



Factors predicting susceptibility of songbirds to nest predation by corvids

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Abstract

Despite the suggestion from several meta-analyses that nest predation is not limiting songbird populations, responses to experimental removal of nest predators, such as corvids, have varied.

The impact of nest predation by corvids on songbird populations is unclear. One potential explanation for this disparity is that susceptibility could vary according to the nesting biology of a species. To investigate this hypothesis, we conducted a review of studies detailing nest predation on UK songbirds and extracted the reported rates of nest predation from 80 papers which attempted to identify the predators responsible. We found that corvids were significant predators of songbird nests (24% of nest predation was attributed to corvids). However, species that construct open nests, and whose breeding season overlaps considerably with the breeding season of magpie and jay, incurred the highest rate of nest predation by corvids specifically (different factors predicted predation by non-corvid predators). We then used attributes of nesting biology to predict predation rates for UK breeding species for which we found no empirical data ($n=31$). Although, in most cases cited in the literature songbird populations are unaffected by changes in corvid numbers, there are some cases in which species we predicted to be more susceptible to corvid predation responded to changes in corvid numbers. However, an understanding of how of other predators and other non-predation-related factors limit both songbird breeding success and songbird population numbers is necessary in any conservation management of songbird populations.

Keywords Nest predation · Corvids · Songbirds · Nesting biology · Management

Introduction

The decline of songbirds in the UK across numerous habitats is well-documented (Donald et al. 2006; Hewson and Noble 2009; Sullivan et al. 2015; Massimino et al. 2019) and, despite widespread conservation efforts, ongoing (DEFRA 2019). Although the enactment of several habitat management initiatives, such as the implementation of agri-environment or woodland creation schemes, have achieved local scale successes (Perkins et al. 2011; McHugh et al. 2016; Scridel et al. 2017), evidence that such management can halt overall songbird population declines is limited (Kleijn et al. 2011).

It has been suggested that habitat improvements have failed to reverse these population declines because the role of other factors, and the interactions between them, has been underplayed (Whittingham and Evans 2004; Nicoll and Norris 2010; McMahan et al. 2020).

One of the most cited of these other factors is predation. UK songbird decline has coincided with the reduction of widespread predator control (Tapper 1992; Douglas et al. 2014), an increase in anthropogenic food sources, changes in agricultural landscapes, and the associated population growth of many generalist mammalian and avian predators (Battersby 2005; Newson et al. 2010; Roos et al. 2018). Predation of eggs and chicks in the nest, hereafter nest predation, is commonly carried out by corvids (Schaefer 2004; Baláz et al. 2007), and, although corvid numbers are now stabilising, their populations have increased substantially in recent decades; in the UK magpie (*Pica pica*) numbers increased by 94% from 1970 to 2017, carrion crow (*Corvus corone*) by 98% and jay (*Garrulus glandarius*) by 7% (DEFRA 2019).

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However, any suggestion of a causal link between falling songbird numbers and predator population growth is disputed (Gibbons et al. 2007; Bell et al. 2010). Studies looking specifically at the correlation between corvid and songbird population change have found little evidence of predators limiting prey populations (Gooch et al. 1991; Thomson et al. 1998). One explanation is that corvids preying on nests are simply causing compensatory mortality, removing part of the population that would have died anyway (the so-called 'doomed surplus' (Errington 1946)). In this case a reduction in corvid numbers would not be expected to have a positive impact on the populations of birds whose nests they prey on. It may be that other predators take nests in the absence of corvids (Parker 1984; Ellis-Felege et al. 2012) or that reduced losses of eggs or chicks due to predation are compensated by other causes of nest mortality (Amundson and Arnold 2011; Ellis et al. 2020) or mortality of individuals at other life history stages. For example, sparrowhawk (*Accipiter nisus*) numbers may not affect great tit (*Parus major*) population numbers because other density-dependent factors such as overwinter food availability or competition for nest holes limit breeding numbers (Cresswell 2010).

Alternatively, it could be that corvids are simply not preying on many nests. Dietary studies have suggested that eggs and nestlings make up a small portion of the diet of corvids and of their nestlings (Holyoak 1968; Díaz-Ruiz et al. 2015). They may attract undeserved blame for nest predation due to their conspicuous, diurnal activity (Birkhead 1991). However, these hypotheses receive only mixed support from removal studies in which predator (corvid) numbers are reduced in one area and the resulting breeding success of the prey (songbird) species is monitored. Such studies are often complicated by the fact that multiple avian and mammalian predators are removed simultaneously alongside other management changes. For example, removal of a suite of predators, including corvids, did lead to an increase in breeding success in some farmland passerine species when combined with sympathetic habitat management (White et al. 2014). Cessation of corvid control (as well as selective mammalian predator control) resulted in a mixed response across a guild of upland songbirds; skylark (*Alauda arvensis*) had lowered abundance, whereas meadow pipits (*Anthus pratensis*) showed no response (Baines et al. 2008). Conversely, in one controlled experimental study where just corvids were removed only very limited effects were found on the productivity of a suite of passerine species (Chiron and Julliard 2007). A systematic review (Madden et al. 2015) drew together correlational and experimental studies from around the world to explore the impact of the removal of corvids on populations of their bird prey of all types. They found that in the majority of cases (81%), corvids had no negative effect on abundance or productivity of birds. The reason why songbird species differ in apparent susceptibility

to correlated corvid population increases, or response to experimental corvid removal, within and across studies may be because, in such a diverse taxonomic group, particular songbird species are differentially preyed on by corvids. At present, there is no overview of how rates of nest predation by corvids differ between songbird species, and consequently there is no way of determining whether removal of corvids is predicted to affect the breeding success or population dynamics of any particular songbird species.

