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Predation by mammalian and avian predators is an important cause of mortality in grouse species during all life stages and has been linked to impaired reproductive performance. Some grouse species are important game birds, but many populations are red-listed at the national level. In consequence, predator control is often conducted as a grouse conservation measure, but remains a contentious issue, also because evidence of its effectiveness is lacking. Here, we review the evidence on predation as a limiting factor for grouse populations and perform a quantitative assessment of the effectiveness of predator control to benefit grouse population parameters. We found support that grouse populations appear to be typically limited by their predators. Predator control was associated with an overall positive effect size on grouse population parameters (i.e. mean of 1.43 times the reference value, 95% CI of 1.22–1.68). We found positive effect sizes for most population parameters (reproductive success; adult abundance and survival), but not all (brood size, nest success). Our results suggest that predator control is likely to achieve short-term conservation benefits for grouse if well-designed and rigorously conducted. We suspect, however, that the majority of control programmes conducted for conservation do not meet this standard.

Keywords: capercaillie, limitation, meta-analysis, nest success, ptarmigan, red fox

Early ideas on predation and its influence on prey species were dominated by the view that prey populations are limited by resource constraints with predators utilizing a 'doomed surplus' of prey (Errington 1946, 1956). Currently, the role of predation in shaping prey populations is recognized to be more complex and dynamic (Sinclair and Krebs 2002, Korpimäki et al. 2004, Ripple et al. 2014). Ecological research has uncovered direct and indirect pathways of top–down influences in trophic networks (Ripple et al. 2001, Elmhagen et al. 2010, Terborgh and Estes 2010) and predator removal experiments have demonstrated that predators may limit their prey populations (Marcström et al. 1988, Tapper et al. 1996, Fletcher et al. 2010; reviews: Salo et al. 2010, Smith et al. 2010, Roos et al. 2018). In birds, high losses to predators are common (Newton 1993, Côté and Sutherland 1997). Predation may severely impact populations already limited by other factors (Newton 1998, Sovada et al. 2001), such as fragmented and degraded habitats (Robinson et al. 1995, Crooks and Soulé 1999, Evans 2004), and particularly when a predator is abundant (Kurki et al. 1997, Smith et al. 2010) and/or invasive in the system (Salo et al.

2007, Doherty et al. 2016). In forest birds, reductions in reproductive success and in particular increased nest predation have been associated with fragmented landscapes (Small and Hunter 1988, Kurki et al. 2000, Storch et al. 2005, Baines et al. 2016), which sustain high densities of generalist mesopredators (Kurki et al. 1998, Güthlin et al. 2013, Pasanen-Mortensen and Elmhagen 2015).

Ground nesting birds, such as grouse (*Tetraonidae*), are especially vulnerable to predation of eggs and chicks and show reduced reproductive success at high predator abundance (Kurki et al. 1997, Jahren et al. 2016). Although the majority of grouse species are not globally threatened (IUCN 2017) and some remain important game species, many populations are red-listed at the national level (Storch 2007). The observed declines in grouse populations are likely to have multifactorial causes, including habitat loss and deterioration (Thirgood et al. 2000a, Storch 2007, Aldridge et al. 2008, Sirkiä et al. 2010), climatic change (Selås et al. 2011, Braunisch et al. 2014) and anthropogenic disturbance (Thiel et al. 2008, Coppes et al. 2017), but also elevated predation risk associated with habitat fragmentation (Kurki et al. 2000, Storch 2000) and predator abundance (Kurki et al. 1997, Baines et al. 2016, Kämmerle et al. 2017). Examples of grouse populations considered to be threatened by predation typically come from landscapes intensively used by humans (Storch 2000). Humans have attempted to control predators to protect livestock or to

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reduce competition over game species since ancient times, but the removal of predators to protect threatened species is a more recent development (Reynolds and Tapper 1996). Previous reviews have shown that predator control is capable of improving population parameters in birds (Côté and Sutherland 1997, Smith et al. 2010, Roos et al. 2018) and other taxa (Salo et al. 2010), but it remains a contentious issue. The removal of both mammalian and avian predators, usually by lethal means, is often an integral part of grouse management for both conservation and harvesting purposes (Suchant and Braunisch 2008, Grant et al. 2012, Conover and Roberts 2017, Storch 2018). In red grouse, for instance, intensive management including predator control is common and has been shown to positively affect grouse population parameters in many (Fletcher et al. 2010, Ludwig et al. 2017) but not all (Calladine et al. 2014) cases. Ambiguous evidence of its effectiveness contributes to the reasons why some interest groups oppose the culling of predators (Perry and Perry 2008). While predator control as a conservation measure has been reviewed for individual species of grouse (Conover and Roberts 2017), a concise summary of empirical data on the effectiveness of predator control for grouse conservation is lacking thus far.

This review collates existing evidence on the suitability of predator control as a conservation measure in favour of grouse populations. In a qualitative review we first assess the evidence on predation as a limiting factor for grouse populations and address how environmental co-determinants of population development may mediate its impact. We then conduct a quantitative review of the effectiveness of predator control, the active removal of predators from an area, to benefit grouse population parameters. Finally, we identify gaps in the current knowledge.

