by the availability of food (Lack 1954, White 1978). Food shortage limits populations of both herbivores and carnivores by reducing reproductive success and survival, while both the abundance and quality of food are determined ultimately by weather (White 2008).

In recent decades, however, this view has again changed with the recognition that predation may represent an additional source of mortality for prey, and therefore that predators can limit or even regulate prey population size (Marcström et al. 1988, Sinclair 1989, Krebs et al. 1995, Korpimäki and Krebs 1996, Tapper et al. 1996, Hubbs and Boonstra 1997, Korpimäki et al. 2004). Introduced predators, in particular, have been shown to have dramatic effects on naïve prey populations (e.g., Johnson 2006, Salo et al. 2007) but, on occasion, even native predators are capable of obliterating prey from local areas (Kavanagh 1988). Furthermore, predation is considered by proponents of top-down regulation to be the major structuring force explaining why "the world is so green" (Hairston et al. 1960). According to this hypothesis, top-down regulation launches a trophic cascade (Paine 1980) in which predators limit the abundance of herbivores, which in turn releases plants from grazing pressure. While the existence of trophic cascades is well established in many aquatic and terrestrial systems (e.g., Schmitz et al. 2000, Shurin et al. 2002, Borer et al. 2005, 2006), examples of the indirect effects of vertebrate predators on plants via impacts on mammalian herbivores are still scarce (Sinclair et al. 2000, Norrdahl et al. 2002, Hambäck et al. 2004, Aunapuu et al. 2008, Fey et al. 2009).

Sinclair (1989) defined population limitation as the processes that set the equilibrium density of a population, whereas population regulation refers to processes by which the population returns to its equilibrium density. However, the issue of population limitation and regulation has been source of endless controversy in ecology: disputes about the meaning of the concepts of "limitation," "regulation," and "equilibrium," about the appropriate methods to study them, and about the interpretation of the results have continued for decades (e.g., Krebs 1995, Turchin 1995, White 2001, 2004, 2007). This lack of general agreement inspired Krebs (1995, 2002, 2003) to advocate a straightforward mechanistic approach that uses experimental manipulations to identify the factors that prevent prey population growth. Caughley and Gunn (1996) proposed a similar experimental approach to identify and then alleviate factors preventing the population growth of threatened species.

Long before the introduction of the mechanistic paradigm, many planned experiments had been set up to study prey population dynamics and to explore more critically whether predation merely removes doomed individuals, limits prey population growth, or actually regulates prey population size. While it is generally agreed that predators may at least limit their prey, no overall consensus appears to have emerged from the plethora of previous studies about the dynamics or the importance of predator–prey interactions. Yet at the same time, predator control is sanctioned and applied commonly by game managers and farmers in many parts of the world, while illegal persecution is a further and very widespread threat to many large predators. For example, some raptor species in Europe are widely persecuted as they are seen as harmful to small game (e.g., grouse) populations (Etheridge et al. 1997, Thirgood et al. 2000, Valkama et al. 2004, Byholm and Nikula 2007); large felids and canids similarly are reviled and hunted in grazing environments for their attacks on domestic stock (Woodroffe 2000). Holt et al. (2008) produced a timely review of the effects of predation on prey abundance in the United Kingdom, but there remains a clear need for a worldwide research synthesis on this topic.

In this paper, we use meta-analysis to review published experimental studies of terrestrial vertebrate predators and quantify their key results. We aim specifically to (1) quantify the extent to which terrestrial vertebrate prey population densities change in response to predator manipulations, (2) identify the factors contributing to the observed density changes, and (3) use the results to provide guidelines and recommendations for future studies.

METHODS

Data searches

We searched for relevant published studies using the on-line databases of the Web of Science, Biosis Previews, and Biological Abstracts using combinations of the following keywords: predator, predation, experiment, manipulation, removal, reduction, control, effect, and impact. We also used the bibliographies of earlier reviews (Côté and Sutherland 1997, Newton 1998, Sundell 2006) and of papers already retrieved. Data searches ended in October 2007.

We selected publications that described the effect of reduction or addition of terrestrial vertebrate predators on terrestrial vertebrate prey, excluding livestock. Acceptable prey responses to predator manipulations were classified as either population size or reproductive responses. Population size responses included those measured directly, such as density, indices such as minimum numbers known to be alive, numbers of breeding pairs, rate of increase, or survival; and catch-per-unit-effort indices such as numbers of animals per trapline or transect. Reproductive responses included numbers of juveniles or broods produced, numbers of females with young, nesting success, survival of young, brood size or number of juveniles per hen, number of broods/fledglings/ducklings per pair, number of fawns per 100 does, and mean recruitment. The selected studies had to have been run for long enough (≥ 1 prey generation) for a prey demographic response to be possible. Studies measuring other parameters or using other units than those described were omitted. No authors were contacted to obtain missing data.

The searches yielded 111 publications which met our criteria (see list of references in Appendix A). These included 61 replicated studies (those with at least two

control and two treatment plots or a before-and-after design where the treatment is reversed between plots) and 50 unreplicated studies (only one treatment or control sample). Fifty-five experiments were included among the unreplicated studies, as one work consisted of six independent experiments conducted at different locations and with different prey species (Appendix A: Table A1). Altogether, our data therefore consisted of 116 predator manipulation experiments. Most were published in international scientific journals on ecology, conservation, and wildlife, but we also included book chapters, Ph.D. and M.Sc. theses. Articles were published between 1939 and 2007, with 48% originating from the last 10 years.

Variables and effect sizes

Publications were scored for prey type (classified as bird, mammal, or other), origin of prey (native or introduced), prey population cyclicity (cyclic or noncyclic as defined in the publication; large irregular fluctuations and eruptions were also classified, for convenience, as cyclic), importance of prey to the predator (main prey, yes or no), importance of predator as a mortality factor to the prey (main predator, yes or no), origin of predator (native or introduced), predator type (bird, mammal, birds plus mammals, or reptile), method of manipulation (addition or removal), experiment type (SEC = simultaneous experiment and control, BA = before-and-after design, NE = natural experiment; predators are naturally absent from or occur at low densities in one study area and are present in higher densities in another area), how many predator species were manipulated (one or more), efficiency of the predator manipulation (high or low; to be classified as "high efficiency" the publication had to provide verbal, tabular, or statistical evidence of the success of the predator manipulation; the study was classified as "low efficiency" if not all targeted predator species responded to manipulation), author's conclusion about predator manipulation effect (positive effect on prey, yes or no), spatial and temporal scales of the experiment (manipulation area and manipulation time), and whether the experiment was conducted in an exclosure or open terrain (manipulation type) (Appendix A). We also recorded the mean mass of prey and predator species to calculate a predator : prey mass ratio for each study. Predators were considered introduced or native based on definitions provided in each study, and confirmed using Long (2003). "Predator addition" means either release of predators or attraction of predators (e.g., attraction of raptors with perch sites) into experimental areas. "Predator removal" refers to either exclosure experiments or manipulations where predators were killed or relocated.

Traditional meta-analyses use effect sizes such as Hedges' d or $\ln(R)$ to quantify the magnitude and direction of the experimental impact (Rosenberg et al. 2000); the response ratio $\ln(R)$ seems especially appropriate for many ecological data sets (Osenberg et al. 1997, Hedges et al. 1999). However, while traditional effect sizes are calculated with their variances, nearly half of our data set consisted of unreplicated studies for which within-study variance could not be determined. Therefore, we defined our effect size as $\ln(X_e/X_c)$ where X_e and X_c are the mean treatment and control prey responses, respectively. An effect size $\ln(X_e/X_c) > 0$ means that the predator manipulation had a positive effect on the prey species (i.e., prey population size or reproductive success increased), $\ln(X_e/X_c) \sim 0$ means that manipulation did not affect the prey species, while $\ln(X_e/X_c) < 0$ means that control prey populations fared better than experimental populations.