Factors that affect the susceptibility of a particular species to nest predation by corvids are likely to relate to aspects of their nesting biology. Birds' nesting strategies vary in several ways which may affect nest predation in general and by corvids particularly. The most striking difference in nesting biology is between species with open nests and species that nest in cavities or nest boxes (hole nesters) which provide physical protection from predation (Ricklefs 1969; Martin and Li 1992). Corvid predators specifically have been found to be unable to access hole nests of some species, such as the northern wheatear (*Oenanthe oenanthe*) (Pärt 2001). Conversely, open cup nesting passerines can be impacted detrimentally by corvids (Baláz et al. 2007; White et al. 2008). Other factors relating to nest position also influence predation risk (Ludvig et al. 1995). For example, nest height has been found to affect concealment of nests within vegetation and consequently predation by corvids (Weidinger 2002). Other aspects of songbird breeding biology can influence a predator's ability to predate the nest. Some rodent species may only be able to attack smaller eggs (Degraaf and Maier 1996; Degraaf et al. 1999), and it has been suggested that corvids may also favour preying on smaller, lighter eggs as they preferentially remove eggs from the nest site, rather than consuming them in situ (Major 1991; Haskell 1995). Finally, life history interactions between predators and prey could be influential. Predators may switch to foraging on more protein-rich prey during their breeding season, to meet the nutritional needs of their own young (Annett and Pierotti 1989). Species which breed at the same time as their predators could therefore suffer increased predation of their eggs and chicks.

We explored how variation in aspects of nesting biology explains variation in rates of nest predation attributable to corvids compared to non-corvid predators. If many potential prey species are not preyed on by corvids due to their nesting biology, then this may explain why they, as a group, do not respond to changes in corvid numbers. We concentrate on UK songbirds as there is a good understanding of their breeding biology (Cramp 1988, 1992; Cramp and Perrins 1993, 1994; Cramp et al. 1994), and there are sufficient detailed previous studies of these species to attribute rates of nest predation to particular predators. These species merit focus as population declines are ongoing and a better understanding of the impact of predation on these species would

provide further insight into this decline (Hayhow et al. 2015). We also predict predation rates for each of the 31 UK breeding species for which we do not have empirical data, based on their nesting attributes. These results permit us to ask which species are likely to be more susceptible to nest predation by corvids and hence may be affected by changes in corvid populations.

Methods

Initial literature search

We conducted a comprehensive search of the literature aimed to find any studies which reported nest predation rates of breeding UK songbirds. The search was limited to resident or migrant songbirds with more than 100 pairs breeding per year on average (Harrop et al. 2013). This encompassed 68 species. Details of the sources searched, and the criteria used are provided below and as electronic supplementary material (S1).

Analysis of papers

Over 5000 papers were initially screened through our literature search and results were extracted from 80 of them for this review (S2). A small number of papers reported predation rates for multiple species ($n = 14$), and in these studies, rates for each species were extracted separately (hereafter referred to as cases). These 14 papers produced 35 cases with the remaining 66 papers each providing predation rates for just one species (1 case per paper) resulting in 101 cases in total. We collected data for 37 of the potential 68 species, with up to 10 separate studies contributing data for any one species. Twenty-eight species were represented by just 1 or 2 cases. The 31 species for which no appropriate results were found included common species such as robin (*Erithacus rubecula*) and starling (*Sturnus vulgaris*) as well as birds which breed less frequently in the UK like Scottish crossbill (*Loxia scotica*). Despite there being no time limit on the search, we found that 81% of studies that reported the required information were published from 1990 onwards.

Predation figures

Studies were only included if the nest predation rate could be extracted, either directly or by calculation, from the presented data. Nest predation rate was defined as the proportion of total nesting effort (eggs or nestlings) lost to predation. This was generally reported in studies as the number of nests predated out of the total number of nests monitored. To avoid false negatives, studies with a nest predation rate of 0 were only included when the authors explicitly stated that no

predation had taken place. If no attempt was made to identify the predators responsible, then data were excluded. This meant that sometimes only a subset of reported data were included, for example in cases where predator identification methods (e.g. cameras) were only utilised for a sample of nests, and no attempt was made to identify predators at other nests. Some non-English language studies were included if the abstract was in English and the required detail could be extracted from the paper (for example Barkow 2005).

When studies manipulated aspects of breeding biology as part of their experimental protocol, for example comparing different nest box densities (Alatalo and Lundberg 1984), results (total number of nests predated and total number of nests monitored) were summed across treatments where possible. Within studies data were also summed across years if site and species were constant. This ensured consistency between studies: due to variation in data presentation across sources it was not always possible to separate data per year. Care was taken to avoid duplication; when the same data or a subset of the same data were reported across multiple studies the report with the clearest predator identification was used.

Predator identification

The proportion of predation attributed to different predators was directly extracted from the text where possible (49% of cases). In other cases, figures were estimated based on the information given (51% of cases). For example, 'most predation due to' was assumed conservatively to be 50% of predation. In 32% of the latter group, broad categories of predators (e.g. avian) were identified conclusively, but the proportion attributed to more specific groupings (e.g. corvids) was qualified, such as 'avian predators (probably mostly jays *Garrulus glandarius* and magpies *Pica pica*)' (Chamberlain 1994). If no qualifiers were used to attribute predation to specific predators, studies were excluded from further analysis. In addition to any events attributed to unknown predators by study authors, any differences between total predation events and predation events assigned to particular predator species were also given the predator identity of 'unknown'. Nest disturbance by man was not consistently categorised as predation by studies so was excluded from our count of predation events.

