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Authors: Sage, Rufus B., and Aebischer, Nicholas J.

Source: Wildlife Biology, 2017(1)

Published By: Nordic Board for Wildlife Research

URL: https://doi.org/10.2981/wlb.00375

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Wildlife Biology 2107: wlb.00375
doi: 10.2981/wlb.00375
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Subject Editor: Christian Hagen. Editor-in-Chief: Ilse Storch. Accepted 29 October 2017

Does best-practice crow *Corvus corone* and magpie *Pica pica* control on UK farmland improve nest success in hedgerow-nesting songbirds? A field experiment

Rufus B. Sage and Nicholas J. Aebischer

R. B. Sage (rsage@gwct.org.uk) and N. J. Aebischer, The Game and Wildlife Conservation Trust, Fordingbridge, Hampshire, SP6 1EF, UK.

The role of predation by corvids on the breeding output of songbirds is unclear. Using a randomised-pair design, we measured how nest success of hedgerow-nesting passerines responded to the experimental removal of carrion crows and magpies. We worked in southern England at 32 paired sites around 4 km^2 each, one with and one without best-practice corvid control, studying four different pairs per year for four years 2011–2014. We counted corvids, and using songbird territory mapping and fledged brood counts without finding nests along transects, we estimated nest success as a brood/territory ratio for the community of songbirds in 4 km of hedgerow at each site. Crows and magpies were still present at most removal sites but numbers were half as high as at paired non-removal sites. Eighteen songbird species were frequently encountered at most sites with on average (±1 SD) 102 ± 30 territories per site. Using a generalised linear mixed model analysis the songbird community as a whole bred less well in treatment sites without corvid removal and in years with more rainfall. Nest success was down by 10% in non-removal sites on average relative to removal sites over the four years. Excluding 2012 data because of exceptionally high spring rainfall that year, nest success was down 16% in the non-removal sites on average in the other three years. For open-cup nesting species as a group there was no difference in nest success between site types. Our data on hole nesters suggest that they were affected by treatment and contributed to our overall result. For species whose numbers are regulated through territoriality, nest-site or habitat availability, spring abundance is unlikely to be affected by a 15% increase in breeding output. For species limited by nest success, it may be more important.

Assessing the potential for predator reduction to have a biologically significant impact on prey species is important for practical and ethical reasons. Carrion crow *Corvus corone* and magpie *Pica pica* control is often undertaken to reduce predation of ground-nesting game birds or waders because there is solid evidence of a predation impact on these groups (Tapper et al. 1996, Summers et al. 2004, Bolton et al. 2007, Fletcher et al. 2010). Protecting breeding farmland songbirds is also sometimes cited by game and other land managers as a reason to undertake crow and magpie control but the evidence supporting this practice is mixed. There have been several reviews and meta-analyses of previous studies of predator impacts on birds in the last 10 or 20 years. Côté and Sutherland (1997), Gibbons et al. (2007, Holt et al. (2008) and Madden et al. (2015) all report that there is a lack of good experimental studies in relation to corvids and passerines. Holt et al. (2008) include none and Madden et al. (2015) refer only to correlative studies.

Gooch et al. (1991) used data from the UK Nest Record scheme (NRS, Crick et al. 2003) from 1966 to 1986 to show no decline in nest success for 15 songbird species, when magpies increased at a rate of 5% per year. However they describe the limitations of a study based on 'associations'.

Siriwardena et al. (2000) looked for relationships between NRS data and population trends in 12 farmland passerines and found that for only one, linnet *Carduelis cannabina*, was fledgling production supressed by increased nest predation. Newson et al. (2010) looked at long-term national monitoring datasets for correlations between spring abundance of 28 lowland farmland songbird species and crows and magpies. They found several positive associations (i.e. prey increases alongside increasing predators), three negative associations for species with magpie and no negative associations for crows. Paradis et al. (2000) showed that spatial variations in nest failure rates for blackbird and song thrush were explained most effectively by variation in corvid abundance.

There is also direct evidence from monitoring studies that crows and magpies can be predators of bird species that nest

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off the ground (Stoate and Szczur 2005, White et al. 2008, Smith et al. 2010) and that targeting generalist nest predators locally (including mammals) can have benefits for non-game lowland farmland bird species (Donald et al. 2002, Stoate and Szczur 2006, White et al. 2008, 2014, Aebischer et al. 2016). There is however little direct evidence that predation by corvids alone can cause a significant reduction in passerine breeding success or that this might reduce recruitment and hence lower population size (Gibbons et al. 2007). Measurement of the breeding success of birds is essential in studies of demographic processes but even if breeding success is reduced by predation this does not mean that breeding population size will be affected (Newton 1998, Thompson 2007).

In their review, Madden et al. (2015) suggested that rigorous corvid-only removal experimental studies were required to assess the biological significance of corvid predation on passerines. Other more general reviews of predators and birds stress the value of experimentally removing predators to see if the prey responds (Paradis et al. 2000, Nicoll and Norris 2010). This has been done for a few sedentary or philopatric ground-nesting birds such as lapwing *Vanellus vanellus* (Bolton et al. 2007), grey partridge *Perdix perdix* (Tapper et al. 1996) and moorland waders (Fletcher et al. 2010). For passerines there are essentially no data of this kind.

