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Detecting an impact of predation on bird populations depends on the methods used to assess the predators

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Summary

1. In recent decades there have been population declines of many UK bird species, which have become the focus of intense research and debate. Recently, as the populations of potential predators have increased there is concern that increased rates of predation may be contributing to the declines. In this review, we assess the methodologies behind the current published science on the impacts of predators on avian prey in the UK.

2. We identified suitable studies, classified these according to study design (experimental/observational) and assessed the quantity and quality of the data upon which any variation in predation rates was inferred. We then explored whether the underlying study methodology had implications for study outcome.

3. We reviewed 32 published studies and found that typically observational studies comprehensively monitored significantly fewer predator species than experimental studies. Data for a difference in predator abundance from targeted (i.e. bespoke) census techniques were available for less than half of the 32 predator species studied.

4. The probability of a study detecting an impact on prey abundance was strongly, positively related to the quality and quantity of data upon which the gradient in predation rates was inferred.

5. The findings suggest that if a study is based on good quality abundance data for a range of predator species then it is more likely to detect an effect than if it relies on opportunistic data for a smaller number of predators.

6. We recommend that the findings from studies which use opportunistic data, for a limited number of predator species, should be treated with caution and that future studies employ bespoke census techniques to monitor predator abundance for an appropriate suite of predators.

Key-words: avian predator, avian prey, mammalian predator, nest predator, population census, predation impact, predator control, predator impact, raptor, review

Introduction

In recent decades there have been widespread fluctuations in the populations of many bird species in the UK (Eaton *et al.* 2006, 2007, 2008). Many species associated with farmland have declined (Fuller *et al.* 1996; Siriwardena *et al.* 1998; Gates & Donald 2000; Gregory *et al.* 2002; Gregory, Noble & Custance 2004) as have a number of woodland (Hewson *et al.* 2007), urban (Summers-Smith 1999; Crick *et al.* 2002) and upland species (Henderson *et al.* 2004b; Sim *et al.* 2005). These declines have been a focus of intense research interest and general public debate and a range of contributory factors have been identified. Across farmland, which covers 70% of the land area in Britain (Newton 2004), changes in agricultural practices and their level of intensity are considered detrimental (Chamberlain & Fuller 2000, 2001; Chamberlain *et al.* 2000, 2001; Newton 2004), in woodlands habitat change is implicated (Fuller *et al.* 2005, 2007; Gill & Fuller 2007) and in the uplands loss of managed grouse moors (Tapper 1992) and the associated loss of habitat combined with changes in management practices are considered important (Tharme *et al.* 2001).

Over a similar time frame to the documented decline of many songbirds, waders and game birds in the UK, there has been a general expansion in the abundance and distribution of many of their potential predators. Raptor populations have increased following the cessation of use of organochlorine pesticides and a reduction in persecution (UKRWG, 2000; Baker *et al.* 2006). Corvid (Baker *et al.* 2006; Eaton *et al.* 2007) and mammal (Battersby 2005) populations have also increased partly in

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response to a relaxation in the intensity of their control as the number of gamekeepers has declined by more than 75% (Tapper 1992). Unsurprisingly this has led to a widespread perception that predation must be contributing to some of the observed avian population declines. This intense interest has resulted in many published studies (Paradis *et al.* 2000; Thirgood *et al.* 2000; Woods, McDonald & Harris 2003; Chamberlain, Glue & Toms 2009), reports (Henderson, Parrott & Moore 2004a; Park *et al.* 2005; Gibbons *et al.* 2007), reviews of the impact of predation on bird populations and the merits of predator control (Newton 1993, 1998; Côté & Sutherland 1997; Valkama *et al.* 2005; Holt *et al.* 2008; Park *et al.* 2008) and even a recent conference (Quinn, Reynolds & Bradbury 2008).

In an ideal scenario studies might alter predation rates by manipulating predator abundance and then record the impact on the target prey populations, i.e. an experimental study. In reality not all studies may be able to achieve this and studies may have to rely on a less rigorous, opportunistic study design, i.e. an observational study. The most convincing evidence for any impact of predators on their prey populations will come from experimental studies (Newton 1998), which allow a causal connection to be established between the predator population(s) and their avian prey. By contrast, observational studies provide evidence that is purely correlative rather than indicative of a causal relationship. Therefore, across study type is a potential decreasing gradient of evidence quality. Practically, examining the impact of predation on a target prey population is complex, but it is essential that detailed data are available on predator (or a suite of predators) abundance and prey demography (e.g. productivity, mortality and abundance), whilst (ideally) all other limiting factors ideally remain unchanged. Therefore, studies wishing to explore the impact of predation on prey populations all need to define a gradient in predation rates, which is usually done through spatial or temporal contrasts in the abundance of specific predators (i.e. more predators equals more predation). Even studies that employ exclusion barriers to create areas with and without specific predators must provide abundance data to demonstrate that the exclusion barriers function accordingly (e.g. Jackson 2001). Establishing a gradient in predation rates is actually very challenging because in many instances there will be a wide range of potential predators and data on the abundance of different predators are likely to be of variable quality depending on the species targeted and the monitoring methods employed. The latter is particularly important as well-designed, national census methods (e.g. Common Bird Census, Breeding Birds Survey, Garden Bird Feeding Survey) or other more specific methods used for many avian prey populations in the UK may not actually be especially effective for monitoring more secretive predator species particularly certain raptors, corvids and mammals. Therefore, the way in which a study defines these gradients in predation rates is likely to have a major impact on its outcome.

A number of previous reviews examining the impact of predation on prey populations both within and outside of the UK (Côté & Sutherland 1997; Holt *et al.* 2008) have employed a technique known as meta-analysis (Hedges & Olkin 1985). This approach can provide a measure of the relative effect of predation or the benefits of predator control. Meta-analysis can also account for the influence of study design and data quality on study outcome by weighting studies according to variables that might be considered indicative of study quality and employing sub-group analyses as done by both Côté & Sutherland (1997) and Holt *et al.* (2008). Côté & Sutherland (1997) examined the role of predator removal experiments in 20 studies published up to 1996 both within and outside of the UK. The more recent review (Holt *et al.* 2008) considered the effect of vertebrate predators on animal prey abundance in the UK but was only able to include nine peer-reviewed publications in the meta-analysis and four of these examined the role of introduced non-native predators on avian prey populations (three of which were in island ecosystems). No published studies included in the meta-analysis examined the potential impact of predators on passerines in the UK. A review of the up-to-date UK (mainland), peer-reviewed, published literature would therefore seem timely and one that considered the impact of predation on a range of avian prey in the UK with a focus on study design and the underlying methodologies would be particularly relevant.