Values for mean treatment (X_e) and mean control (X_c) prey responses were extracted from the text, tables or figures of the publications. We collected three kinds of treatment and control values to address different aims of the study. (1) For all prey, we collected terminal data at the end of experiments (or mean values obtained over the course of the study, if no other information was available) to examine the overall effects of predator manipulation. (2) For cyclic prey, we extracted data from peak and low prey densities, as predator impacts are expected to differ between phases (Korpimäki et al. 2004). These values were compared to the impacts on non-cyclic prey where, if predator limitation occurs, the early phase of predator manipulation should show low prey population sizes, while the later phases should show increased population sizes (i.e., the effect of predator manipulation should increase with time). (3) For all experiments that lasted long enough, at least three values were taken more than one prey generation apart for calculating the coefficient of variation (CV; the ratio of standard deviation to the mean, expressed as a percentage) to examine the temporal stability of treatment and control prey populations.

In 104 experiments predators were removed or excluded, in five studies the density of predators was enhanced, and two studies used both methods. The setups in the four natural experiments included in the data set were interpreted as removal experiments, as was the only study where manipulation included addition of refugia for prey rather than the direct manipulation of predator numbers. In cases where predator density was enhanced we reversed the treatment and control, so that "predator manipulation effect" always refers to the response of prey to reduced predator density. Prey were considered to be limited by predation if their population size or reproductive success increased after predator manipulation.

Statistical analyses of predator manipulation effects

All statistical tests were performed using SAS statistical software (SAS Institute 2008) and the level of statistical significance was set at 0.05. For univariate tests and Pearson correlations we had to omit some experiments to reach the assumption of normality, as the

effect size $\ln(X_e/X_c)$ in these experiments (Greenwood et al. 1990, Towns 1991, Banks et al. 2000, Kinnear et al. 2002: Appendix A, cases 1, 2a, 2b, 4 and 5) ranged from 2.50 to 3.38 compared to the mean of 0.53 (range −0.91–2.29) in the other experiments. This made the tests considerably more conservative for finding an effect. We also performed a repeated-measures analysis with $\ln(X_e/X_c)$ as a response variable to study the impacts of prey cyclicity (cyclic or non-cyclic) and phase of prey population dynamics (peak and low for cyclic prey, early and late for non-cyclic prey) on predator manipulation effects (procedure MIXED in SAS).

A generalized linear model with a gamma distribution of the response and a log link function was built to explore the most important factors influencing the ratio X_e/X_c of predator manipulation experiments (procedure GENMOD in SAS; note that here the response values are simple ratio X_e/X_c values and scaling to natural logarithm is achieved using the log link function). The global model included the following classifying variables: number of predator species removed (one or more, OM), cyclicity of prey (cyclic or non-cyclic, C), predator origin (introduced or native, PO), predator type (bird, mammal, or both, Ptype), efficiency of the experiment (high or low, E), manipulation type (open or exclosure, Mtype), replication of the experiment (replicated or unreplicated, RU) and response type (population size or reproduction, Rtype). The three continuous variables in the model were predator : prey mass ratio (Pm), area of the manipulation (Marea), and duration of the manipulation (Mtime). All second-order interactions of these variables were first tested individually in a model with only main effects, and those with a P value < 0.10 were included in the model selection process. However, some interactions had to be omitted because they produced zero or near-zero cells (OM × Ptype, OM × Mtype, C × PO, C × E, C × Rtype, PO × Ptype, PO × E, PO × Mtype, E × Mtype, Ptype × E, Ptype × Mtype, Ptype × Rtype, Mtype × Rtype). We used backward elimination of nonsignificant factors ($P > 0.05$) to find the best model, starting from a global model including factors OM, C, PO, Ptype, E, Mtype, RU, Rtype, Pm, Marea, Mtime, Pm × OM, Mtime × C, Pm × PO, Pm × Ptype, Pm × Mtype, RU × Pm, Rtype × Mtime, OM × PO, OM × Rtype, C × Mype, PO × Rtype, RU × Rtype. We also calculated the associated AIC_c values, AIC_c differences (Δ_i), and Akaike weights (w_i) for each step. The number of experiments included in the models was 89, since many studies had missing values for one or more of the variables. To account for the possible confounding effects of introduced predators and prey (Salo et al. 2007), the model selection procedure was repeated for experiments including only native species ($n = 60$), starting with a global model including variables OM, C, Ptype, E, Mtype, RU, Rtype, Pm, Marea, Mtime, Marea × OM, Pm × C, C × Mtime, Mtype × Mtime, OM × RU.

Publication bias

We calculated Hedges' d for the 61 replicated experiments to examine the possibility of publication bias (Rosenthal 1979) using the normal quantile plot method (Wang and Bushman 1998; Appendix B: Fig. B1) in MetaWin 2.1 (Rosenberg et al. 2000). For Hedges' d we extracted the sample sizes, mean responses of control and treatment samples at the end of the experiment, and their standard deviations/standard errors/confidence limits from the articles. If error bars were not symmetrical about means, variances were calculated conservatively using the longest bars provided and, if no variances were given, these were calculated from raw results. As the normal quantile plot method was not possible for the unreplicated studies, we also used the funnel plot method by plotting the sample size of all the experiments against their effect size $\ln(X_e/X_c)$ (Appendix B: Fig. B2). No evidence of publication bias was found with either of these methods.

RESULTS

Description of the study systems and overall predation impact

Vertebrate predator manipulations were dominated by experiments on mammalian prey (55% of 116 experiments) compared to 39% on bird prey (Table A1). Predation impacts on small rodents were examined in 30% of experiments, ungulate prey was studied in 10%, hares and rabbits in 4%, and marsupials in 7%. Waterfowl (ducks, geese, swans; 13%) and grouse (9%) were the most frequently studied bird prey groups, while a variety of other birds (seabirds, passerines, waders, parrot) represented 15% of experimental prey. Reptiles and amphibians were studied in a further 4% of experimental setups, and in 7% the responses of several of the aforementioned groups were evaluated during the same experiment.

Predators manipulated in the experiments were mostly mammals (69% of 115 experiments; one study did not specify which predator species were manipulated), followed by experiments where both avian and mammalian predators were manipulated (21%). Avian predators were targeted in only 9% of the experiments. Medium-sized carnivores (e.g., red fox, raccoon, American mink) were manipulated in 41% of 80 experiments on mammalian predators, whereas large carnivores (e.g., wolf, lynx, coyote) were targeted in 15%, small mustelids in 8% and other predatory mammals (e.g., rat, hedgehog, red squirrel) in 10% of experiments.

Overall, predator manipulation experiments resulted in highly significant positive effects on prey, with prey populations increasing 1.7-fold after predator manipulation (Student's t test, mean $\ln(X_e/X_c) \pm 95\%$ confidence limit $= 0.53 \pm 0.12$, $t = 9.01$, df $= 107$, $P < 0.0001$, $n = 108$). This result also held when introduced predators were excluded from the analysis (mean $\ln(X_e/X_c) \pm 95\%$ confidence limit $= 0.50 \pm 0.13$,

TABLE 1. Means, 95% confidence limits (CL), and P values for the effect of different variables on the effect size in the predator manipulation experiments reviewed.