Here we present the results of a four-year experimental study based on a randomised pair design, with corvid control as the treatment. We measured the effectiveness of the corvid control and compared songbird nest success between the treatment (corvid removal) and an untreated 'control' site in each pair. To avoid biases that can arise when using traditional nest monitoring or mist-netting techniques in an experimental context (Bart 1977, Peach et al. 1996, Crick et al. 2003, Weidinger 2009) we measured nest success of hedgerow-nesting farmland passerines as a brood-to-territory ratio using fledged brood counts without finding nests.

Material and methods

Study sites

Songbird territory mapping, songbird fledged brood counts and corvid counts were undertaken at 16 pairs of farmland sites with hedges, songbirds, crows and magpies in southern England (Table 1). Each pair of sites was studied in one year only with four pairs per year for four years. Paired sites were either located on the same farm or estate or on different but nearby holdings. The minimum distance between nearest site boundaries in a pair was 2 km although normally it was greater than this. Our songbird pilot work (Sage et al. 2015) suggests that at this minimum distance, sites within pairs would be independent in terms of breeding songbirds. We anticipated that sites would also remain independent in terms of the effects of corvid control, which targets territorial birds, because crows and magpies maintain small territories during and after breeding (Vines 2008). However non-territorial birds move around the landscape more and may have moved between sites within pairs. The possibility that this might reduce our ability to detect differences in corvid numbers between paired sites is discussed in the context of our results. Estates already practising corvid control for gamebird management on potential sites were not excluded as long as there were crows and magpies present in the early spring. Assessments of site suitability in terms of crow and magpie numbers and pre-existing predator control activities were made by observations and through discussions with land managers.

To collect sufficient data on songbird breeding success we aimed to include at least 4 km of suitable hedgerow in a central area within a larger overall site where corvid control was possible. Hinsley and Bellamy (2000) provide guidance on the potential suitability of hedgerows for breeding songbirds in the UK. We were interested in defining transects that contained a significant proportion of hedges 2 m or higher, with the shrubby part extending to meet the ground

Table 1. The 16 pairs of sites used in the study and the total number of crows and magpies caught and dispatched at each of the 16 treatment sites. Control type: 1 – professional gamekeeper, 2 – other pest control expert, 3 – farmer or assistant. Survey is the surveyors initials (see Acknowledgements). Site code refers to each pair of sites – see also Fig. 1 for corvid count data by site code. No effect was detected ($p > 0.1$) of controller type on numbers of magpies or crows caught and dispatched.

Pairs				Corvid control result		
Year	Site code	Survey	County/shire	Control type	Magpies	Crows
2011	A	TP	Warwick	2	24	18
2011	B	SW	Dorset	3	4	20
2011	C	JS	Leicester	1	15	25
2011	D	TP	Hereford	2	35	5
2012	E	SW	S Hants	1	68	287
2012	F	MS	Norfolk	1	34	9
2012	G	TP	Oxford	1	37	22
2012	H	TP	Warwick	2	30	32
2013	I	TP	Oxford	1	48	14
2013	J	SW	N Hants	1	27	91
2013	K	AG	E Hants	3	6	61
2013	L	TP	Warwick	2	46	16
2014	M	TP	Oxford	1	60	79
2014	N	TP	Wilts	3	61	40
2014	O	AG	W Sussex	1	38	63
2014	P	SW	Hants	1	31	55
Total					564	837

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vegetation and not excessively thin in cross-section. Larger unmanaged hedges with standard trees were included but not shelter-belts or woodland strips. Hedgerow transects tended to zig-zag through the sites with variable orientations. We made no attempts to assess songbird abundance at prospective study sites. Paired sites needed to have broadly similar hedgerows in relation to their typical gross structure (i.e. shrubby density and presence/absence of standard trees), be roughly the same size, have similar overall cropping and similar previous game management protocols especially in relation to corvid control.

Treatments

Within each pair, one of the two sites was chosen at random to have crows and magpies removed, while the other was left alone. While it is permissable to kill or take crows and magpies in order to 'conserve wild birds, and conserve flora and fauna' under the arrangements of a General Licence in the UK, crows and magpies are protected under the Wildlife and Countryside Act 1981. The corvid control work at the four study sites in each of the four years 2011 to 2014 was undertaken in accordance with four separate Natural England Licences for which we applied each year (20111309, 20121198, 20130733, 20140390).

We asked participating sites to employ best-practice crow and magpie control, to run at least four Larsen traps on the corvid control site from early April to the end of June, to adhere to the project licence and to follow Game & Wildlife Conservation Trust guidelines (GWCT 2014). A Larsen trap is a small cage trap with a live decoy bird and trap door, specifically designed to catch crows and magpies. Some sites also used other corvid control techniques allowed by the project licence, including ladder traps (a larger multi-catcher with slotted opening) and shooting with a shot-gun.