In this review, we wished to explore how the design of a study and the way in which gradients in predation rates were inferred might influence study outcome. To do this we first identified studies published in the peer-reviewed literature that examined the impact of predators on avian prey in the UK. Next, we classified these studies according to study type, ranging from experimental to observational studies conducted at a single site. As all studies must use either spatial or temporal contrasts in predator abundance to define a gradient in predation rates we critically reviewed the evidence on which variation in predation rates were inferred. Lastly, we explored whether the quality of evidence on predation rates had implications for study outcome in terms of the detection of an impact on avian prey.

Systematic literature review

This review focuses on the impact of predators on avian populations in mainland UK. We chose to omit studies that examined the impact of non-native mammals on small islands as the impact of predators in these particular circumstances is well documented (Craik 1997; Jackson, Fuller & Campbell 2004; De Leon *et al.* 2006) but particular to the circumstances. We also exclude any island-based studies involving colonial seabirds due to the idiosyncratic nature of that particular study system (Oro & Furness 2002). We restrict our review to only those studies that have been published in scientific journals, whereby they have undergone the peer review process. This provides a level of quality control that is accepted within the wider scientific community. We were interested in studies that attempt to explore whether and how predators impact on the dynamics of prey populations through experiments, observational studies or the retrospective analysis of long-term data sets. We therefore exclude those studies that are either based solely on a modelling approach and examine the potential impact of a predator on an avian prey population (e.g. Beckerman, Boots & Gaston 2007) or those studies that use estimated population-level losses to predation through scaled-up per capita predation rates for a specific predator, e.g. predation by domestic cats (Baker *et al.* 2005, 2008). In order to be systematic in the identification of the appropriate published studies we conducted literature searches using key words and phrases in the ISI web of Knowledge database (http://apps.isiknowledge.com/) and the search engine Google Scholar (http://scholar.google.co.uk/) up to and including December 2008. We also used the reference sections from published reviews (Newton 1993, 1998; Côté & Sutherland 1997; Valkama *et al.* 2005; Holt *et al.* 2008; Park *et al.* 2008) to identify additional suitable studies. Once an identified study met with the above selection criteria it was reviewed as an independent piece of research irrespective of the information or findings from other published studies that had been conducted on the same species or study system. This ensured that the approach we employed and the information we extracted were consistent across all reviewed studies.

REVIEW PROCESS

A number of approaches have been used to study the impact (or potential impact) of predators on avian prey populations (for an overview, see Newton 1998; Park *et al.* 2008). The most convincing evidence for any impact of predators on their prey populations will come from experimental studies, whereas observational studies provide evidence that is purely correlative and those conducted at a single site rely on the local temporal variation in predator abundance and as such are strongly influenced by the circumstances associated with that study site. Therefore, across study type is a potential decreasing gradient of evidence quality – experimental studies, followed by quasi-experimental, then multisite observational and finally single-site observational studies.

We categorized each study according to its type as follows: (i) experimental, whereby a predator population is manipulated and the response of the target prey population monitored. A formal control site is an essential component of this design and for enhanced robustness a degree of replication is required; (ii) quasi-experimental, which are similar to experimental in design but typically lack formal controls and/or the random assignment of groups or treatments; (iii) observational (multisite), involving a correlative study typically based on concurrent data on the abundance of predator populations and prey abundance and/or key demographic parameters (productivity & survival) across multiple sites; (iv) observational (single site), which in principle is the same as an observational study conducted across multiple sites but is only conducted at one site. While multisite observational studies typically utilize spatial variation in predator populations, single-site studies utilize temporal variation in predator populations at the one site. A modelling component can be incorporated into any of the above study types to make use of the ecological data collected on a particular component of prey demography to assess the potential impact of the predator(s) on prey abundance.

It is clear that for any study to explore the impact of these predators on their avian prey, data are required on any changes in abundance of the predator populations under examination. Across the UK there is evidence that many predators of birds are now widespread resulting in a community of potential predators in any given habitat. We therefore examined the range of predators that a study covered, the methods it used to quantify predator abundance and hence how a study established and defined predation rates. For each study we established: (i) the number of predators species included, i.e. those predators that were monitored, controlled or mentioned as potential predators; (ii) whether or not data were provided on changes in abundance of the target predator(s); and (iii) whether predator abundance data were collected using a census method specifically designed for the predators (i.e. bespoke) or via a generic method from which data were made available. A list of all predators (common and scientific names) that were mentioned in at least one or more of the studies is provided in Table S1.

Assuming that the abundance of a target predator population varies then it may impact on two aspects of prey demography – productivity and survival (mortality), and ultimately (potentially) on population abundance. Therefore, for each study we identified which of these three aspects of prey demography were studied. We classified measures of nest success, nest survival, brood size and various measures of fledglings as a measure of productivity. Mortality post-fledging, i.e. of fledglings and adults, was classed as survival and measures relating to population trends, such as numbers of individuals or pairs, density estimates, abundance indices, counts of territorial males, were considered measures of population abundance. We then identified (as specified by the study) which aspect of prey demography showed evidence of an impact from a change in predator abundance.

For each published study we extracted the information outlined above, plus study duration and scale and if predator control was employed or not. Full descriptions of the information extracted from the published studies are provided in Table S2.

STATISTICAL ANALYSES

We wished to examine how different types of study treated the predator community. To do this, we examined how study type might affect (i) the number of predator species included in a study, (ii) the number of predator species for which data on abundance were available, and (iii) the number of predator species with abundance data collected using bespoke census techniques. Analyses were conducted at the study level with the above predator measures as the response variables (in turn) in a series of log-linear regression models with a quasi-Poisson error in a general linear modelling framework (GLM). Models were fitted with the four categories of study type, then three category types [experimental, quasi-experimental and observational (multi- and single site)] and finally two categories [experimental (experimental and quasi-experimental) and observational].