Methods

Literature search

We searched for literature on the Web of Science and Google Scholar until August of 2017 using combinations of 'grouse' (incl. common names of the species) and 'predation', 'predator', 'predator removal' or 'predator control'. We also used literature cited in the studies thus obtained as well as in existing reviews (Côté and Sutherland 1997, Holt et al. 2008, Smith et al. 2010, Conover and Roberts 2017). Here, we define predator control as the active removal of predators from within a specific experimental area by lethal or non-lethal means (i.e. not considering predator fencing studies). We grouped the resulting studies into two groups: 1) studies investigating population limitation of grouse species by predators and 2) studies assessing the effects of predator control (as defined) on grouse reproductive success or adult abundance and survival. All studies not matching any of these two groups were not considered in this review. For a quantitative analysis of the effects of predator control on grouse population parameters we selected all studies resulting from group 2 of our literature search (journal articles and research reports) that either conducted the removal of one or more potential predators or utilized such a setting (e.g. control conducted by authorities), while simultaneously

recording population parameters of grouse species using a type of experimentally paired design (i.e. either employing a 'treatment-control' or a 'before–after' design or a 'before–after-control-impact' design) and reported quantitative results. We considered all studies that fulfilled these criteria and were accessible as journal papers or conference proceedings. We did not consider unpublished grey literature (e.g. student thesis work) although this would have increased the sample, because 1) we aimed for replicability of the study and 2) because accessibility rather than scientific rigour may have determined inclusion of individual studies.

With regards to population limitation of grouse by predators, we found a total of 15 peer-reviewed studies investigating the effects of differences in predator abundance on grouse population development and/or reproductive success (Supplementary material Appendix 1 Table A1), using data from Fennoscandia (5), the US (3), the UK (4), Germany (1), Canada (1) and the eastern Alps (1). The studies cover six grouse species (Europe: *Tetrao urogallus*: 7, *Lyrururs tetrix*: 4, *Lagopus lagopus* incl. *L. l. scotica*: 3 and *Bonasa bonasia*: 2; North America: *Centrocercus urophasianus*: 3, *Tympanuchus phasianellus*: 1).

With regards to predator control, we found 17 publications describing studies during which predators were removed at one or more sites (either experimentally during the study or utilizing differences in predator management between study sites) and the effect of predator control on grouse population parameters was monitored (Table 1, Supplementary material Appendix 1 Table A2). These studies covered eight grouse species across Europe and North America (Europe: *Tetrao urogallus*, *Lyrurus tetrix*, *Bonasa bonasia* and *Lagopus lagopus* incl. *L. l. scotica*, America: *Centrocercus urophasianus*, *Tympanuchus cupido*, *Bonasa umbellus*). There was one study that was considered in both groups, but is listed here (Baines et al. 2004).

Of the 17 studies on predator control (Table 1, Supplementary material Appendix 1 Table A2), 14 reported numerical data potentially suitable for re-analysis (Europe: 10; North America: 4). We excluded two of those studies, because the reported effects of grouse population performance were not clearly attributable to predator control (full details in Supplementary material Appendix 1 Table A2 and Results). Both studies had a large mean effect size (Supplementary material Appendix 1 Table A2) and their exclusion makes the analysis more conservative. Accordingly, we used data of 12 studies in the quantitative review. Table 1 gives full details on the studies used in the analysis and Supplementary material Appendix 1 Table A2 provides an overview of removal studies not used in the quantitative review and the reasons for excluding those studies.

Quantitative review: extracting data from studies

We obtained numerical values for parameters of interest from the text, tables and figures of the original 12 publications (Table 1). We extracted pairs of treatment (i.e. predator control) and reference (i.e. no predator control) values. For studies describing removal experiments at several independent sites, over several years, or involving several grouse species, we obtained paired values of each measured entity for each respective set of treatment and reference sites and

Table 1. List of predator control studies used in quantitative analysis in chronological order. The country of the study, the grouse species for which parameters were recorded, the predator species removed, the study design (site design and study type, number of sites), the timeframe of the study, the mean test statistic (with SD of the mean in brackets for n≥3)†, the number of data points for each type of data, the sample size used as weight in analysis (sample size: number of sites×number of years) and the standard of impact control (measured as a) whether the number of removed predators was monitored and (b predator populations were monitored) are provided. *Study types were: C and T for studies featuring control and treatment sites, B–A for studies employing a before after design. The number of sites in each class are given in parentheses. †Values >0 denote a positive effect of predator control. [1]Partly, by comparison of removal rates; [2]crows partially monitored.