Sites had one of three types of predator control practitioner employed on the study, either a professional gamekeeper, a pest control contractor, or an experienced farmer or farm worker (Table 1). At most sites corvid control was previously practised on all or part of the holding. At about half of these, the project requirement was to stop controlling crows and magpies at the non-removal site. We asked the corvid control person at each site to record the number of crows and magpies that they caught and dispatched within their removal site.

Data collection

The method used to estimate the breeding success of hedgerow-nesting songbirds in this study is described in detail in Sage et al. 2015 (see also Sage et al. 2011). It involved a survey programme of adult breeding territories and of fledged broods at each plot. The basic approach is commonly used for ground-nesting bird species (Gilbert et al. 1998), which involves counting adults and fledged young to calculate a young-to-old ratio.

Bird surveys

We used three experienced bird surveyors each year, one of whom worked full time and surveyed two pairs of sites, while the other two surveyed one pair each. The same surveyor was used at each of the two sites in a pair (to avoid possible surveyor bias within the pair). They surveyed the pre-defined 4-km hedgerow transect running through the site twice a week, avoiding wet and windy weather. Surveyors were able to do one pair of sites per day. Although transects were all close to 4 km long, survey time varied considerably from around 1.5 hours up to about 3.5 h depending on walking conditions, gaps within transects and the workload in terms of observations and recording.

For the territory assessments the surveyor used standard territory mapping techniques similar to those described in the BTO Common Birds Census (CBC) methods (Marchant 1983). Encounters with birds and basic types of behaviour were recorded onto visit maps. Each hedgerow was initially surveyed six to eight times during April/early May and then twice a week after that until early July so that in total around 20 surveys were conducted at each study site. This intensive programme was designed to provide a near-complete count of songbird territories in the study sites, with two or more registrations indicating a territory. Commencing in early May we also looked for fledged broods during surveys. These fledged-brood surveys were undertaken in the morning and late afternoon (Sage et al. 2015). The emphasis was on looking for signs of breeding and counting fledged broods before broods matured and broke up. Nest searches were not conducted. All encounters with fledglings were recorded on separate visit maps for each survey and allocated to the nearest territory of that species. It was usually not possible to record the number of individuals in each brood so the data were brood presence or absence.

Predator surveys

Numbers of crows and magpies, other corvids, raptors and possible predatory mammals at our 32 sites were recorded during our songbird assessment surveys. A transect survey along hedgerows is not the ideal method for assessing the presence and abundance of certain avian and especially mammalian predators, but to do dedicated predator surveys was beyond the resources of the study. The strength of the predator records was the amount of time over which data could be collected (typically 20 surveys and 50 h per site). We recorded numbers of individuals at each site on each survey. The landscape at all sites consisted of farmland and hedgerows and the likelihood of detecting crows and magpies was similar across sites. We used these data to calculate mean numbers per hour of crows and magpies and for other common potential predator species during the main part of the study period (April, May and June).

Analysis

For fledged broods, our analysis took into account brood detectability to adjust for missed broods, thereby reducing the likelihood of bias in our estimates of productivity. Where the possibility of error or bias might exist is discussed in detail in Sage et al. (2011, 2015) and in the Discussion.

We calculated brood detection and occupancy probabilities using the software package 'Presence' (< www.mbr-pwrc.usgs.gov/software/presence.html >; MacKenzie et al.

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2002, 2006). First, the analysis calculated simple daily detection probabilities for each species at any one site using encounter rates with fledged broods during the fledging to maturity period. These are the probabilities of detecting a brood in any one survey. The fledging to maturity period is the average number of days from when a brood leaves the nest to when it breaks up and was taken from the literature as summarized in Cramp (1985, 1988, 1992) and Cramp and Perrins (1993, 1994). Fledging to maturity period for species encountered in this study varied between about 10 and 18 days, equivalent to the period covered by three or four surveys. For a particular species at a site, if the mean encounter rate of broods was two and there were four visits before maturity the detection probability for the species would be 0.5. This assumed that broods seen on several occasions were first detected soon after fledging. When, very occasionally, surveyors identified a second (later) fledged brood from a territory, only the first was included in analysis.

The Presence software then adjusted the observed probability of territory occupancy by a fledged brood (simply the number of fledged broods encountered for each species/hedgerow, divided by the number of breeding territories) by taking account of the brood detection probability at that site.

This new adjusted occupancy probability included fledged broods estimated to have been present but not detected. For species where fledged broods were seen infrequently, i.e. had a low detection probability, the new adjusted occupancy probability estimated by Presence differed more from the observed occupancy probability than for species where broods were seen frequently (Sage et al. 2015).

We took this adjusted occupancy probability as an estimate of songbird nest success (Success) and examined its relationship with our treatment and other variables using generalised linear mixed modelling (GLMM) in Systat ver. 12. Year and Pair within Year were included as random factors. We first tested whether songbird nest success (Success) differed between removal and non-removal sites within pairs using a two-way fixed treatment variable Treat. Rainfall during April–June for southern England was included as a fixed variable (Rain). Rainfall was 320 mm in 2012 and half this or less in the other three years (<www.metoffice.gov.uk/climate/uk/summaries>). The Rain × Treat interaction was included but then dropped if it was not significant. We then tested whether Success was related to our corvid count data (Count) included as a fixed continuous variable. To do this we repeated the GLMM analysis above except that Treat was replaced with Count.