Next, we wished to examine how the different types of study affected study outcome. To do this, we examined how study type might affect the probability of detecting an impact of predation on: (i) prey productivity, (ii) population abundance, and (iii) any measure of prey demography. Analyses were conducted at the prey species level using logistic regression models with 'impact' defined as a binary response variable (i.e. whether or not a study detected an impact of predation on each of the prey species under examination) and study specified as a random factor (to account for repeated measures on the same species across studies) within a general linear mixed modelling framework (GLMM). As above, study type was categorized using four, three and two categories.

Finally, we wished to examine whether the way in which predators were accommodated in a study influenced study outcome. To do this, we examined how (i) the number of predator species included in a study, (ii) the number of predator species with data on abundance, and (iii) the number of predator species with data collected using bespoke census techniques, affected the probability of a study detecting an impact of predation on prey demography. Analyses were conducted at the prey species level (on productivity, population abundance and any measure of prey demography) using a series of logistic regression models with 'impact' defined as a binary response variable and study as a random factor in a GLMM. All analyses were conducted using the statistical software R (RDCT 2005).

Results

OVERVIEW

We identified 32 published studies that met our selection criteria. We included one recent experimental study from outside of

Table 1. General study information

Study	Study type*	Study duration (years) and scale	Prey†	Demography‡	Predator§	Predator control
Bolton *et al.* (2007)	Exp	8, local	W	Pp, Pd, S	C, M	Yes
Chiron & Julliard (2007)	Exp	3, local	S	Pp, Pd	C, M, R	Yes
Parr (1993)	Exp	9, local	W	Pp, Pd	C, M, O	Yes
Summers *et al.* (2004)	Exp	11, local	G	Pd	C, M	Yes
Tapper, Potts & Brockless (1996)	Exp	8, local	G	Pp, Pd	C, M, R, O	Yes
Amar *et al.* (2008)	Qexp	8, local	W, S	Pp	R	Yes
Baines *et al.* (2008)	Qexp	15, local	G, W, S	Pp	C, M, R	Yes
Hill (1988)	Qexp	39, local	W	Pp, Pd	R, O	Yes
Stoate & Szczur (2001)	Qexp	7, local	S	Pp, Pd	C	Yes
Stoate & Szczur (2006)	Qexp	12, local	S	Pp, Pd	C, M	Yes
White *et al.* (2008)	Qexp	16, local	S	Pp, Pd	C, M	Yes
Thirgood *et al.* (2000)	Qexp¶	7, local	G	Pp, Pd, S	R	Yes
Baines (1996)	Ob(m)	3, local/regional	G	Pp, Pd	C	Yes
Baines, Moss & Dugan (2004)	Ob(m)	11, local	G	Pd	C, R	Yes
Chamberlain, Glue & Toms (2009)	Ob(m)	30, national	S, O	Pp	R	No
Donald *et al.* (2002)	Ob(m)	3, local/regional	S	Pd	U	Yes
Draycott *et al.* (2008)	Ob(m)	14, local	G	Pd	C, M	Yes
Gooch, Baillie & Birkhead (1991)	Ob(m)	20, national/regional	S	Pp, Pd	C	No
Grant *et al.* (1999)	Ob(m)	3, local	W	Pd	U	No
Groom (1993)	Ob(m)	3, local	S	Pp, Pd	C	No
Lewis *et al.* (2007)	Ob(m)	1, regional	S	Pp	O	No
MacDonald & Bolton (2008)	Ob(m)	8, local	W	Pd	C, M	Yes
Paradis *et al.* (2000)	Ob(m)	15, national	S	Pd	C, R	No
Redpath (1991)	Ob(m)	3, local	G	Pd	R	Yes
Tharme *et al.* (2001)	Ob(m)	2, regional	G, W, S	Pp	C, M	Yes
Thomson *et al.* (1998)	Ob(m)	30, national	S	Pp	C, R	No
Watson *et al.* (2007)	Ob(m)¶	2, local	G	Pp	R	Yes
Ferreras & Macdonald (1999)	Ob(s)	0·5, local	O	Pp, Pd	M	Yes
Geer (1978)	Ob(s)	2, local	S	Pd	R	No
Newton, Dale & Rothery (1997)	Ob(s)	31, local	S	Pp	R	No
Parr (1992)	Ob(s)	14, local	W	Pp, Pd	C, M, O	Yes
Petty *et al.* (2003)	Ob(s)	23, local	O	Pp	R	No

Studies are grouped according to study type.
*Exp, experimental; Qexp, quasi-experimental; Ob(m), observational at multiple sites; Ob(s), observational at single sites.
†G, game birds; W, waders; S, songbirds; O, others.
‡Pp, population abundance; Pd, productivity; S, survival.
§C, corvids; M, mammals; R, raptors; O, others; U, unspecified predators.
¶Studies have a strong modelling component.

the UK (Chiron & Julliard 2007) that had not been included in any previous published reviews (Newton 1993, 1998; Côté & Sutherland 1997; Holt *et al.* 2008; Park *et al.* 2008). This was included on the grounds that it was a novel study, where the landscape (parkland) prey species and suite of potential predators were similar to those found in the UK. Studies were conducted in managed game bird systems using manipulated predator populations to explore the impact on populations of all native Galliformes (Tapper, Potts & Brockless 1996; Thirgood *et al.* 2000), a number of wader species (Tharme *et al.* 2001; Amar *et al.* 2008) and passerines (Stoate & Szczur 2001; White *et al.* 2008). Other studies controlled specific predators that were thought to impact on certain prey species (Hill 1988; Bolton *et al.* 2007). Whilst some used long-term data sets of up to 30 years to explore the impact of fluctuating predator populations on songbird populations at both national (Thomson *et al.* 1998; Chamberlain, Glue & Toms 2009) and local scales (Newton, Dale & Rothery 1997). In all 25 different study systems were utilized and further study-specific information is provided in Table 1. The 32 studies were comprised of five experimental, seven quasi-experimental, 15 observational (multisite) and five observational (single-site) studies.

