

# Population change of avian predators and grey squirrels in England: is there evidence for an impact on avian prey populations?

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## Summary

1. Using novel analytical methods applied to extensive national bird and mammal monitoring data, we examine whether 29 English bird populations may have been depressed by increases in the abundance of two broad categories of predators. The first includes predators of juvenile and adult birds: Eurasian sparrowhawks *Accipiter nisus*, common kestrels *Falco tinnunculus* and common buzzards *Buteo buteo*, and the second comprises five nest predators: carrion crow *Corvus corone*, black-billed magpie *Pica pica*, Eurasian jay *Garrulus glandarius*, great spotted woodpecker *Dendrocopos major* and grey squirrel *Sciurus carolinensis*.

2. For 22 avian prey species, there is no evidence that increases in common avian predators and grey squirrels are associated with large-scale depression of prey abundance or population declines. For the remaining seven, some negative correlations are biologically unlikely but we cannot exclude the possibility that some of the negative associations are causally related. For example, a particularly strong negative relationship between sparrowhawk and tree sparrow during the Common Birds Census period (1967–2000) could indicate a causal relationship. In contrast, the negative association between buzzard and goldfinch during the Breeding Bird Survey period (1995–2005) is, on ecological grounds, unlikely to do so. Whilst a correlative study such as this cannot prove causation, it provides a focus for more detailed work on particular species.

3. Unexpected was a large number of positive associations between predators and prey, particularly for native avian nest predators, which largely exonerates these predators as driving declines in passerine numbers.

4. *Synthesis and applications.* Analyses of large-scale and extensive national monitoring data provides little underlying evidence for large-scale impacts of widespread avian predators and grey squirrels on avian prey populations, although we cannot exclude the possibility that a small number of negative associations between particular predator and prey species reflect causal relationships or that predators affect prey species at smaller spatial scales.

**Key-words:** predation, predators, rates of population change

## Introduction

Over the past 40 years many wild bird species have declined in abundance in the UK (Baillie *et al.* 2009). Whilst many of these declines are associated with changes in agricultural practices (e.g. Vickery *et al.* 2004), increases in the abundance of com-

mon and widespread avian and mammalian predators may be depressing population levels of some species (Holt *et al.* 2008). These predators can be grouped into two broad categories: predators of juvenile and adult birds (Eurasian sparrowhawk *Accipiter nisus* L., common kestrel *Falco tinnunculus* L. and common buzzard *Buteo buteo* L.), and nest predators (carrion crow *Corvus corone* L., black-billed magpie *Pica pica* L., Eurasian jay *Garrulus glandarius* L., great spotted woodpecker *Dendrocopos major* L. and grey squirrel *Sciurus carolinensis*

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Gmelin 1788). Sparrowhawks feed on avian prey and their abundance in England increased by 170% between 1975 and the early 1990s, remaining relatively stable thereafter (Baillie *et al.* 2009). This predator is perhaps most likely to affect wild bird populations, because for many species, abundance is more strongly influenced by juvenile and adult mortality than by nesting success (e.g. Robinson *et al.* 2004). However, breeding bird populations can be buffered against increasing predation pressure through density-dependent mechanisms, including compensatory reduction in mortality rates through reduced competition for resources and recruitment of surplus, non-breeding individuals (Newton 1993). There is no doubt that the eight predators considered here prey on the nests, fledglings or adults of a wide range of bird species (Moller 1983; Fuller *et al.* 2005). There is also some evidence for population depression of passerines (e.g. Groom 1993; Stoate & Szczyr 2001, 2006) and ground-nesting waders and gamebirds (e.g. Tapper, Potts & Brockless 1996; Summers *et al.* 2004) at a local scale. However, previous analyses of UK garden bird data and national bird monitoring data, focussing in each case on a single predator species, have failed to detect any marked effects (Gooch, Baillie & Birkhead 1991; Thomson *et al.* 1998; Chamberlain, Glue & Toms 2009). Here we use the larger national data set that has accumulated across a wider suite of predators and apply novel analytical methods to reassess this question.

## Materials and methods

### SURVEY METHODS

This study uses two extensive volunteer surveys, the BTO/JNCC Common Birds Census (CBC) and the BTO/JNCC/RSPB Breeding Bird Survey (BBS). The CBC was introduced in 1962 to provide the first systematic annual monitoring of bird abundance in the UK. Operating until 2000, the CBC was based mainly on farmland and woodland mapping census plots selected by volunteers. About 200 plots of different sizes were surveyed in England each year, producing trends that were broadly representative of breeding bird populations (Fuller, Marchant & Morgan 1985). Bird territories were mapped from observations made on between seven and ten site visits per year (Marchant *et al.* 1990), providing reasonably robust estimates of the absolute number of breeding territories within each census plot. The CBC covers a period when sparrowhawks, buzzards and magpies spread eastward into intensive arable farming areas (Newton & Haas 1984; Gregory & Marchant 1995). This survey therefore offers an exceptionally large-scale long-term data set with which to look for associations between changes in predator numbers at individual sites and the rates of avian prey population change at these sites between consecutive years. We focus here on the period 1967–2000 during which predators and prey have been recorded on a sufficient number of sites for change in relative abundance to be monitored over time.

Introduced in 1994 and continuing to the present, the BBS provides a more rigorous approach to the monitoring of widespread bird species. The BBS is based on a formal sampling framework where 1-km squares are randomly selected from those in the National Grid according to a stratified random sampling design, providing trends that are representative of the UK and its constituent countries. For comparability, we focus on analyses of the CBC and BBS for England. BBS fieldwork involves two visits to each square to count birds,

where birds are recorded along two 1-km transects and their perpendicular distance from the transect line recorded in three distance bands (0–25, 25–100, 100 m or more). This allows for a correction for detectability to be made via the use of distance sampling (Buckland *et al.* 2001), allowing counts to be converted to densities. This is necessary for the BBS because just two visits to a square underestimates the number of individuals present, and provides less detailed information than the CBC. In addition to recording birds, the BBS monitors large and easily detectable mammal species, including grey squirrel on the same sites since 1995. In this study we use BBS data for the period 1995–2005. The increase in predators was largely over by the start of the BBS. For example, there was no change in sparrowhawk numbers on BBS squares in England between 1994 and 2006 (Baillie *et al.* 2009). However, the coverage of the BBS is considerably greater than the CBC with over 2000 BBS squares surveyed annually in England combined with systematic habitat recording.