Variable and levels	All predators ($n = 108$)							Native predators ($n = 75$)						
	n	Mean	CL low	CL high	t	df	P	n	Mean	CL low	CL high	t	df	P
Efficiency of manipulation														
High	75	0.63	0.48	0.78	2.96	42.1†	0.005	50	0.57	0.38	0.76	2.03	54.6†	0.048
Low	19	0.26	0.06	0.47				15	0.33	0.17	0.49			
Replication														
Replicated	59	0.60	0.44	0.76	1.35	106	0.18	43	0.50	0.33	0.67	0.01	73	0.99
Unreplicated	49	0.44	0.28	0.61				32	0.50	0.27	0.72			
Response														
Reproduction	28	0.62	0.38	0.87	−0.96	106	0.34	19	0.68	0.42	0.93	−1.54	73	0.13
Population size	80	0.50	0.36	0.63				56	0.44	0.28	0.60			
Main prey														
Yes	27	0.43	0.19	0.66	0.66	77	0.51	22	0.42	0.18	0.65	0.34	52	0.73
No	52	0.53	0.35	0.71				32	0.47	0.25	0.69			
Main predator														
Yes	82	0.56	0.43	0.69	−1.27	85	0.21	60	0.52	0.37	0.66	−1.42	62	0.16
No	5	0.20	−0.73	1.14				4	0.10	−1.21	1.41			
Predator type														
Bird	10	0.36	−0.05	0.77	−0.90	80	0.37	10	0.36	−0.05	0.77	−0.67	48	0.51
Mammal	72	0.55	0.40	0.71				40	0.51	0.30	0.71			
Manipulation type														
Open	82	0.51	0.40	0.63	−0.49	28.4†	0.63	53	0.52	0.38	0.65	−0.77	27.3†	0.45
Exclosure	23	0.43	0.11	0.76				21	0.38	0.05	0.72			
Number of predators														
One	39	0.63	0.41	0.85	−1.30	106	0.20	19	0.46	0.17	0.76	0.31	73	0.75
More	69	0.47	0.34	0.61				56	0.51	0.36	0.67			

Note: We defined our effect size as $\ln(X_e/X_c)$ where X_e and X_c are the mean treatment and control prey responses, respectively. Student's t tests were run separately for experiments with both introduced and native predators and with native predators only.

† Satterthwaite degrees of freedom were used in these cases, where variances were found to be unequal.

$t = 7.41$, df $= 74$, $P < 0.0001$, $n = 75$). Studies in which authors concluded that there was an effect of predator control had a significantly higher effect size than studies concluding that there was no effect (Student's t test, "yes" mean $= 0.76 \pm 0.13$, $n = 68$, "no" mean $= -0.05 \pm 0.19$, $n = 21$; $t = -6.18$, df $= 87$, $P < 0.0001$).

Across the entire data set, manipulations that clearly had an effect on predator densities (i.e., high efficiency) produced higher effect sizes than manipulations deemed to be low efficiency, and this result remained significant also when only native predators were considered (Table 1). There were no evident differences in effect size between replicated and unreplicated experiments, between population size effects and reproductive responses, between main and alternative prey, main and secondary predators, between different manipulation types or the number and type of predator species manipulated (Table 1). However, experiments manipulating only birds of prey or predators not considered as the main source of prey mortality had no apparent impact on prey populations (Table 1). There were no obvious correlations between effect size and predator : prey mass ratio, spatial or temporal scale of the experiments (Pearson correlation, r values ranged from −0.05 to 0.10, with associated P values

ranging from 0.32 to 0.71). Overall, experiments lasted from 2 months to 15 years (median $= 36$ months), while the spatial scale of the experiments ranged from 0.13 ha to 20 000 km^2 (overall median $= 2.5$ km^2; predator exclosures median $= 2$ ha, open areas median $= 5.3$ km^2).

Replication of experiments was more common in the case of rodent and bird prey compared with larger mammalian prey (chi-squared test, $\chi^2 = 10.35$, $P = 0.006$, $n = 108$): numbers of replicated vs. unreplicated experiments were 24 vs. 14 for rodents, 26 vs. 19 for birds, and 6 vs. 19 for larger mammals. The same was true for predators, where only one out of 11 manipulations of large carnivores was replicated. Overall, experiments manipulating both avian and mammalian predators were replicated more often than manipulations of only mammalian or avian predators: numbers of replicated vs. unreplicated experiments were 18 vs. 6 for both predator types, 31 vs. 42 for mammalian predators, and 5 vs. 4 for avian predators (Fisher's exact test, $\chi^2 = 7.73$, $P = 0.018$, $n = 106$).

Model selection of experimental variables

The backward elimination procedure retained the following main variables: number of predators manip-

TABLE 2. Effects of different explanatory variables on effect size in a total of 89 predator manipulation studies.

Model	k	$\log(L)$	AIC_c	Δ_i	w_i
OM, C, PO, E, RU, Rtype, Pm, Mtime, Pm × OM, Mtime × C, Rtype × Mtime, OM × PO, PO × Rtype, RU × Rtype	16	−150.16	339.88	0	0.87
OM, C, PO, Ptype, E, RU, Rtype, Pm, Mtime, Pm × OM, Mtime × C, Rtype × Mtime, OM × PO, PO × Rtype, RU × Rtype	17	−149.28	344.33	4.45	0.09
OM, C, PO, Ptype, E, RU, Rtype, Pm, Mtime, Pw × OM, Mtime × C, Pm × Ptype, Rtype × Mtime, OM × PO, PO × Rtype, RU × Rtype	18	−147.32	346.99	7.11	0.02
OM, C, PO, Ptype, E, RU, Rtype, Pm, Mtime, Pm × OM, Mtime × C, Pm × Ptype, RU × Pm, Rtype × Mtime, OM × PO, PO × Rtype, RU × Rtype	19	−146.28	348.35	8.47	0.01
OM, C, PO, Ptype, E, Mtype, RU, Rtype, Pm, Mtime, Pm × OM, Mtime × C, Pm × Ptype, RU × Pm, Rtype × Mtime, OM × PO, PO × Rtype, RU × Rtype	20	−146.11	351.56	11.68	0.00
OM, C, PO, Ptype, E, Mtype, RU, Rtype, Pm, Marea, Mtime, Pm × OM, Mtime × C, Pm × Ptype, RU × Pm, Rtype × Mtime, OM × PO, PO × Rtype, RU × Rtype	21	−145.37	353.72	13.84	0.00
OM, C, PO, Ptype, E, Mtype, RU, Rtype, Pm, Marea, Mtime, Pm × OM, Mtime × C, Pm × Ptype, RU × Pm, Rtype × Mtime, OM × PO, C × Mtype, PO × Rtype, U × Rtype	22	−144.78	356.31	16.43	0.00
OM, C, PO, Ptype, E, Mtype, RU, Rtype, Pm, Marea, Mtime, Pm × OM, Mtime × C, Pm × Ptype, RU × Pm, Rtype × Mtime, OM × PO, OM × Rtype, C × Mtype, PO × Rtype, RU × Rtype	23	−144.38	359.40	19.52	0.00
OM, C, PO, Ptype, E, Mtype, RU, Rtype, Pm, Marea, Mtime, Pm × OM, Mtime × C, Pm × PO, Pm × Ptype, RU × Pm, Rtype × Mtime, OM × PO, OM × Rtype, C × Mtype, PO × Rtype, RU × Rtype	24	−144.30	363.24	23.36	0.00
OM, C, PO, Ptype, E, Mtype, RU, Rtype, Pm, Marea, Mtime, Pm × OM, Mtime × C, Pm × PO, Pm × Ptype, Pm × Mtype, RU × Pm, Rtype × Mtime, OM × PO, OM × Rtype, C × Mtype, PO × Rtype, RU × Rtype	25	−144.12	367.03	27.15	0.00