Predator identification evidence quality was categorised and used to assess the reliability of the study's results. Studies which inferred the predators' identity from evidence at the nest were considered separately, categorised as 'field signs', to studies which directly observed predation, often using cameras, which were categorised as 'observed'. All other methods of identification, which were considered generally less reliable, such as utilising information from previous studies of the site or knowledge of the local predator population were categorised as 'other'.

Prey species nesting biology parameters

Characteristics of the prey species' nesting biology considered likely to influence susceptibility to corvid nest predation were taken from Ferguson-Lees et al. (2011) and Harrison and Castell (2002). The first two characteristics that we considered, which might affect accessibility of the nest to corvids, were nest type, which was classified as open or hole and, nest height, which was categorised as either ground, low (≤ 2 m) and high (> 2 m) based on descriptions in the literature. As specific individual nest heights were generally not given in the studies included in this review, and the wider literature reported a range of possible nest heights for each species, this categorisation provided a solution which allowed consistency between species which have been more or less well studied. A height of 2 m was chosen to distinguish species which nest low in shrub from those who nest higher in hedgerows and in trees (Sullivan et al. 2017). Thirdly, egg size, which might affect corvids' ability to handle eggs, was taken as egg length multiplied by width. Finally, the proportion of the songbird's breeding season that overlapped with either jay or magpie breeding season was calculated to assess whether songbirds which breed during their predators' breeding season are more susceptible. Breeding seasons were defined as the period 90% of eggs or young were produced using data collected from 2000 to 2009 (Ferguson-Lees et al. 2011). For example, for goldfinch (*Carduelis carduelis*), this period was late April (22nd) to mid-August (15th), whereas for the long-tailed tit, (*Aegithalos caudatus*), this period was late March (22nd) to early June (7th). In the case of jay and magpie, this encompassed early March (7th) to early July (7th). The overlap ranged from 40% (house martin (*Delichon urbicum*); breeding season from mid-May to late September) to 100% (blackcap (*Sylvia atricapilla*); breeding season late April to early July). The breeding seasons of jay and magpie were used as they were by far the most often cited corvids in the studies found in our literature search which identified specific corvid species as nest predators. Magpie and/or jay were cited as nest predators in 93% of studies where specific corvids were identified whereas the next most frequently identified was carrion crow which was identified in only 24% of studies where specific corvid species were identified. In addition, magpies particularly, are the corvids most frequently controlled in predator removal studies focussing on passerine populations.

Study type

Studies of natural nests were distinguished from those using artificial nests. The ability of artificial nest studies to represent natural nest biology has been questioned; therefore we only included these studies if they attempted to mimic

nesting biology of specific species, and, as the factors influencing predation of artificial nests may differ from those affecting predation of natural nests (Weidinger 2001), we first analysed studies on natural nests together with artificial nest studies and then analysed studies on natural nests alone. In the case of artificial nest studies, equivalent values for the other characteristics of nesting biology (height, nest type, egg size and breeding season overlap) were extracted directly from the studies' methods. For example, the specific dates and duration of artificial nest exposure given in the methods of these studies were taken as the breeding season and used in the calculation of breeding season overlap with magpie and jay and when non-songbird eggs were used (such as quail's eggs) the size of those eggs was taken as the egg size.

Statistical analysis

The number of nests predated by corvids, the number of nests predated by non-corvid predators and the total number of nests were extracted from each study. Corvid predation was defined as predation attributed to any or all UK corvid species. Corvid species may differ in their nest predation of different songbird species, but many studies did not distinguish between corvid species when identifying nest predators, so it was not possible to include any distinction in our analysis. Non-corvid predation was defined as predation conclusively attributed to non-corvids, therefore excluding predation attributed to unknown predators or unknown avian predators. The effect of prey species biology on these nest predation rates was analysed using a generalised linear mixed model (GLMM) approach.

In order to identify specific factors affecting corvid nest predation, we constructed two models: the first model with nest predation attributed to corvids as the response (1) and the second with all nest predation attributed to non-corvid predators as the response (2). In addition, due to the aforementioned possible discrepancy of the results of artificial nest studies, we constructed both these models firstly including all studies on natural and artificial nests (artificial nest studies were grouped by the species they aimed to mimic) (a) and secondly including studies only on natural nests only (b).

To allow for the overdispersion in the response variable, we assumed a beta-binomial distribution with a logit link for the response variable (Harrison 2015). The number of nests predated and total number of nests extracted from papers were fitted as a binomial response with number of nests predated (successes)/total nests—number of nests predated (failures). To account for non-independence of studies on the same species, species identity was fitted as random effect.

Parameters of prey nesting biology (nest type, nest height, egg size and breeding season overlap with magpie and jay)

and category of evidence (field signs, observed, and other) were all included as explanatory variables in the GLMMs. In models 1a and 2a, the type of study (artificial or natural nests) was also included. A first-order interaction term was fitted between nest height and nest type to examine potential differences in nest height distribution between hole and open nesting species. The majority of studies of hole nesting species reported nest heights of > 2 m (80% of cases on hole nesting species) with studies on coal tit (*Periparus ater*) and northern wheatear reporting nests at ground level (11% of cases) and studies on redstart (*Phoenicurus phoenicurus*), willow tit (*Poecile montanus*) and marsh tit (*Poecile palustris*) reporting nest heights of ≤ 2 m but above ground level (9% of cases). Conversely for studies identifying predation of open nesting species, the nest heights reported were more evenly distributed (21.5% of cases on the ground, 41.5% low (≤ 2 m) and 37% high (> 2 m)).

