IBIS
BOU international journal of avian science
Ibis (2015), **157**, 1–16

Review article

A review of the impacts of corvids on bird productivity and abundance

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Corvids are often viewed as efficient predators capable of limiting prey species populations. Despite this widely held belief, a comprehensive review quantifying the effect of corvids on the demography of prey species is lacking. We examine the impacts of crows, ravens *Corvus* spp. and Eurasian Magpies *Pica pica* on the population parameters of other bird species. We summarize results from 42 studies, which included 326 explicit evaluations of relationships between a corvid and a potential prey species. Population parameters of studied prey species were categorized as abundance-related (numbers, nest density) or productivity-related (nest success, brood size). Information from both experimental removal studies and correlative studies was examined. Combining all studies, no negative influence of corvids on either abundance or productivity of prey species was found in 81% of cases. Negative impacts were significantly more likely in cases examining productivity rather than abundance (46 vs. 10%). Experimental studies that removed only corvid species were significantly less likely to show a positive impact on productivity than those removing corvids alongside other predators (16 vs. 60%). This suggests that the impact of corvids is smaller than that of other predators, or that compensatory predation occurs. The impact of corvids was similar between diverse avian groups (such as gamebirds, passerines and waders; or ground-nesting and other species). Crows were found to be significantly more likely to have a negative impact on prey species productivity than were Magpies (62 vs. 12%), but no differences were found in relation to prey abundance. We conclude that while corvids can have a negative impact on bird species, their impact is small overall, and nearly five times more frequent for productivity than for abundance. These results suggest that in most cases bird populations are unlikely to be limited by corvid predation and that conservation measures may generally be better targeted at other limiting factors. However, negative impacts were found in a minority of cases, and those may require further investigation to develop management tools to mitigate such impacts where they are of economic or conservation concern.

Keywords: correlation, *Corvus*, experiment, game management, ground-nesting species, meta-analysis, *Pica pica*, predation, predator removal.

Predator control is often implemented to boost breeding performance and population densities of prey species, for either game management or conservation purposes (Butchko & Small 1992,

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Meckstroth & Miles 2005). This practice is based on the assumption that predation is a limiting factor in prey populations, and that predator control results in population increases (Holt *et al.* 2008). However, despite the widespread use of predator control, its efficacy in enhancing species' populations is still contentious (McDonald & Harris 2002, Park *et al.* 2008). The impacts of predator removal on prey populations may be complicated by compensatory predation, whereby predation from one predator is replaced by another, or by meso-predator release, whereby removal of one predator leads to increased abundance of another (Palomares *et al.* 1995, Courchamp *et al.* 1999). Additionally, the goals and objectives of predator control may differ depending on the management objectives. For example, game management is primarily concerned with post-breeding abundance (i.e. abundance at the start of the hunting season), whereas conservation actions are typically aimed at enhancing breeding population densities (Gibbons *et al.* 2007). Predator control may have effects on one of these parameters but not the other. Coupled with this, predator control by lethal removal of predators is controversial, potentially socially unacceptable, time-consuming, difficult, expensive and may only have short-term benefits (Ivan *et al.* 2005, Shwiff *et al.* 2005, Valkama *et al.* 2005, Smith *et al.* 2010a). Given these factors, and limited resources for either management or conservation, it is important to evaluate the efficacy of such management tools and allocate resources to management options that produce the desired results (O'Connor 1991).

Several reviews have assessed whether predator control is effective in reducing predation or increasing breeding populations of prey species (Côté & Sutherland 1997, Newton 1998, Gibbons *et al.* 2007, Holt *et al.* 2008, Smith *et al.* 2010b). Côté and Sutherland's (1997) meta-analysis on the effectiveness of predator removal to enhance bird populations concluded that predator removal improved hatching success and increased post-breeding population sizes by 75%. However, they found that predator removal did not generally result in subsequent increases in breeding population sizes. Thus, they concluded that although it might be useful for game-managers, it was unlikely to be effective in the conservation of declining species. Smith *et al.* (2010b) updated this review using many, more recently published studies and also concluded that predator removal enhanced hatching and fledging success, as well as post-breeding numbers (on mainlands, but not on islands). They also found, in contrast to Côté and Sutherland (1997), that predator removal enhanced breeding population size. Nordström (2003) reviewed studies of ground-nesting birds in the Baltic and again found that predator removal resulted in a general increase in nest success, post-breeding population size and breeding population size. Holt *et al.* (2008) conducted a meta-analysis of studies of birds in the UK and found an average 1.6-fold increase in avian prey breeding population size following mammalian and avian predator removal. These authors also found that removing multiple predator species had a much stronger effect than removing a single species, an idea previously suggested by Newton (1998), who postulated that removing single predator species was less effective due to compensatory predation. Newton (1993) also suggested that the prey species studied tend to be biased toward ground-nesting birds, which may be particularly prone to predation, and therefore may be more likely to respond to predator control, although neither Côté and Sutherland (1997) nor Smith *et al.* (2010a,b) found significant differences between ground-nesting and other species.

In the northern hemisphere, and particularly northern and western Europe, management of generalist predators most frequently involves the control of Red Fox *Vulpes vulpes* and corvids, both of which are common and usually not legally protected (Parker 1984, Tapper *et al.* 1996, Draycott *et al.* 2008, Bodey *et al.* 2009). However, whether fox or corvid control makes the greater contribution to management objectives has not been evaluated. Corvids are also frequently identified as major nest predators of bird species of conservation concern (Andrén 1992, Soderstrom *et al.* 1998, Baláž *et al.* 2007, Klausen *et al.* 2009). Yet, despite many studies and experiments on corvid predation, their overall impact on other birds remains to be assessed. Because corvids are diurnal and conspicuous nest predators, their importance in prey population regulation is often assumed prior to any assessment of the evidence (Marzluff & Angell 2005). There are several biological reasons why corvids may have a negative impact on birds and could be a conservation or management problem; they are adaptable, opportunistic, generalist predators with high cognitive abilities. However, further problems, such as misplacement of conservation resources, may result if corvid management decisions are based on misconceptions or poorly substantiated conclusions about their ecological impact on prey populations (Amar *et al.* 2010).