The adjusted estimates of nest success (Success) calculated by Presence had associated standard errors. In our GLMM analysis we gave less weight to estimates with high standard errors, using the inverse of the variance (standard error squared) as a weighting factor. Residuals from proportional data are usually not normally distributed so Success was transformed using a logit transformation log(Success/(1 – Success).

We analysed data for the all-birds group, and then for hole (or cavity) nesters and for open-cup nesters separately (Supplementary material Appendix 1). If our analysis identified differences in Success with treatment or corvid numbers, we calculated mean and maximum differences between sites within pairs using weighted site estimates as before.

Our fledged brood count data were collected with the aim of calculating brood detection and occupancy (nest success) probabilities only. We were unable to undertake analysis of brood survival because we did not know if or when broods failed and could not be certain about brood identity.

Results

Crows and magpies

The number of crows and magpies caught at each study site was not related to controller type ($F_{2,13} = 0.984$, $p > 0.1$, Table 1). The number of crows recorded per hour during our survey programme was lower at the removal site than in the corvid non-removal site at 14 of the 16 pairs of sites (Fig. 1). On average crow abundance was reduced significantly by 50% (Fig. 2). The number of magpies per survey hour was lower in the corvid control plots at 11 of the 15 sites that had magpies (Fig. 1), with a significant average reduction of 44%. For crows and magpies combined there was a significant reduction of 49% (Fig. 2).

Other predator data

Jay *Garrulus glandarius*, sparrowhawk *Accipiter nisus* and kestrel *Falco tinnunculus* occurred at many sites in low numbers. Buzzard *Buteo buteo* was also widespread and occurred frequently at sites. Rook *Corvus frugilegus* and jackdaw *Corvus monedula* were common at some sites but not at others. The mean difference in the number of any of these raptors or other corvids between plot types was not different to zero ($p > 0.1$ in all cases). Too few mammalian predators were encountered to test for differences between plot types.

Songbirds

Twelve songbird species were seen at every site in the study and a further six were seen at most (Supplementary material Appendix 1). These 18 species dominated our nest success data in this study. We found on average (± 1 SD) 102 ± 30 passerine territories in each of the 32 study sites (Supplementary material Appendix 2). The overall simple occupancy probability (ratio of broods to territories as surveyed), the detection probabilities and the adjusted nest success as calculated by Presence and used in the analysis are also shown in the Supplementary material Appendix 2.

Songbirds and corvid control

All-birds group

At 10 of the 16 sites in our study, our adjusted estimate of nest success in the all-birds group, Success, was higher at removal sites than in the paired non-removal sites (Fig. 3). In our GLMM model the interaction term Treat × Rain and Treat were both significant at $p < 0.05$ (Table 2). Nest

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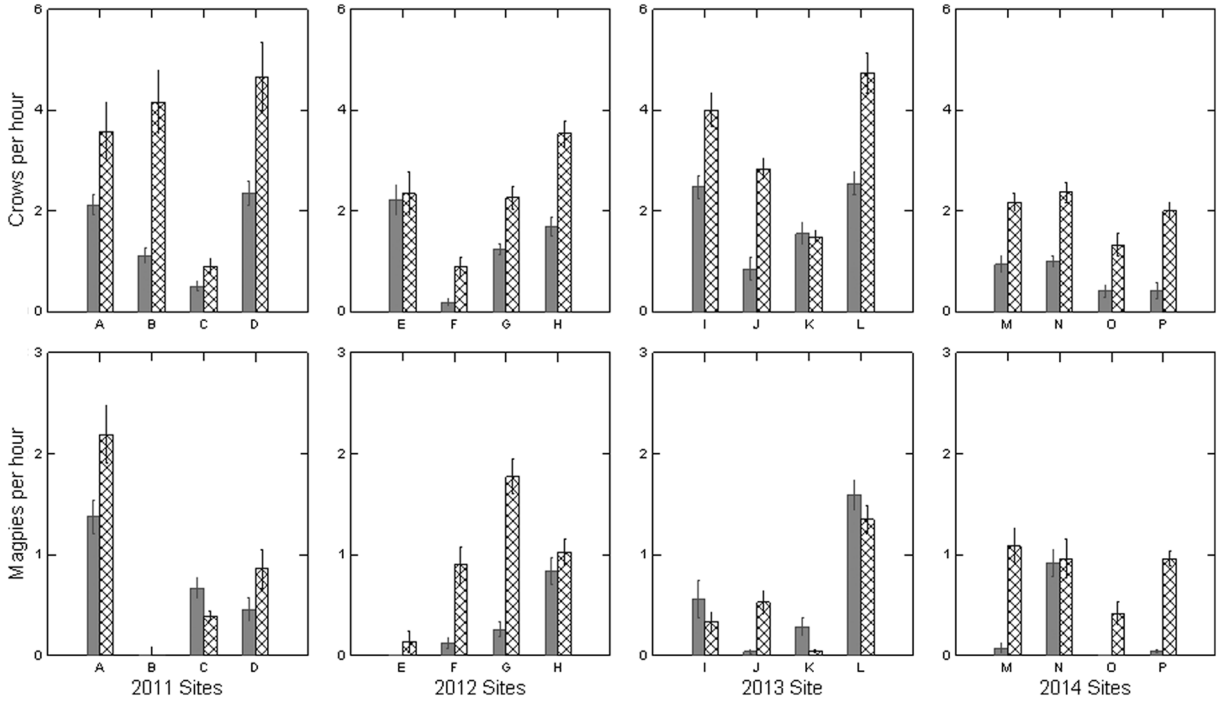