Notes: The table shows a succession of models where nonsignificant variables have been removed in a backward elimination process (Model). In addition, the number of parameters in each model (k), log-likelihood value ($\log[L]$), corrected Akaike's information criterion value (AIC_c), AIC difference (Δ_i), and Akaike weights (w_i) are shown. The main variables in the models are: number of predator species removed (one or more, OM), cyclicity of prey (cyclic or non-cyclic, C), predator origin (introduced or native, PO), predator type (bird, mammal, or both, Ptype), efficiency of the experiment (high or low, E), experimental manipulation type (open or exclosure, Mtype), replication of the experiment (replicated or unreplicated, RU), response type of prey species (population size or reproduction, Rtype), predator : prey mass ratio (Pm), area of the manipulation (Marea), and duration of the experiment (Mtime).

ulated (OM, $\chi^2 = 12.93$, $P = 0.0003$), cyclicity of prey (C, $\chi^2 = 0.80$, $P = 0.37$), predator origin (PO, $\chi^2 = 0.01$, $P = 0.93$), efficiency (E, $\chi^2 = 4.62$, $P = 0.03$), replication (RU, $\chi^2 = 6.67$, $P = 0.010$), response type (Rtype, $\chi^2 = 6.96$, $P = 0.008$), predator : prey mass ratio (Pm, $\chi^2 = 8.33$, $P = 0.004$), and duration of the experiment (Mtime, $\chi^2 = 2.48$, $P = 0.12$), together with the following interactions: Pm × OM ($\chi^2 = 10.65$, $P = 0.001$), Mtime × C ($\chi^2 = 5.11$, $P = 0.024$), Mtime × Rtype ($\chi^2 = 8.42$, $P = 0.004$), OM × PO ($\chi^2 = 8.87$, $P = 0.003$), PO × Rtype ($\chi^2 = 5.66$, $P = 0.017$), and RU × Rtype ($\chi^2 = 8.18$, $P = 0.004$; Table 2). The interaction between duration of the experiment and prey cyclicity showed an increase in effect size for non-cyclic species with time, whereas there was a slight decrease in effect size for cyclic species (Fig. 1A). The interaction between prey response type and duration of the experiment showed a rapidly increasing effect size for reproductive responses with time, while the increase for population size responses was more moderate (Fig. 1B). The interaction between predator : prey mass ratio and number of predators manipulated showed a decreasing effect size with increasing mass ratio for those experiments where only one predator species had been manipulated; experiments where several species were manipulated showed practically no change in effect size with increasing mass ratio (Fig. 1C).

High efficiency predator manipulations showed effect sizes 2.4-fold higher than those deemed to be low efficiency; low efficiency predator removals had no obvious positive impact on prey as their confidence limit overlaps zero (Fig. 2A). The interaction between predator origin and number of manipulated predator species showed different responses for alien and native predator manipulations: manipulating only one alien predator species had a large positive impact on prey populations whereas experiments where several alien predator species were manipulated showed no impact at all (Fig. 2B). The opposite was true for native predators: studies manipulating only one predator species showed no clear positive impact on prey (mean effect size 0.39 but confidence limit overlaps zero) while manipulating several native predator species simultaneously resulted in a distinct positive impact (Fig. 2B). The interaction between predator origin and prey response type showed a 2.5-fold greater effect size for reproductive responses over population size responses when native predators were manipulated, whereas the opposite was true for alien predators (Fig. 2C). Finally, the interaction between level of experimental replication and prey response type revealed that both replicated and unreplicated experiments reached similar effect sizes for population size responses (Fig. 2D). Replicated experiments on reproductive prey responses yielded at least 1.9-fold greater effect size compared to population size responses, while unreplicated experiments recording reproductive responses showed no positive impacts on prey (Fig. 2D).
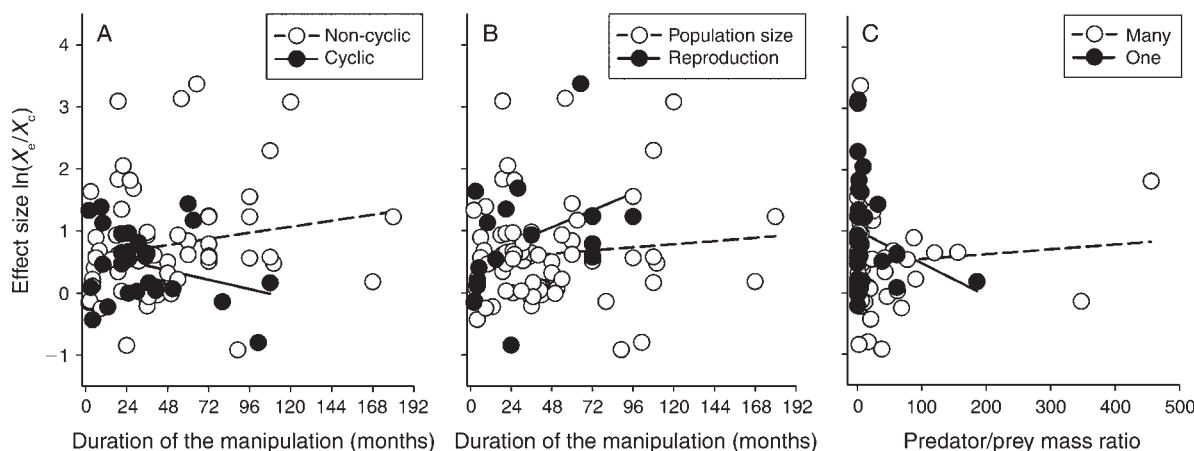
FIG. 1. Trends in effect sizes $\ln(X_e/X_c)$ of significant interactions from a generalized linear model explaining prey responses to predator manipulation, showing the relationship between (A) duration of the manipulation and cyclicity of prey (cyclic prey, $n = 27$; non-cyclic prey, $n = 62$); (B) duration of the manipulation and prey response type (population size, $n = 73$; reproduction, $n = 16$); and (C) predator : prey mass ratio and the number of predator species manipulated (only one predator species manipulated, $n = 35$; several predator species manipulated, $n = 54$) The variables X_e and X_c are the mean treatment and control prey responses, respectively. Figures are drawn from raw data.

Repeating the backward elimination process using experiments with only native species ($n = 60$) yielded a model with the following variables: number of predators manipulated (OM, $\chi^2 = 0.09$, $P = 0.76$), prey cyclicity (C, $\chi^2 = 1.13$, $P = 0.29$), predator manipulation efficiency (E, $\chi^2 = 6.83$, $P = 0.009$), replication of the experiment (RU, $\chi^2 = 1.35$, $P = 0.25$), duration of the manipulation (Mtime, $\chi^2 = 3.86$, $P = 0.049$), and the interactions Mtime × C ($\chi^2 = 8.72$, $P = 0.003$) and OM × RU ($\chi^2 = 11.98$, $P = 0.0005$; Table 3). As in the overall model, the impacts of high-efficiency experiments were on average

