Predation and songbird populations

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In order to consider whether the widespread declines of British songbirds may be linked with the spread of their avian predators, we provide an overview of two studies. In one, the abundance of Magpies *Pica pica* and Carrion Crows *Corvus corone* were manipulated at three farms in Leicestershire and the breeding success and abundance of songbirds was studied. In the other, extensive historical data from the Common Birds Census were used to look at whether the presence of Magpies or Sparrowhawks *Accipiter nisus* at individual sites affected the rates of songbird population change. In Leicestershire, songbird breeding success was higher and breeding abundance increased when corvids were controlled, although the effects of predators on the latter could not be distinguished from possible effects of habitat changes over the same period. Any local effect of Magpies on songbird breeding success did not translate into a significant effect on the rates of songbird population change at sites throughout the country. There was also no evidence that Sparrowhawks affected rates of population change. It would appear that while individual songbirds can clearly suffer from predation, the national populations are resilient. The two different approaches discussed here each have their advantages and disadvantages, and this overview highlights the benefits of combining insights from both intensive local studies and from the modelling of extensive national data.

Over the last thirty years populations of many British songbirds have declined substantially. Although correlated with agricultural change and often particularly severe on farmland, the actual causes of these population declines are not well understood. Some have suggested that increased predation caused by expanding populations of Magpies *Pica pica* and Sparrowhawks *Accipiter nisus* should be investigated as a potential contributing factor (Fuller *et al*. 1995). Predation remains politically contentious even though the scientific evidence suggests that songbird breeding populations are in fact resilient to it (Newton 1993). With mounting evidence that gamebird populations can be affected by predation (Tapper *et al*. 1996, Redpath & Thirgood 1997), and with predation on songbirds being witnessed ever more commonly in the countryside, there is a popular belief that avian predators could have played a significant role in the songbird declines.

This paper provides an overview of two studies that shed light on the impact of avian predators on songbird population dynamics. In one, at three sites in Leicestershire, we have reduced the abundance levels of Magpies, Carrion Crows *Corvus corone* and other nest predators, and monitored both the nesting success and the abundance of breeding songbirds. In the other (Thomson *et al*. 1998), we have used 30 years of the British Trust for Ornithology (BTO) Common Birds Census (CBC) data (Marchant *et al*. 1990) from hundreds of sites across Great Britain to study whether the rates of songbird population change are lower in the presence of either Magpies or Sparrowhawks than in the absence of these predators. We aim to synthesise the results of these two approaches, quantifying the effect of nest predation on songbird breeding performance locally, and then considering whether such local effects are likely to have any sustained impact on the numbers of breeding songbirds.

METHODS

The Loddington study

Study areas

The research was conducted on three areas of mixed arable and livestock farmland in Leicestershire, namely Loddington (333 ha), Horninghold (144 ha) and Owston (196 ha). Each site comprised arable fields and grassland interspersed with hedges and small woods. Loddington and Owston included a length of the same disused railway. Loddington is a research and demonstration farm, owned and managed by the Allerton Research and Educational Trust. The two other sites were selected at 5 km from the centre of Loddington in each direction along a random bearing through the centre of the farm (Fig. 1).

Loddington includes a small-scale pheasant shoot, which depends exclusively on production of wild pheasants on the farm. Potential nest predators, such as Magpie, Carrion Crow, Brown Rat *Rattus norvegicus*, Stoat *Mustela erminea*, Weasel *M. nivalis* Mink *M. vison* and Fox *Vulpes vulpes* are therefore removed during the period in which gamebirds are nesting (April – July) in an attempt to increase both autumn and spring numbers of gamebirds (Tapper *et al*. 1996). Other forms of management intended to benefit gamebirds at Loddington include thinning and replanting of woodland, hedge management and the provision of seed-bearing cover crops on set-aside. Such management started in 1993, following a year of baseline monitoring (see below). This study is concerned mainly with the period 1995 – 1998, when nest monitoring was conducted at all three sites.