Figure 1. Abundance (mean ± 1 SE) of crows (top) and magpies (bottom) recorded per hour of survey in the two study sites (shaded = removal, hatched = corvid) in each of the 16 pairs of sites based on the 15 or so surveys undertaken between late April and June. See Table 1 for site codes.

success of the songbird community was higher at the corvid removal site in lower rainfall years and overall. Over the four years, the mean adjusted nest success in non-removal corvid sites was 0.519 ± 0.021 and the mean difference between sites within pairs was 0.053 ± 0.020, representing an increase of 10 ± 4% on removal sites compared to non-removal sites (Table 3). Over the three years with average or lower rainfall (April–June) the mean difference was 16% ± 3%. In 2012, with three times the average rainfall, there was no improvement in nest success in the removal site (Table 3).

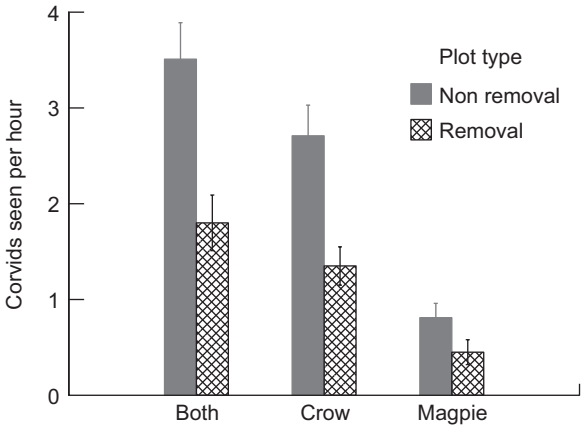


Figure 2. Mean number of crow and magpie sightings per survey hour per site type, in relation to corvid control treatment (undertaken in, typically, March–June). Difference between site types was significant for crows (paired $t_{15} = 6.51$, $p < 0.001$), magpies ($t_{15} = 2.69$, $p = 0.017$) and both ($t_{15} = 6.96$, $p < 0.001$).

Open-nesting and hole-nesting species

For open-nesting species, there were nine pairs of sites where nest success was greater at the plot with corvid removal and seven where it was lower (Fig. 3). For this group there was no overall effect of Treat, Rain or the interaction between these terms on Success (Table 2).

At 10 of the 16 sites, nest success of hole-nesters was higher at sites with corvid removal. Figure 2 also shows much better nest success for this group of species than for open nesters. At some sites every breeding territory produced a fledged brood. For Success in hole-nesting species, the interaction between Treat and Rain was not significant. Rain was significant at $p < 0.05$. Treat was not significant at $p < 0.05$ but was at $p < 0.1$ (Table 2).

Songbirds and corvid count data

For the all-birds group there was no relationship between Success and the corvid count data Count ($F_{1,15} = 0.34$, $p = 0.56$) or with Rain ($F_{1,15} = 2.63$, $p = 0.13$). For hole-nesters Success was affected by Rain ($F_{1,14} = 5.32$, $p = 0.04$) only (Count, $F_{1,15} = 0.01$, $p = 0.95$) with reduced productivity in wetter years. For open nesters there was no relationship between Success and Count ($F_{1,15} = 0.93$, $p = 0.35$) or Rain ($F_{1,15} = 1.06$, $p = 0.32$).

Discussion

This study used best-practice corvid control at the 16 treatment sites, as currently implemented by typical countryside trappers working under the UK general licence