In this study we undertake a systematic literature review to explore the relationships between corvids and populations of their bird prey species, and assess whether widely held perceptions about the demographic impact of corvid predation are well founded. Specifically, we examine the impacts of corvids on various prey population parameters related to both productivity and breeding population size, and use information from both removal experiments and correlative studies.

METHODS

Literature survey

The scope of the study included species of the genus *Corvus* and the Eurasian Magpie *Pica pica*. The *Corvus* genus includes a third of all corvid species, and most of them are nest predators (dos Anjos *et al.* 2009). We also included the Eurasian Magpie as this species is a common and widespread nest predator, and is one of the main targets of legal predator control (at least for game purposes) in many European countries (Jokimäki *et al.* 2005). There were too few appropriate studies to include North American *Pica* species (*Pica hudsonia* and *Pica nuttalli*). Corvid is used hereafter to refer to any species of *Corvus* or the Eurasian Magpie, unless otherwise stated. When examining differences between effects of *Corvus* species and Magpies, we refer to the former as crows.

To ensure robustness and repeatability, a systematic process was employed to obtain all relevant studies for this review (Pullin & Stewart 2006). Comprehensive literature searches were generated through Web of Science (apps.webofknowledge.com) to obtain relevant studies using the following keywords and combinations: (corvid* OR crow* OR raven* OR Corvus) OR (magpie OR "Pica pica") AND (predat* OR experiment*). The start year for the search was 1950 and studies were refined to include only those within the Science and Technology research domain. The search was further refined to include only studies under the following topics: environmental science, ecology, zoology and biodiversity conservation. A total of 1191 studies was identified from this search in August 2013.

Papers were included that might be broadly of relevance, and excluded later after further examination based on relevance at a finer scale (Pullin & Stewart 2006). Titles of the studies obtained from the searches were scanned for relevance, and 352 studies remained after this. The abstracts from each of these were read to ensure they were relevant for the purposes of this study, and 172 studies were eliminated based on the abstract. The remainder were further assessed to see whether they contained information appropriate for analyses. Non-English studies were included if the abstract was in English and provided sufficient information about which breeding parameters were used, outlined the study design, and gave the statistical significance of the outcomes. We did not examine relationships of corvid predation on artificial nests, as they are known not to be directly equivalent to natural nests (Zanette 2002). In all, 42 studies met all the above-mentioned criteria, and were used in this review.

We classified each study as experimental or correlative (see below) and noted the location of study (country), corvid species involved, prey species and relevant parameters analysed (abundance and/or productivity, see below) in response to corvids. A second independent researcher checked the papers and nature of the relationships. Several different studies investigated more than one species, or more than one abundance or productivity parameter. Therefore, we make a distinction between the terms 'study' and 'case', where the case is a response (i.e. abundance/productivity) of a single species to corvids. Hence, there can be several cases in a single study, if multiple species were studied, or multiple responses measured for a species.

Overall, our literature search produced information on the effect of corvid removal or changes in corvid abundance from six different corvid species on productivity or abundance of 67 bird prey species, with a total of 326 cases. For productivity measures there were 108 cases from 49 different prey species and for prey abundance there were 218 cases from 52 species.

Experimental corvid removal or natural variation in corvid abundance could significantly increase, decrease or have no effect on the prey species' parameters measured. Henceforth, when we describe an impact, it is always one that is statistically significant at $P < 0.05$. When abundance or productivity parameters increased with corvid removal, this is considered indicative of a negative effect of corvids on prey species.

Study types

Experimental studies

We classified studies as experimental when (1) corvids were intentionally removed, (2) there were controls (i.e. no corvid removal) in either space or time and (3) specific population parameters of prey species were measured. Studies that removed corvids alongside other predators (e.g. foxes and raptors) were also included, and identified as multiple-species predator removal experiments. Some quasi-experimental studies that removed corvids, but did not have controls, were treated as correlative studies (e.g. Erikstad *et al.* 1982). Twenty of the 42 studies in this review were classified as experimental (see Supporting Information Table S1).

Correlative studies

These studies explore the relationships between various corvid abundance measures and prey species populations to draw inferences on impacts. The explanatory variable in these relationships was expressed in one of five ways: corvid numbers, presence, activity, proximity or predation levels. Abundance (as presence or density of corvids) was the most commonly used measure. Tested correlations may be temporal, spatial or both. Thus, Newson *et al.* (2010) used temporal correlations in bird survey data from annual national monitoring schemes to explore whether the population trends of 29 British bird populations were associated with increases in avian predator abundance. Baláž *et al.* (2007) made spatial comparisons of nest success in habitats with low or high corvid abundance. Amar *et al.* (2010) explored the relationships between both corvid and prey species abundance and population trends. A few studies described changes in predator populations of *Corvus* species grouped together with other predators into a single variable (e.g. Baines *et al.* 2004, Sims *et al.* 2008, Dunn *et al.* 2010). Quasi-experimental studies were included in this section when the authors did not provide adequate temporal (i.e. before–after values) or spatial controls. These included Erikstad *et al.* (1982), Stoate and Szczur (2001), and Baines *et al.* (2004).

Several studies presented correlations between corvid abundance and prey species, but effects of corvids were confounded by management (Stoate & Szczur 2005, Baines *et al.* 2008, Beja *et al.* 2009) or disturbance (e.g. Brambilla *et al.* 2004). Other studies did not quantify an effect on prey species (Kelly *et al.* 2005), or measured behavioural effects of corvids on prey species nest characteristics (Kazama *et al.* 2010). To ensure robust inference, these studies were excluded. Two papers (Rodewald & Yahner 2001, Tryjanowski 2001) were relevant in terms of showing the relationships between corvids and prey species but were excluded because they measured the impact on multiple prey species combined together into one metric so that species-specific impacts could not be distinguished. Overall, after these exclusions, correlative studies comprised 22 of the 42 studies in this review (Table S1).