In this paper, we consider the impact of two broad classes of predator on 29 avian prey species, primarily passerines (Table S1 Supporting information), of the three predators of juvenile and adult birds, and the five nest predators described earlier. The 29 prey species were chosen on the basis that they had been recorded in the diet of one or more of the eight predators and had been recorded on a sufficient number of CBC and BBS sites for change in relative abundance to be monitored through both schemes (Baillie *et al.* 2009).

### ANALYTICAL METHODS

A simple correlation of population changes for a given bird species with predator abundance at a large spatial scale may result in spurious results, as changes in the abundance of each group may be driven by different, but concurrent, processes. When examining relationships between songbirds and avian predators, Thomson *et al.* (1998) dealt with this problem by relating changes in abundance between consecutive years to predator abundance at the individual site level. More recently, Freeman & Newson (2008) extended this approach to increase the efficiency of data use and the precision of parameter estimates. We extend Freeman & Newson (2008) to implement a change in passerine abundance as a response variable, with changes in predator abundance as predictors. We chose a change/change approach in preference to a change/abundance model to take into account density-dependent effects. Under the hypothesis that predator and prey numbers are inter-related at a given site, changes in predator numbers will lead to density-dependent compensation in the prey population dynamics that allows prey numbers to stabilize at a new level, i.e. the rate of change in prey density will return to zero as the change in predator numbers returns to zero. In a change/abundance approach, the same situation results in a zero rate of prey change for two different levels of predator abundance, in contradiction with the underlying regression model. Moreover, at different sites the levels at which prey and predator densities are in balance will vary markedly according to local conditions. The change/change model will match a zero rate of prey change with a zero rate of predator change in these cases, whereas under the change/abundance model, a zero rate of prey change will again wrongly correspond to more than one level of predator abundance. Several biotic and abiotic covariates were also included to control for environmental variability and sharpen the focus of our question regarding the influence of change in predator numbers upon change in passerine numbers.

For the BBS, it is important to control for any apparent change in numbers that might reflect a temporal change in detectability. We used a distance-sampling approach and fitted half normal

distributions to the data for each passerine species (see Newson *et al.* 2008). For each surveyed square we determined the principal habitat according to Centre for Ecology and Hydrology (CEH) Land Class data (Barr *et al.* 1993), which assigns a single landclass from a possible 32 categories to each 1-km square. Using data for England, we modelled the detection probability,  $P$ , for each prey species on each 1-km square without and including one and then both habitat and year as factors to see whether the model fit improved. The best fitting model for each prey species was defined as the model with the lowest Akaike's Information Criterion (AIC) value (Table S1) and estimates of  $P$  from this model were retained and used as offsets in the main analyses.

To determine the impact of a single predator on a prey species, it is necessary to control for the impact that other predators may have on the prey species of interest, by including all predators in the model. When considering the biology of the predators and prey species here, it could be argued that for nest predators there might be a lag of a year following predator change before there was an impact on prey populations, because it is primarily the number of adults present at the start of the breeding season that will determine the predation level not the breeding success of the predators. This argument could also be used for predators like sparrowhawk that take full-grown birds, but a case could also be made here for there being no lag. For example, if the increase in predators occurs because of a good breeding season the previous year, it could mean that the parents will have been busy feeding large numbers of nestling predators by depleting the nest contents of the prey. This would reduce prey productivity and hence deplete numbers in the current year, i.e. no lag. So overall, there are good biological arguments both for and against a 1 year lag. If we were to consider all combinations of lagged and not lagged for each predator, we would have to fit  $2^8 = 256$  models for each prey species, which is clearly not practical and would considerably increase the problem of multiple testing and resulting interpretation. For this reason we fitted four sets of models that consider either a lag or no lag for predators of full-grown bird and nest predators with the same number of years and used AIC to identify the best fitting model for subsequent analysis.

Multiple predators were incorporated into the model as follows. Suppose that  $E[N_{i,t}]$  is the expected count of prey,  $P_{k,i,t}$  the count of predator  $k$  at site  $i$  in year  $t$ ,  $R_t$  is the instantaneous rate of change of the passerine population during the period  $t-1$  to  $t$  in the absence of any covariate effect,  $\alpha_k$  is the effect on that rate of change of the predator  $k$ , and  $P_{i,t}$  is the detection probability for the prey species at site  $i$  in year  $t$  in the BBS analysis only. We assume that  $N_{i,t}$  has a Poisson distribution, and account for annual changes, predator effects and climatic effects. The predator-prey relationship adopted here models the instantaneous rate of change in prey abundance as a linear function of the instantaneous rate of change in predator abundance during the same period, with  $\alpha_k$  as the slope and  $R_t$  as the intercept. Parameter  $\alpha_k$  therefore measures the response in instantaneous rate of change of the prey species per unit of instantaneous predator change rate; if it is negative it indicates that the instantaneous rate of change of the prey species drops, and vice versa.

To control for the availability of alternate prey, which may buffer against impact on the prey species of interest, we included the change in total biomass of alternate prey present at each surveyed site as a covariate in the model. We multiplied counts of 36 common and widespread prey species by their species-specific biomass values taken from Snow & Perrins, [(2004); Table S1 Supporting information] after first, in the analyses of BBS data, adjusting species counts by the species-specific detection probabilities. Climate may influence prey abundance, so we included changes in rainfall (number of days having

a rainfall  $\geq 1$  mm) and temperature (mean daily minimum temperature) during the preceding breeding season (prey-specific according to Joys & Crick 2004; see Table S1) and preceding winter period (December–February) as further covariates in the model; with associated estimated coefficients,  $\gamma_{\text{weather}}$ . We used spatial monthly weather data provided at a 5-km resolution matched to the appropriate 1-km square, provided by the Meteorological Office through the UK Climate Impact Programme (UKCIP, <http://www.ukcip.org.uk>).