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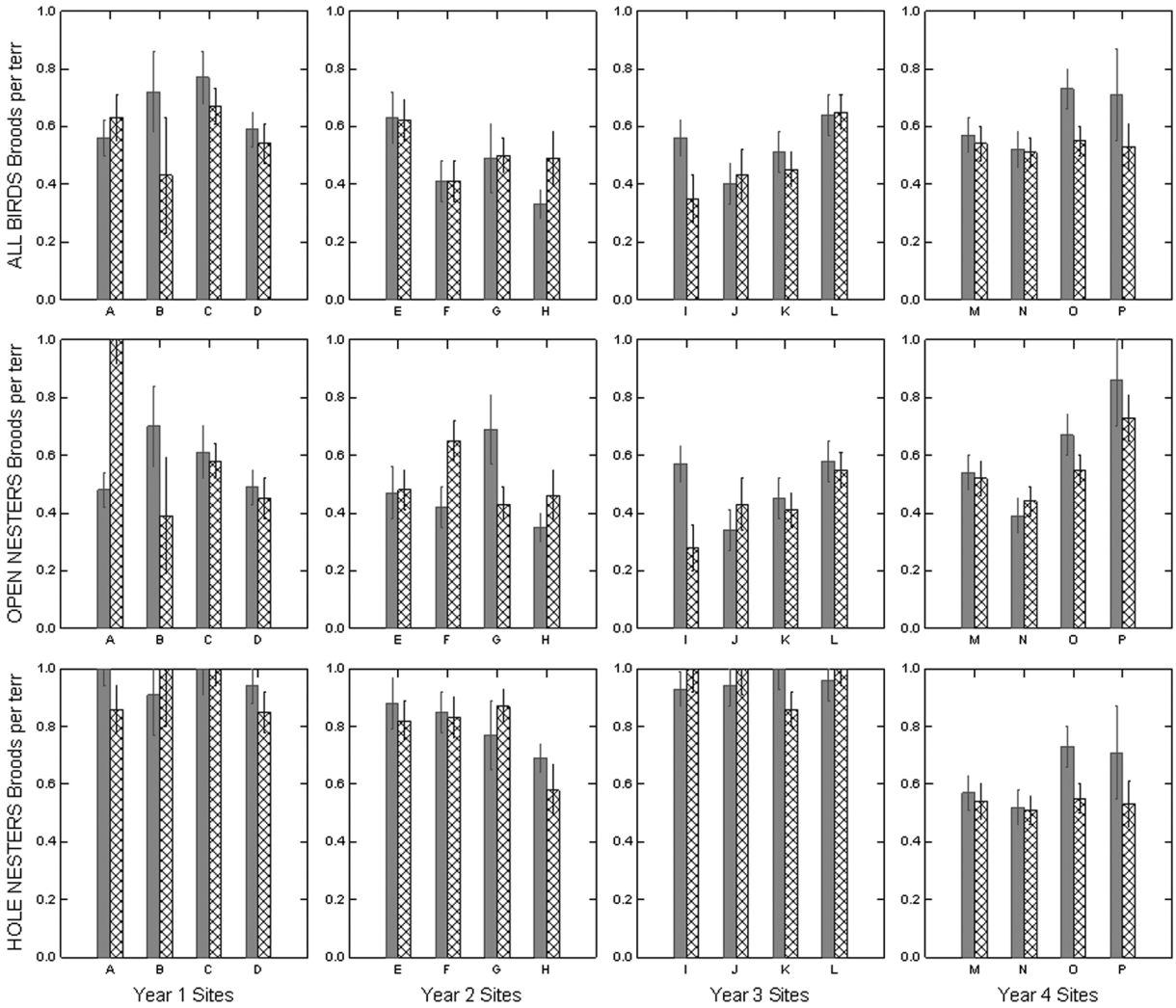


Figure 3. Adjusted mean (± 1 SE) nest success at each pair of sites (shaded = removal, hatched = non-removal). Data shown for each study year separately, and for all birds (top row), open-nesters and hole-nesters. Values with low precision (large error bars) have less weight in the analysis.

(GWCT 2014). These treatments made significant reductions in the numbers of crows and magpies at most removal sites but did not eliminate them from most (Fig. 1). On average there were still around half as many crows and half as many magpies at removal sites compared to the 16 paired non-removal ones (Fig. 2). We could not detect a difference in the abundance of other potential avian predators between site types.

Over the four years and 16 pairs of sites our calculations of adjusted occupancy or nest success using the Presence software for the passerine community as whole indicated that around 55% of the territories of all the songbird species encountered produced a brood. This is broadly in line with figures on nest success from the literature, which are highly variable, e.g. chaffinch *Fringilla coelebs* 18–60%, linnet 25–55%, blue tit *Cyanistes caeruleus* 33–95%, yellowhammer *Emberiza citronella* 31–70%, blackbird *Turdus merulus* 30–56% (Cramp 1985, 1988, 1992, Cramp and Perrins 1993, 1994). Our corvid removal treatments lead to an overall improvement in nest success of around 10% by hedgerow-nesting birds in those plots compared to the non-removal plots (Table 2, 3). While the overall difference in nest success within paired sites was significant, the hedgerow-nesting bird community that we studied bred

Table 2. Tests of the effect of corvid control treatment (Treat) and rainfall in April – June (Rain) on adjusted songbird nest success (Success). The final model is shown without the interaction term if not significant.

Success	Treat	Rain	Treat × Rain
All birds	$F_{1,14}=6.61$, $p=0.022$	$F_{1,14}=3.08$, $p=0.101$	$F_{1,14}=4.79$, $p=0.046$
Open nesters	$F_{1,15}=0.53$, $p=0.480$	$F_{1,15}=0.81$, $p=0.380$	
Hole nesters	$F_{1,15}=3.32$, $p=0.089$	$F_{1,15}=6.52$, $p=0.022$	

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Table 3. Summary statistics for adjusted nest success in relation to estimates and differences between plot types ± 1 SE for the all-bird group. Means for all 4 years and because of the significant effect of rainfall means for the three years excluding 2012. In the three months April to June, 2011, 2013 and 2014 had average or lower rainfall while 2012 had three times the average rainfall over the same period. Mean % difference is the mean difference between paired sites as a percentage of the nest success at the non-removal site.