PREDATORS

The potential impacts of a broad range of predators (32 species) were studied in the reviewed publications, including corvids (e.g. crow and magpie), mammals (wild mammals, e.g. stoat and fox), raptors (e.g. sparrowhawk and hen harrier) and others (e.g. domestic/feral cat, gull) (for study-specific details, see Table S3). The most frequently studied species were the fox, stoat, weasel, carrion crow, magpie and sparrowhawk. Across the four different study types these were all well represented with the exception of the sparrowhawk, which was considered in only one experimental study (Tapper, Potts & Brockless 1996) and no quasi-experimental studies. Despite being frequently mentioned as important predators of songbirds in the UK (Ruxton, Thomas & Wright 2002; Hewson *et al.* 2004; Nelson, Evans & Bradbury 2005) the grey squirrel and domestic cat were included in few studies. Twenty-eight of the 32 studies provided/used data that represented a change in abundance for 17 of the predator species (for details, see Table S4). Predator control was implemented in 22 studies (Table 1) and details of the different species controlled in each study are provided in Table S3. Predator control was found to reduce the abundance of crows (Tapper, Potts & Brockless 1996; Tharme *et al.* 2001; Summers *et al.* 2004; Baines *et al.* 2008), magpies (Tapper, Potts & Brockless 1996), gulls (Hill 1988; Parr 1992, 1993) and foxes (Tapper, Potts & Brockless 1996; Baines *et al.* 2008). None of the studies provided evidence to indicate that the implemented control programmes reduced the abundance of mustelids or other small mammals. However, not all studies that implemented predator control provided evidence that control effectively reduced predator abundance, principally because many studies monitored only part or none of the suite of predators controlled (for details, see Tables S3 and S4). Across the studies a range of census techniques were employed to monitor predator abundance and for the 17 predators where changes in abundance were observed 14 were censused using bespoke techniques in 22 studies (Table 2). For study specific details see Table S5.

We found no compelling evidence to indicate that the number of predators included in a study and the number of predators for which a change in abundance were recorded varied according to study type. However, there was significant evidence that the number of predators monitored using bespoke census techniques were lower in observational studies (multi- and single site combined) than in experimental (experimental and quasi-experimental combined) studies (coefficient: −0·773, SE ±0·371; $t = -2{\cdot}09$, $P = 0{\cdot}046$). For observational studies, the mean number of predators monitored with bespoke census techniques was 1·0, SE ±0·34 and for experimental studies was 2·17, SE ±0·27.

IMPACTS ON PREY

The review encompassed published studies that examined the impact of predation across a wide range of avian prey populations. This included five species of game birds (Galliformes), e.g. capercaillie, red grouse and grey partridge, five species of wader (Charadriiformes), e.g. golden plover, lapwing and avocet, in excess of 25 species of songbird (Passeriformes), including finches, thrushes, tits and warblers, and a number of other species, e.g. collared dove, coot and common kestrel. While population abundance (23 studies) and productivity (23 studies) were relatively well studied, survival was only examined in two studies. Evidence for an impact of predators on productivity was identified in 16 studies and on population abundance in 11. Further study-specific details relating to demographic components studied and evidence of an impact of predation or not are provided in Table S6 (a–d).

Our analyses revealed that study type did not significantly affect the probability of detecting an impact of predation in a study or more specifically on prey productivity or population abundance (trend). Twenty-two studies employed bespoke predator census techniques to examine the potential impact of predation and 18 (82%) of these studies detected a predation impact on prey productivity or abundance. By contrast, of the 10 that employed generic predator census techniques only five (50%) detected an impact. This difference approached statistical significance (Fisher's exact test, one-tailed, $P = 0{\cdot}078$). Our analyses provided no compelling evidence to indicate that the number of predator species studied and how they were censused influenced the probability of detecting any impact on prey productivity. However, our analyses did provide strong evidence that the probability of detecting an impact of predation on prey abundance (population trend) was positively influenced by the number of predators studied ($P = 0{\cdot}03$), the number of predators for which abundance data were recorded ($P = 0{\cdot}05$) and the number of predator species for which abundance was monitored using bespoke census techniques ($P = 0{\cdot}01$). Full models for each of these three findings are shown in Table 3. The number of predators studied and the number of predators monitored with bespoke census tech-

Table 2. A summary of the number of studies providing data on a change in abundance and the implementation of bespoke census techniques for each listed predator

Predator species	Number of studies	Data for a difference in abundance available	Bespoke census technique employed
Badger	3	0	0
Brown rat	5	0	0
Cat (Feral or domestic)	2	0	0
Fox	18	7	5
Grey squirrel	2	0	0
Hedgehog	1	0	0
Mink	3	1	1
Pine marten	2	2	1
Stoat	8	0	0
Weasel	6	0	0
Carrion crow	19	13	11
Jackdaw	2	0	0
Jay	3	1	0
Magpie	11	9	6
Raven	2	0	0
Common buzzard	3	3	2
Common kestrel	5	2	1
Goshawk	2	2	2
Hen harrier	6	5	5
Merlin	3	1	1
Peregrine	4	4	4
Sparrowhawk	8	7	3
Black-headed gull	1	1	1
Common gull	2	2	2
Great black-backed gull	1	0	0
Herring gull	1	0	0
Lesser black-backed gull	1	0	0

Studies in which an appropriate census technique was applied but inconsistently across space or time are excluded from the third column.

niques were correlated (correlation coefficient: $r = 0{\cdot}69$, $SE = 0{\cdot}05, n = 127, P < 0{\cdot}001$).