The general model where predator change and biomass of alternative prey are not lagged by a year is shown as follows (a model with time lags is produced by modifying the  $t$  subscripts to  $t-1$  subscripts for the predator and biomass terms). We start with a change/change model, which is converted to a recursive form in the manner of Freeman & Newson (2008), after which the summation terms are simplified. This gives us the following model.

$$E[N_{i,t}] = \exp\left[\sum_{j=1}^{t-1} R_j + \alpha_{\text{Squirrel}} \ln\left(\frac{P_{\text{Squirrel},i,t} + 1}{P_{\text{Squirrel},i,1} + 1}\right) + \alpha_{\text{Crow}} \ln\left(\frac{P_{\text{Crow},i,t} + 1}{P_{\text{Crow},i,1} + 1}\right) + \alpha_{\text{Magpie}} \ln\left(\frac{P_{\text{Magpie},i,t} + 1}{P_{\text{Magpie},i,1} + 1}\right) + \alpha_{\text{Jay}} \ln\left(\frac{P_{\text{Jay},i,t} + 1}{P_{\text{Jay},i,1} + 1}\right) + \alpha_{\text{Woodpecker}} \ln\left(\frac{P_{\text{Woodpecker},i,t} + 1}{P_{\text{Woodpecker},i,1} + 1}\right) + \alpha_{\text{Hawk}} \ln\left(\frac{P_{\text{Hawk},i,t} + 1}{P_{\text{Hawk},i,1} + 1}\right) + \alpha_{\text{Kestrel}} \ln\left(\frac{P_{\text{Kestrel},i,t} + 1}{P_{\text{Kestrel},i,1} + 1}\right) + \alpha_{\text{Buzzard}} \ln\left(\frac{P_{\text{Buzzard},i,t} + 1}{P_{\text{Buzzard},i,1} + 1}\right) + \alpha_{\text{Dove}} \ln\left(\frac{P_{\text{Dove},i,t} + 1}{P_{\text{Dove},i,1} + 1}\right) + \beta \ln\left(\frac{\text{Biomass}_{i,t}}{\text{Biomass}_{i,1}}\right) + \gamma_{\text{STemp}} \ln\left(\frac{W_{\text{STemp},i,t}}{W_{\text{STemp},i,1}}\right) + \gamma_{\text{SRain}} \ln\left(\frac{W_{\text{SRain},i,t}}{W_{\text{SRain},i,1}}\right) + \gamma_{\text{WTemp}} \ln\left(\frac{W_{\text{WTemp},i,t}}{W_{\text{WTemp},i,1}}\right) + \gamma_{\text{WRain}} \ln\left(\frac{W_{\text{WRain},i,t}}{W_{\text{WRain},i,1}}\right) + \ln(N_{i,1}) + \ln\left(\frac{\hat{p}_t}{\hat{p}_1}\right)\right]$$

Some algebraic manipulation shows that, under this model,

$$\ln\left(\frac{E[N_{i,t}]}{E[N_{i,t-1}]}\right) = R_{t-1} + \alpha_{\text{Squirrel}} \ln\left(\frac{P_{\text{Squirrel},i,t} + 1}{P_{\text{Squirrel},i,t-1} + 1}\right) + \alpha_{\text{Crow}} \ln\left(\frac{P_{\text{Crow},i,t} + 1}{P_{\text{Crow},i,t-1} + 1}\right) + \alpha_{\text{Magpie}} \ln\left(\frac{P_{\text{Magpie},i,t} + 1}{P_{\text{Magpie},i,t-1} + 1}\right) + \alpha_{\text{Jay}} \ln\left(\frac{P_{\text{Jay},i,t} + 1}{P_{\text{Jay},i,t-1} + 1}\right) + \alpha_{\text{Woodpecker}} \ln\left(\frac{P_{\text{Woodpecker},i,t} + 1}{P_{\text{Woodpecker},i,t-1} + 1}\right) + \alpha_{\text{Hawk}} \ln\left(\frac{P_{\text{Hawk},i,t} + 1}{P_{\text{Hawk},i,t-1} + 1}\right) + \alpha_{\text{Kestrel}} \ln\left(\frac{P_{\text{Kestrel},i,t} + 1}{P_{\text{Kestrel},i,t-1} + 1}\right) + \alpha_{\text{Buzzard}} \ln\left(\frac{P_{\text{Buzzard},i,t} + 1}{P_{\text{Buzzard},i,t-1} + 1}\right) + \alpha_{\text{Dove}} \ln\left(\frac{P_{\text{Dove},i,t} + 1}{P_{\text{Dove},i,t-1} + 1}\right) + \beta \ln\left(\frac{\text{Biomass}_{i,t} + 1}{\text{Biomass}_{i,t-1} + 1}\right) + \gamma_{\text{STemp}} \ln\left(\frac{W_{\text{STemp},i,t} + 1}{W_{\text{STemp},i,t-1} + 1}\right) + \gamma_{\text{SRain}} \ln\left(\frac{W_{\text{SRain},i,t} + 1}{W_{\text{SRain},i,t-1} + 1}\right) + \gamma_{\text{WTemp}} \ln\left(\frac{W_{\text{WTemp},i,t} + 1}{W_{\text{WTemp},i,t-1} + 1}\right) + \gamma_{\text{WRain}} \ln\left(\frac{W_{\text{WRain},i,t} + 1}{W_{\text{WRain},i,t-1} + 1}\right) + \ln\left(\frac{\hat{p}_t}{\hat{p}_{t-1}}\right)$$

so that change between successive years in log abundance is being modelled as a function of change in the logarithm of the covariates, i.e. a change-change model. Note that our predictor variables are subject to sampling error, and some are themselves predictions from other models. It is accepted that this may lead to attenuation of the estimated coefficients (Carroll *et al.* 2006), possibly leading to an underestimate of the number of significant effects.

Models were implemented by fitting generalized linear models using the GENMOD procedure in SAS (SAS Institute. 2001) with Poisson

errors and a logarithmic link function. Because the deviance divided by the degrees of freedom was close to one in all cases, it was not necessary to account for overdispersion. The magnitude of multicollinearity between predators was assessed by calculating variance inflation factor (VIF) values for each predictor (Kutner, Nachtsheim & Neter 2004). They were  $< 5$  in all cases, suggesting that any multicollinearity was low. Sites were included in each prey-specific model only if the species concerned had been recorded in at least one of the survey years and there was a minimum of 2 years to calculate a measure of change. Plots of residuals vs. fitted predator change were used to provide a visual assessment of the adequacy of each fitted model.

Because sparrowhawks, buzzards and kestrels have relatively large territories, the surveyed sites were not the appropriate scale at which to measure the local abundance of these species. For this reason, we used Generalized Cross Validation (GCV) selected penalized regression spline Generalized Additive Models (GAMs) with logarithmic link function and quasi-Poisson error structure (after Wood 2006) to produce a smoothed relative abundance surface for each raptor species across England, fitting a separate model with land class and easting and northing as predictor variables to each year of data. The amount of smoothing was established automatically, with the maximum degrees of freedom equal to 15. The fitted models were then used to produce year-specific predicted raptor abundances for each surveyed BBS and CBC site. These predicted raptor abundances were used as predictors in the subsequent GLM analyses.