Parameters and avian groups analysed

One of the challenges of a systematic review is to collate the variety of response parameters used in different studies and condense them into biologically meaningful groups. In this review, we focused on abundance-related parameters and productivity-related parameters. Because one of the main aims of predator control for hunting management is to increase post-breeding population size, it would have been desirable to analyse effects on this variable separately. However, there was not sufficient information for this (only two cases evaluated this specifically). Thus, we included these two cases with those evaluating productivity responses (giving a total of 108 cases) because post-breeding population sizes frequently reflect productivity variation more than breeding density variation (Gibbons *et al.* 2007). Productivity measures included any measure relating to brood size, or nest, clutch or fledging success, but we also included in this group measures that affect these parameters (e.g. provisioning rates or nestling condition, 17 cases). Indicators of abundance were reported in 218 cases; these included reports on breeding population size, number of adults or nest densities, but also population trends (one case) and adult survival rates (one case), as the latter is likely to directly affect abundance (Fuller *et al.* 1995).

Bird prey species were condensed into common categories, including gamebirds, passerines, waders, herons, cranes, seabirds, waterfowl and raptors. For analyses, the two waterfowl studies (Johnson *et al.* 1989, Clark *et al.* 1995) were placed into the wader category for convenience. We further categorized bird prey species as ground-nesting, which were those that exclusively nested on the ground or under low shrubs, or other. This was established through species descriptions in the papers and other sources (Harrison 1975, Gibbons *et al.* 1993).

Statistical analyses

Because we were mainly interested in testing whether corvids had negative impacts on prey species (and thus whether management of corvid populations can be justified on scientific grounds) we grouped studies that found no impacts with those in which a positive effect on prey species (a minority of studies – see Results) was found; these were combined into a single category termed 'no negative impacts'. Generalized linear mixed models, with a binomial error distribution and a logit link function, were used to evaluate the impacts on prey species as a binary variable (i.e. negative impact or no negative impact). We included study as a random effect in all models, to account for the non-independence of cases from the same study. This approach does not formally incorporate effect sizes of each study because very few studies reported the necessary mean values and estimates of variation, and because our literature spanned some 60 years we would be unlikely to be able to obtain such data from the original authors. Separate models were implemented to assess whether the likelihood of finding a negative impact on either abundance or productivity of prey species varied between different avian groups (i.e. ground-nesting or other or different taxa), between experimental and correlative studies, between locations (for countries with sufficient sample sizes, namely USA, France and UK), between experiments removing only corvids and those removing corvids with other predators, or between studies on crows or Magpies (cases where studies removed both Magpies and crows simultaneously were excluded from this analysis).

To determine the overall probability of finding a negative effect on either productivity or abundance, accounting for the lack of independence between studies, we used the same model as above with these two categories as a single two-vector explanatory variable. We used this model both to determine the mean probability of an effect for each category, and to contrast the probability of a negative effect between these two measures. Analyses were carried out in R (version 3.0.3, R Core Development Team 2013), using the lme4 package. The chi-squared test statistic, degrees of freedom (df) and *P*-values from these models are presented. Additionally, means are presented as back-transformed parameter estimates, with the upper and lower 95% confidence limits.

RESULTS

Literature search

The 42 studies that met the criteria for this review were focused on a variety of corvid species (Table 1) but showed a strong geographical bias, with most of the studies being carried out in the UK (Table 2).

In relation to prey species, Northern Lapwings *Vanellus vanellus* were the most frequently studied species, with 17 cases examined in nine different studies (Parr 1993, Tharme *et al.* 2001, Bolton *et al.* 2007, MacDonald & Bolton 2008, Amar *et al.* 2010, 2011, Fletcher *et al.* 2010, Newson *et al.* 2010, Bodey *et al.* 2011). The top five species investigated in correlative studies were all passerines (Yellowhammer *Emberiza citrinella*, $n = 11$; Song Thrush *Turdus philomelos*, $n = 10$; Common Blackbird *Turdus merula*, $n = 9$; Common Chaffinch *Fringilla coelebs*, $n = 9$; Dunnock *Prunella modularis*, $n = 9$). In contrast, the top five species studied in experimental studies were two waders (Northern Lapwing, $n = 9$; European Golden Plover *Pulvialis apricaria*, $n = 4$), a passerine (Common Blackbird, $n = 7$) and two gamebirds (Grey Partridge *Perdix perdix*, $n = 4$; Ring-necked Pheasant *Phasianus colchicus*, $n = 4$).

Effects of corvids on bird productivity

The influence of experimental corvid removal (in isolation or combined with other predators) on productivity was examined for 53 cases in 19 studies (Table 3A). Six studies found no effect at all of corvid removal on prey species (Clark *et al.* 1995, Amar & Redpath 2002, Stoate & Szczur 2005, Struthers & Ryan 2005, Steen & Haugvold 2009, Bodey *et al.* 2011). The remaining 13 studies (45 cases) found varying effects of corvid removal on

Table 1. Sample sizes (studies and cases) for productivity and abundance of target prey for each corvid species, and a combination thereof, studied in both experimental and correlative studies. Percentages are shown in parentheses. These studies were from a total of 20 experimental removal studies and 22 correlative studies.

	Productivity		Abundance		Total	
Corvid species	Studies	Cases	Studies	Cases	Studies	Cases
American Crow *Corvus brachyrhynchos*	4 (11)	8 (7)	1 (5)	2 (1)	4 (9)	10 (3)
Carrion Crow *Corvus corone*	7 (19)	24 (22)	6 (29)	82 (38)	10 (22)	106 (33)
Common Raven *Corvus corax*	4 (11)	7 (6)	1 (5)	5 (2)	5 (11)	12 (4)
Hooded Crow *Corvus cornix*	4 (11)	6 (6)	2 (10)	5 (2)	5 (11)	11 (3)
Western Jackdaw *Corvus monedula*	1 (3)	1 (1)	1 (5)	4 (2)	1 (2)	5 (2)
Eurasian Magpie *Pica pica*	6 (16)	41 (38)	5 (24)	96 (44)	8 (17)	137 (42)
Unidentified	1 (3)	1 (1)	–	–	1 (2)	1 (0)
American Crow & Common Raven	1 (3)	1 (1)	–	–	1 (2)	1 (0)
American Crow & Eurasian Magpie	1 (3)	1 (1)	–	–	1 (2)	1 (0)
Carrion Crow & Hooded Crow	1 (3)	2 (2)	–	–	1 (2)	2 (1)
Carrion Crow & Eurasian Magpie	5 (14)	11 (10)	6 (13)	33 (10)	5 (11)	15 (5)
Hooded Crow & Common Raven	1 (3)	1 (1)	–	–	1 (2)	1 (0)
Hooded Crow, Common Raven & Eurasian Magpie	1 (3)	4 (4)	1 (5)	1 (0)	1 (2)	5 (2)
Hooded Crow & Eurasian Magpie	–	–	1 (5)	1 (0)	1 (2)	1 (0)
Total	37	108	21	218	46[a]	326

[a]There were 42 studies in total; however, some studies reported the impacts on several corvid species individually, making the total here 46. The percentages are calculated using 46 as the total studies.