2.7-fold higher compared to experiments deemed to be low efficiency; low efficiency predator removals had no obvious positive impact on prey (Fig. 3A). Manipulating several predator species either in a replicated or unreplicated design yielded clear positive impacts on prey (Fig. 3B). However, manipulating only one predator species in a replicated design produced at least 1.4-fold greater effects compared to manipulating many predators, while unreplicated single-predator experiments showed no obvious impacts on prey populations (Fig. 3B). Similar to the overall model, the interaction
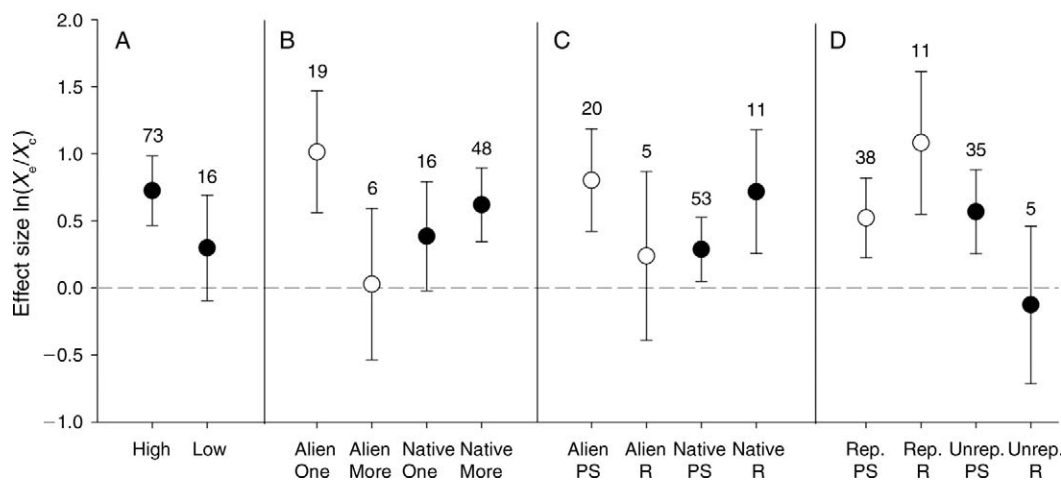

FIG. 2. Effect size $\ln(X_e/X_c)$ and 95% confidence limits of categorical variables in the generalized linear model explaining prey responses to predator manipulation. (A) Effect of predator manipulation efficiency (high or low). (B) Interaction between predator origin (alien or native) and number of predator species manipulated (one or more). (C) Interaction between predator origin (alien or native) and type of measured prey response (PS, population size; R, reproduction). (D) Interaction between replication of the experiment (Rep., replicated; Unrep., unreplicated) and type of measured prey response (PS, population size; R, reproduction). The number of studies is shown above bars (total $n = 89$). Effect size ≤ 0 means that prey species did not benefit from predator manipulation.

TABLE 3. Effects of different explanatory variables on effect size in a total of 60 predator manipulation studies, where only native species were included.

Model	k	log (L)	AIC$_c$	Δ_i	w_i
OM, C, E, RU, Mtime, C × Mtime, OM × RU	9	−74.86	171.31	0	0.40
OM, C, E, RU, Pm, Mtime, C × Mtime, OM × RU	10	−73.84	172.17	0.86	0.26
OM, C, E, RU, Pm, Mtime, Pm × C, C × Mtime, OM × RU	11	−72.40	172.29	0.98	0.24
OM, C, Ptype, E, RU, Pm, Mtime, Pm × C, C × Mtime, OM × RU	12	−70.44	174.80	3.49	0.07
OM, C, Ptype, E, RU, Pm, Marea, Mtime, Pm × C, C × Mtime, OM × RU	13	−69.78	176.90	5.59	0.02
OM, C, Ptype, E, Mtype, RU, Pm, Marea, Mtime, Pm × C, C × Mtime, OM × RU	14	−69.19	179.28	7.97	0.01
OM, C, Ptype, E, Mtype, RU, Pm, Marea, Mtime, Pm × C, C × Mtime, Mtype × Mtime, OM × RU	15	−68.72	182.08	10.77	0.00
OM, C, Ptype, E, Mtype, RU, Rtype, Pm, Marea, Mtime, Pm × C, C × Mtime, Mtype × Mtime, OM × RU	16	−68.44	185.45	14.14	0.00
OM, C, Ptype, E, Mtype, RU, Rtype, Pm, Marea, Mtime, Marea × OM, Pm × C, C × Mtime, Mtype × Mtime, OM × RU	17	−68.42	189.52	18.21	0.00

Notes: The table shows a succession of models where nonsignificant variables have been removed in a backward elimination process (Model). In addition, the number of parameters in each model (k), log-likelihood value (log[L]), corrected Akaike's information criterion value (AIC$_c$), AIC difference (Δ_i), and Akaike weights (w_i) are shown.

between prey cyclicity and experiment duration showed a decrease in effect size for cyclic species with time, and a slight increase in effect size for non-cyclic prey (Fig. 3C).

Prey cyclicity and prey population stability

The repeated-measures model on the effects of predator manipulation on cyclic and non-cyclic prey showed a significant interaction between prey cyclicity and phase of prey population dynamics ($F_{1,45} = 11.343$, $P = 0.002$, $n = 47$; Fig. 4). In non-cyclic species the predator manipulation had a significant positive effect on prey already at the beginning (early phase) of the experiment. In the case of cyclic prey, predator manipulation had a large positive effect on prey populations at low prey densities whereas no effect was observed in high prey densities.

Overall, control populations were just as stable as experimental populations, when stability was measured using coefficients of variation (signed rank test, mean difference CVcontrol – CVexperiment = 3.87 ± 33.5 [mean ± SD], $S = 86.5$, $P = 0.28$, $n = 42$). There was a marginally significant tendency for the CVs. of non-cyclic prey populations to be larger in control than in experimental areas (mean difference CVcontrol – CVexperiment = 11.2 ± 33.2, $S = 50$, $P = 0.06$, $n = 20$), while there was no obvious difference in the CVs. of cyclic prey populations (mean difference CVcontrol – CVexperiment = −2.79 ± 33.1, $S = −5.5$, $P = 0.86$, $n = 22$).

DISCUSSION

Overall response of prey populations

Our analysis shows that manipulations of predator densities produced a positive and significant 1.7-fold overall effect on prey populations, meaning that most vertebrate predators appear to limit populations of their
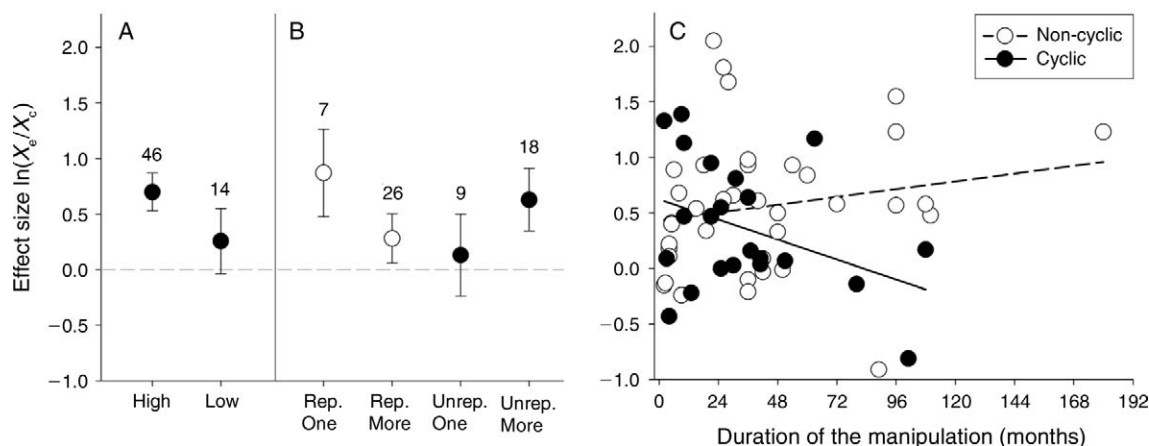