For the CBC only, plot size varied, so we included the logarithm of plot area as an offset in each GAM. For the analysis of BBS data, where detection is certainly less than 100%, raw counts were corrected by including estimates of the detection probability  $\log(P_{i,t})$  of each species (see above) as offsets.

To reduce the degree of multiple testing, we fitted a single model for each prey species that included all predator terms and the overall effect of those predator terms was tested using a likelihood ratio (LR) test. Further investigation of the individual coefficients was only undertaken if a significant result was found at this stage. To examine the possibility that independent but coincident national population changes could give rise to spurious correlations, we followed the approach of Thomson *et al.* (1998) to include collared dove *Streptopelia decaocto* as an additional dummy predator. Collared doves expanded their range during the same period as magpies and sparrowhawks, but they spread from the east rather than from the west (Marchant *et al.* 1990).

We also considered whether any broad pattern emerged across the full suite of predator coefficients in two ways. First, we calculated a weighted mean predator coefficient across prey species for each predator, using the reciprocal of the variance of the coefficient as a weight. This provided a way of evaluating the relative predation impact of the different predators. Secondly, we compared the average proportion of negative associations among prey species that declined during 1995–2005 (BBS) or 1967–2000 (CBC) with the average proportion among those that were stable or increasing during the same period, using a generalized linear model with binomial error and logistic link function.

## Results

### PREPARATORY ANALYSIS

Using the appropriate lagged or no lag measure of predator change (Table S1 Supporting information), and likelihood

ratio tests for an overall predator effect, a significant result was found for 2 of 29 (7%) prey species in the BBS analyses and for 10 of 29 (35%) prey species in the CBC analyses (Table 1). For BBS, this was approximately the number expected by chance 1.45, but for CBC it was much larger ( $\chi^2_1 = 53.1$ ,  $P < 0.001$ ). Plots of residuals vs. fitted predator change values provided no reason to doubt the validity of the fitted models (Fig. S1 Supporting information).

### BREEDING BIRD SURVEY ANALYSIS

For the BBS predator analysis, from 232 possible correlations between rates of change of predators and prey populations, we found 24 (10%) significant at the nominal 5% level. This reduced to seven statistically significant relationships for species with a significant LR test (Table 1). Of these, two results suggested negative associations and five positive associations. The coefficients here are perhaps best expressed in terms of a percentage increase or reduction in annual prey rate of population change in response to a doubling in the number of predators by calculating  $100 \times \{\exp[\text{coefficient} \times \log(2)] - 1\}$ . Looking more closely at the two negative associations, the association between greenfinch/grey squirrel ( $-0.015$ ) is small and equivalent to 1% reduction in the rate of annual population change with a doubling in grey squirrel numbers, whereas the association between goldfinch/buzzard ( $-0.542$ ) is larger, but as we discuss later is very unlikely to represent a real association. In terms of the positive relationships, sparrowhawk/goldfinch is notable as being particularly large.

The weighted mean coefficient across prey species for each predator was negative for buzzard, sparrowhawk and grey squirrel, and positive for the remaining five predators. In all negative cases, this is equivalent to a less than 7% reduction in the rate of annual population change in relation to a doubling in the number of predators.

Exploring the associations in relation to the conservation status of the prey species (Baillie *et al.* 2009) over the period of analysis (1995–2005), we found no significant difference in the proportion of negative and positive associations for declining or stable/increasing prey species as a whole ( $\chi^2_1 = 0.21$ ,  $P = 0.65$ ) and separately for predators of juvenile and adult birds ( $\chi^2_1 = 0.15$ ,  $P = 0.70$ ) and for nest predators ( $\chi^2_1 = 0.28$ ,  $P = 0.60$ ).

Treating collared dove as a dummy predator, there are two statistically significant but small positive relationships between rates of change of predators and prey population. The significant results for collared dove and predators are statistically independent of one another ( $\chi^2_1 = 2.95$ ,  $P = 0.08$ ).

### COMMON BIRDS CENSUS ANALYSIS

For the CBC predator analysis, 58 of 203 (29%) relationships were significant at the nominal 5% level. This reduced to 30 when restricted to the 10 species with a significant LR test. Of these, nine suggested negative associations and 21 positive associations (Table 1, Fig. 1b). Most notable is a highly significant negative association between sparrowhawk and tree

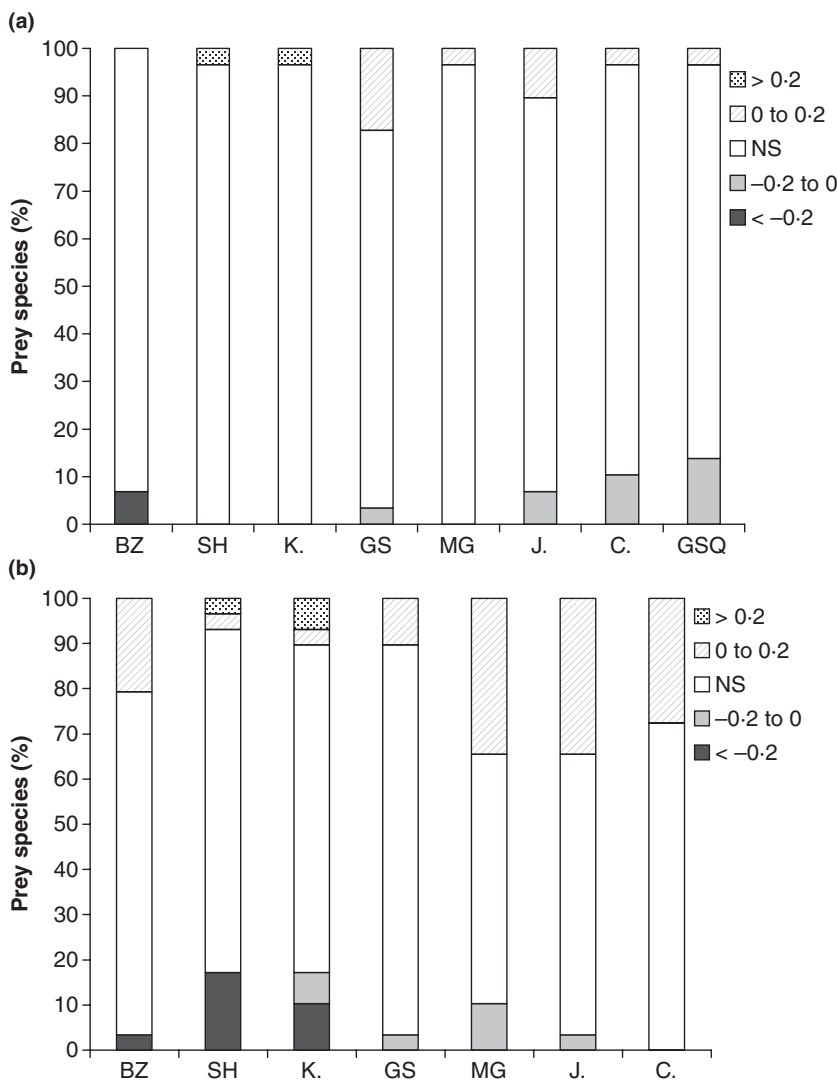
**Table 1.** Change in avian prey populations in relation to a change in predators according to (a) Breeding Bird Survey data 1995–2005, and (b) Common Birds Census (CBC) data 1970–2000. The likelihood ratio (LR) tests for an effect of one or more predator on a species (or for collared dove as a dummy predator). Species scientific names are given in Table S1