Table 2. Sample sizes (studies and cases) in relation to country where the study was conducted. Percentages are shown in parentheses.

	Productivity		Abundance		Total	
Country	Studies	Cases	Studies	Cases	Studies	Cases
Canada	1 (3)	1 (1)	–	–	1 (2)	1 (0)
France	1 (2)	10 (3)	1 (2)	10 (3)	1 (2)	20 (6)
Norway	3 (7)	7 (2)	2 (5)	2 (1)	4 (10)	9 (3)
Poland	–	–	1 (2)	1 (0)	1 (2)	1 (0)
Slovakia	1 (2)	1 (0)	–	–	1 (2)	1 (0)
Spain	1 (2)	3 (1)	1 (2)	1 (0)	1 (2)	4 (1)
Sweden	1 (2)	3 (1)	1 (2)	12 (4)	1 (2)	15 (5)
UK	17 (40)	67 (21)	11 (26)	190 (58)	23 (55)	257 (79)
USA	9 (21)	16 (5)	1 (2)	2 (1)	9 (21)	18 (6)
Total	34	108	14	205	42	326

productivity (53% of cases having negative effects, 47% having no effect; Supporting Information Table S2).

We provide further detail on those studies which detected a negative effect and, where the results allowed it, presented the magnitude of effects. Parker (1984) found that nest losses of Black Grouse *Tetrao tetrix* in Norway decreased following corvid removal, but no effect was seen on chick productivity. Magpie removal increased productivity in only one case (the Blue Tit *Cyanistes caeruleus*) from the 10 passerine species studied in France (Chiron & Julliard 2004). Hatching success of Common Eider *Somateria mollissima* in one of two colonies studied in Norway improved from 61 to 80% following Hooded Crow *Corvus cornix* removal (Stien *et al.* 2010). The lack of an effect on the other studied colony was attributed by the authors to compensatory predation. Productivity increased when Carrion Crows *Corvus corone* were removed alongside Common Gulls *Larus canus* (Parr 1993), Red Foxes (Summers *et al.* 2004, Bolton *et al.* 2007), and other corvids and mammals (Stoate & Szczur 2006, White *et al.* 2008, Fletcher *et al.* 2010). The magnitude of effect differed for these studies.

Table 3. Effects of experimental predator removal (Experimental) and corvid abundance (Correlative) studies on prey productivity (A) and abundance (B) in relation to avian groups. Number of studies and cases showing a negative (neg.) impact on prey species (indicated by increases in either abundance or productivity after corvid removal, or decreases in prey abundance with increasing corvid abundance), a positive (pos.) impact of corvids on prey species (as indicated by reductions in productivity or abundance after corvid removal), or no (none) impact. For full details of the studies used see Supporting Information.

		Experimental		Correlative	
Avian group	Impact of corvids	Studies	Cases	Studies	Cases
A. Productivity					
Cranes	Neg.	1	2	–	–
Gamebirds	Neg.	6	9	3	3
	None	3	6	1	2
Passerines	Neg.	4	4	5	12
	None	3	13	4	24
	Pos.	–	–	1	4
Raptors	None	1	1	–	–
Waders	Neg.	4	9	2	3
	None	6	9	2	2
Herons	Neg.	–	–	1	3
Seabirds	Neg.	–	–	1	1
	None	–	–	1	1
Total		28[a]	53	21	55
B. Abundance					
Gamebirds	Neg.	2	3	1	1
	None	3	4	–	–
	Pos.	–	–	1	1
Passerines	Neg.	2	2	2	6
	None	3	13	5	151
	Pos.	–	–	2	12
Waders	Neg.	1	2	2	2
	None	3	4	5	16
	Pos.	–	–	1	1
Total		14[b]	28	19	190

[a]Some studies reported the impacts of corvids on multiple species. There were 19 experimental removal studies that investigated prey productivity. [b]Some studies reported the impacts of corvids on multiple species. There were 10 experimental removal studies that investigated prey abundance.

For example, Bolton *et al.* (2007) found a two-fold increase in Northern Lapwing productivity, whereas Fletcher *et al.* (2010) found that predator control led to an average three-fold increase in breeding success for a number of species (Lapwing, Golden Plover *Pluvialis apricaria*, Curlew *Numenius arquata*, Red Grouse *Lagopus lagopus scoticus* and Meadow Pipit *Anthus pratensis*), and Stoate and Szczur (2006) found that predator control increased hatching success of Spotted Flycatchers *Muscicapa striata* from 16 to 77%. The removal of Common Ravens *Corvus corax* (alongside Coyotes *Canis latrans* and Common Racoons *Procyon lotor*) improved Sandhill Crane *Grus canadensis* productivity, with numbers of chicks per pair nearly doubling from 5.1 chicks without removal to 9.1 chicks with removal (Littlefield 2003), while removing American Crows *Corvus brachyrhynchos* and a multitude of other predators improved Ring-necked Pheasant hatching success from 16% to 36% and led to a two-fold increase in clutch size (Chesness *et al.* 1968). Survival of Red-legged Partridge *Alectoris rufa* chicks increased when Magpies and Red Foxes were removed (Mateo-Moriones *et al.* 2012). Similarly, the removal of Carrion Crows, Magpies and Red Foxes improved the productivity of the Grey Partridge (Tapper *et al.* 1996). Parr (1993) also found some effects of Carrion Crow removal on Eurasian Curlew, Common Redshank *Tringa totanus* and Northern Lapwing productivity. Stoate and Szczur (2006) removed Carrion Crows and Magpies, together with several other predators, and found this improved Spotted Flycatcher productivity.

Only in three of these studies (Parker 1984, Chiron & Julliard 2004, Stien *et al.* 2010) were corvids removed alone.