Nest type	All four years	Three years 2011, 2013, 2014	2012
Mean nest success removal site	0.572 ± 0.024	0.607 ± 0.026	0.465 ± 0.050
Mean nest success non-removal site	0.519 ± 0.021	0.524 ± 0.017	0.505 ± 0.027
Mean difference between paired sites	0.053 ± 0.020	0.083 ± 0.018	–0.040 ± 0.019
Mean % difference	10.2 ± 3.9 %	15.8% ± 3.4%	<0

reasonably well in the presence of crows and magpies at all sites in all paired plots (Fig. 3).

Rainfall during April to June affected nest success in our analysis. Both April and June 2012 experienced between three and four times the average rainfall for those months (< www.metoffice.gov.uk/climate/uk/summaries/2012/summer > or .../spring >). Of the 22 migrant and resident passerines in the UK BTO Nest Record Scheme report for 2012, all but one had reduced fledging success compared to the long-term average (NRS: < www.bto.org/volunteer-surveys/nrs/results/nrs-preliminary-results-2012 >). Fledglings per breeding attempt for both magpie and crow were also substantially reduced in 2012 (< http://app.bto.org/birdtrends/species.jsp?year=2015&s=carcr or …&s=magpi >). In the other three years of study, corvid control increased nest success of the songbird community as a whole by over 15%.

While treatment was significant, we did not see an effect of our corvid count variable on nest success. Larsen traps use decoy birds and are effective at attracting and catching territorial individuals (GWCT 2014). These are considered more likely to exert predation pressure on songbirds than non-territorial birds (Vines 1981, Erikstad et al. 1982). Our counts could not distinguish between territorial and non-territorial birds, so it is possible that they did not reflect the predation potential of corvids at sites because of this.

We do not have a scientific comparison for our data as there are no previous studies that have attempted to quantify predation by these corvids or the effect of corvid control on passerines (Madden et al. 2015). Experimental studies of the effect of predator control and birds have focused on waders and other ground-nesting birds. For (mainly) these bird species, Côté and Sutherland's (1997) meta-analysis suggested that predator removal (mammalian and avian) increased hatching success by on average 75% and in over 80% of studies produced a larger post-breeding population size. Using a similar approach Smith et al. (2010) found that predator removal sometimes enhanced breeding population size as well. Holt et al. (2008) found a 1.6-fold increase in prey abundance with predator control (or 'predator absence'). In their review, a minority of studies found an effect of corvid predation specifically on the breeding output of ground-nesting birds but there was no quantification of this (Madden et al. 2015).

Our data quantify the effect of corvid control on songbirds for the first time. If corvids were somehow completely removed from our treatment plots we may have seen an improvement in songbird productivity greater than 10%. It may also be that the actual predation rate by corvids is higher than our study suggests because of compensatory predation (Newton 1998). This is where one predator is replaced by another, or where a second predator increases following removal of the first. We also found high variation in treatment effect between plot pairs. Corvids are opportunistic generalist predators with high cognitive abilities. The importance of particular food items to individuals will vary depending on alternative food sources and other factors (Holyoak 1968, Birkhead 1991). It is also likely that crows and magpies were not similarly predatory. Magpies are smaller than crows, adept at moving through dense shrubby hedges and capable of predating a wider variety of nest types in hedges (Cramp and Perrins 1994, Vines 2008). It may be that magpies were more predatory in our study than crows and hence controlling magpies may be more beneficial to songbirds.

Individual songbird species were not sufficiently abundant to provide useful estimates of nest success in relation to treatment in each site in our study. We have not investigated groupings based on perceived susceptibility to predation (other than hole-/open-nesting) because the risk of predation varies with a variety of potentially subtle environmental parameters within species as well as between them. This includes nest location or concealment (Söderström et al. 1998, Weidinger 2002) and nest height (Ludvig et al. 1995, Weidinger 2002). For example long-tailed tit *Aegithalos caudatus* nests located higher up in the shrub layer were more likely to be predated by corvids than those lower down (Hatchwell et al. 1999) and for reed warbler *Acrocephalus scirpaceus* nests the reverse was true (Catchpole 1974). The timing of breeding (Mallord et al. 2008) and parental behaviour (Weidinger 2002) are also important. Predation risk for hedgerow-nesting songbirds varies with hedge structure and its potential to provide cover and reduce accessibility to corvids (Dunn et al. 2016).

Given our overall significant effect, it is perhaps odd that we did not see a significant effect for open-nesters when we looked at this group separately and that predation of the common hole-nesters (mainly blue tit and great tit *Parus major*) may have contributed to our overall finding. We think that both groups were being predated in our study and these counter-intuitive group results are partly an artefact of the analysis. For open-nesting species, detection probabilities or encounter rates at some sites were low (Supplementary material Appendix 2) and hence produced poor estimates of adjusted nest success as indicated by the error bars in Fig. 2. MacKenzie et al. (2002) suggested that the detection probabilities need to be around 0.25 or more to provide reasonable estimates of occupancy. While our weighted analysis reduced the influence of sites with relatively poor estimates of productivity, it could not overcome the fact that at some

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sites our estimates were not accurate enough to identify an effect in a noisy dataset. Detection probabilities for hole-nesters were much better, which means that our nest success estimates were generally more precise for this group.