At Horninghold and Owston, no attempt was made to influence numbers of potential nest predators in 1995 and 1996. In 1997, Magpies were removed from Horninghold (by a land-owner) but not from Owston, and in 1998 Magpies were removed from both Horninghold and Owston, with Carrion Crows also being removed from Owston. At all three sites corvids were removed from early April to early July using Larsen traps and a shotgun. Emphasis was placed on Magpies because previous studies (e.g. Møller 1988, Groom 1993), and our own observations, had suggested that Magpies were major predators of passerine eggs and chicks. Other forms of management remained relatively constant at each site throughout the four years of the study.

Within these study areas, six species were selected for intensive study because they were present in sufficient numbers to provide adequate samples for nest survival analysis, and because they represented a range of avian guilds. These species comprised Blackbird *Turdus merula*, Song Thrush *T. philomelos*, Dunnock *Prunella modularis*, Whitethroat *Sylvia communis*, Chaffinch *Fringilla coelebs* and Yellowhammer *Emberiza citrinella*. All these species construct 'open-cup' nests, but vary in their choice of nest site. While most nest in trees or shrubby vegetation, all Whitethroats and most Yellowhammers nest in herbaceous vegetation. With the exception of Song Thrush at Owston, all species were present at each of the three sites.

Breeding bird abundance

The breeding abundances of Magpies and Carrion Crows at all three sites were monitored using annual nest counts. At Loddington, where game management began in 1993, transects across all habitats were used to provide an abundance index for all species. Transects were conducted in fine weather in May and June, in the first three hours of the day, four times each year. Transect routes were constant between visits and years. Rates of change in breeding abundance at Loddington from 1992 to 1998 for the study species were subsequently expressed relative to national changes in abundance over the 1992-1998 period (derived from CBC data), using the difference between the two figures for each species.

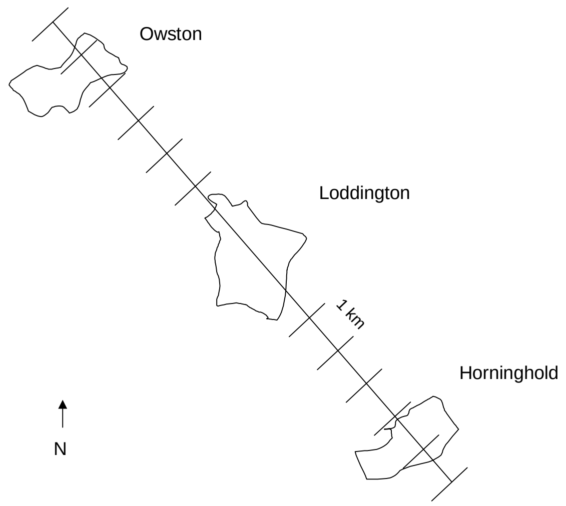

Figure 1. Relative positions of the three sites used for the intensive study of nest predation in Leicestershire.

Nest survival

Nest monitoring was conducted on all three sites from 1995 to 1998, from early April to late July each year. Nests were located by a combination of searches and observations of breeding birds and visited at 3- to 7-day intervals. Predation was assumed to have occurred if the contents of the nest had been removed since the previous visit, or if clear signs such as broken egg shells or partially eaten young were visible. It was rarely possible to determine the identity of nest predators from signs left at the nest. Nest height above ground and nesting habitat were recorded on the first visit, and nest concealment was recorded using a three-point scale of 'well hidden', 'part hidden' and 'exposed'. Meteorological data, comprising average daily temperature (mean of minimum and maximum) and daily rainfall, were provided by the Leicester Botanical Gardens located approximately 12 km west of our study area.

Statistical analysis

To avoid bias associated with locating a disproportionately large number of nests experiencing high levels of nesting success, estimation of daily probability of nest survival was based on the method of Mayfield (1975). We used an extension of this method (Aebischer 1999) to examine nest survival rates in relation to environmental variables comprising nest height and concealment, mean daily rainfall and temperature, as well as corvid abundance. We modelled nest outcome as a binary variable by logistic stepwise regression, incorporating the observation period (the time between nest discovery and either success or failure) as the binomial denominator. Laying, incubation and nestling stages of the nesting period were treated separately. Where nests failed between visits, failure was assumed to have occurred half-way between the penultimate and final visit. Where eggs hatched, or nestlings fledged between visits, the half-way point between visits was again assumed, unless the resulting timespan fell outside the known incubation or nestling period for the species concerned, when the nearest known period was adopted.