Comparing experimental studies removing only corvids with those removing corvids and other predators, we found a significant difference in the probability of finding a negative impact (χ^2 = 5.69, df = 1, P = 0.01, Fig. 1). Controlling for the non-independence of studies, the probability of finding a negative impact on productivity in experiments removing only corvids was 16% (95% CL 4–46%) and for experiments removing corvids together with other predators it was 60% (95% CL 41–77%). Combining both types of experiments (i.e. corvid-only removal and corvid with other predator removal), the probability of finding a negative impact of corvids on productivity was 49% (95% CL 28–70%). Most cases (83%, n = 15) from those studies that only removed corvids found no effect on prey productivity, whereas only 17% (n = 3) found a negative effect (Fig. 1).

In correlative studies, the relationships between corvid abundance and prey species productivity were also mixed, with 40% of cases (n = 55) showing a negative relationship. Controlling for the non-independence of studies, the probability of corvid abundance being negatively correlated with prey species productivity was 43% (95% CL 13–79%). Interestingly, a positive association was found in 4% of cases (n = 4; from 108 productivity cases), indicating that when corvid abundance was higher, prey productivity was also higher (Table 4).

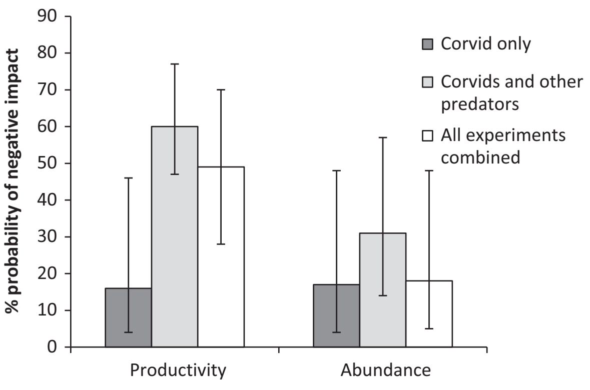

Figure 1. Probability of finding a negative impact on bird productivity and abundance from experimental removal studies. Data are split for experiments involving corvid-only removal, corvid and other predator removal, and all experiments combined. Results are from a generalized linear mixed model controlling for the non-independence of cases from the same studies. Means and their 95% confidence limits are shown.

Combining both types of studies (i.e. experimental and correlative), the probability of corvids being negatively associated with prey productivity was 46% (95% CL 26–67%). There was, however, no significant difference between study types (i.e. correlative and experimental) in finding a negative effect of corvids on productivity (χ^2 = 0.20, df = 1, P = 0.64, Fig. 2), with experimental and correlative studies having a probability of 47% (95% CL 24–71%) and 56% (95% CL 28–81%), respectively.

For the three countries with sufficient samples (France, UK and USA; Table 2), there was no significant difference between the effects of corvids on prey species productivity (χ^2 = 1.78, df = 2, P = 0.40), with the probability of a negative effect for France, UK and USA being 7% (95% CL 0.1–85%), 55% (95% CL 27–80%) and 65% (95% CL 23–92%), respectively.

Variation in the impacts of corvids on productivity between bird groups

For three avian groups, sample size was sufficient to compare the probability of finding a positive effect of experimentally removing corvids on productivity (passerines, gamebirds and waders; Table 3A). There were no statistical differences in effect on prey productivity between gamebirds (64%, 95% CL 29–88%), waders (44%, 95% CL 16–76%) and passerines (26%, 95% CL 7–63%; χ^2 = 2.21, df = 2, P = 0.33). Similarly, no significant differences were found among the responses of these three avian groups using the correlational data (χ^2 = 0.82, df = 2, P = 0.66; gamebirds 78%, 95% CL 10–99%, waders 59%, 95% CL 6–97%, passerines 40%, 95% CL 9–81%), or when combining both correlative and experimental studies (χ^2 = 2.49, df = 2, P = 0.28; gamebirds 68%, 95% CL 33–90%, waders 46%, 95% CL 18–76%, passerines 33%, 95% CL 14–61%, Table 3A).

We also compared whether the impact was different in relation to nesting habits of prey species. In the 108 cases from both experimental and correlative studies, 63 (58%) cases involved ground-nesting species, and 45 (42%) non-ground nesting species. We found no significant difference in the probability of cases finding a negative impact of corvids on productivity for either ground-nesting (51%, 95% CL 22–78%) or non-ground-nesting species (50%, 95% CL 31–71%; χ^2 = 0.01, df = 1, P = 0.91).

Table 4. Results of the impact of each corvid species (or combination of species) on either prey species productivity (A) or abundance (B) derived from the 42 experimental or correlative studies. Increasing corvid abundances could have a positive (pos.), negative (neg.) or no (none) influence on prey species abundance or productivity. Percentages are shown in parentheses.

Corvid species	Pos.	Neg.	None	Cases (total)
A. Productivity				
American Crow *Corvus brachyrhynchos*	–	6 (75)	2 (25)	8
Carrion Crow *Corvus corone*	–	17 (71)	7 (29)	24
Common Raven *Corvus corax*	–	4 (57)	3 (43)	7
Hooded Crow *Corvus cornix*	–	2 (33)	4 (67)	6
Western Jackdaw *Corvus monedula*	–	–	1 (100)	1
Eurasian Magpie *Pica pica*	4 (10)	5 (12)	32 (78)	41
Unidentified	–	1 (100)	–	1
American Crow & Common Raven	–	–	1 (100)	1
American Crow & Eurasian Magpie	–	1 (100)	–	1
Carrion Crow & Hooded Crow	–	2 (100)	–	2
Carrion Crow & Eurasian Magpie	–	7 (64)	4 (36)	11
Hooded Crow & Common Raven	–	–	1 (100)	1
Hooded Crow, Common Raven & Eurasian Magpie	–	1 (25)	3 (75)	4
Total	4 (4)	46 (43)	58 (54)	108
B. Abundance				
American Crow *Corvus brachyrhynchos*	–	–	2 (100)	2
Carrion Crow *Corvus corone*	7 (9)	6 (7)	69 (84)	82
Common Raven *Corvus corax*	–	–	5 (100)	5
Hooded Crow *C. Corvus cornix*	–	3 (60)	2 (40)	5
Western Jackdaw *Corvus monedula*	–	–	4 (100)	4
Eurasian Magpie *Pica pica*	6 (6)	4 (4)	86 (90)	96
Carrion Crow & Eurasian Magpie	1 (5)	2 (9)	19 (86)	22
Hooded Crow, Common Raven & Eurasian Magpie	–	–	1 (100)	1
Hooded Crow & Eurasian Magpie	–	1 (100)	–	1
Total	14 (6)	16 (7)	188 (86)	218