FIG. 3. Effect sizes ln(X_e/X_c) from a generalized linear model explaining prey responses to predator manipulation, when only native predators were manipulated ($n = 60$). (A) Effect size and 95% confidence limits of the effect of predator manipulation efficiency (high or low). (B) Effect size and confidence limits for the interaction between number of predator species manipulated (one or more) and replication of the experiment (Rep., replicated; Unrep., unreplicated). The number of studies is shown above bars. Effect size ≤ 0 means that prey species did not benefit from predator manipulation. (C) Effect of the duration of the manipulation and cyclicity of prey (cyclic prey, $n = 22$; non-cyclic prey, $n = 38$), based on raw data.

prey. We have earlier demonstrated that introduced predators suppress prey populations more than do native predators (Salo et al. 2007), but our results here confirm that the positive impact of predator manipulation on prey remains even when introduced predators are removed from the data set. Our worldwide meta-analysis thus supports the conclusions of recent work on vertebrates in the UK that predator removal induces a 1.6-fold increase in prey populations (Holt et al. 2008). Earlier reviews reported a 75% increase in hatching success in birds following predator removal but no effect on breeding population size (Côté and Sutherland 1997), and clear effects of predation in 21 of 33 predator manipulations on small mammals (Sundell 2006). These studies suggest a surge of interest in vertebrate predator studies since the review of Sih et al. (1985), which concentrated on the effects of predation and competition, but did not include studies of vertebrates preying on other vertebrates. In the meta-analysis by Gurevitch et al. (2000) on interactions between competition and predation, anurans were the only vertebrates included.

While our review indicates that predators usually limit their prey, one in six experiments (16.4%, 19 of 116) did not show a predator manipulation effect (i.e., effect size was ≤0; Appendix A). Lack of effect may be related to the experimental setup or to specific environmental circumstances. For example, an experiment may produce no impact if predator numbers do not change substantially in response to manipulation, or if the experiment is too short in duration. Predator species may compensate for mortality, especially if predator removal allows the release of mesopredators that in turn suppress the prey species (Courchamp et al. 1999, Glen and Dickman 2005). There may be other sources of mortality that compensate for predator removal (i.e., the doomed surplus sensu Errington 1956 might occur in some circumstances); prey may not increase after predator removal if they represent alternative prey for the predator (Norrdahl and Korpimäki 2000), or if the predator preys on a major competitor of the studied prey (Abrams 1992). Prey may also escape predator limitation during an outbreak caused, for example, by sudden increases in resources (Letnic and Dickman 2010); predator manipulation in these circumstances will have no effect because prey population growth is regulated by food. These observations suggest that, while predator limitation may be general, more focus is needed on cases where limitation does not seem to occur. Indeed, the possibility that researchers have pursued experimental studies in systems where a strong role for predators was already suspected, may be a subtle source of bias in this and other reviews.

Experimental design and the efficiency of predator manipulation

Predator manipulation efficiency emerged as an important factor in all our analyses: manipulations deemed to be highly efficient had a strongly positive
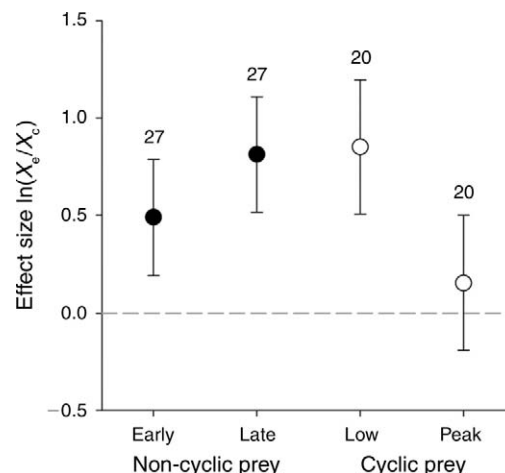

FIG. 4. Effect size $\ln(X_e/X_c)$ and 95% confidence limits from a mixed model, showing the interaction between prey species cyclicity (cyclic or non-cyclic) and phase of prey population dynamics (early and late phase of experiment for non-cyclic prey; low and peak phase for cyclic prey) in predator manipulation experiments. The number of experiments included is shown above bars (total $n = 47$). Effect size ≤ 0 means that prey species did not benefit from predator manipulation.

impact on prey populations whereas those of low efficiency had no apparent impact (effect size 0.71 vs. 0.28; Figs. 2A and 3A). Nineteen experiments were classified as low efficiency while 18 could not be classified at all. The existence of low-efficiency experiments indicates that manipulating and monitoring populations of mobile vertebrate predators is very difficult. On the other hand, there were also large differences between studies in recording manipulation impacts on predator populations: some provided no data or even comments about the success of manipulations, while others used continuous monitoring, quantitative methods and statistical evaluation to confirm changes in predator densities between control and experimental populations. The importance of quantifying the effectiveness of predator manipulations is being recognized increasingly as a crucial component of the experimental design (Kinnear et al. 2010).

The majority of experiments deemed "low efficiency" were conducted in open areas (17 of 19), as were most experiments where efficiency could not be determined. Open-area predator removals usually suffer from immigration of predators from neighboring areas (Norrdahl and Korpimäki 1995, Korpimäki et al. 2002), especially when predators aggregate in areas of high prey density ("pantry effect"; Ford and Pitelka 1984). In order to succeed, such experiments usually need to remove predators continuously: Holt et al. (2008) found that field experiments using game keepers yielded stronger positive effects on prey than those not using game keepers. However, traditional methods of open-area predator removal, like trapping and shooting, are laborious and expensive, while poison baiting is

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effective but illegal in many countries because of ethical concerns or effects on non-target species (Glen et al. 2007). Increasing predator densities via experimental introduction is even less popular as predators usually emigrate swiftly or, if captive-born and raised, experience high mortality because of poor hunting skills and naivety towards other predators (Sundell 2003, Hellstedt and Kallio 2005). Despite these challenges, 77% of open-area experiments (56 of 73) achieved "high" efficiency.

Exclosure experiments could be expected to reach higher manipulation efficiency more often than open-area experiments: indeed, nearly all (91%) exclosure experiments achieved "high" efficiency. However, building and maintaining predator-proof fences with roofs is both expensive and laborious. An example of an heroic effort is provided by Krebs et al. (2001), who built two 1 km^2 mammalian-predator-proof exclosures in boreal forest and maintained the fences and their corresponding control areas for 10 years, even under harsh winter conditions. In addition, exclosure experiments may be confounded by the "fence effect" whereby enclosed prey populations reach high densities when emigration is prevented (Krebs et al. 1969, Ostfeld 1994). We could not test this idea, as there were only four exclosure experiments out of 24 where prey dispersal was not allowed; many experiments used "dispersal sinks" to prevent the fence effect (e.g., Klemola et al. 2000).

In general, experiments should run for at least one generation for a prey population size response to be detectable. This is a demanding requirement for slowly maturing, long-lived vertebrate species, which often are also of greatest conservation and management concern. We observed no overall temporal trend in effect size but found an interaction between prey cyclicity and experiment duration: effect sizes for non-cyclic prey species increased with time, while the opposite was true for cyclic prey. Our results for non-cyclic species accord with those of Holt et al. (2008), who found that "temporal" studies in Britain reported stronger effects with a mean study duration of 5 years compared to "spatial" studies lasting on average 1.67 years. Cyclic small mammals may suffer from crowding effects faster than non-cyclic prey after being released from predation pressure, because they typically have high intrinsic rates of increase (Hennemann 1983). Thus bottom-up effects such as food limitation could explain the negative trend in effect size exhibited by cyclic prey species with manipulation duration.