For each site and year, daily survival rates were estimated for each nesting stage, and combined to give the overall rate of nest success for each of the six main study species (Hensler 1985). Survival rates were first estimated from a model incorporating only 'site' and 'year' variables. To estimate the effect of corvid abundance on nest survival, independently of other variables, adjusted nest survival rates were then estimated using a model incorporating all non-corvid variables (site, year, habitat and meteorological variables). The relationship between overall nest survival rates and breeding abundance of Carrion Crows and Magpies was then assessed using Pearson correlation for each set of survival estimates.

The national study

We constructed a simple population model and, using data from the CBC, estimated its parameters statistically so as to test whether songbird population growth rates between consecutive years on individual CBC plots were lower when Magpies or Sparrowhawks were seen there. We used CBC data for the period 1965-1995, and we used only data collected with standard methods from those plots where seven estimates of population change between consecutive years could be made. We examined data for 23 species: Skylark *Alauda arvensis*, Meadow Pipit *Anthus pratensis*, Wren *Troglodytes troglodytes*, Dunnock, Robin *Erithacus rubecula*, Blackbird, Song Thrush, Mistle Thrush *Turdus viscivorus*, Chiffchaff *Phylloscopus collybita*, Willow Warbler *Phylloscopus trochilus*, Coal Tit *Parus ater*, Blue Tit *Parus caeruleus*, Great Tit *Parus major*, Nuthatch *Sitta europaea*, Starling *Sturnus vulgaris*, Tree Sparrow *Passer montanus*, Chaffinch, Greenfinch *Carduelis chloris*, Goldfinch *Carduelis carduelis*, Linnet *Carduelis cannabina*, Bullfinch *Pyrrhula pyrrhula*, Yellowhammer and Reed Bunting *Emberiza schoeniclus*.

The population model we used was:

$$\log_e(N_{t+1,i}/N_{t,i}) = R_t + a(S_{t,i}) + b(H_{t,i}) + c(M_{t,i})$$

where $N_{t,i}$ is the abundance of songbird territories in year t on plot i, R_t is the expected population growth rate $\log_e(N_{t+1,i}/N_{t,i})$ in year t in the absence of predation and intra-specific competition, b and c are the amounts by which the population growth rate is reduced below R_t if a Sparrowhawk or a Magpie is present respectively ($H_{t,i}$ and $M_{t,i}$ are therefore dummy variables which take the values 0 if Sparrowhawks or Magpies respectively are absent, and 1 if they are present). In the analysis we did not seek to test formally for the presence of density dependence, but we accommodated it in the analysis – a is the amount by which songbird population growth rates are reduced below R_t for each standardised unit of songbird abundance ($S_{t,i}$) on plot i in year t. We standardised songbird abundances because plots differed in their size and habitat, and because they were studied during different time periods. For each songbird species in turn, we therefore divided abundance by the average abundance of that species on the plot during the years over which it was censused, and multiplied by the average national population index during the period over which the plot was censused.

To estimate the relevant parameters of this model, and thus to test whether songbird population growth rates were affected by the predators, we constructed a generalised linear model with $N_{t+1,i}$ as the dependent variable. We used Poisson errors and a logarithmic link function, and because we fitted $\log_e(N_{t,i})$ as an offset (an explanatory variable with a fixed coefficient of 1) we excluded all cases where $N_{t,i} = 0$. We estimated R_t by fitting year as a factor. In order to find whether predators significantly reduced songbird population growth rates, we used Wald c^2-tests, adjusted for over-dispersion, to test whether b and c differed significantly from zero.