Species	Predators										LR test $\chi^2$ (d.f. = 9)	
	Buzzard	Sparrowhawk	Kestrel	GS Woodpecker	Magpie	Jay	Carrion Crow	Grey Squirrel	Collared Dove	Dummy predator		
(a) Breeding Bird Survey												
Lapwing	0.476 (0.408)	-0.390 (0.321)	0.057 (0.567)	-0.044 (0.030)	0.001 (0.009)	0.050 (0.030)	0.003 (0.002)	-0.005 (0.022)	0.009 (0.009)	0.009 (0.009)	6.817	
Green Woodpecker	-1.000 (0.651)	-0.091 (0.684)	0.467 (1.053)	-0.012 (0.018)	0.010 (0.007)	<b>0.039 (0.018)*</b>	0.000 (0.002)	-0.005 (0.015)	0.008 (0.009)	0.008 (0.009)	5.580	
Skylark	-0.381 (0.196)	0.037 (0.059)	0.434 (0.312)	0.016 (0.012)	0.006 (0.004)	-0.010 (0.010)	0.000 (0.001)	0.003 (0.011)	0.004 (0.004)	0.004 (0.004)	5.785	
Meadow Pipit	0.086 (0.224)	-0.031 (0.056)	0.289 (0.340)	-0.040 (0.040)	-0.012 (0.010)	-0.038 (0.039)	0.003 (0.002)	0.005 (0.039)	0.013 (0.014)	0.013 (0.014)	3.190	
Yellow Wagtail	0.411 (1.284)	0.910 (1.270)	0.751 (1.367)	<b>0.134 (0.059)*</b>	-0.008 (0.017)	<b>-0.076 (0.035)*</b>	0.000 (0.004)	-0.054 (0.053)	0.006 (0.014)	0.006 (0.014)	6.707	
Wren	<b>-0.244 (0.122)*</b>	0.067 (0.072)	0.279 (0.245)	-0.011 (0.006)	0.001 (0.002)	0.005 (0.006)	-0.001 (0.001)	<b>-0.018 (0.005)**</b>	0.000 (0.002)	0.000 (0.002)	11.95	
Dunnock	-0.148 (0.152)	0.126 (0.097)	0.268 (0.316)	<b>0.019 (0.007)**</b>	0.004 (0.002)	0.004 (0.007)	0.000 (0.001)	-0.002 (0.007)	0.004 (0.002)	0.004 (0.002)	9.422	
Robin	-0.191 (0.126)	-0.179 (0.109)	0.468 (0.259)	-0.007 (0.006)	0.002 (0.002)	-0.004 (0.006)	-0.001 (0.001)	-0.005 (0.005)	<b>0.005 (0.002)*</b>	<b>0.005 (0.002)*</b>	9.093	
Blackbird	0.132 (0.12)	-0.182 (0.100)	-0.477 (0.259)	-0.003 (0.006)	0.000 (0.002)	-0.009 (0.006)	0.000 (0.000)	<b>-0.016 (0.005)**</b>	<b>-0.006 (0.002)*</b>	<b>-0.006 (0.002)*</b>	12.25	
Song Thrush	-0.285 (0.208)	-0.025 (0.210)	-0.007 (0.441)	-0.007 (0.009)	0.001 (0.004)	0.011 (0.009)	-0.001 (0.001)	0.004 (0.007)	0.003 (0.003)	0.003 (0.003)	2.928	
Mistle Thrush	-0.421 (0.369)	0.417 (0.393)	<b>1.454 (0.727)*</b>	0.019 (0.016)	0.008 (0.005)	0.000 (0.015)	0.001 (0.002)	-0.002 (0.011)	0.001 (0.001)	0.001 (0.001)	5.626	
Garden Warbler	0.431 (0.591)	0.035 (0.339)	2.561 (1.543)	0.017 (0.025)	-0.011 (0.014)	-0.018 (0.031)	0.004 (0.004)	0.007 (0.033)	-0.006 (0.018)	-0.006 (0.018)	3.012	
Chiffchaff	-0.211 (0.174)	0.048 (0.259)	-0.101 (0.424)	0.011 (0.008)	-0.002 (0.004)	<b>0.023 (0.008)**</b>	0.001 (0.001)	-0.005 (0.007)	0.007 (0.004)	0.007 (0.004)	8.630	
Willow Warbler	-0.046 (0.172)	0.024 (0.081)	0.025 (0.412)	0.004 (0.013)	<b>0.010 (0.004)*</b>	0.001 (0.009)	0.001 (0.001)	-0.001 (0.011)	0.005 (0.007)	0.005 (0.007)	3.460	
Spotted Flycatcher	1.270 (0.789)	0.936 (1.450)	-1.343 (1.996)	-0.034 (0.040)	-0.015 (0.022)	-0.018 (0.054)	0.001 (0.006)	-0.040 (0.032)	-0.011 (0.019)	-0.011 (0.019)	3.461	