Study	Country	Grouse species	Predator	Design* (sites)	Timeframe	$\bar{x}$ ln(X_e/X_c)	Data types	Sample size	Impact	contr.
Edminster 1939	USA	ruffed grouse	multiple avian and mammalian	adjacent C and T (1 and 1)	1931–1935	0.22 (0.30)	'NEST': 4 'ADULT': 4	1931: 2×1 1932: 2×1	yes	no[1]
Parker 1984	Norway	black grouse willow ptarmigan	corvids	adjacent C and T (1 and 1)	1978–1981	0.20 (0.16)	'BROOD': 2 'ADULT': 1	2×4	yes	yes
Marcström et al. 1988	Sweden	black grouse capercaillie hazel grouse willow ptarmigan	red fox pine marten	multiple C and T/B–A (1 and 1, then reversed)	1976–1984	0.35 (0.30)	'BROOD': 1 'JUV/ADL': 1 '%CHICK': 1 'ADULT': 2	2×9	yes	yes
Baines 1991	UK	black grouse	'gamekeeping'	multiple C and T (5 and 5)	1989–1990	0.47 (0.41)	'BROOD': 2 'JUV/ADL': 2 '%CHICK': 2	1989: 10×1 1990: 10×1	no	no
Lawrence and Silvy 1995	USA	Attwater's prairie-chicken	striped skunk opossum raccoon	adjacent C and T (1 and 1)	1980–1981	0.91	'NEST': 1	2×2	yes	yes
Baines 1996	UK	black grouse	carrion crows 'gamekeeping'	multiple C and T (10 and 10)	1991–1993	−0.06 (0.17)	'BROOD': 1 'JUV/ADL': 2 '%CHICK': 1 'ADULT': 2	20×3	no	no[2]
Kauhala et al. 2000	Finland	black grouse capercaillie hazel grouse willow ptarmigan	red fox pine marten stoat raccoon dog	multiple C and T (2 and 2)	1993–1998	0.46 (0.66)	'BROOD': 7 'JUV/ADL': 2 'ADULT': 2	North: 2×5 South: 2×6	yes	yes
Baxter et al. 2007	USA	sage-grouse	several canids badger skunk corvids	single B–A (1)	1998–2005	0.71	'JUV/ADL': 1 'ADULT': 1	1×8	yes	no
Fletcher et al. 2010, 2013	UK	red grouse	red fox stoat weasel carrion crow	multiple B–A, T and C (4, reversed)	2000–2008	0.62 (0.31)	'BROOD': 1 'JUV/ADL': 1 '%CHICK': 1 'ADULT': 2	4×9	yes	yes
Moreno-Opo et al. 2015	Spain	capercaillie	2 marten spp. red fox badger wildcat gennet	multiple B–A, T and C (1 and 1)	1999–2013	0.71	'JUV/ADL': 1	2×6	yes	yes
Dinkins et al. 2016	USA	sage-grouse	raven (coyote)	multiple C and T (7+5)	2008–2011	0.04	'NEST': 2	12×3	yes	yes

per recorded species and/or over separate time frames as they were provided in the original publications (i.e. multiple pairs were possible per study; Table 1). For two publications describing the same experiment (Fletcher et al. 2010, 2013) we averaged over two values for the ratio of young to adult birds, because they slightly differed between publications. In total, we thus obtained 51 value pairs of population parameters (i.e. treatment and reference values) from 12 publications (Table 1).

To account in our analysis for the different types of data reported in the original studies, we grouped the data (i.e. n = 51 value pairs) into seven types of grouse population parameters, including four types of reproductive parameters: A) brood size (mean number of chicks counted; abbreviated as 'BROOD'), B) the ratio of juveniles to adult birds counted ('JUV/ADL'), C) the proportion of female birds observed with chicks ('%CHICK') and D) measures of nest success ('NEST'); and three measures of adult population parameters: E) proportional changes in adult counts, F) adult density or density indices and G) adult survival. We assigned all values such as that higher values indicated better performance across all seven types (e.g. higher reproductive success, higher adult abundance). The set of 51 value pairs fell into our seven types as follows: reproductive parameters n = 36 value pairs (brood size: 14; juvenile/adult birds: 10; % hen with chick: 5; nest success: 7) and adult population parameters n = 15 (% change adult count: 4; density index: 8; adult survival measures: 3).

We characterized differences among studies by a number of metrics. To partially account for differences in experimental design during the quantitative analysis, we differentiated between removal experiments in which treatment and control sites were spatially independent or had multiple spatial replication ('independent') and those that had dependent sites ('dependent', i.e. single directly adjacent sites or single-site before–after designs). In order to account for the strong heterogeneity in environmental context among studies, we grouped the habitat types covered by the studies into three factor levels: 'forest', 'forest mosaic' (depicting mosaics of forest stands and open habitat types) and 'open' (covering open habitat types dominated by shrubs such as steppe, prairie and moors). The data did not permit a more detailed categorization of environmental context or target species. In addition, we qualitatively assessed whether studies monitored 1) the number of predators removed during the treatment and/or 2) the predator populations at the study sites following the cull (Table 1).

Quantitative review: data analysis

Data analysis was conducted in software R ver. 3.5.0 (<www.r-project.org>). In a first step, we tested whether treatment values were significantly higher than their paired reference values. To do so, we standardized the reported parameters for each type of data (i.e. population parameters) by subtraction of the within-group mean and dividing by the within-group SD to bring all data to the same scale, before testing for an effect of predator control using a paired Wilcoxon signed rank test comparing treatment values with their respective reference value; first testing for each individual type of data (for $n \geq 5$) and then on the pooled dataset.

To quantify the size of the effect in the data and control for the effect of covariates on the effect size of predator control we obtained an effect size statistic for each value pair. A technical requirement of meta-analysis is the assessment of individual effect sizes with their respective variances (Vetter et al. 2013). A larger number of the metrics we found were, however, reported without an estimate of the associated variance. We thus calculated the test statistic as $\ln(X_e/X_c)$ with X_e and X_c being the mean treatment and control responses (cf. Salo et al. 2010). A test statistic larger than zero indicates a positive effect of the treatment, a value of zero no effect and values below zero a negative effect. For further analysis we pooled the test statistic of the three types of adult parameters (i.e. abundance change and survival, types E and G into class F; 'ADULT') due to low sample sizes for types E (n = 4) and G (n = 3).

We assessed the data for signs of publication bias by initially plotting effect size by $\sqrt{\text{sample size}}$ of the study in a funnel plot around the mean effect size (sample size was calculated as the number of study sites × number of study years for each value pair; Fig. 1b–c). Since other fail-safe statistics require variance estimates, we then calculated Orwin's fail-safe N (Orwin 1983, Rosenberg 2005) that quantifies the number of studies required to reduce an effect in the data below an ecologically meaningful threshold. A common small threshold is an effect size of 0.2 (Rosenberg 2005). We thus calculated Orwin's fail-safe N for a minimum effect size of 0.2 and additionally for a ratio of treatment to control value of $X_e/X_c = 1.1$ (i.e. a 10% increase).