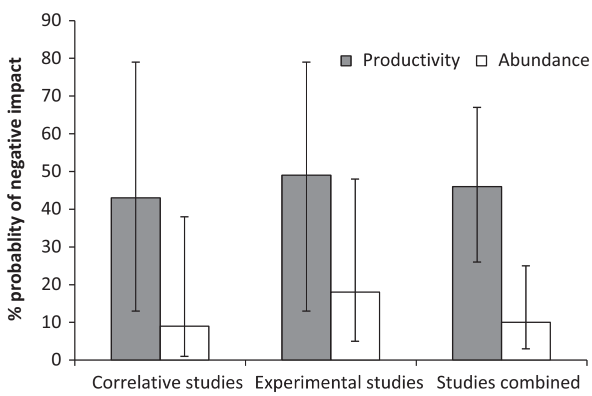

Figure 2. Probability of finding a negative impact on bird productivity or abundance between different types of studies (correlative, experimental and both types combined). Results are from a generalized linear mixed model controlling for the non-independence of cases from the same studies. Means and their 95% confidence limits are shown.

Variation in the impacts on productivity between corvids

In experimental studies, crows were significantly more likely to have a negative effect on prey species productivity than were Magpies (χ^2 = 4.29, df = 1, *P* = 0.03), with crows having a 60% probability (95% CL 38–79%) compared with only 15% (95% CL 3–52%) for Magpies (Fig. 3). Similarly, for correlative studies, crows were more likely to be negatively associated with prey productivity (64%, 95% CL 39–83%) than were Magpies (11%, 95% CL 3–33%; χ^2 = 9.80, df = 1, *P* = 0.001). Finally, combining both types of studies, crows were again found to be significantly more likely to have a negative impact on prey species productivity (62%, 95% CL 46–76%) than were Magpies (12%, 95% CL 4–29%; χ^2 = 14.78, df = 1, *P* = 0.0001; Fig. 3).

We also attempted to explore differences between corvid species. For experimental studies, only Carrion Crows and Magpies had sufficient sample sizes. Carrion Crows had a higher probability of producing a negative effect on their prey (75%, 95% CL 45–92%) compared with Magpies (15%, 95% CL 4–45%; χ^2 = 7.5, df = 1, *P* = 0.006). For correlative studies there was sufficient data to explore the difference between three corvid species: Carrion

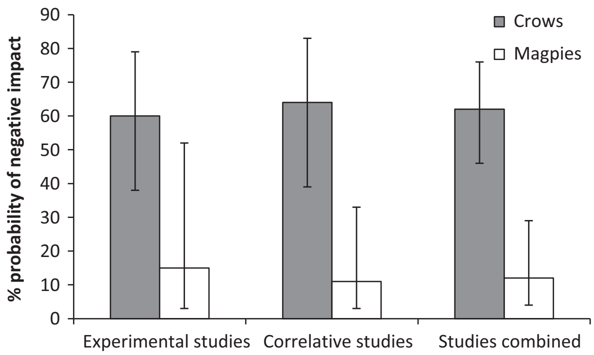

Figure 3. Probability of finding a negative impact on bird productivity for crows (*Corvus* spp.) or Magpies from experimental studies, correlative studies or both studies combined. Results are from a generalized linear mixed model controlling for the non-independence of cases from the same studies. Means and their 95% confidence limits are shown.

Crow, Common Raven and Magpie. There was a significant difference in the probability of finding a negative effect between these three species (χ^2 = 6.61, df = 2, *P* = 0.04), with values for Carrion Crows being higher (61%, 95% CL 23–89%) than for Common Ravens (40%, 95% CL 9–82%) or Magpies (11%, 95% CL 3–32%). Pairwise comparisons showed significant differences between Magpies and Carrion Crows (*P* = 0.03), but not between Common Ravens and either Magpies or Carrion Crows (*P* > 0.10). Similarly, combining both types of studies, there was a significant difference in the probability of finding a negative effect on prey species productivity between these three corvid species (χ^2 = 16.79, df = 2, *P* = 0.002; Carrion Crows: 72%, 95% CL 48–87%; Common Ravens: 58%, 95% CL 22–87%; Magpies: 12%, 95% CL 5–28%). Again, our pairwise comparisons revealed significant differences between Magpies and Carrion Crows (*P* = 0.0002), and a near significant difference between Common Ravens and Magpies (*P* = 0.05), but no differences between Carrion Crows and Common Ravens (*P* = 0.79).

Effect of corvids on bird abundance

The influence of experimental removal of corvids on bird abundance was assessed in 10 studies and 28 cases (Table 3B). Negative impacts were found in only seven cases. Predator removal including Carrion Crows led to increases in the abundance of Northern Lapwing, Eurasian Curlew and Red Grouse, whereas numbers declined in the absence of predator control (Fletcher *et al.* 2010). Similarly, Tapper *et al.* (1996) found predator removal including Carrion Crows and Magpies improved the abundance of the Grey Partridge, leading to a 3.5-fold increase in subsequent years. Fieldfare *Turdus pilaris* breeding population size increased significantly when Hooded Crows were removed in Norway (Slagsvold 1980), although this was attributed to the reduction in interspecific competition rather than predation risk. Lastly, Magpie removal in France increased the abundance of the Long-tailed Tit *Aegithalos caudatus* (Chiron & Julliard 2004). In one case of experimental removal, a positive impact of corvids on bird abundance was found (Chiron & Julliard 2004). In that study, adult Eurasian Blackcaps *Sylvia atricapilla* decreased after removal of Magpies. However, this response was believed to be a spurious relationship, as the Blackcap population was already declining prior to Magpie removal, potentially due to changes in habitat preference.