Blue Tit	-0.218 (0.126)	-0.174 (0.101)	-0.228 (0.265)	-0.001 (0.007)	-0.001 (0.002)	<b>-0.012 (0.006)*</b>	0.000 (0.000)	<b>0.017 (0.005)**</b>	0.004 (0.002)	0.004 (0.002)	12.40	
Coal Tit	-0.156 (0.360)	0.328 (0.291)	-1.189 (0.769)	-0.023 (0.015)	-0.009 (0.008)	0.014 (0.015)	0.001 (0.001)	<b>-0.025 (0.013)*</b>	-0.002 (0.011)	-0.002 (0.011)	6.789	
Great Tit	0.148 (0.140)	0.014 (0.147)	-0.015 (0.288)	<b>0.013 (0.006)*</b>	-0.002 (0.002)	-0.009 (0.006)	0.001 (0.001)	0.000 (0.005)	<b>0.007 (0.002)**</b>	<b>0.007 (0.002)**</b>	9.427	
Nuthatch	-0.226 (0.454)	-0.585 (0.887)	0.515 (1.257)	-0.007 (0.019)	0.009 (0.010)	0.012 (0.020)	-0.001 (0.003)	0.016 (0.015)	0.014 (0.012)	0.014 (0.012)	2.521	
Starling	-0.143 (0.206)	-0.134 (0.143)	-0.522 (0.355)	0.016 (0.009)	0.002 (0.003)	0.005 (0.008)	-0.002 (0.001)	0.001 (0.007)	0.004 (0.002)	0.004 (0.002)	7.523	
House Sparrow	0.176 (0.168)	0.074 (0.158)	-0.636 (0.353)	0.009 (0.009)	-0.001 (0.003)	0.013 (0.008)	0.000 (0.001)	-0.005 (0.007)	<b>-0.005 (0.002)*</b>	<b>-0.005 (0.002)*</b>	6.938	
Tree Sparrow	0.970 (1.241)	-0.077 (0.134)	3.044 (1.737)	-0.055 (0.055)	0.030 (0.016)	-0.063 (0.044)	<b>-0.014 (0.006)*</b>	-0.065 (0.067)	-0.011 (0.014)	-0.011 (0.014)	9.544	
Chaffinch	-0.096 (0.114)	-0.138 (0.111)	0.099 (0.243)	<b>-0.021 (0.007)**</b>	-0.004 (0.002)	0.005 (0.006)	0.000 (0.001)	-0.010 (0.005)	0.000 (0.002)	0.000 (0.002)	10.060	
Greenfinch	0.132 (0.154)	0.029 (0.215)	-0.188 (0.276)	<b>0.016 (0.006)*</b>	0.000 (0.002)	<b>0.024 (0.006)**</b>	<b>0.001 (0.001)*</b>	<b>-0.015 (0.006)*</b>	<b>0.010 (0.002)**</b>	<b>0.010 (0.002)**</b>	<b>39.700*</b>	
Goldfinch	<b>-0.542 (0.204)**</b>	<b>0.292 (0.107)**</b>	0.122 (0.450)	<b>0.028 (0.012)*</b>	0.001 (0.004)	0.014 (0.012)	0.001 (0.001)	-0.002 (0.011)	<b>0.012 (0.004)**</b>	<b>0.012 (0.004)**</b>	<b>18.106*</b>	
Linnet	-0.118 (0.229)	0.042 (0.094)	-0.473 (0.456)	-0.009 (0.014)	-0.001 (0.005)	-0.001 (0.016)	0.002 (0.001)	-0.005 (0.015)	0.003 (0.005)	0.003 (0.005)	3.157	
Bullfinch	-0.546 (0.764)	-0.994 (1.055)	-0.626 (1.364)	0.018 (0.026)	0.005 (0.010)	0.014 (0.021)	0.005 (0.004)	0.018 (0.027)	0.001 (0.013)	0.001 (0.013)	2.420	
Yellowhammer	-0.023 (0.214)	0.136 (0.145)	0.202 (0.449)	0.005 (0.011)	0.002 (0.004)	-0.018 (0.011)	<b>-0.003 (0.001)**</b>	0.010 (0.012)	<b>0.009 (0.005)*</b>	<b>0.009 (0.005)*</b>	8.437	
Reed Bunting	-1.487 (0.729)*	-0.171 (0.295)	-0.647 (1.049)	0.038 (0.041)	0.008 (0.011)	0.004 (0.024)	0.003 (0.003)	0.011 (0.064)	0.018 (0.014)	0.018 (0.014)	4.745	
Weighted Mean (se) <sup>a</sup>	-0.096 (0.036)	-0.001 (0.023)	0.007 (0.073)	0.000 (0.002)	0.001 (0.001)	0.003 (0.002)	0.000 (0.000)	-0.004 (0.002)	0.003 (0.001)	0.003 (0.001)		