Figure 1a and c shows the relationship between two measures of the predator species' and the probability of detecting an impact on prey population abundance. Both figures indicate that as the number of predator species increases the probability of detecting an impact of predation on prey abundance increases. These findings suggest that: (i) by including more predator species in a study the probability of a study detecting an impact on prey abundance improves, and (ii) by monitoring an increasing number of predator species with bespoke census techniques in a study the probability of detecting an impact on prey abundance improves. Therefore, as the quantity and quality of predator abundance data used to define predation gradient(s) increase, the chances of detecting a population-level impact on prey also increase. In Fig. 1a the relationship implies that once 10 or more predator species are included then the probability of detecting a predation impact exceeds 90% and in Fig. 1c including at least five predator species (censused with bespoke techniques) results in a detection probability in excess of 90%. While we can be reasonably confident in the shape of the relationship when the number of predator species are relatively low due to the abundance of data (see Fig. 1b and d) this is not the case when the number of predator species is relatively high (i.e. >6 in Fig. 1b and >3 in Fig. 1d) due to few data from a limited number of studies upon which the relationship is based.

Our findings imply that if you have good quality data on the abundance of a range of predator species then you are more likely to detect an effect (if it is there) than if you rely on opportunistic data on a smaller number of predator species. Based on this and the relationship presented in Fig. 1c we conducted a basic assessment of the quality of the evidence presented by each of the studies that found no impact of predation on prey abundance. Using the probability of a study detecting an impact (see Fig. 1c) four grades were identified: very low ($<0{\cdot}1$), low ($0{\cdot}1$–$0{\cdot}25$), medium ($>0{\cdot}25$–$0{\cdot}80$) and high ($>0{\cdot}80$). An assessment of the quality of the evidence presented by each study is provided in Table 4. For studies that found no impact of predation on abundance (eight studies) in songbirds the evidence presented was typically of low or very low quality. In game birds only two (low quality) studies found no impact of predation on prey abundance and in waders only three (medium quality) studies found no impact of predation on prey abundance.

Discussion

Of the 32 reviewed studies, 23 provided some evidence of an impact of predators on an aspect of avian prey demography.

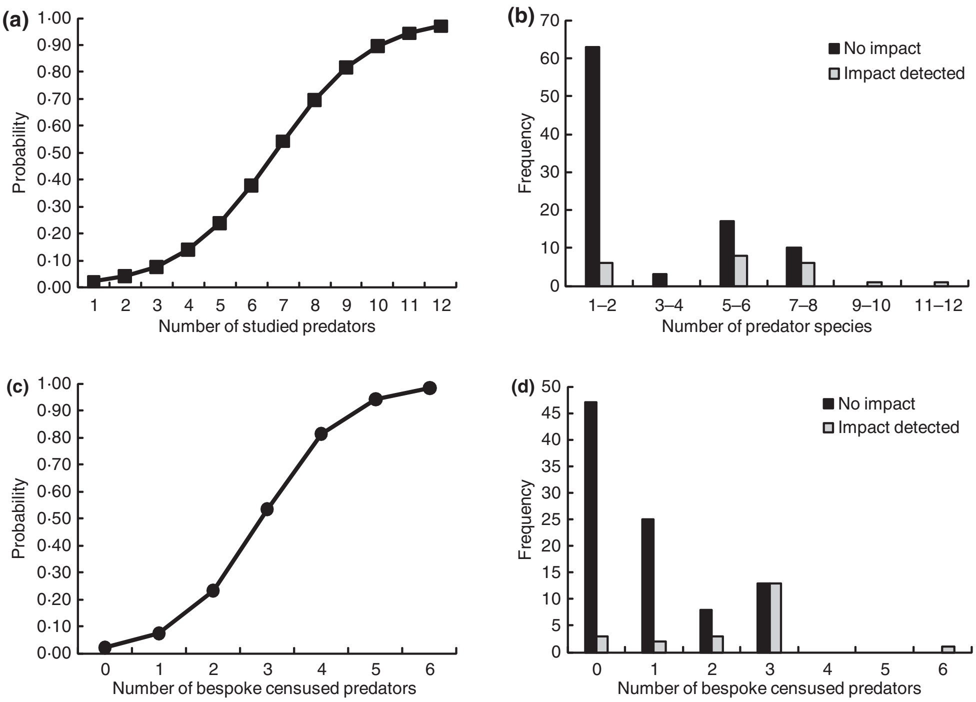

Fig. 1. The relationship between the probability of detecting an impact of predation on the abundance of a prey species and (a) the number of predator species studied and (c) the number of predator species for which abundance data were collected using bespoke census techniques. The models used to generate the figures are models (a) and (c) in Table 3. (b) and (d) provide a summary of the raw data upon which the modelled relationships are based and in each figure the sum of the frequencies represents the total number of prey species for which abundance was studied in the 32 reviewed studies ($n = 115$). These are presented in two categories – impact detected and no impact detected.

Table 3. The logistic regression models used to explore the influence of (a) the number of predator species studied, (b) the number of predator species for which abundance data were collected and (c) the number of predator species for which abundance data were collected using bespoke census techniques, on the probability of detecting a predation impact on prey population abundance

Variable	Estimate (SE)	Z-value	*P*-value
(a)			
Intercept	−4·468 (1·53)	−2·91	< 0·01
No. predator species studied	0·663 (0·31)	2·14	0·03
(b)			
Intercept	−4·592 (1·68)	−2·74	0·01
No. predator species with abundance data	1·486 (0·76)	1·95	0·05
(c)			
Intercept	−3·86 (1·13)	−3·40	< 0·01
No. predator species monitored using bespoke census methods	1·33 (0·53)	2·52	0·01

However, the overall quality of this evidence was variable coming from experimental, quasi-experimental and observational studies. We found no strong evidence to suggest that study type significantly influenced the probability of detecting an impact of predation. We did find strong evidence that the probability of detecting an impact of predation on prey abundance was positively influenced by the quantity and quality of the data upon which the gradients in predation rates were inferred.