As described previously, in most removal studies, corvids were removed along with other predators. However, in contrast to the results for our productivity analysis, the likelihood of finding a negative impact on prey abundance did not differ significantly between removing only corvids, or corvids together with other predators (χ^2 = 0.75, df = 1, *P* = 0.38; Fig. 1). Controlling for the non-independence of studies, the probability of finding a negative impact on abundance in experiments removing only corvids was 17% (95% CL 4–48%) and for experiments involving removal of corvids together with other predators it was 31% (95% CL 14–57%). Combining both types of experiments (i.e. corvid only and corvid with other predator removal), the probability of finding a negative impact of corvids on abundance was significantly lower than for productivity (χ^2 = 4.05, df = 1, *P* = 0.04), with the likelihood of finding a negative impact for abundance being 18% (95% CL 5–48%), compared with 49% (95% CL 28–70%) for productivity. As with our finding for productivity, in most cases (83%, i.e. 10 of the total of 12 cases) of experimental studies removing only corvid species, no negative effect on prey abundance was found (Fig. 1).

For correlative studies, most cases (95%, i.e. 181 of the 190 correlative cases) found no negative association between corvid and prey species abundance (Table 3B). Again, as was the case for productivity, a small number of cases (*n* = 14, 7%) showed a positive association, indicating that species abundance increased with increased corvid abundance. Controlling for non-independence between studies, there was a marginally non-significant difference in the probability of finding a negative impact on prey productivity or abundance (χ^2 = 3.53, df = 1, P = 0.060), with 9% (95% CL 1–38%) for abundance and 43% (95% CL 13–79%) for productivity (Fig. 2).

Comparing study types (i.e. correlative and experimental) we found no significant difference in the probability of finding a negative effect of corvids on prey species abundance (χ^2 = 1.02, df = 1, P = 0.31; Fig. 2), with experimental and correlative studies having a probability of 11% (95% CL 1–66%) and 2% (95% CL 0.2–66%), respectively.

Combining both types of studies (i.e. experimental and correlative), the probability of finding a negative impact of corvids on prey abundance was significantly lower (10%, 95% CL 3–25%) than on productivity (46%, 95% CL 26–67%; χ^2 = 11.72, df = 2, P = 0.0006; Table 3B).

Sample size across countries was insufficient to test for geographical differences in impacts on abundance.

Variation in the impacts of corvids on abundance between bird groups

For the three avian groups with sufficient sample size to explore the impact of experimental corvid removal on prey abundance (Table 3B), no statistical differences were found (χ^2 = 2.31, df = 2, P = 0.31; gamebirds: 43%, 95% CL 14–77%, passerines: 13%, 95% CL 3–41%, waders: 33%, 95% CL 8–73%).

For correlative studies, sample size was sufficient to make comparisons only between waders and passerines and again we found no significant difference in the probability of finding a negative effect (χ^2 = 1.03, df = 1, P = 0.30), the difference being very low in both of these bird groups (passerines 0.4%, 95% CL 0–68%; waders 3%, 95% CL 0–87%).

Combining data from experimental and correlative studies, the probability of finding a negative impact on abundance still did not differ between gamebirds (25%, 95% CL 1–90%), passerines (1%, 95% CL 0.04–31%) and waders (6%, 95% CL 0.3–58%; χ^2 = 3.77, df = 2, P = 0.15, Table 3B); nor was there a difference between species with different nesting habits (i.e. ground-nesting (3%, 95% CL 0–29%) and non-ground-nesting (6%, 95% CL 0–38%) species; χ^2 = 0.41, df = 1, P = 0.52).

Variation in the impacts on abundance between corvids

The probability of finding an effect of experimental removal on prey abundance was not significantly different for crow (33%, 95% CL 13–62%) or Magpie removal (9%, 95% CL 1–44%; χ^2 = 1.76, df = 1, P = 0.19). We found the same result for correlative studies, where there was no significant difference in finding a negative effect on prey abundance between crows (0.5%, 95% CL 0–47%) and Magpies (2%, 95% CL 0–67%, χ^2 = 1.10, df = 1, P = 0.29). Similarly, when combining both types of studies, there was no significant difference between crows (3%, 95% CL 0–29%) and Magpies (6%, 95% CL 0–38%) in the likelihood of finding a negative impact on prey species abundance (χ^2 = 0.40, df = 1, P = 0.52).

Sample size at the level of the corvid species was too small to examine differences in their impacts for correlative, experimental or combined studies.

DISCUSSION

Our review shows that although there is no consistent pattern with regard to corvid impacts on other bird species, the most commonly reported effect is that corvids have no negative impact on prey species abundance or productivity. When combining experimental and correlative studies (326 cases), most cases (81%, n = 264) showed no negative influence of corvids on either abundance or productivity of birds, and even some apparently beneficial relationships were observed (6%, n = 18). Where negative impacts were observed, these were more common for productivity than for abundance. This suggests that corvid control may be less useful for conservation than for game management purposes, as conservation frequently aims to increase population size (i.e. our abundance measures), whereas game management aims to maximize the shootable surplus (i.e. post-breeding abundance, which is more often related to productivity). This conclusion is therefore similar to that found by Côté and Sutherland (1997), who examined the influence of mammalian and avian predator removal on bird populations.

Negative impacts on productivity were more frequently observed in experimental studies when corvids were removed alongside other predators than when corvids were removed alone. This reinforces the idea that removing multiple species may have a greater effect on prey species, as previously suggested by Newton (1998) and Holt *et al.* (2008). The smaller effect on productivity observed in experimental studies which removed only corvids suggests that the effect of corvids on prey species may be less marked than that of other predators, or else that compensatory predation or meso-predator release may occur (Bodey *et al.* 2009). The most frequent predators of corvids are corvids themselves, and culling one species of corvid could result in higher predation rates on prey species by other, non-culled, corvid species (Yom-Tov 1974). For example, Bodey *et al.* (2009) detected the competitive release of Common Ravens when Hooded Crows were culled; as a result, predation by Common Ravens potentially obscured changes in predation rates when Hooded Crows were removed. This emphasizes that corvid removal may be an inadequate management or conservation option in situations when correlated responses to corvid removal cannot also be controlled.

One of the novel findings from this study was the higher likelihood of finding a negative impact on productivity from crow species as compared with Magpies. This difference was present in both correlative and experimental studies, and combining both types of studies showed that crows were five times more likely to negatively impact prey species productivity than were Magpies. No such differences were found for the probability of finding an effect on abundance, but the likelihood of finding an effect on abundance by any corvid was much smaller.