We observed no obvious positive relationship of effect size with the spatial scale of the experiment. This implies that most experiments are performed at an adequate spatial scale which should cover many home ranges of the manipulated predator species, not just the ranges of its prey (Korpimäki et al. 2002, 2005). Too small a scale, for example in exclosures, may result in over-dense prey populations, which then suffer from intense intraspecific competition (Koivisto et al. 2007, 2008), obscuring the positive effects of predator exclusion. Also, even one predator in an experiment at too small a scale may cause unnaturally high predation pressure.

The importance of replication

While both replicated and unreplicated experiments showed similar positive impacts on prey population size responses (Fig. 2D), unreplicated predator manipulations had on average no effect on prey reproduction (Fig. 2D), and the same was true for unreplicated experiments manipulating only one predator species (Fig. 3B). These observations most likely reflect the higher risk of "nondemonic intrusion" (Hurlbert 1984); that is, unreplicated experiments are more vulnerable to chance effects, which may defeat the objectives of the study. Despite the obvious advantages of replication, the difficulties of manipulating vertebrate predators and prey at large scales and/or over long periods often render replicated designs unfeasible. For example, 76% of studies on larger mammal prey were unreplicated compared to 37% on rodents and 42% on avian prey, and 58% of all experiments manipulating mammalian predators.

Replication in open areas also appears more common than in exclosure experiments (47 vs. 13 experiments, respectively; Appendix A: Table A1), perhaps reflecting the capital cost and effort of maintaining exclosures. In addition, some experimental setups like "natural experiments" usually leave no opportunity for replication. For example, Jarnemo and Liberg (2005) utilized a nationwide decline of red fox (*Vulpes vulpes*) populations due to a sarcoptic mange epidemic to study changes in the survival of roe deer (*Capreolus capreolus*) fawns in Sweden over 14 years. Replication may also be impossible in cases involving rare or endangered species; indeed many of the unreplicated studies in our data set come from species that are threatened by introduced predators (e.g., Robertson et al. 1994, Dilks 1999, Innes et al. 1999, Cuthbert 2002, Kinnear et al. 2002). As replication especially in large-scale environmental gradients is nearly impossible, it may be that in many cases the spatial and temporal scales of experiments are more important than replication (Oksanen 2001).

Different types of manipulated predators

We included the origin of the predator species in the analyses as we have shown earlier that introduced predators suppress prey populations more than do native predators (Salo et al. 2007). This was reconfirmed here, especially in the interaction between predator origin and number of predators manipulated: the removal of one alien predator had a positive impact of the same magnitude on prey as the removal of several native predators (Fig. 2B). This result appears to stem from many removals of one particularly destructive introduced species, the red fox (Kinnear et al. 2002, Saunders et al. 2010). Curiously, however, manipulating several alien predators at the same time appeared to have no impact on prey (Fig. 2B). One possible

explanation for this result is small sample size, as only six studies have manipulated several alien species simultaneously. Alien invasive species are becoming an increasingly important issue worldwide, with research focusing, in particular, on the impacts and control of invasive predators. However, many aspects of the ecology and impacts of abundant native predators are also still unknown and should not be overlooked (Glen and Dickman 2005, 2008, Korpimäki et al. 2005, Holt et al. 2008).

Removal of several predator species could be expected to impact more positively on prey than removing just one, because mortality caused by the removed predator may be compensated by mortality caused by other predators still present (Norrdahl and Korpimäki 1995). Indeed, manipulations of one native predator species had no detectable impact on prey (mean 0.39 but confidence limit overlaps zero), whereas manipulating several native predators clearly had a positive effect (mean 0.62; Fig. 2B). In some cases multiple predators have been shown to cause risk enhancement because of conflicting predator-specific prey defenses (Sih et al. 1998): when multiple predators have different hunting modes, a functioning antipredator response against one predator may put prey at greater risk of being preyed upon by another. However, the impacts of multiple predators are usually not additive because of compensatory prey defenses and predator interference (Sih et al. 1998, Schmitz 2007). For example, intraguild predation may have positive impacts on prey whereas removing top predators may actually increase predation pressure via mesopredator release (sensu Courchamp et al. 1999; Korpimäki and Norrdahl 1989, Polis and Holt 1992, Henke and Bryant 1999, Sergio et al. 2006, Vance-Chalcraft et al. 2007, Salo et al. 2008, Sergio and Hiraldo 2008, Letnic et al. 2009). Because of these complex interactions within the predator trophic level, the role of large top predators as keystone species in ecosystems should be carefully assessed (Sergio et al. 2008, Dickman et al. 2009), especially if the areas over which species are removed are large (Letnic et al. 2009).

There was an apparent imbalance in our data set towards mammalian predator impacts: reptiles were manipulated in only one and birds of prey in 10 experiments compared to 80 experiments manipulating mammalian predators. Overall, ectothermic vertebrates have received a lot less attention in ecological studies although there are over twice as many ectothermic species compared to endothermic ones (Shine and Bonnet 2000, Bonnet et al. 2002). Raptor experiments suffer from difficulties in manipulating predator densities; besides exclosures, the most efficient methods (shooting and trapping) are illegal in most countries. One successful method has been the removal of nest sites (e.g., nest-boxes, natural cavities, and stick nests) of tree-nesting species (Norrdahl and Korpimäki 1995), but this leaves manipulation areas accessible for breeding ground-nesting birds of prey and hunting of non-

breeding individuals. On the other hand, perch-hunting birds of prey may be attracted to manipulation areas by provision of artificial perches (Kay et al. 1994, Widén 1994). There also appears to be a common belief that mammalian predators are more detrimental to populations of small game species (grouse, waterfowl) than are birds of prey because mammalian predators are better able to find and destroy eggs and broods with hens; this has probably reduced the impetus to plan experiments for birds of prey. Holt et al. (2008) showed that avian predators indeed seem to have less impact on prey than mammalian predators, and our results confirm this: mammalian predator manipulations had a positive impact on prey while there was no obvious impact of manipulating birds of prey (mean effect size 0.36 but confidence limit overlaps zero; Table 1). Other studies have shown further that removal of avian predators can be compensated easily by mammalian predators (Parker 1984, Norrdahl and Korpimäki 1995, Korpimäki and Norrdahl 1998).

We found no difference in the impacts of predators on main vs. alternative prey, but manipulations of predators that had been identified as the main source of mortality of the studied prey species had a clearly positive effect on prey populations (Table 1). In many studies, especially early ones, little was mentioned about the predator-prey relationships of the species involved, with no indication given of whether the studied prey species constituted main or alternative prey for the predator, or which of the manipulated predators was the main cause of mortality for the prey species in question. Thus our classification of main and alternative prey and predators often had to be based on sources other than the original paper itself, and should be treated with caution, as predator–prey relationships will often be ecosystem dependent. The test for main and alternative predators also suffered from imbalance, as our analysis included only five studies where the predator manipulated was not deemed to be the main source of mortality of the studied prey species. As 60% of experiments (in 70 of 116 experiments) manipulated more than one predator, this set of predators usually included also the main predator of prey. Overall, the data indicate serious gaps in our knowledge of predator-prey relationships. This also poses a challenge for experimental designs, since recording prey survival and assigning causes of death is notoriously difficult even when closely tracking prey individuals such as by radio-telemetry.