We then fitted weighted linear-mixed effect models (LMM) using R-package lme4 (Bates et al. 2015) with our test statistic as dependent variable and the ID of the respective predator control study as random intercept to account for the grouped nature of the data. We included the $\sqrt{\text{sample size}}$ as model weights (i.e. sample size per study as specified above) to account for the differences in sample size and the higher likelihood of a small study to be associated with larger uncertainty or to produce an extreme effect size. We used the square root of the sample size to distribute the weight more evenly across the range of values in our data (compare Table 1).

We first fitted a null-model containing only the intercept, weights and the random effect to obtain a weighted mean effect size that accounts for the nested structure of our data.

In order to obtain individual mean effect size estimates for all grouse population parameters, we then refitted the model with the different types of population parameters (i.e. type 'BROOD', 'JUV/ADL', '%CHICK', 'NEST' and 'ADULT') as predictor. We also included the categorical habitat type ('forest', 'forest mosaic' and 'open') and the type of study site design ('dependent' and 'independent') as control variables for potential differences among studies and then performed an all-subset model selection using Akaike's corrected information criterion (AICc), fixing the grouse population parameters in the selection process. We set the level of significance at $\alpha = 0.05$ and computed p-values using the Satterthwaite approximation as implemented in R-package lmerTest (Kuznetsova et al. 2017). We calculated marginal and conditional R^2 (Nakagawa and Schielzeth 2013) for the final model. Parametric assumptions for the use of a linear
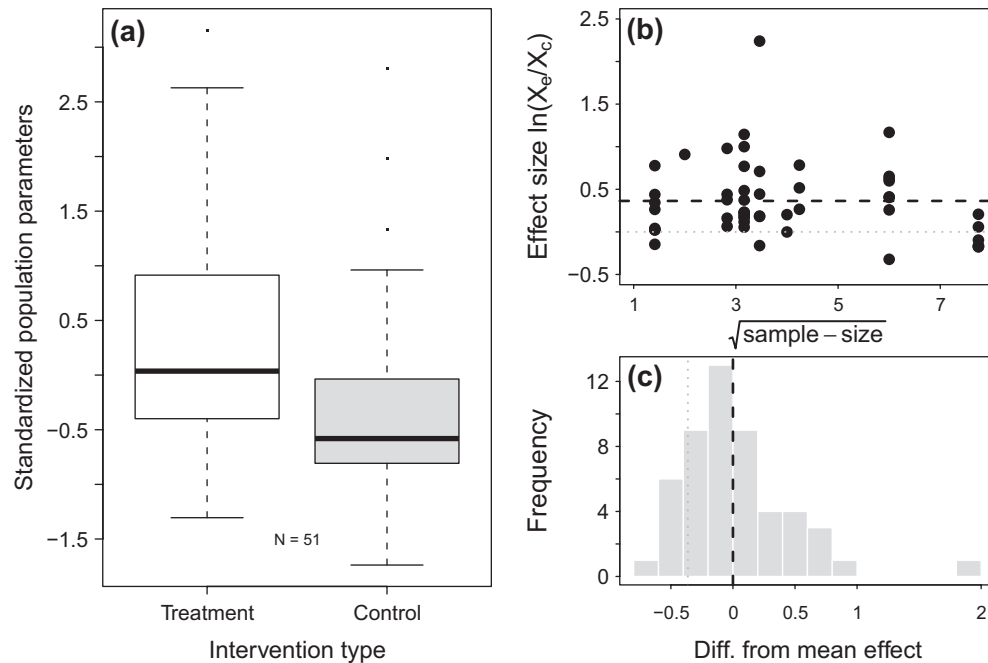
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Figure 1. (a) Raw differences in standardized grouse population parameters between treatment and reference plots for predator control studies. Values were standardized by subtracting the within-group mean and dividing by the within-group SD for each type of data; higher values indicate better grouse performance. (b) Funnel plot of effect size by the sample size of the study for all data (sample size as the number of study sites times the number of study years). Horizontal lines denote an effect size of zero (grey, i.e. no effect of the treatment) and the mean effect size (black). (c) Distribution of effect sizes around the mean effect size. Vertical lines correspond to lines in (b).

mixed-effect model were met. We obtained effect plots and associated conditional confidence intervals for the final model using the R-package effect (Fox 2003). Finally, we performed sensitivity analysis by refitting the final model excluding data points that we considered potentially influential to exclude a strong influence of their use on the results. This was done for 1) outliers, 2) using only adult abundance data points without the inclusion of adult survival and 3) red grouse data points, because we considered moors managed for shooting purposes as a highly artificial management situation.

Results

Overall, we found a strong bias in published research towards European and North American grouse. The majority of European studies on the effects of predation and predator control on grouse were from Fennoscandia and the UK.