RESULTS

The Loddington study

There was a negative correlation between overall nest survival and Carrion Crow breeding density for all species, this relationship being significant for Blackbird, Song Thrush, Dunnock and Yellowhammer. A negative relationship between overall nest survival and Magpie density was also apparent for all species except Whitethroat, and was significant for Blackbird and Song Thrush (Table 1). After considering habitat and meteorological effects, the negative correlation between nest survival and corvid abundance was maintained for all species except for that between Whitethroat nest survival and Carrion Crow abundance, and, of the previously significant correlations only that between Song Thrush and Magpie ceased to be so.

Of the eight species for which nest survival data were available, Blackbird and Song Thrush showed the greatest difference in survival between Loddington and the mean of the other sites. Relative to the national trend, all species increased in abundance at Loddington, with Blackbird and Song Thrush showing the greatest increases (Table 2).

Table 1. Pearson coefficients of correlation between corvid breeding density and overall nest survival for the six main study species at three sites in Leicestershire, derived from regression models incorporating site and year, and models based also on habitat and meteorological variables. *: $P < 0.05$; **: $P < 0.01$.

	Model incorporating site and year		Model incorporating all non-corvid variables	
	Carrion Crow	Magpie	Carrion Crow	Magpie
Blackbird	-0.786 **	-0.626 *	-0.769 **	-0.584 *
Song Thrush	-0.904 **	-0.751 *	-0.945 **	-0.694
Dunnock	-0.653 *	-0.348	-0.592 *	-0.342
Whitethroat	-0.396	0.164	0.140	0.477
Chaffinch	-0.172	-0.304	-0.139	-0.267
Yellowhammer	-0.821 **	-0.353	-0.794 **	-0.420

The national study

Out of the 23 songbird species, we found only three cases where one or other of the predators had a statistically significant effect on the population growth rate (Table 3). The sign of the coefficients shown in Table 3 might be taken to imply that Sparrowhawks had a negative effect on the growth rates of Song Thrush populations and a positive effect on Mistle Thrushes, while Magpies had a negative effect on Wrens. However, given that 46 statistical tests were conducted, this was approximately the frequency of significant effects that would be expected by chance. After correcting for multiple tests, we found no evidence of any effects of either predator species on songbird population growth rates. We therefore had no indication that predators had a general effect on songbird population growth rates or that they could have played a significant role in the songbird population declines.

DISCUSSION

The results from Loddington suggest that the presence of breeding Carrion Crows and Magpies, at the densities recorded, can reduce nest survival rates of some species, especially those of Blackbird and Song Thrush. These were the species that showed the greatest increase in breeding numbers at Loddington through the study period. It is possible that the increased nest survival associated with corvid removal contributed to this increase in breeding numbers at Loddington, although habitat management conducted over the same period may also have contributed to increased breeding abundance. Although managed and unmanaged habitats are not totally independent, direct effects of breeding habitat management are unlikely, as breeding numbers of Blackbird and Song Thrush have increased in both managed and unmanaged habitats.

The two studies considered different predators, as well as Magpies considered by both studies. Sparrowhawk presence on CBC plots was not associated with year-to-year declines in prey numbers, suggesting that this species does not limit breeding densities. Although no data were collected on Sparrowhawk abundance at Loddington, the species was present throughout the period of increasing prey abundance, supporting the CBC findings. The Loddington results reveal a strong relationship between nest survival of some species and the breeding abundance of Carrion Crows. This nest predator was not considered in the CBC study and the possibility that this and other potential nest predators such as Grey Squirrel *Sciurus carolinensis* and Jay *Garrulus glandarius* could affect songbird breeding populations cannot be discounted without further work.

While there is a strong suggestion that corvid abundance can influence nesting success of some songbird species,

Table 2. Average annual percentage changes in breeding abundance at the national and local levels based on territory mapping data from the CBC and from Loddington (1992-1998).