LITERATURE REVIEW

Our approach to identifying potential studies for inclusion in this review utilized tried and tested approaches and literature search engines that have been employed in previous reviews that have examined the role of predation in prey population dynamics (Côté & Sutherland 1997; Valkama *et al.* 2005; Holt *et al.* 2008; Park *et al.* 2008). It is of course feasible that we may have overlooked some publications but this will be minimized by also employing a strategy of searching reference sections from identified studies and previous reviews. We included only those studies that met certain criteria including publication in a peer-reviewed journal. While this will have excluded a number of studies it provides a consistent measure of quality control and acceptance regarding the methodologies and statistical analyses employed by the studies within the wider scientific community. Studies that are likely to have been excluded, on these grounds, include those published as reports, certain conference proceedings, PhD theses, commissioned reviews and general and technical reports. Numerous examples of these are provided in recent comprehensive reviews (Park *et al.* 2005; Gibbons *et al.* 2007). A potential concern associated with any review of a particular topic is that it does not provide a realistic representation of the research conducted due to the potential for

Table 4. An assessment of the quality of the evidence presented by studies that found no impact of predation on prey abundance

Studied predator type	Bespoke censused predator type	Predation impact	Quality of evidence	Study
(a)				
C	–	No	Very low	Baines (1996)
R	R	No*	Low	Thirgood *et al.* (2000)
(b)				
R	R	No	Medium	Amar *et al.* (2008)
C, M, O	C, M, O	No	Medium	Parr (1992)
C, M, O	C, M, O	No	Medium	Parr (1993)
(c)				
C, M, R	C	No	Low	Chiron & Julliard (2007)
C	–	No	Very low	Gooch, Baillie & Birkhead (1991)
C	C	No	Low	Groom (1993)
O	–	No	Very low	Lewis *et al.* (2007)
R	R	No	Low	Newton, Dale & Rothery (1997)
C, M	C	No	Low	Stoate & Szczur (2001)
C, M	C, R	No	Medium	Tharme *et al.* (2001)
C, R	–	No	Very low	Thomson *et al.* (1998)
(d)				
R	–	No	Very low	Chamberlain, Glue & Toms (2009)

This is based on the quality of the underlying data upon which a gradient in predation rates is inferred (i.e. the number of bespoke censused predator species) and its influence on the probability of detecting a predation impact. Based on the probability of a study detecting an impact (see Fig. 1c) four grades were identified: very low ($<0{\cdot}1$), low ($0{\cdot}1$–$0{\cdot}25$), medium ($>0{\cdot}25$–$0{\cdot}80$) and high ($>0{\cdot}80$). Studies are grouped according to prey (a) game birds, (b) waders, (c) songbirds and (d) others. The types of predators included in the study are C, corvids; M, mammals; R, raptors; O, others.
*In this study an impact of predation on prey abundance was identified but only through modelling the potential impact of an observed impact of predator abundance on prey survival.

a bias in the published research findings, i.e. there is a bias in favour of publishing research that demonstrates a positive result. In this review of predation and its impact on bird populations in the UK we suggest that this is of little concern because identifying or not identifying an impact are of equal importance when understanding this issue, hence equal support should be given to the publication of both results. It therefore seems unlikely that there will be a bias in favour of those studies that identified an impact of predation in the published studies reviewed.

THE STUDIES

Our review indicates that for every one experimental/quasi-experimental study around two observational studies have been conducted. Exactly why this is the case is unclear, but it could be that observational studies utilized either readily available data or data that could have been collected with minimal logistical and financial investment and were hence easier to conduct. By contrast, studies that involved an experimental/quasi-experimental component were less frequently conducted as they were likely to be logistically and financially more demanding to implement. This is illustrated by the seven quasi-experimental studies, which were conducted in only three different study systems, maximizing the research returns from the investments made.

PREDATORS

The potential impact of both common, widespread and less common, localized predators of nest contents, fledglings and adults was examined in the reviewed studies. Across study types, corvids and mammals were well represented, but raptors were largely restricted to observational studies. This imbalance is more than likely a reflection of the protected status of raptors in the UK and hence their exclusion from studies where predator populations were manipulated through lethal control, e.g. all experimental studies. By contrast, corvids and some mammals can legally be controlled and effective methods are well known. In addition a reduction in the illegal persecution of raptors in the UK, which was common last century (UKRWG 2000), has led to the local recovery of certain raptor populations on moorland which has allowed their impact on populations of moorland birds to be explored in a limited number of quasi-experimental studies.

While numerous predators were often included in the different studies, data on a change in abundance were available for around half the listed predator species and for only 14 of these were bespoke census techniques employed in 22 studies. By comparison, reliable population abundance data were available for >35 prey species implying that considerably less effort is expended when monitoring predator populations compared with prey populations across the reviewed studies. This is emphasized by studies that implemented (or took advantage of) a predator control programme and either assumed that control reduced the local abundance of all controlled predator species, or monitored only part of the suite of controlled predators and assumed that all controlled predators responded in the same way. Our analyses indicated that the inadequate monitoring of predator populations was most prevalent in observational studies. As a generalization these studies may therefore possibly be based on either (i) an assumption that the population of certain predators has changed or (ii) poor quality data that may inaccurately represent any genuine spatial or temporal change in predator abundance and hence predation pressure. Note that this is a generalization and does not apply to all observational studies as some conducted bespoke censuses for the predators included in the study.

IMPACTS ON PREY

Our assessment of the quality of the evidence presented by studies which found no impact of predation on songbird abundance typically graded this evidence as low or very low quality (see Table 4). For these studies this raises the issue of whether or not a null result is believable based on the evidence presented. Below we discuss this further.

We found that by including more predator species in a study the probability of detecting an impact on prey abundance improves. We suggest that this may arise through either an increased chance of the study including predator species that exhibit a genuine change in predation rates or that the combined predation impact by multiple predator species may be more readily detectable than that of a single species. Monitoring an increasing number of predator species with bespoke census techniques also increased the probability of detecting an impact on prey abundance. This may arise through a study identifying and including true representations of changes in predation rates across a suite of predators. Typically, experimental studies include more, well-censused predators than observational studies and the findings from experimental studies are considered to be more plausible than those from single-site observational studies. Together these imply that if you have good quality data on the abundance of a range of predator species, particularly from different sites, then you are potentially more likely to correctly identify differences in predation pressure and thereby improve the probability of detecting an effect (if it is there) than if you rely on opportunistic data on a smaller number of predator species. In the latter scenario the chances of a type II error must be increased, i.e. accepting the null hypothesis of no impact of predation when the opposite is actually true. Therefore, we suggest that we should be sceptical about observational studies that use opportunistic predator data particularly if they are claiming to have found no evidence of an impact of predation on population trends. In such cases, the burden of proof should be on studies to show that their methods for describing spatial or temporal differences in predator abundance (and hence predation pressure) are appropriate for the predators concerned. This is particularly relevant to some of the observational (multi- and single site) studies of songbirds. By contrast, for studies where high-quality data on a range of predators are used, then the likelihood of detecting a population-level impact is very high. However, as indicated in the results this is based on only one study where an impact of a large number of bespoke censused predators (i.e. ≥4) on prey abundance were examined.