Predation on grouse

All grouse species featured in published predation studies are reportedly killed by both mammalian and avian predators. Across Europe and North America, foxes (mainly red foxes *Vulpes vulpes*, Marcström et al. 1988, Lindström et al. 1994), mustelids (Kurki et al. 1997, Summers et al. 2009) and coyotes *Canis latrans* (Conover and Roberts 2017) prey on adult grouse, as well as their nests and chicks. Birds of prey e.g. goshawk *Accipiter gentilis* (Linden and Wikman 1983, Tornberg 2001), hen harrier *Circus cyaneus* (Thirgood et al. 2000a, b), *Accipitridae*, mainly golden eagle *Aquila chrysaetos* (Lyly et al. 2016, Conover and Roberts 2017) are likewise

considered important predators of grouse. Corvids are often implicated as nest predators, especially for species living in open habitats such as prairie grouse (Bui et al. 2010, Coates and Delehanty 2010, Dinkins et al. 2016), ptarmigan and black grouse (Erikstad et al. 1982, Parker 1984), but also in forest grouse like the capercaillie (Baines et al. 2004, Summers et al. 2004). There appears to be no clear pattern in the grouse literature as to the relative importance of mammalian versus avian predation. Dominant predator species vary dependent on habitat characteristics and community composition, but studies assigning individual depredation events to a specific predator species are rare (but see Coates et al. 2008, Summers et al. 2009, Coates and Delehanty 2010, Taylor et al. 2017). Several studies name predation as the most important cause of nest failure (Hewitt et al. 2001, Saniga 2002, Moynahan et al. 2007, Coates et al. 2008, Ludwig et al. 2010) and the main cause of chick mortality (Wegge and Kastdalen 2007, Manzer and Hannon 2008, Rhim et al. 2015). Video monitoring of greater sage-grouse nests (*Centrocercus urophasianus*, hereafter sage-grouse) indicates that nest defence of female grouse is rare and seldom successful (Coates et al. 2008). Favourable vegetation cover at nest sites may result in lower nest predation in various grouse species (Gregg et al. 1994, Coates and Delehanty 2010, Ludwig et al. 2010, Rhim et al. 2015).

Qualitative review

Predation and population limitation

We found eight studies concluding that predator abundance may limit grouse populations or significantly affect their development (Lindström et al. 1994, Smedshaug et al. 1999, Thirgood et al. 2000a, b, Čas 2010, Baines et al.

2016, Lyly et al. 2016, Kämmerle et al. 2017), while one study found such a relationship only for one of several grouse species (Tornberg et al. 2013). In Sweden, Lindström et al. (1994) monitored red foxes and three grouse species at several spatial scales during a sarcoptic mange outbreak and concluded that predation by foxes is limiting grouse abundance. Similar results were obtained by Smedshaug et al. (1999) using Norwegian hunting bag data. Thirgood et al. (2000a) also used bag data to show that red grouse abundance was negatively correlated to raptor abundance in addition to habitat quality, and Thirgood et al. (2000b) conclude that predation by raptors was additive to other losses and reduced autumn abundance of grouse by 50%. In contrast, coupled models using Finnish count data provided evidence of limiting effects of goshawks on capercaillie, but not on black grouse or hazel grouse (Tornberg et al. 2013). Baines et al. (2016) used grouse count data from 26 forests in Scotland to show that adult densities of grouse were negatively correlated to red fox abundance. Similarly, Kämmerle et al. (2017) linked capercaillie range contractions in Germany to variation in red fox abundance. Finally, Lyly et al. (2016) used Finnish triangle counts to show that red fox, pine marten and golden eagle abundance negatively correlated with adult abundance of black grouse and hazel grouse. Danvir (2002) reported that sage grouse lek attendance was negatively correlated with golden eagle abundance, but that golden eagle abundance was negatively correlated to coyote abundance through prey availability, thus benefitting sage grouse.

We found eight studies concluding that reproductive success of grouse was negatively related to the abundance of mammalian or avian predators (Kurki et al. 1997, Baines et al. 2004, 2016, Manzer and Hannon 2005, Bui et al. 2010, Coates and Delehanty 2010, Ludwig et al. 2010, Lyly et al. 2016). Kurki et al. (1997) and Lyly et al. (2016) used Finnish wildlife triangle census data to show that reproductive success of capercaillie, black grouse and hazel grouse decreased with mammalian predator density. The same pattern has been described indirectly by linking predator abundance to forest fragmentation (Kurki et al. 1998) and forest fragmentation to reduced reproductive success of grouse (Kurki and Linden 1995, Kurki et al. 2000). Baines et al. (2004, 2016) showed that capercaillie breeding success was negatively related to the abundance of mammalian and avian predators in Scotland. In North America, nest success of sage-grouse and sharp-tailed grouse has been found to be negatively related to the abundance of ravens (Bui et al. 2010, Coates and Delehanty 2010) and corvids in general (Manzer and Hannon 2005), whose abundance was related to human land use (Manzer and Hannon 2005, Bui et al. 2010). Effects of predator abundance on adult survival of grouse are, however, less clear. Thirgood et al. (2000b) found raptor predation an important cause of mortality for adult red grouse. Baxter et al. (2013) found only weak support for an effect of predator abundance on survival rates in sage-grouse, but they used canids killed each year as a debatable proxy for predator abundance. In their review, Schroeder and Baydack (2001) concluded that most prairie grouse individuals are eventually predated and that predation has substantial effects on adult survival.

Environmental factors and impacts of predation

There is limited published information on how environmental conditions and site characteristics affect the impact of predation on grouse populations. Baines (1991) compared the effects of predator removal between years with more and less favourable environmental conditions for reproduction of grouse and concluded that predation may limit grouse recruitment only if environmental conditions are unfavourable, as adverse conditions may predispose chicks to predation (Wegge and Kastdalen 2007). Similarly, Thirgood et al. (2000a) conclude that predation limits red grouse populations as an additional effect following habitat deterioration. Ludwig et al. (2010) could ultimately ascribe the majority of nest losses to predation, but nest survival rates were best explained by environmental determinants, whose effect varied with predator abundance. For Germany, Kämmerle et al. (2017) found the relative impact of predator abundance on capercaillie range persistence probability to increase if climate, forest structure and other site characteristics were suboptimal. In the US, Coates and Delehanty (2010) also linked nest loss of sage grouse to habitat configuration (mainly shrub cover) and Bui et al. (2010) found reproductive success of sage grouse to be related to human-altered sagebrush habitat that favours raven abundance. Finally, there are indications that parasite loads of grouse may interact with predation risk (Hudson et al. 1992, Isomursu et al. 2008). Overall, there is need for research to target how predation and the severity of its impact on grouse vary with changes in environmental conditions (e.g. precipitation, climate change), habitat suitability (e.g. forest structure, food availability), body condition (e.g. parasites) and other site characteristics (e.g. disturbance, land use) and how these interact.