To assess the significance of explanatory terms, the variables were removed one at a time and likelihood ratio tests were used to assess the changes in the models' deviance (Crawley 2012). First-order interaction terms that were not significant were removed from the minimal adequate models using backwards deletion, but all main effects were retained in final models.

In order to examine the between species difference in nest predation rates by corvids specifically, model predictions on the scale of response variable (proportion of nests predated by corvids) were extracted from both minimal models (1a and 1b), and the predictive ability of both these models were assessed by comparing the predicted number of nests predated by corvids and the actual number of nests predated by corvids for each species. The predicted numbers of nests predated were calculated by multiplying the predicted proportion of nests predated by the total number of nests given as the denominator in the original response variable. The balanced accuracy of models was calculated as $[(\text{specificity} + \text{sensitivity})/2]$. Sensitivity is the proportion of true positives (positives correctly predicted as such) as opposed to false positives (negatives incorrectly predicted as positives) and specificity is the proportion of true negatives (negatives correctly predicted as such) as opposed to false negatives (positives incorrectly predicted as negatives). As per the original response, variable nests predated by corvids were classed as positives and nests that were not were deemed negative. Balanced accuracy was used, as opposed to other metrics of model performance, to take into account the large difference in probability between positive and negative results (Féret and Asner 2013), nests were far more likely to not be predated (negative) than be predated (positive). If this difference in likelihood is not considered, then the ability of the model to predict the more likely outcome has a greater influence in defining total error (Sebastián-González et al. 2015; Graves et al. 2016).

We then used the minimal model which had the best predictive ability to predict nest predation rates for species included in the literature search for which nest predation data were not found. Predictions on the scale of the response variable were calculated based on specified values of the explanatory variables: the attributes of nesting biology of the specific species (nest type, nest height, egg size, breeding season overlap with magpie and jay), study type was defined as natural and evidence category as other (the most common result).

All analyses were carried out in R ver. 3.6.0 (R Core Team 2019). Models were constructed using the glmADMB package (Skaug et al. 2016), and model accuracy was calculated using the confusion matrix function in the caret package (Kuhn 2017). All mean averages are presented ± 1 SE.

Results

Factors effecting rates of predation

Predation of songbird eggs and nestlings attributed to corvids varied widely across the studies included in this review (ranging from 0 to 75% of breeding effort lost to corvid predation), with a mean of $10.63 \pm 1.52\%$ of nests/eggs lost to corvid predation. Across all studies in which any nest predation was reported ($n = 96$) an average of $24.11 \pm 2.76\%$ of total nest predation was attributed to corvids and, of predation allocated to identified predators (an average of $69.94 \pm 2.43\%$ of total predation), corvid predation comprised of $36.54 \pm 4.02\%$. Overall, of predation allocated to identified predators, $42.88 \pm 4.02\%$ was attributed to mammalian predators, whereas $54.01 \pm 4.09\%$ was attributed to avian predators (including corvids).

The rate of nest predation experienced by a songbird species was predicted by some aspects of its nesting biology (Tables 1 and 2). The aspects which significantly affected predation differed depending on whether predation by corvids (Table 1) or predation by non-corvid predators (Table 2) was considered. When only corvid predation was considered nest type influenced predation rate: open nesting species experienced higher predation (corvid predation rate $16.11 \pm 2.05\%$) than hole nesting species (corvid predation rate $0.74 \pm 0.42\%$) (Fig. 1). The degree of overlap between the breeding seasons of the focal songbird species and those of magpies and jays also predicted corvid nest predation rates. Species with breeding seasons which overlapped more with the breeding season of magpie and jay suffered higher predation by corvids.

When variation in corvid nest predation rates were analysed, including, or excluding artificial nest studies in the analysis had no effect on the results (Table 1). However,

Table 1 Generalised linear mixed models showing the effect of nesting biology on the reported rates of nest predation by corvid predators including artificial nest studies (a) and excluding artificial nest studies (b). Non-significant interaction terms are not shown

Fixed effects	Estimate	SE	Test statistic (X^2)	df	P value
a					
Intercept (nest height, ground; nest type, hole; evidence category, field signs)	-6.10	1.30			
Nest height (Low)	0.51	0.45	1.77	2	0.414
Nest height (High)	0.13	0.48			
Overlap with J and MG breeding season	2.45	0.84	11.23	1	0.001*
Nest type (Open)	3.63	0.61	40.82	1	<0.001*
Egg size	<0.01	<0.01	2.74	1	0.098
Evidence category (Observed)	0.11	0.63	0.19	2	0.911
Evidence category (Other)	-0.10	0.35			
Study type (Natural nests)	-1.03	0.62	2.80	1	0.094
b					
Intercept (nest height, ground; nest type, hole; evidence category, field signs)	-7.17	1.23			
Nest height (Low)	0.84	0.51	3.35	2	0.187
Nest height (High)	0.22	0.51			
Overlap with J and MG breeding season	2.30	1.06	4.76	1	0.029*
Nest type (Open)	3.67	0.66	34.29	1	<0.001*
Egg size	<0.01	<0.01	1.38	1	0.240
Evidence category (Observed)	0.08	0.61	0.58	2	0.748
Evidence category (Other)	-0.21	0.35			

when predation by non-corvid predators was considered, the inclusion of artificial nest studies did affect the results of the analysis. When artificial nest studies were included, nest type did not influence predation rate (open nesting species $9.99 \pm 2.18\%$; hole nesting species $12.61 \pm 1.75\%$).