Finally, we suggest that future studies which intend to explore the impact of predation on avian prey populations in the UK employ bespoke census techniques to monitor predator abundance and consider including all appropriate widespread and local predators (i.e. a suite of predators where appropriate) in order to maximize the potential of detecting a predator impact if it exists. The latter point is of particular relevance today with the re-establishment of a community of predators across the UK, potentially resulting in prey populations experiencing a cumulative predation impact by multiple predator species rather than a single predator species in isolation.

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References

Amar, A., Thirgood, S., Pearce-Higgins, J. & Redpath, S. (2008) The impact of raptors on the abundance of upland passerines and waders. *Oikos*, **117**, 1143–1152.

Baines, D. (1996) The implications of grazing and predator management on the habitats and breeding success of black grouse *Tetrao tetrix*. *The Journal of Applied Ecology*, **33**, 54–62.

Baines, D., Moss, R. & Dugan, D. (2004) Capercaillie breeding success in relation to forest habitat and predator abundance. *Journal of Applied Ecology*, **41**, 59–71.

Baines, D., Redpath, S., Richardson, M. & Thirgood, S. (2008) The direct and indirect effects of predation by hen harriers *Circus cyaneus* on trends in breeding birds on a Scottish grouse moor. *Ibis*, **150**, 27–36.

Baker, P.J., Bentley, A.J., Ansell, R.J. & Harris, S. (2005) Impact of predation by domestic cats *Felis catus* in an urban area. *Mammal Review*, **35**, 302–312.

Baker, H., Stroud, D.A., Aebischer, N.J., Cranswick, P.A., Gregory, R.D., McSorley, C.A., Noble, D.G. & Rehfisch, M.M. (2006) Population estimates of birds in Great Britain and the United Kingdom. *British Birds*, **99**, 25–44.

Baker, P.J., Molony, S.E., Stone, E., Cuthill, I.C. & Harris, S. (2008) Cats about town: is predation by free-ranging pet cats *Felis catus* likely to affect urban bird populations? *Ibis*, **150**, 86–99.

Battersby, J.E. & Partnership (2005) UK mammals: species status and population trends. First report by the tracking mammals partnership. JNCC/Tracking mammals partnership, Peterborough.

Beckerman, A.P., Boots, M. & Gaston, K.J. (2007) Urban bird declines and the fear of cats. *Animal Conservation*, **10**, 320–325.

Bolton, M., Tyler, G., Smith, K.E.N. & Bamford, R.O.Y. (2007) The impact of predator control on lapwing *Vanellus vanellus* breeding success on wet grassland nature reserves. *Journal of Applied Ecology*, **44**, 534–544.

Chamberlain, D.E. & Fuller, R.J. (2000) Local extinctions and changes in species richness of lowland farmland birds in England and Wales in relation to recent changes in agricultural land-use. *Agriculture Ecosystems & Environment*, **78**, 1–17.

Chamberlain, D.E. & Fuller, R.J. (2001) Contrasting patterns of change in the distribution and abundance of farmland birds in relation to farming system in lowland Britain. *Global Ecology and Biogeography*, **10**, 399–409.

Chamberlain, D.E., Glue, D.E. & Toms, M.P. (2009) Sparrowhawk *Accipiter nisus* presence and winter bird abundance. *Journal of Ornithology*, **150**, 247–254.

Chamberlain, D.E., Fuller, R.J., Bunce, R.G.H., Duckworth, J.C. & Shrubb, M. (2000) Changes in the abundance of farmland birds in relation to the timing of agricultural intensification in England and Wales. *Journal of Applied Ecology*, **37**, 771–788.

Chamberlain, D.E., Fuller, R.J., Garthwaite, D.G. & Impey, A.J. (2001) A comparison of farmland bird density and species richness in lowland England between two periods of contrasting agricultural practice. *Bird Study*, **48**, 245–251.

Chiron, F. & Julliard, R. (2007) Responses of songbirds to magpie reduction in an urban habitat. *Journal of Wildlife Management*, **71**, 2624–2631.

Côté, I.M. & Sutherland, W.J. (1997) The effectiveness of removing predators to protect bird populations. *Conservation Biology*, **11**, 395–405.

Craik, J.C.A. (1997) Long-term effects on North American mink *Mustela vison* on seabirds in western Scotland. *Bird Study*, **44**, 303–309.

Crick, H.Q.P., Robinson, R.A., Appleton, G.F., Clark, N.A. & Rickard, A.D. (2002) *Investigation into the Causes of the Decline of Starlings and House Sparrows in Great Britain*. BTO Research Report No. 290. DEFRA, London.

De Leon, A., Minguez, E., Harvey, P., Meek, E., Crane, J.E. & Furness, R.W. (2006) Factors affecting breeding distribution of stormpetrels *Hydrobates pelagicus* in Orkney and Shetland. *Bird Study*, **53**, 64–72.

Donald, P.F., Evans, A.D., Muirhead, L.B., Buckingham, D.L., Kirby, W.B. & Schmitt, S.I.A. (2002) Survival rates, causes of failure and productivity of skylark *Alauda arvensis* nests on lowland farmland. *Ibis*, **144**, 652–664.

Draycott, R.A.H., Hoodless, A.N., Woodburn, M.I.A. & Sage, R.B. (2008) Nest predation of common pheasants *Phasianus colchicus*. *Ibis*, **150**, 37–44.

Eaton, M.A., Ausden, M., Burton, N., Grice, P.V., Hearn, R., Hewson, C.M., Hilton, G.M., Noble, D.G., Ratcliffe, N. & Rehfisch, M.M. (2006) *The State of the UK's Birds 2005*. RSPB, BTO, WWT, CCW, EN, EHS, SNH, Sandy.