Hole nesting is primarily a predator-avoidance strategy in birds (Newton 1998) and open-cup nests are usually shown to be more vulnerable to predation (Thompson et al. 1998, Stoate and Szczur 2001, Morosinotto et al. 2012). We suggest it may be that hole-nesting passerines are more likely to use sub-optimal nest sites in hedgerows where holes or other cavities in timbers may be absent or uncommon (Cramp and Perrins 1993, Ferguson-Lees et al. 2011). Blue and great tit broods are also particularly noisy and conspicuous (Cramp and Perrins 1993). In our study, fledged broods of these two species had the highest encounter rates and hence detection probabilities of any species. It is noteworthy that in their investigations of avian predators and 28 lowland farmland songbird species (i.e. not woodland communities), Newson et al. (2010) identified blue tit as one of three species negatively associated with magpie.

In summary, both groups of hedgerow birds, open- and hole-nesting, were probably predated by corvids at most sites in our study to a varying extent. Despite this variation, overall nest success at our 16 pairs of sites was significantly lower in the presence of uncontrolled crows and magpies but not hugely so. Our findings provide new evidence that best-practice magpie and crow control can lead to improvements in the nest success of farmland hedgerow birds. We do not know if there was a differential effect between the two corvid species but suggest that magpie may be more important. The scale of the improvement was not large and the impact of a 10–15% increase in nest success on autumn or spring abundance will vary between species. For species whose numbers are regulated through territoriality, nest-site or habitat availability, the number of breeding adults in the following spring is unlikely to be affected; for species where breeding output is limiting adult numbers the following spring the effect of corvid control could be important (Newton 1998).

Assumptions and limitations

In relation to our corvid control treatment, while we cannot be sure that non-territorial individuals did or did not move from one site to another within a pair, our overall significant treatment difference for combined crows and magpies suggests that such movements were relatively uncommon compared to the overall abundance of individuals within sites. Further experimental studies could assess this and aim to further or completely remove corvids from study plots for comparison. Corvid control undertaken year after year would be expected to lead to greater suppression of their numbers over time (GWCT 2014).

Using fledged brood count data to evaluate passerine nest success makes some assumptions that have not been properly explored (Sage et al. 2015). In particular mortality and dispersal of fledged broods at the edges of study plots may affect counts in discrete plots such as those used in this study. Dispersal or fate of fledged songbird broods pre independence has not been well documented but the evidence available suggests that distances are small compared to the size of our study plots (Cox et al. 2014, Sage et al. 2015). Late-summer surveys of young game birds and waders encounter these potential problems, but are widely and successfully used to calculate young-to-old ratios as an annual index of breeding success (Gilbert et al. 1998). Another potential source of bias in our study is the possibility of songbirds creating territories and producing nests to predate before the territory was identified. We addressed this to an extent by applying a regular survey programme from a start date in early April but recognize that it is possible that one or two early-nesting species, in particular song thrush *Turdus philomelos*, may have slipped through this net. Analyses of Nest Record Scheme data, which are widely used to provide estimates of nest success for UK bird populations, make some similar assumptions that have been more fully explored (Crick et al. 2003). We also assume that broods were initially detected soon after fledging. For broods seen several times the likelihood of this was high. For broods seen only once, the likelihood is lower but the sighting was still likely to be during the fledgling-to-maturity period so the calculated detection probability was unaffected. A further limitation of the method is that fledged broods were counted, not the number of young (which was too difficult to measure in the field). While predation is considered to usually cause complete nest failure rather than partial losses (Gooch et al. 1991), our study does not take account of possible partial nest losses. This too may reduce sensitivity in detecting an effect of predation.

We suggest that while our brood survey techniques may produce a slightly inaccurate measure of local nest success because of some of these factors, in a paired study of this kind, it is unlikely to be biased in relation to treatment to any great extent. Further improvements in the fledged brood survey technique that allows the date of fledging to be evaluated, and the accurate identification of individual fledged broods on subsequent occasions, may facilitate the application of survival analysis techniques. If we had undertaken three fledged-brood surveys per week rather than two, the study may have had a better chance of detecting a significant effect of corvid control on nest success in the open-cup nesting group of birds (Sage et al. 2015).

Acknowledgements – We are very grateful to the owners of participating estates, and to their land and game managers who altered pre-existing management plans to accommodate this study. We thank our skilled bird surveyors Sue Wilson, Tony Powell, John Szczur, Alan Goddard and Mikel Salvador for undertaking the fieldwork.
Funding – The study was funded by SongBird Survival.

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Supplementary material (available online as Appendix wlb-00375 at <www.wildlifebiology.org/appendix/wlb-00375>). Appendix 1–2.

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