However, when only studies on natural nests were considered, the effect of nest type on non-corvid predation rate was influenced by nest height; open-nesting species which nest at ground level suffered relatively higher predation compared those nesting above ground level. Nest height did

Table 2 Generalised linear mixed models showing the effect of nesting biology on the reported rates of nest predation by non-corvid predators including artificial nest studies (a) and excluding artificial nest studies (b). Non-significant interaction terms are not shown

Fixed effects	Estimate	SE	Test statistic (X^2)	df	P value
a					
Intercept (nest height, ground; nest type, hole; evidence category, field signs)	-0.46	1.06			
Nest height (Low)	-0.70	0.43	2.57	2	0.277
Nest height (High)	-0.38	0.39			
Overlap with J and MG breeding season	-1.47	0.60	5.36	1	0.021*
Nest type (Open)	-0.39	0.38	1.09	1	0.297
Egg size	<0.01	<0.01	0.31	1	0.575
Evidence category (Observed)	0.35	0.58	6.26	2	0.044*
Evidence category (Other)	-0.65	0.31			
Study type (Natural nests)	0.22	0.55	0.17	1	0.684
b					
Intercept (nest height, ground; nest type, hole; evidence category, field signs)	-2.94	1.09			
Overlap with J and MG breeding season	1.11	0.91	1.56	1	0.212
Egg size	<0.01	<0.01	0.50	1	0.480
Evidence category (Observed)	-0.23	0.52	9.95	2	0.007*
Evidence category (Other)	-0.91	0.29			
Nest height (Low) * Nest type (Open)	-3.16	0.96	9.69	2	0.008*
Nest height (High) * Nest type (Open)	-1.18	0.78	0.00		

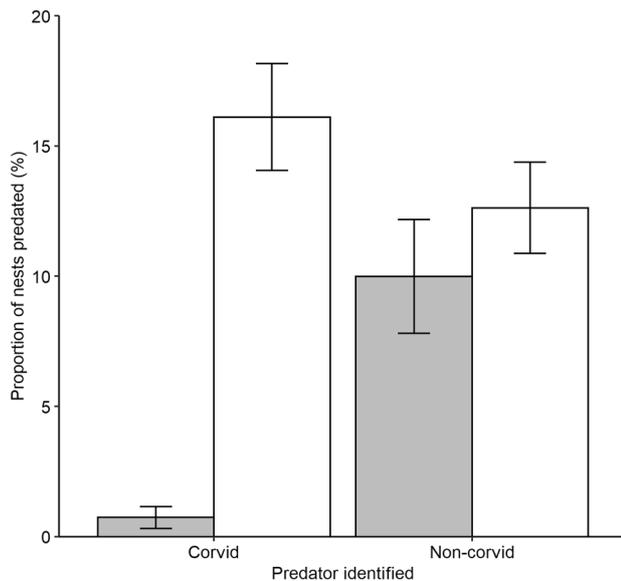


Fig. 1 The difference in proportion of nests predated by corvid and non-corvid predators between hole and open nesting species (dark grey bars, hole nesting species; white bars, open nesting species)

not have the same effect on non-corvid predation suffered by hole nesting species (Fig. 2). In addition, when artificial nest studies were included, jay and magpie breeding season overlap had a negative effect on predation rate, but no effect when these studies were excluded. In both cases (Table 2a and b) rates of reported predation rates were influenced by the type of evidence used to identify predator type. Studies

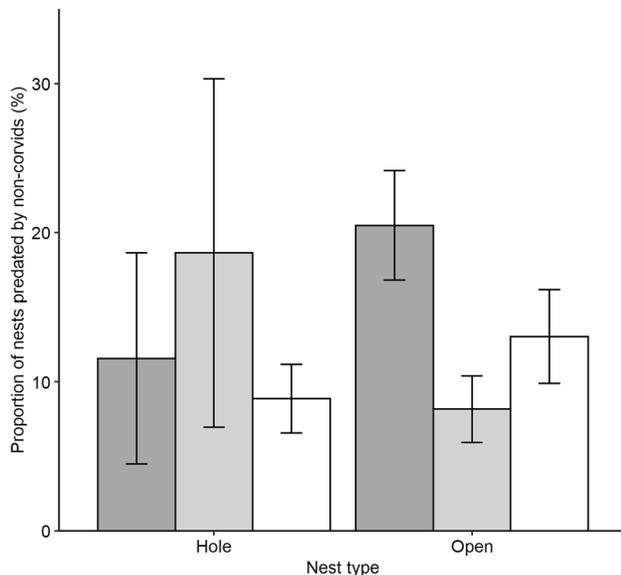


Fig. 2 The difference in the effect of nest height on the proportion of nests predated by non-corvid predators between hole and open nesting species (dark grey bars, ground nests; light grey bars, low nests; white bars, high nests)

which used indirect evidence (such as observations of predators in the general vicinity of the study site), classed as other, were likely to report lower rates of predation than studies which used physical evidence of damage to nest and eggs (field signs).

Model predictions

The minimal models of corvid nest predation rate both had good predictive performance, whether they included (Table 1a) or excluded (Table 1b) artificial nest studies (balanced accuracy values of 82.0% and 87.0%, respectively). As the latter model had a slightly higher predictive performance, it was used to predict values on the scale of the response for the 31 UK breeding songbird species for which reliable data on rates of corvid nest predation were not found in the literature (Table 3). All model predictions fell within the range of reported natural predation rates for other songbird species collected in the literature search.