Table 1. (Continued)

Species	Predators							LR test $\chi^2$ (d.f. = 8)	
	Buzzard	Sparrowhawk	Kestrel	GS Woodpecker	Magpie	Jay	Carrion Crow		Dummy predator Collared Dove
(b) Common Birds Census									
Lapwing	<b>-0.540 (0.244)*</b>	<b>-0.453 (0.210)*</b>	<b>-0.315 (0.125)*</b>	0.013 (0.040)	<b>0.039 (0.015)*</b>	0.007 (0.039)	0.026 (0.015)	<b>-0.048 (0.015)**</b>	<b>18.889*</b>
Green Woodpecker	-0.139 (0.096)	0.102 (0.146)	-0.007 (0.132)	0.029 (0.024)	<b>0.034 (0.015)*</b>	<b>0.049 (0.023)*</b>	<b>0.040 (0.014)**</b>	0.021 (0.017)	<b>18.529*</b>
Skylark	<i>0.049 (0.054)</i>	<i>-0.120 (0.127)</i>	<i>0.064 (0.076)</i>	<i>-0.022 (0.023)</i>	<b>0.022 (0.009)*</b>	<i>0.016 (0.022)</i>	<i>0.013 (0.008)</i>	0.005 (0.008)	7.554
Meadow Pipit	<i>0.034 (0.096)</i>	<i>0.052 (0.242)</i>	<i>0.115 (0.133)</i>	<i>-0.074 (0.060)</i>	<i>0.025 (0.019)</i>	<i>0.034 (0.053)</i>	<b>0.090 (0.020)**</b>	<i>-0.018 (0.027)</i>	14.796
Yellow Wagtail	<i>-0.112 (0.679)</i>	<b>0.921 (0.314)**</b>	<i>-0.140 (0.211)</i>	<i>-0.064 (0.068)</i>	<b>-0.068 (0.024)**</b>	<b>-0.167 (0.070)*</b>	0.005 (0.020)	0.008 (0.021)	12.841
Wren	0.023 (0.038)	-0.046 (0.081)	<b>-0.142 (0.058)*</b>	0.005 (0.015)	0.001 (0.008)	0.006 (0.013)	-0.006 (0.007)	0.008 (0.007)	4.428
Duncock	-0.068 (0.036)	0.100 (0.068)	-0.053 (0.056)	0.000 (0.015)	0.006 (0.007)	<b>0.032 (0.013)*</b>	0.000 (0.007)	-0.012 (0.007)	8.263
Robin	<i>0.069 (0.040)</i>	<b>0.163 (0.076)*</b>	-0.060 (0.059)	-0.015 (0.015)	-0.013 (0.008)	0.005 (0.013)	<b>0.015 (0.007)*</b>	0.002 (0.008)	7.375
Blackbird	-0.003 (0.038)	-0.024 (0.080)	-0.041 (0.057)	-0.016 (0.015)	<b>-0.033 (0.007)**</b>	<b>0.030 (0.013)*</b>	-0.002 (0.007)	0.007 (0.007)	13.751
Song Thrush	<b>0.091 (0.041)*</b>	-0.108 (0.070)	0.060 (0.056)	0.011 (0.014)	-0.003 (0.007)	<b>0.027 (0.012)*</b>	0.011 (0.007)	0.007 (0.007)	9.756
Mistle Thrush	0.002 (0.067)	-0.077 (0.106)	<b>0.208 (0.087)*</b>	0.019 (0.020)	<b>0.027 (0.010)**</b>	0.003 (0.018)	0.014 (0.010)	0.009 (0.009)	12.344
Garden Warbler	0.015 (0.062)	0.010 (0.147)	-0.056 (0.101)	-0.004 (0.010)	0.009 (0.014)	0.038 (0.020)	<b>0.031 (0.012)*</b>	0.026 (0.014)	8.879
Chiffchaff	-0.010 (0.047)	0.030 (0.079)	-0.049 (0.073)	0.018 (0.015)	-0.002 (0.009)	<b>0.033 (0.014)*</b>	-0.011 (0.009)	<b>0.019 (0.009)*</b>	7.437
Willow Warbler	<b>0.083 (0.039)*</b>	0.134 (0.074)	0.116 (0.061)	<b>0.041 (0.015)**</b>	-0.014 (0.008)	-0.023 (0.014)	<b>0.020 (0.007)**</b>	-0.007 (0.008)	<b>15.231*</b>
Spotted Flycatcher	0.022 (0.071)	-0.124 (0.187)	0.016 (0.133)	<b>0.077 (0.029)**</b>	-0.028 (0.017)	<b>0.076 (0.027)**</b>	0.010 (0.014)	<b>0.034 (0.013)**</b>	<b>15.420*</b>
Blue Tit	<b>0.099 (0.038)*</b>	-0.106 (0.080)	0.030 (0.057)	0.018 (0.014)	-0.016 (0.007)	<b>0.012 (0.013)</b>	0.003 (0.007)	<b>-0.017 (0.008)*</b>	10.629
Coal Tit	<b>0.132 (0.051)**</b>	-0.031 (0.106)	-0.047 (0.087)	<b>0.049 (0.018)**</b>	0.010 (0.012)	0.016 (0.016)	-0.017 (0.011)	-0.012 (0.014)	10.017
Great Tit	0.030 (0.037)	-0.094 (0.067)	-0.011 (0.054)	0.012 (0.014)	-0.001 (0.007)	-0.023 (0.012)	0.001 (0.007)	0.004 (0.007)	3.523
Nuthatch	0.020 (0.060)	<b>-0.373 (0.149)*</b>	<b>-0.453 (0.122)**</b>	0.041 (0.023)	0.002 (0.017)	0.033 (0.020)	-0.005 (0.014)	0.011 (0.018)	14.917
Starling	-0.001 (0.051)	0.133 (0.076)	-0.157 (0.073)*	0.029 (0.018)	<b>0.037 (0.009)**</b>	0.008 (0.016)	0.015 (0.008)	0.004 (0.008)	<b>20.327**</b>
House Sparrow	<b>0.155 (0.058)**</b>	-0.038 (0.196)	-0.227 (0.124)	0.052 (0.036)	<b>0.045 (0.015)**</b>	<b>0.089 (0.034)**</b>	-0.006 (0.013)	-0.007 (0.014)	14.742
Tree Sparrow	-0.284 (0.415)	<b>-1.053 (0.227)**</b>	<b>-0.471 (0.126)**</b>	0.036 (0.031)	<b>0.055 (0.014)**</b>	-0.051 (0.027)	<b>0.025 (0.012)*</b>	<b>0.028 (0.011)*</b>	<b>39.853***</b>
Chaffinch	0.061 (0.042)	0.033 (0.074)	0.050 (0.058)	0.007 (0.014)	-0.004 (0.007)	0.011 (0.013)	-0.002 (0.007)	-0.019 (0.008)*	5.592
Greenfinch	0.089 (0.053)	-0.193 (0.113)	-0.015 (0.070)	-0.006 (0.020)	<b>0.027 (0.008)**</b>	0.033 (0.017)	0.012 (0.008)	0.006 (0.007)	13.764
Goldfinch	0.079 (0.048)	-0.279 (0.148)	-0.175 (0.090)	-0.029 (0.024)	<b>0.036 (0.010)**</b>	0.041 (0.023)	0.012 (0.010)	-0.013 (0.008)	<b>15.505*</b>
Linnet	<b>0.198 (0.046)**</b>	-0.158 (0.122)	0.054 (0.070)	-0.008 (0.023)	-0.001 (0.009)	<b>0.046 (0.021)*</b>	<b>0.023 (0.009)**</b>	0.003 (0.008)	<b>16.554*</b>
Bullfinch	0.118 (0.072)	<b>-0.262 (0.116)*</b>	-0.076 (0.086)	-0.004 (0.019)	<b>0.047 (0.010)**</b>	<b>0.033 (0.016)*</b>	-0.013 (0.010)	-0.003 (0.009)	<b>19.118*</b>
Yellowhammer	0.117 (0.063)	0.024 (0.119)	<b>0.157 (0.075)*</b>	-0.027 (0.020)	0.004 (0.009)	0.002 (0.017)	0.008 (0.009)	0.006 (0.008)	5.584
Reed Bunting	0.195 (0.127)	<b>-0.430 (0.178)*</b>	<b>0.243 (0.099)*</b>	-0.065 (0.030)*	0.012 (0.012)	<b>0.079 (0.028)**</b>	<b>0.023 (0.011)*</b>	0.011 (0.010)	<b>16.817*</b>
Weighted mean (se) <sup>a</sup>	0.052 (0.010)	-0.030 (0.019)	-0.018 (0.014)	0.007 (0.004)	0.005 (0.002)	0.017 (0.003)	0.008 (0.002)	0.002 (0.002)	