Predator control

Most studies returned by our literature search (17 studies in group 2) attempted removal of multiple predators (16 studies), two studies removed only corvids. While the majority of studies concluded that predator removal benefitted reproductive success of grouse, fewer studies also monitored changes in adult abundance or survival. In contrast to the large amount of predation-related literature, we only found 4 published studies describing the effect of predator control on populations of North American grouse. All studies report effects of removal on reproductive success with nest success being most commonly measured (3 of 4), including the oldest published predator control experiment (Edminster 1939). Most published predator control studies (13 of 17 studies) targeted grouse species in Europe, mainly capercaillie, black grouse and ptarmigan (including red grouse) in the UK (7) and Fennoscandia (6). The studies differ greatly in the intensity and type of predator control, in the grouse population parameters measured and the spatial scale of analysis. The classic experiment by Marcström et al. (1988) still represents one of the most solid studies, characterized by a robust design and good reporting standards.

All of the studies used in the quantitative analysis removed mammalian predators, except for Parker (1984), and most removed multiple species, typically both avian and mammalian predators, although some did not specify all removed species (Table 1). Some UK studies used professional

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gamekeepers for predator control, who removed multiple avian and mammalian species (Table 1). American studies also commonly used professional personnel for predator control.

The studies not included in our quantitative review show overall mixed results. In Scotland, reproductive success of capercaillie and black grouse was found to be higher in years with corvid control compared to years without at the same site (Summers et al. 2004), but predator control years coincided with years of low precipitation in early summer. In another study from Britain (Ludwig et al. 2017), grouse moor management was found to positively affect abundance and reproductive success of red grouse, but the effects of predator control could not be separated from those of other management measures. One study found lower nest predation rates after removing a single pair of breeding hooded crows from the study site, but did not conduct a thorough removal experiment (Erikstad et al. 1982). Finally, Smedshaug (2001) found ambiguous effects of a large-scale governmental predator control programme on grouse population indices.

Quantitative review

When conducting pairwise tests, grouse population parameters were significantly larger at treatment sites than at reference sites for brood size ($V = 101$, $p = 0.003$; 14 pairs), the ratio of young to adult birds ($V = 50$, $p = 0.02$; 10 pairs) and nest success ($V = 26$, $p = 0.047$; 7 pairs). Treatment values were not significantly higher than reference values for the proportion of hens with chicks ($V = 15$, $p = 0.063$, 5 pairs) and adult abundance ($V = 25$, $p = 0.076$; 8 pairs), although p-values were <0.1. We did not test for differences in the % change in adult abundance (n = 4 pairs) and adult survival (n = 3 pairs) due to low sample size. When pooling standardized values, treatment values were significantly higher than the reference values for reproductive parameters ($V = 618$, $p < 0.001$, 36 pairs), adult parameters ($V = 91$, $p = 0.017$, 15 pairs) and the whole dataset ($V = 1165$, $p < 0.001$; 51 pairs).

The funnel plot of the data did not display signs of publication bias (Fig. 1b–c) and Orwin's fail-safe N indicated that 42 studies with a mean effect size of 0 (i.e. $X_e = X_c$) were required to reduce the mean effect size of removal to 0.2 and 144 studies were needed to reduce the mean treatment effect to 10% higher than the reference mean. The weighted mean test statistic was significantly different from zero after accounting for the nested structure of the data (LMM intercept only: mean = 0.36, 95% CI 0.20–0.52, Fig. 2). This corresponds to a LMM-based mean positive ratio of treatment to reference parameters (i.e. X_e/X_c) of 1.43 (95% CI: 1.22–1.68).

The final LMM only contained the predictor 'grouse population parameters' (Table 2), had a ΔAICc = 2.70 to the next best model in the set, an Akaike weight of 0.73 (full model selection results in Supplementary material Appendix 1 Table A3) and a low R^2 (marginal: 0.02; conditional: 0.08). The ratio of juvenile to adult birds (mean = 0.54; CI: 0.27–0.80), the proportion of hens with chicks (mean = 0.40; CI: 0.06–0.75) and the pooled adult parameters (mean = 0.38; CI: 0.14–0.62) had positive mean effects with confidence intervals excluding zero. Brood size (mean = 0.22; CI: −0.03 to 0.47) and nest success (mean = 0.30; CI: −0.12 to 0.72) had confidence intervals overlapping zero. Brood size was the parameter least affected by predator control. The largest effect ('JUV/ADL') was significantly larger than brood size, the smallest effect. For those data types with confidence intervals excluding zero this corresponded to a mean increase in population parameters in treatment sites compared to reference sites of 1.46 (1.15–1.87) for pooled adult abundance and survival, 1.71 (1.31–2.23) for the ratio of young to adult birds and 1.50 (1.06–2.12) for the proportion of hens with chicks.

The results were overall unaffected by the sensitivity analysis, except that confidence intervals for 'BROOD' did not overlap zero after removal of one outlier with large effect size.