Unlike some other predation studies, we found that corvid effects did not vary significantly among prey species groups. Previous research has suggested that ground-nesting birds, such as waders, are particularly prone to predation (Newton 1993, Nordström 2003). Gibbons *et al.* (2007) also concluded that populations of ground-nesting species, especially waders and some gamebirds, are more likely to be limited by predation, as their nests and young are likely to be more vulnerable to predation. Our review found that neither waders, nor gamebirds nor ground-nesting species were disproportionately affected by corvid predation when compared with other avian groups. The opposite is often claimed and predator control experiments have often been justified due to a perceived negative effect on ground-nesting species (see Bolton *et al.* 2007, Evans *et al.* 2009, Bodey *et al.* 2011). Our study therefore suggests that the generality of this conclusion may be weak, at least with respect to corvid predation.

An unexpected finding was that correlative studies detected several positive relationships with both abundance and productivity, suggesting the possibility of beneficial impacts of corvids on some species. Passerines (both abundance and productivity measures) were positively correlated with corvid abundance in 18 cases (6%), and there was also one case involving a wader (Northern Lapwing). In most cases, it is difficult to see what mechanisms might account for these relationships, and in some cases they might have arisen by chance. However, this finding certainly suggests that not all impacts of corvids should necessarily be assumed to be negative.

Study limitations

Studies that met the criteria for the review had a strong geographical bias, with the majority (79, $n = 257$) being from the UK. Nevertheless, we found no significant differences in the impact of corvids on productivity for the three countries with sufficient sample sizes to examine geographical differences in the effects of corvids. These countries represent different ecological and geographical contexts and this result suggests that our conclusions may well be valid across the studied areas. However, further studies in other geographical areas would help to confirm our overall conclusions (particularly with respect to impacts on prey species abundance) and would help to expand their geographical validity.

Given that in our analysis we reduced our study results to a binary (negative/no negative effect) response, it could be argued that our approach over-simplified the results of these studies, and in doing so we perhaps underestimate any negative effect. However, any such bias could have only arisen if there had been a systemic tendency for 'no-negative effect' results to have come from poorly replicated studies and 'negative effect' results to have come from better replicated more robust studies, a situation which we consider unlikely.

Our review also has implications for the utility of different methods to investigate the impacts of corvids. Experimental studies are often favoured to examine the impacts of predators on their prey because they allow causal relationships to be determined (Nicoll & Norris 2010). Correlative studies, on the other hand, often make use of existing datasets on corvid and prey species abundances by making comparisons either temporally (e.g. Newson *et al.* 2010) or spatially (e.g. Tharme *et al.* 2001). They are therefore often less expensive and can be carried out opportunistically (e.g. Newson *et al.* 2010, Amar *et al.* 2011). Our review found no significant differences in the impacts of corvids using these two approaches, suggesting that both types of studies may be equally informative on this issue. However, a well-designed experiment will always engender greater confidence (Newton 1998).

Many of the experimental studies removed corvids alongside other predators (frequently mammalian carnivores), thereby confounding the impacts of corvids and those of other predators, as specified above. To improve our understanding of the impacts of corvids it would be useful to conduct further rigorous corvid-only removal experiment studies, which would test for effects not only on the parameters of interest (e.g. prey bird abundance or productivity) but also on other processes in order to understand the mechanisms underlying observed impacts. For example, disentangling the proportion of predation accounted for by different species (corvid and other predators) is needed. This might provide improved insight into the relative impact of corvids on bird productivity or abundance (as compared with other predators) and also on when and how corvid removal may be a necessary and efficient management tool.

Conclusions and Management Implications

Corvids are often assumed to be highly detrimental to bird populations, and this perception is often reinforced due to their conspicuous predatory behaviour (Marzluff & Angell 2005). However, while this review confirms that corvids can have negative impacts on bird species, the probability of finding a negative impact was almost six times more frequent for productivity than for abundance, and was only 10% for abundance. These results therefore suggest that in most cases bird species are unlikely to be limited by corvid predation. Given these results, conservation management may not necessarily be well served by the removal of corvids, and resources may be better targeted at other limiting factors (Amar *et al.* 2010). The efficacy of corvid removal (alongside other predators) to increase the surplus of game birds available for shooting appears to be higher, although not consistently so, with still a large proportion of cases showing no effect. In the context of game management, the relative effect of corvids and other predators remains to be assessed. This is quite surprising, given the financial resources devoted to corvid control for game management across many countries. Furthermore, the relative effects of predator control and other management options (e.g. habitat management) directed at increasing abundance or reducing predation still remain underexplored.

Finally, despite the general pattern described above, serious negative impacts of corvids may still occasionally occur for both avian and non-avian taxa. For example, Kristan and Boarman (2003) found that Common Ravens in the Mojave desert can reach unnaturally large numbers, due to supplementary food from anthropogenic sources, which has resulted in hyper-predation on the native Desert Tortoise *Gopherus agassizii*. They concluded that this increase in predation pressure is affecting the tortoise population and could potentially result in the extinction of this reptile. This illustrates that in certain cases direct intervention may be needed to prevent the extinction of certain species. Further research on species-specific impacts needs to be conducted to guide management decisions in specific contexts. Monitoring of corvid populations and experimental studies quantifying their impacts on specific species should therefore be continued.

We are grateful to Jessica Shaw, Alex Thompson, Katherine Forsythe, Margaret Koopman and Phoebe Barnard for their assistance and comments on the manuscript. We thank the NRF/DST South Africa for their funding. B.A. enjoyed a Mobility Grant (Salvador de Madariaga call, funded by the Spanish Ministry of Education and Culture) to CEBC while writing the paper.

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Received 14 November 2013;
revision accepted 16 October 2014.
Associate Editor: Jose A. Sanchez-Zapata.

SUPPORTING INFORMATION

Additional Supporting Information may be found in the online version of this article:

Table S1. Summary of 42 experimental and correlative studies (326 cases) showing the effect (prey response) of corvids on the abundance or productivity of prey species.

Table S2. Summary of 326 experimental and correlative cases showing the effect (prey response) of corvids on the abundance or productivity of prey species.