Discussion

Corvids were found to be common predators of UK songbird nests, with approximately 24% of predated nests reportedly lost to corvids (37% of identified predation), but the level of nest predation by corvids varied markedly across songbird species. Specific attributes of songbird species' nesting biology can predict this variation in corvid nest predation, and these are different to the attributes of nesting biology affecting predation by non-corvid species. Species which nest in holes generally suffer very low rates of nest predation by corvids (86% of studies on hole-nesting species reported 0% corvid nest predation). Conversely, species with open cup nests and with a high degree of overlap with magpie and jay breeding season suffered up to ~55% of their nests being predated by corvids (Cresswell 1997). These findings suggest that different songbird species may not respond in the same way to either population changes in corvids or experimental removal of corvids. Changes in corvid numbers are unlikely to directly affect hole nesting species such as great tit (predicted corvid predation rate 1%), but other species such as the open nesting blackcap may be very sensitive to corvid prevalence during the breeding season (predicted corvid predation rate 28%) (Table 3).

Factors influencing nest predation by corvids.

The attributes of species' nest sites can explain how susceptible they are to predation by particular predator species. Open nests are more accessible than hole nests to predators generally (Martin and Li 1992) and, as shown in our results, to corvids in particular (Møller 1987). When predation by non-corvid predators was considered, hole nesting species did suffer lower predation rates than open

Table 3 Species with predicted proportion of nesting effort predated by corvids and count of studies from which values were taken. Where count of studies is 0, only model predictions on the scale of the response variable are shown (bold), for other studies averages from literature included in this review are also shown

Species	Count of cases included	Proportion of nests predated by corvids (%)	
		Prediction of the scale of the response	Average taken from the literature (data used to fit model)
Bearded tit (<i>Panurus biarmicus</i>)	0	28	
Blackbird (<i>Turdus merula</i>)	9	12	14
Blackcap (<i>Sylvia atricapilla</i>)	3	28	28
Blue tit (<i>Cyanistes caeruleus</i>)	6	1	0
Bullfinch (<i>Pyrrhula pyrrhula</i>)	0	13	
Cetti's warbler (<i>Cettia cetti</i>)	0	28	
Chaffinch (<i>Fringilla coelebs</i>)	1	16	23
Chiffchaff (<i>Phylloscopus collybita</i>)	2	32	8
Cirl bunting (<i>Emberiza cirlus</i>)	1	14	16
Coal tit (<i>Periparus ater</i>)	1	1	0
Common crossbill (<i>Loxia curvirostra</i>)	1	8	
Corn bunting (<i>Emberiza calandra</i>)	1	4	1
Crested tit (<i>Lophophanes cristatus</i>)	1	1	0
Dartford warbler (<i>Sylvia undata</i>)	0	29	
Dipper (<i>Cinclus cinclus</i>)	1	12	2
Duncock (<i>Prunella modularis</i>)	1	23	32
Firecrest (<i>Regulus ignicapillus</i>)	0	20	
Garden warbler (<i>Sylvia borin</i>)	1	21	19
Goldcrest (<i>Regulus regulus</i>)	0	15	
Goldfinch (<i>Carduelis carduelis</i>)	0	9	
Grasshopper warbler (<i>Locustella naevia</i>)	0	14	
Great tit (<i>Parus major</i>)	5	1	0
Greenfinch (<i>Chloris chloris</i>)	2	11	0
Grey wagtail (<i>Motacilla cinerea</i>)	0	19	
Hawfinch (<i>Coccothraustes coccothraustes</i>)	0	13	
House martin (<i>Delichon urbicum</i>)	0	5	
House sparrow (<i>Passer domesticus</i>)	2	0	0
Lesser redpoll (<i>Acanthis cabaret</i>)	0	9	
Lesser whitethroat (<i>Sylvia curruca</i>)	2	24	31
Linnet (<i>Carduelis cannabina</i>)	3	19	37
Longtailed tit (<i>Aegithalos caudatus</i>)	2	21	20
Marsh tit (<i>Poecile palustris</i>)	1	1	14
Meadow pipit (<i>Anthus pratensis</i>)	0	11	
Mistle thrush (<i>Turdus viscivorus</i>)	0	10	
Nuthatch (<i>Sitta europaea</i>)	5	1	0
Pied flycatcher (<i>Ficedula hypoleuca</i>)	6	1	1
Pied wagtail (<i>Motacilla alba</i>)	0	15	
Redstart (<i>Phoenicurus phoenicurus</i>)	1	1	0
Redwing (<i>Turdus iliacus</i>)	1	21	16
Reed bunting (<i>Emberiza schoeniclus</i>)	0	22	
Reed warbler (<i>Acrocephalus scirpaceus</i>)	1	19	0
Ring ouzel (<i>Turdus torquatus</i>)	1	8	0
Robin (<i>Erithacus rubecula</i>)	0	26	
Rock pipit (<i>Anthus petrosus</i>)	0	13	
Sand martin (<i>Riparia riparia</i>)	0	0	

Table 3 (continued)