<sup>a</sup>Weighted by 1/variance  
P-values are: \* < 0.05, \*\* < 0.01, \*\*\* < 0.001.  
Significant results are further highlighted in bold and results where the LR test is not significant are highlighted in italics. Columns are estimated coefficients for the predictors, and their standard errors in parenthesis.



**Fig. 1.** Percentage of prey species for which the predator coefficient is significant and <math>< -0.2</math>, between

sparrow and to a lesser degree negative associations between sparrowhawk and both bullfinch and reed bunting. The predator coefficient for sparrowhawk and tree sparrow (

Calculating a weighted mean predator coefficient across prey species for each predator produces a mean that is negative for two predators, sparrowhawk and kestrel, but which is posi-

tive for the remaining five predators. For the kestrel the mean negative association is fairly small (

Examining the CBC associations in relation to the conservation status of the prey species (declining or stable/increasing; Baillie *et al.* 2009) over the period 1967–2000, shows a significant difference in the proportion of negative and positive associations for declining or stable/increasing prey species as a whole (

Treating collared dove as a dummy predator in the analysis, two statistically significant positive relationships were found between rates of change of predators and prey population and one negative relationship. The BBS and CBC analyses are consistent with the assumption that whether an association is significant or not is independent across the two sets of results ( $\chi^2_1 = 0.46, P = 0.50$ ).

## Discussion

For 22 of the prey species considered in this study, analyses of extensive national bird and grey squirrel monitoring data from England provides no statistical evidence that increases in common avian predators and grey squirrels in recent years have resulted in population declines. Indeed, declining prey species were no more likely to be negatively associated with an increase in predators than stable and increasing species. These results are largely in agreement with past analyses of garden bird data (Chamberlain, Glue & Toms 2009) and national monitoring data for magpie (Gooch, Baillie & Birkhead 1991) and sparrowhawk and magpie (Thomson *et al.* 1998). However, we cannot exclude the possibility that the populations of some of the remaining predators and prey species are causally related. It is interesting for example that the mean predator coefficient calculated across prey species was most highly negative for sparrowhawk during the CBC period. Sparrowhawk is the species believed most likely to have an impact on passerines at a time when sparrowhawks were increasing in England. The fact that such a relationship between sparrowhawks and passerines is not found more recently in the BBS, suggests that if sparrowhawks have reduced numbers of some species in the past, predator and prey numbers have now stabilized. From a biological viewpoint, a negative relationship between sparrowhawk and tree sparrow during the CBC period (1967–2000) seems feasible, whilst a significant negative association between buzzard and goldfinch during the BBS period (1995–2005) considering the recorded prey of buzzard (Snow & Perrins 2004), does not. Whilst a correlative study cannot prove causation, a number of negative associations uncovered here may warrant further work to establish or refute causation. Field experiments for example could complement this study by focusing on particular predator/prey pairs for which a negative association was identified here.

There was no consistency in the direction of the relationships (negative or positive) between predator and prey species during the CBC and BBS periods. The CBC and BBS largely represent different periods in time during which predator and prey populations have in many cases shown very different trends, so this finding is perhaps not unexpected. Moreover, the BBS covers only 11 years compared with the 34 years of the CBC, so the scope for discovering relationships through the BBS is correspondingly reduced. The fact that a small number of negative relationships were found between collared dove as a dummy predator and prey species provides support for the idea that some negative associations may have occurred by chance. One caveat is that collared dove contributes to the alternative prey biomass variable, so is in effect present twice in

the analysis. The correlation between collared dove and alternative prey biomass is not significant (Spearman rank-order correlation,  $P = 0.40$ ), suggesting that this is unlikely to affect the results. Unexpected in these analyses, particularly for the CBC and for our native nest predators in general was the large number of positive associations. This appears to largely exonerate native nest predators as driving declines in passerines numbers. These positive associations could represent a behavioural response of birds to an increased predation threat (e.g. Székely, Szép & Juhász 1989) or perhaps an attraction of predators to increased prey caused by confounding effects of improvement in site quality.

In contrast to this study, there is currently better evidence for an impact of predators on populations of ground-nesting birds, such as breeding waders and gamebirds (Tapper, Potts & Brockles 1996; Summers *et al.* 2004). These species are perhaps more likely to be limited by predation than the species considered here.

Our analyses here focus on the potential impact of avian predators and grey squirrels on avian prey populations at a national scale. Whilst more detailed habitat-specific analyses are beyond the scope of this manuscript, an important development of the analytical approach here could be to incorporate habitat and to use this to explore questions relating to the spatial dynamics of different populations of the same species in different habitats.

In conclusion we still have much to learn about the mechanisms underlying the declines of many species of wild birds. For several of the prey species here associated with farmland habitat, there is growing evidence that agricultural change has been the major cause of decline (e.g. Vickery *et al.* 2004). A review of the recent literature (Newton 2004) for example concluded that 27 of 30 farmland species were affected by a loss of nest sites, a lack of winter or summer food or a combination of these factors. Whilst there has been concern that increases in common avian predators and grey squirrels may be depressing national breeding population levels of some bird species, we found little underlying evidence for a generalized impact of predators on the majority of avian prey populations considered here.

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## Supporting Information

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

**Fig. S1.** Plots of residuals vs. fitted predator change for six key predator/prey associations discussed in the manuscript.

**Table S1.** Prey species and information relevant to the analyses of Common Birds Census (CBC) and Breeding Bird Survey (BBS) data. Species for which not appropriate (NA) is recorded in the first seven columns are used in alternative prey calculations only.

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