Discussion

Our re-analysis of published data shows that predator control was associated with an overall positive effect on grouse population parameters, reflected by a net positive effect in
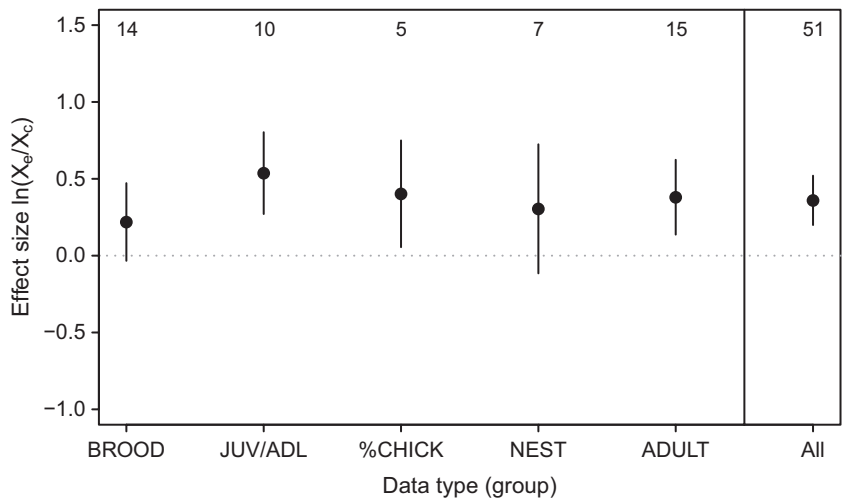

Figure 2. Final model results. Differences in the mean size of the test statistic (i.e. values >0 denote a positive effect of predator control) for the different types of population parameters as predicted by the final linear model.

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Table 2. Linear mixed-effect model results. Parameter estimates, associated SE and approximate p-values are provided.

Predictor	Estimate	SE	p
Intercept	0.220	0.126	0.089
Type 'JUV/ADL' (B)	0.320	0.158	0.049
Type '%CHICK' (C)	0.200	0.192	0.344
Type 'NEST' (D)	0.086	0.242	0.725
Type 'ADULT' (E, F, G)	0.150	0.150	0.286

The test statistics was defined as $\ln(X_e/X_c)$, where X_e and X_c are the mean treatment and control responses of the removal experiments. For factor levels see Methods section. Reference category (intercept): 'BROOD'.

our null model (i.e. range of 1.22–1.68 times the reference value) that already accounted for differences between studies and heterogeneity in sample size. Although there were differences in mean effect size and associated variance among the different parameters, the conclusion holds for both reproductive and adult abundance parameters and the associated effect sizes were independent of habitat type and study design. Accordingly, predator control as a management measure appears capable of benefitting grouse populations, similar to other taxa (Côté and Sutherland 1997, Salo et al. 2010, Smith et al. 2010). We also found considerable evidence in the literature that predation and predator abundance may limit adult abundance and reproductive success of grouse. This implies that grouse populations are often limited by their predators, a conclusion that is in line with studies on numerous terrestrial prey species (Holt et al. 2008, Salo et al. 2010).

Effects on grouse population parameters

Although we found a net increase of adult abundance parameters following predator control (i.e. 1.46 times the reference value), mean effect sizes varied among measures of reproductive success. Predator control did not have a net positive effect on nest success or brood size and we found a significantly larger effect on the ratio of juveniles to adult birds than on brood size. This may indicate that fewer broods are lost to predators during predator control, resulting in a larger contribution of juvenile birds to the total population. Although many studies controlled potential nest predators (mammalian and avian) and predation is often named as the most important cause of nest failure (Hewitt et al. 2001, Saniga 2002, Moynahan et al. 2007, Coates et al. 2008, Ludwig et al. 2010), nest success had confidence intervals clearly overlapping zero (Fig. 2). The mean effect on nest success was, however, clearly positive (i.e. 1.35 times the reference value), albeit having the largest confidence interval of all parameters. This points to considerable heterogeneity in predator control effects on nest success among studies (e.g. due to differences in the study systems and removed predators) that we could not account for.

In addition, previous reviews on other taxa have concluded that, while breeding parameters benefit, adult post-breeding populations are often unaffected by predator control (Côté and Sutherland 1997, Smith et al. 2010). Although this is in contrast to our findings, we are unable to conclude whether effects on abundance are due to increased survival of specific age classes, purely a consequence of higher reproductive success or will lead to a sustained increase in the breeding population. Evidence from before–after designs suggests that effects on grouse population size are only temporary (Marcström et al. 1988, Fletcher et al. 2013, Ludwig et al. 2017). Accordingly, benefits must be expected to subside quickly when predator removal activity ceases and predator populations recover.

Predator control as a conservation measure

Predator control – even for the conservation of threatened species – is a highly contentious subject (Perry and Perry 2008, Smith et al. 2010). Predator control is firmly accepted in the context of invasive species management (Myers et al. 2000). The matter is different when predators are native: some interest groups (e.g. animal-rights activists) and parts of the general public oppose culling of predators for conservation purposes (Perry and Perry 2008), also because evidence of the effectiveness of such programmes is often lacking owing to the difficulty of quantifying their effectiveness. This is problematic, however, because predator control is difficult to justify without quantitative evidence of its effectiveness.