Species	Count of cases included	Proportion of nests predated by corvids (%)	
		Prediction of the scale of the response	Average taken from the literature (data used to fit model)
Scottish crossbill (<i>Loxia scotica</i>)	0	8	
Sedge warbler (<i>Acrocephalus schoenbaenus</i>)	0	17	
Siskin (<i>Carduelis spinus</i>)	0	9	
Skylark (<i>Alauda arvensis</i>)	3	8	2
Song thrush (<i>Turdus philomelos</i>)	2	13	25
Spotted flycatcher (<i>Muscicapa striata</i>)	1	10	20
Starling (<i>Sturnus vulgaris</i>)	0	0	
Stonechat (<i>Saxicola torquata</i>)	0	14	
Swallow (<i>Hirundo rustica</i>)	2	5	1
Tree pipit (<i>Anthus trivialis</i>)	0	10	
Tree sparrow (<i>Passer montanus</i>)	0	0	
Treecreeper (<i>Certhia familiaris</i>)	3	1	0
Twite (<i>Carduelis flavirostris</i>)	0	7	
Wheatear (<i>Oenanthe oenanthe</i>)	2	0	1
Whinchat (<i>Saxicola rubetra</i>)	0	17	
Whitethroat (<i>Sylvia communis</i>)	1	20	15
Willow tit (<i>Poecile montanus</i>)	1	1	0
Willow warbler (<i>Phylloscopus trochilus</i>)	0	16	
Wood warbler (<i>Phylloscopus sibilatrix</i>)	2	14	15
Woodlark (<i>Lullula arborea</i>)	1	13	13
Wren (<i>Troglodytes troglodytes</i>)	0	18	
Yellow wagtail (<i>Motacilla flava</i>)	1	7	4
Yellowhammer (<i>Emberiza citrinella</i>)	2	12	17

nesting species, but the difference was not significant. This likely reflects the ability of species such as woodpeckers, snakes and rodents to physically access nests in cavities (Kuitunen and Aleknonis 1992; Czeszczewik 2004). We included studies using nest boxes, which are generally designed to reduce predation rates (Skwarska et al. 2009) and may have lower predation rates than nests in natural holes (Kuitunen and Makinen 1993) but we do not believe this affected these trends. Approximately half of the studies of hole nesting species included in our review were on populations nesting in natural holes, and although they suffered higher predation rates by corvids ($1.52\% \pm 1.15$) than nest box studies ($0.14\% \pm 0.14$), the reported predation rates were much lower than corvid nest predation observed on open nesting species. For non-corvid predators, there was no difference in predation rates between natural holes and nest boxes (natural holes predation rate $8.4\% \pm 2.78$; nest box predation rate $7.53\% \pm 2.65$).

Nest type did moderate the effect of nest height on non-corvid predation rates when only natural nests were considered. Open nesting species nesting at ground level suffered relatively higher predation rates compared to nests above

ground, but this relationship was not seen for hole nesting species. Open nests at ground level may be more accessible to some non-corvid predators, such as larger mammals like badgers (Brickle et al. 2000), whereas predators which prey on hole nests (such as woodpeckers or mustelids) may be less affected by nest height.

The timing of songbird breeding has often been related to variation in the risk of nest predation due to factors such as temporal variation in physical nest site attributes and in predator activity (Sperry et al. 2008). However, how the effect of the timing of songbird breeding may interact with the breeding phenology of predatory species has been less frequently examined. The extent of overlap between the breeding season of the songbird and jay and magpie breeding season provided a strong predictor of a nest's likelihood of being predated by corvids. Magpies, jays and other corvids may switch prey during their breeding season to meet the nutritional needs of their own young. A concentration on more nutrient rich prey when feeding nestlings is seen in a number of bird species including tawny owls (*Strix aluco*) (Sasvari and Hegyi 1998) and western gulls (*Larus occidentalis*), for example, the latter switch from foraging

mainly on garbage to taking mainly small fish when provisioning chicks (Annett and Pierotti 1989). Nest predation could also be a response to availability; the magpie and jay breeding season could correspond with a general peak in nesting. It has been proposed that corvids are capable of forming a search image following repeated encounters of the same prey (Croze cited in Montevecchi 1976). Therefore, it may be that a sudden increase in nests triggers the formation of such an image, facilitating subsequent predation of this prey (Isaksson et al. 2007). Corvids can also associate other cues including auditory cues (such as parental alarming (Bonnington et al. 2013) or chick begging (McDonald et al. 2009)) with songbird nests and an increase these other cues could further facilitate recognition, and consequent predation, of nests. The finding that the extent of overlap between the focal songbird breeding season and jay and magpie breeding season did not increase non-corvid predation of natural nests supports the conclusion that the effect of breeding season overlap on corvid nest predation rate is related to an ecological interaction between predator and prey, rather than a simple effect of time of year.

Interestingly, when artificial nest studies were included in analyses considering non-corvid predators, there was a negative relationship between the amount of overlap with jay and magpie breeding season and nest predation rate. Studies using artificial nests vary in methodology and can differ from natural nests in numerous ways which might explain this relationship. For example, the exposure period of artificial nest studies can be shorter than natural nesting periods, which could lead to much lower overlap with jay and magpie breeding season than seen for natural songbirds. Artificial nests studies generally found higher predation rates (corvid predation rate $14.66\% \pm 4.26$; non-corvid predation rate $16.51\% \pm 3.83$) than studies on natural nests (corvid predation rate $9.69\% \pm 1.58$; non-corvid predation rate $10.56\% \pm 1.42$). We suggest that the inclusion of some artificial nests studies with lower breeding season overlap and relatively high predation by non-corvid predators may explain the overall negative relationship between breeding season overlap and non-corvid predation rate (see Gregoire et al. 2003; Lopez-Iborra et al. 2004).