	Blackbird	Song Thrush	Dunnock	Whitethroat	Chaffinch	Yellowhammer
National	0.2	1.3	1.0	2.5	-0.2	-2.1
Loddington	5.7	9.3	4.6	4.2	2.0	-0.3
Difference	5.5	8.0	3.6	1.7	2.2	1.8

there is no convincing evidence of an impact of these corvids, or of Sparrowhawks, on songbird breeding abundance. The evidence indicates that songbird populations are resilient to predation, even though predation can affect breeding performance (this study) and local survival (Dhondt *et al*. 1998); the demographic mechanisms underlying this resilience are not yet well understood and require further investigation. Given that breeding productivity is much higher than is needed to replace losses due to mortality of breeding adults, it is widely thought that bird populations include many surplus birds, particularly juveniles, and that this buffers the size of the breeding population against any effects of predation (Newton 1993, 1998, Newton *et al*. 1997, Perrins & Geer 1980).

Also not well understood are the contrasting effects of predation on songbird and gamebird populations, the potential interactions between predation and habitat, and the impact of other species of predators on songbird populations. It is difficult to perform experiments on large spatial and temporal scales, or to include in some other way the replication required for conclusive answers,

Table 3. Sample sizes and statistical results from the national study of songbird population growth rates in relation to the presence of predators on individual CBC plots. Values shown are the amounts by which $\log_e(N_{t+1,i}/N_{t,i})$ is affected by the presence of each of the predators, i.e. negative values show that the rate of population change is lower when predators are present. Standard errors are shown in brackets. Significant associations between the presence of predators and rates of songbird population change are shown in bold and are followed by an asterisk. These are the results before significance levels were corrected for multiple tests. The significant correlations should not be regarded as showing a causal effect of predation because none is significant after correcting for multiple tests.

Species	*N*[†]	No. plots	Sparrowhawk	Magpie
			b (*se*)	*c* (*se*)
Skylark	2048	157	-0.161 (0.0148)	-0.009 (0.0138)
Meadow Pipit	844	65	-0.001 (0.0283)	-0.003 (0.0262)
Wren	3743	286	0.006 (0.0097)	**-0.028 (0.0135)***
Dunnock	3649	278	-0.015 (0.0112)	0.002 (0.0131)
Robin	3751	289	-0.004 (0.0088)	-0.022 (0.0122)
Blackbird	3874	294	-0.007 (0.0074)	0.004 (0.0092)
Song Thrush	3623	276	**-0.030 (0.0131)***	0.007 (0.0138)
Mistle Thrush	2606	202	**0.037 (0.0189)***	-0.013 (0.0263)
Chiffchaff	2190	178	0.009 (0.0168)	-0.015 (0.0286)
Willow Warbler	3368	264	0.003 (0.0110)	0.004 (0.0124)
Coal Tit[#]	2033	164	-0.003 (0.0185)	-0.010 (0.0223)
Blue Tit[#]	3741	285	-0.0004 (0.008)	-0.013 (0.0116)
Great Tit[#]	3643	278	0.011 (0.0106)	-0.010 (0.0149)
Nuthatch[#]	1035	86	0.006 (0.0260)	-0.013 (0.0383)
Starling[#]	1156	105	0.045 (0.0313)	-0.023 (0.0344)
Tree Sparrow[#]	1000	86	-0.054 (0.0475)	0.003 (0.0321)
Chaffinch	3763	287	0.004 (0.0074)	-0.011 (0.0089)
Greenfinch	2723	217	-0.014 (0.0195)	0.016 (0.0206)
Goldfinch	1786	146	0.042 (0.0264)	-0.019 (0.0333)
Linnet	2234	172	-0.007 (0.0227)	0.026 (0.0229)
Bullfinch	2645	212	-0.026 (0.0186)	0.017 (0.0258)
Yellowhammer	2471	191	-0.007 (0.0140)	0.002 (0.0166)
Reed Bunting	1350	104	-0.018 (0.0276)	0.009 (0.0276)

[†]The number of observations of the rate of inter-annual songbird population change.
[#]Hole-nesting species whose eggs and chicks are therefore mostly protected from Magpies.

although they can, if designed appropriately, be less influenced by confounding variables than purely correlative studies. It is therefore worthwhile pursuing the study of predation and songbird population dynamics through a blend of small-scale intensive experimental studies and large-scale correlative analyses.

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