Across most of Europe, grouse are considered threatened species (Storch 2007) and – as (former) game species – they are popular and often of major conservation concern. Predator control is typically an integral part of grouse management plans (Suchant and Braunisch 2008, Grant et al. 2012). Control activities are sometimes conducted by professionals, e.g. by gamekeepers or state authorities, but in other cases hunting legislation assigns the responsibility for predator control to local stakeholders and interest groups (e.g. recreational hunters, land owners). Large variation in commitment among individual hunters (e.g. in Germany: Langgemach and Bellebaum 2005), may dilute an effect of predator control, because culls become spatially structured harvests from continuously distributed populations (Conner and Morris 2015). For this reason, even predator control efforts perceived as 'intense' by local hunters and conservation managers may actually have little effect on predator populations and the grouse they prey on (Kämmerle et al. in prep.).

Our data do not allow for a complete technical evaluation of the characteristics of an effective predator control programme, owing to the differences among studies in, for instance, removal intensity and technique, the removed predator species and the grouse species involved. Nonetheless, most experiments in our quantitative review fully monitored the impact of predator control by quantifying how many predators were removed and how predator populations responded to the cull (Table 1). While monitoring standards are unlikely to affect outcomes per se, clear objectives are important (Reynolds and Tapper 1996) and programmes with monitoring of success are likely to have clear objectives and thus be more professional and more rigorously conducted. While less rigorous removal programmes may certainly produce an effect as well, professional programmes have a higher chance of achieving their goals. Qualitative assessment of the studies in our data indicates that successful studies are characterized not only by rigorous monitoring of success, but also by removing the largest possible number

of predators from an area with effective removal techniques. Accordingly, predator removal programmes that are rigorously conducted can significantly reduce predator populations and may thus result in short-term benefits for grouse. The sample of published studies available for our analysis is, however, small in comparison to the frequent application of predator control in management. This indicates that predator control programmes are rarely designed with the goal of quantitatively assessing their effectiveness. Most published studies in our dataset are well-designed and thus effective experiments. By contrast, we suspect that a large part of predator control programmes in local grouse conservation contexts (e.g. in Germany: Braunisch and Suchant 2013) may lack such rigorous designs and may thus remain both ineffective and undetected.

Predator community effects

In our review we found considerable evidence that predators may limit grouse populations and that grouse populations can benefit from predator control. Our mechanistic understanding of this process is, however, still limited and especially so concerning interactions with environmental conditions and habitat suitability or the importance of individual predator species. Only little attention has been directed at competitive interactions (i.e. resource and interference competition) among predator species and how they shape predation risk for grouse (but see Mezquida et al. 2006, Lyly et al. 2016) and even less on how these interactions are affected by selective predator control targeting individual predator species. While some predator species may profit from selective removal of competitive species (e.g. pine martens from red fox declines, Smedshaug et al. 1999), it is unclear how this might affect grouse populations and whether cascading effects are dependent on other environmental characteristics. Some evidence suggests that higher order predators, although preying on grouse themselves, may sometimes provide grouse with relief from mesopredators (Mezquida et al. 2006, Lyly et al. 2016), although the evidence is ambiguous (Taylor et al. 2017). Grouse populations reported as threatened by predation typically inhabit severely fragmented and degraded habitats, often in Europe (Storch 2000). Accordingly, grouse population development has been linked to predation or mesopredator abundance mainly in areas with high mesopredator abundance and an absence or low influence of top–down control (e.g. UK: Baines et al. 2016, central Europe: Kämmerle et al. 2017, southern Finland: Kurki et al. 1997). There is clearly a need for research to address these issues and the results would be of high relevance for management.

Technical limitations

In general, the precision of the effect sizes used in meta-analyses is dependent on the sample size and the design of the individual studies (Borenstein et al. 2009) and small studies have a particularly high risk of producing extreme effect sizes and/or high variances. Our use of a test statistic based on the mean treatment and reference values without incorporation of the respective individual variances bears the risk of not appropriately representing the precision of the mean effect size of individual studies, especially for small studies and studies with heterogeneous results (that still sum up to a mean positive effect size). Since the data prevented us from using individual study variances, we tackle this issue by reducing the effect of smaller studies, typically with dependent designs, in the analysis by using sample size as a weight in the model in favour of larger, often more rigorous ones.

Moreover, the availability of published information on the effects of predator control on grouse is strongly biased towards Europe (i.e. 13 of 17 studies). In our quantitative review data from North America are scarce, and lacking for Asia, and we are unable to quantify the potential influence of studies from other parts of the world on our results. Conover and Roberts (2017) recently provided an overview of North American grey literature regarding the role of predation for sage-grouse populations. While this review lists a number of studies in the grey literature, the authors also note that many, but not all, unpublished experiments were limited by methodological problems. In our quantitative analysis we chose not to include unpublished studies on predator control (e.g. thesis works, government reports), although this would have increased the sample, for two reasons. First, in order to increase the replicability of our work and second, owing to general inaccessibility of those studies (also to third parties), so that accessibility instead of quality would have determined inclusion or exclusion of individual studies. Finally, differences between studies, reproductive parameters and our set of control variables only explained only very little variation in the data (i.e. low R^2), indicating large variation in effect sizes that we could not account for. This implies that a range of other habitat-related and, potentially, site-specific factors can influence the effectiveness of predator control. Accordingly, we suggest that responsible parties bear this in mind when conducting predator control.

In summary, the current published evidence does not allow for conclusions other than that predator control is potentially capable of benefitting grouse populations, at least in the short-term, and that an intensive removal effort combined with rigorous monitoring of its impact is recommended to achieve the desired effect. Highly intensive predator control may, however, not be publicly acceptable everywhere, nor easily implemented in all settings and hunting systems.

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Supplementary material (available online as Appendix wlb-00464 at <www.wildlifebiology/appendix/wlb-00464>). Appendix 1.