The ability of some artificial nests to represent natural patterns of predation, and composition of predator fauna, has been widely questioned (Pärt and Wretenberg 2002; Zanette 2002; Moore and Robinson 2004). However, the effects of nest type and breeding season overlap with jay and magpie on corvid nest predation were maintained whether or not artificial nests were included in the analysis. It may be that artificial nests can be used, with caution, to assess how some nest attributes influence predation risk.

Other aspects of study design also appear to affect reported nest predation rates. Accurate identification of nest predators is essential but often difficult (Schaefer 2004;

Ibáñez-Álamo et al. 2015). The results of our analysis suggest studies using indirect methods (such as observations of the predator fauna on the study site or signs obtained from concurrent studies using plasticine eggs) did differ in the nest predators they identified; these studies were likely to attribute a lower proportion of predation to non-corvids. The increasing use of video technology, and consequent increase in predator identification accuracy, may facilitate more detailed understanding of how differences in nest predator fauna relate to prey breeding biology (Ibáñez-Álamo et al. 2015).

Due to an absence of data available, we did not account for local variations in predator abundance or ecology at each of the study sites which could have influenced the occurrence and distribution of nest predation by specific predators. The data extracted from these studies were collected from 21 countries (mainly Western Europe) and over a relatively broad time scale (1954 – 2014; > 84% from 1990 onwards). This made it very difficult to account for variation in predator population density in either time or space. Such variation may explain differences in the relative contribution of different predator species across studies. However, analysis of European wide trends of predator populations suggests that, for corvids at least, there has been geographically widespread, long-term population growth (Voříšek et al. 2008).

Implications of findings

Our models indicate that particular attributes of nesting biology may make some songbird species susceptible to nest predation by corvids specifically; these attributes differ from those that affect nest predation by other predators. This could partially explain why correlational studies between corvid and songbird populations, and corvid removal studies, detect effects on productivity and abundance for some songbird species but not others. Some of these previous studies which do not find an effect have included more resilient species, such as hole nesting species in their analysis (Thomson et al. 1998; Bolton et al. 2007). Conversely some studies that focused on songbird species which we predict to be vulnerable to corvid predation (open-nesting species with high breeding season overlap with magpie and jay breeding season; Table 3) have found prey responses to changes in corvid number; Baláz et al. (2007) found black-caps had relatively high productivity in areas where corvids were absent, and a significant negative relationship has been found between corvid density and blackbird (*Turdus merula*) and song thrush (*Turdus philomelos*) nest survival rate (Stoate and Szczer 2001; White et al. 2008).

However, many studies do not find relationships between changes in corvid numbers and songbird species, even for species we predict should be vulnerable to corvid nest

predation such as dunnoek (*Prunella modularis*) (predicted corvid predation rate 23%) or chiffchaff (*Phylloscopus collybita*) (predicted predation rate 32%) (Table 3) (Gooch et al. 1991; Thomson et al. 1998; Chiron and Julliard 2007; Newson et al. 2010). It may be that studies exploring the relationship between corvids and songbird populations are themselves not equally likely to detect an impact of corvids if present. Study methodology could have an effect (Holt et al. 2008) experimental studies may be more likely than correlational studies to show an impact of corvids on particular species that we predict to be vulnerable. Some experimental studies do report a negative impact of corvids on songbirds we consider susceptible (Stoate and Szczur 2001). The paucity of such controlled experimental studies (cases classed as experimental studies in Madden et al.'s (2015) review of the impact of corvids on other bird species are sourced from just five papers, the majority (60%) from Chiron & Julliard (2007)) could affect the detection of relationships between corvid numbers and songbird species in the literature.

Study design or methodology is not the only factor influencing whether a study detects an impact of corvid nest predation on songbirds. There are several cases where species that we predict should be susceptible to corvid nest predation did not benefit from experimental corvid removal. Some of these mismatches between our model predictions and the population changes recorded may arise because corvid nest predation was affected by factors other than songbird nesting biology. There are a range of additional factors, including variation in habitat (Dunn et al. 2016), in landscape context (Pedersen et al. 2009), in land management (Ponce et al. 2018), in corvid population numbers and in other predator populations (Bodey et al. 2009), likely to affect the impact of corvid nest predation on songbird populations. The influence of other predator populations could be particularly important; a review of studies examining the impact of corvids on other bird species suggested that in many cases predation by corvids is likely to be compensatory (Madden et al. 2015). In many ecosystems songbirds are threatened by a number of nest predator species, and in the absence of one predator species, another is likely to take the nest (see Parker (1984)).

It could also be that breeding success is limited by factors other than nest success. Post-fledging survival is rarely studied (Cox et al. 2014), and it was not possible to include the impact of corvid predation on fledgling survival in this review; it may be that some species where we did not find an effect of corvid predation at the nest stage are predated by corvids in the fledgling stage (Chiron and Julliard 2007). This could also explain mismatches between corvid removal and songbird population response. Finally, it may be that success at the breeding stage is less likely to influence overall population numbers; variation in other demographic factors

such as overwinter survival may be important (Siriwardena et al. 1998) (see S3).

Developing a better understanding of the mechanisms which limit songbird populations will be critical in halting further population decline (Newton 2004). The results of this review suggest that a negative impact of corvid nest predation on UK songbirds cannot be entirely discounted. Some songbird species, defined by aspects of their nesting biology, may benefit in terms of their nesting success from a reduction in corvid nest predation. However, further exploration of the possible impact of compensatory predation and non-predation related factors, on both songbird breeding success and songbird population numbers, would be necessary when considering different conservation management strategies.

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