Reproductive and population dynamic responses

We found no overall difference in the magnitude of impact between reproductive and population size measures, but a slight tendency for stronger reproductive than population size responses for native species (Fig. 2C). Our model also implied that experiments measuring prey reproductive responses may reach higher effect sizes more rapidly than those measuring population size responses (Fig. 1B), but this result was affected

by an aberrant effect size in one study on reproductive responses (Greenwood et al. 1990). In addition, while replicated experiments on both response types and unreplicated experiments on population size responses resulted in positive impacts on prey, unreplicated predator manipulations had on average no effect on prey reproduction (Fig. 2D). This may be due to the paucity of such studies (five), or the fact that unreplicated experiments, especially on reproduction, are more vulnerable to stochastic effects such as adverse weather which may mask the impacts of predator manipulation.

Holt et al. (2008) also reported a tendency for larger effects on prey reproduction than on population size while both Newton (1998) and Côté and Sutherland (1997) documented strong positive impacts of predator removals on bird prey productivity. However, it is usually not known to what extent increased reproductive success actually converts into larger population size. For example, raptor predation may decrease nesting success of game birds, but this does not necessarily affect the breeding population size next spring (Valkama et al. 2004). Only a few studies in our data set actually recorded changes in prey survival in predator manipulation experiments (e.g., Reid et al. 1995, Wilson et al. 1999), although this is clearly needed to confirm the direct mechanism of predator impact.

Body sizes of prey and predator

Model selection revealed a strong interaction between predator:prey mass ratio and the number of predators manipulated (Fig. 1C). When only one predator was manipulated, the interaction showed a decrease in effect size with increasing predator:prey mass ratio; manipulating multiple predators revealed no relationship between effect size and predator:prey mass. Several studies have already shown a positive relationship between the body sizes of predators and their prey (e.g., Rosenzweig 1966, Gittleman 1985, Fisher and Dickman 1993), and even between the sizes of predators and their intraguild prey (Korpimäki and Norrdahl 1989, Sergio and Hiraldo 2008). This relationship may arise because of a morphological upper limit to the size of prey that can be handled by the predator (e.g., predators cannot kill prey that are too large; Janes and Barss 1985), or because of differences in habitat use between different-sized predators (e.g., King and Moors 1979, Dickman 1988). Foraging theory suggests that prey size should maximize the net rate of energy intake (Stephens and Krebs 1986), whereby larger predators do not benefit from foraging on small prey (Griffiths 1980).

Our results show that large predators do not have great influence on populations of small-sized prey, probably because the optimum prey size increases with predator mass (Wilson 1975, Fisher and Dickman 1993). A study with a high predator:prey mass ratio most likely involves small-sized prey that are smaller than the optimum prey size for the predator in question. For example, the mass ratio for least weasel (*Mustela nivalis*)

and its most common prey, the field vole (*Microtus agrestis*), is around 2.8, and for Canadian lynx (*Lynx canadensis*) and snowshoe hare (*Lepus americanus*) it is 6.9, but that for Canadian lynx and northern red-backed vole (*Clethrionomys rutilus*) it is 356. Large predators often eat a wider range of prey sizes than smaller predators (Wilson 1975, Gittleman 1985, Korpimäki 1985), taking small prey as alternatives if optimum-sized prey are not available. Manipulating multiple predator species with different optimum prey sizes thus blurs species-specific patterns so no relationship can be observed (Fig. 1C).

Conclusions

Overall, our worldwide meta-analysis on predator density manipulation experiments has shown that vertebrate predators can indeed suppress the population sizes and reproductive success of their prey. However, we also recognized many factors that affected the outcome of manipulation studies; the single most important factor explaining variation between the effect sizes in different experiments was predator manipulation efficiency. The spatial scale of experiments had no obvious effects, but cyclic prey species tended to show decreasing effect sizes with experimental duration, while the opposite was true for non-cyclic prey. Overall, the impacts of predators on cyclic prey were larger in the decline and low phases than in the peak phases of the population cycle. We suggest, finally, that control of introduced vertebrate predators can be used to manage wildlife. However, care should be taken in managing native predators, because control of top predators may cause mesopredator release, and the habitats occupied by apex predators often have high biodiversity value (Sergio et al. 2005, 2006, 2008, Letnic et al. 2009).

Future studies will likely concentrate on the ecological mechanisms driving the varying magnitudes of predator impact on prey, and the nature of compensatory processes that prevent predator limitation. What, then, makes a successful predator manipulation experiment?

1) Before setting up a predator manipulation experiment one should have detailed observational information on the system to be studied, on its most important predators, what they eat, and also on the factors causing prey mortality. On this basis, one should be able to formulate reasonable working hypotheses to be tested in the experiments.

2) One essential precondition of a successful predator manipulation experiment was not fulfilled in many studies: that of establishing and demonstrating that the predator manipulation actually worked effectively. Careful monitoring of predator numbers before and during experiments is the only way to ensure that observed changes in prey populations are caused by changes in predation impacts. In addition, it would be wise to monitor other predators in addition to the one manipulated, as other predators may increase and

compensate for reduced predation pressure from the target species.

3) Planning the experimental design includes solving multiple compromises and realizing their limitations for interpreting the results: experiments usually are a trade-off between spatial and temporal scale and the degree of replication that can be achieved. Our review suggests that the spatio-temporal scale of predator manipulation experiments is usually addressed adequately, in line with a prevailing view among ecologists that the scale of experiments is more important than replication. In addition, unreplicated studies also can yield important results, especially if replication is impossible because of prey rarity, lack of finances or other factors. Sufficient "replication" of predator manipulation experiments can also be achieved by carrying out unreplicated studies in various environments and by analyzing the effect sizes afterwards.

4) In many studies, the impacts of predator manipulations on target species have been measured by estimating various density indices of prey species in treatment and control areas. There is an urgent need in future to validate these index measures, and to use robust methods of density estimation such as Program Mark for capture–recapture data (White and Burnham 1999). While there is growing interest in recent noninvasive sampling techniques for density estimation, such as camera traps (Rowcliffe et al. 2008) and DNA-based sampling (Boulanger et al. 2004, Mondol et al. 2009), there is still a need to also study survival and movements of prey species by using radio-marked or otherwise individually known prey individuals.

5) While the relative impacts of lethal and nonlethal effects of predators could not be teased out with our data set, where both effects were manipulated simultaneously, future studies should pay more attention to nonlethal effects, which may be as strong as the lethal ones (Lima 1998, Werner and Peacor 2003, Preisser et al. 2005). Our review also revealed some largely unstudied predator and prey groups, such as birds as predators and amphibians and reptiles as prey.

6) It has become clear that more large-scale replicated predator manipulation studies are still needed. This offers a challenge to granting agencies, because such laborious experiments need long-term and substantial financing. One way to proceed is for wildlife managers and ecologists to plan and conduct these experiments in collaboration (see, e.g., Nordström et al. 2002, 2003, Holt et al. 2008 for examples), and thus achieve common goals in applied ecology and conservation management.

While our review supports the notion of top-down control, it is likely that both top-down and bottom-up processes alternate depending on both biotic and abiotic factors in the system (Sinclair and Krebs 2002). In addition, recent advances in understanding predator-prey interactions emphasize not only the impacts at population levels but also the behavior of individuals: predators and prey are involved in a foraging game where both sides respond behaviorally to each other and to changes in their environment, and these individual decisions ultimately determine population densities (Lima 2002).

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APPENDIX A

Predator manipulation studies included in the meta-analysis (*Ecological Archives* M080-018-A1).

APPENDIX B

Two methods to examine the possibility of publication bias in our data set (*Ecological Archives* M080-018-A2).