Eaton, M.A., Austin, G.E., Banks, A.N., Conway, G., Douse, A., Grice, P.V., Hearn, R., Ratcliffe, N., Rehfisch, M.M., Worden, J. & Wotton, S. (2007) *The State of the UK's Birds 2006*. RSPB, BTO, WWT, CCW, EHS, NE, SNH, Sandy.

Eaton, M.A., Balmer, D., Burton, N., Grice, P.V., Musgrove, A.J., Hearn, R., Hilton, G., Leech, D., Noble, D.G., Ratcliffe, N., Rehfisch, M.M., Whitehead, S. & Wotton, S. (2008) *The State of the UK's Birds 2007*. RSPB, BTO, WWT, CCW, EHS, NE, SNH, Sandy.

Ferreras, P. & Macdonald, D.W. (1999) The impact of American mink Mustela vison on water birds in the upper Thames. *Journal of Applied Ecology*, **36**, 701–708.

Fuller, R.J., Gregory, R.D., Gibbons, D.W., Marchant, J.H., Wilson, J.D., Baillie, S.R. & Carter, N. (1996) Population declines and range contractions among lowland farmland birds in Britain (vol 9, pg 1425, 1995). *Conservation Biology*, **10**, 7.

Fuller, R.J., Noble, D.G., Smith, K. & Vanhinsbergh, D. (2005) Recent declines in populations of woodland birds in Britain: a review of possible causes. *British Birds*, **98**, 116–143.

Fuller, R.J., Smith, K.W., Grice, P.V., Currie, F.A. & Quine, C.P. (2007) Habitat change and woodland birds in Britain: implications for management and future research. *Ibis*, **149**, 261–268.

Gates, S. & Donald, P.F. (2000) Local extinction of British farmland birds and the prediction of further loss. *Journal of Applied Ecology*, **37**, 806–820.

Geer, T.A. (1978) Effects of nesting sparrowhawks on nesting tits. *The Condor*, **80**, 419–422.

Gibbons, D.W., Amar, A., Anderson, G.Q.A., Bolton, M., Bradbury, R.B., Eaton, M.A., Evans, A.D., Grant, M.C., Gregory, R.D., Hilton, G.M., Hirons, G.J.M., Hughes, J., Johnstone, I., Newbery, P., Peach, W.J., Ratcliffe, N., Smith, K.W., Summers, R.W., Walton, P. & Wilson, J.D. (2007) The predation of wild birds in the UK: a review of its conservation impact and management. Research Report no 23. RSPB, Sandy.

Gill, R.M.A. & Fuller, R.J. (2007) The effects of deer browsing on woodland structure and songbirds in lowland Britain. *Ibis*, **149**, 119–127.

Gooch, S., Baillie, S.R. & Birkhead, T.R. (1991) Magpie *Pica pica* and songbird populations. Retrospective investigation of trends in population density and breeding success. *The Journal of Applied Ecology*, **28**, 1068–1086.

Grant, M.C., Orsman, C., Easton, J., Lodge, C., Smith, M., Thompson, G., Rodwell, S. & Moore, N. (1999) Breeding success and causes of breeding failure of curlew *Numenius arquata* in Northern Ireland. *Journal of Applied Ecology*, **36**, 59–74.

Gregory, R.D., Noble, D.G. & Custance, J. (2004) The state of play of farmland birds: population trends and conservation status of lowland farmland birds in the United Kingdom. *Ibis*, **146**, 1–13.

Gregory, R.D., Wilkinson, N.I., Noble, D.G., Robinson, J.A., Brown, A.F., Hughes, J., Procter, D., Gibbons, D.W. & Galbraith, C. (2002) The population status of birds in the United Kingdom, Channel Islands and Isle of Man: an analysis of conservation concern 2002–2007. *British Birds*, **95**, 410–448.

Groom, D.W. (1993) Magpie *Pica pica* predation on Blackbird *Turdus merula* nests in urban areas. *Bird Study*, **40**, 55–62.

Hedges, J.V. & Olkin, I. (1985) *Statistical Methods for Meta-analysis*. Academic Press, Orlando, FL.

Henderson, I., Parrott, D. & Moore, N. (2004a) *Racing Pigeons – Impact of Raptor Predation*. CSL, York.

Henderson, I.G., Fuller, R.J., Conway, G.J. & Gough, S.J. (2004b) Evidence for declines in populations of grassland-associated birds in marginal upland areas of Britain. *Bird Study*, **51**, 12–19.

Hewson, C.M., Fuller, R.J., Mayle, B. & Smith, K. (2004) Possible impacts of Grey squirrels on birds and other wildlife. *British Wildlife*, **15**, 183–191.

Hewson, C.M., Amar, A., Lindsell, J.A., Thewlis, R.M., Butler, S., Smith, K. & Fuller, R.J. (2007) Recent changes in bird populations in British broadleaved woodland. *Ibis*, **149**, 14–28.

Hill, D. (1988) Population-dynamics of the Avocet (*Recurvirostra avosetta*) breeding in Britain. *Journal of Animal Ecology*, **57**, 669–683.

Holt, A.R., Davies, Z.G., Tyler, C. & Staddon, S. (2008) Meta-analysis of the effects of predation on animal prey abundance: evidence from UK vertebrates. *PLoS ONE*, **3**, e2400.

Jackson, D.B. (2001) Experimental removal of introduced hedgehogs improves wader nest success in the Western Isles, Scotland. *Journal of Applied Ecology*, **38**, 802–812.

Jackson, D.B., Fuller, R.J. & Campbell, S.T. (2004) Long-term population changes among breeding shorebirds in the Outer Hebrides, Scotland, in relation to introduced hedgehogs (Erinaceus europaeus). *Biological Conservation*, **117**, 151–166.

Lewis, A.J.G., Amar, A., Cordi-Piec, D. & Thewlis, R.M. (2007) Factors influencing willow tit (*Poecile montanus*) site occupancy: a comparison of abandoned and occupied woods. *Ibis*, **149**, 205–213.

MacDonald, M. & Bolton, M. (2008) Predation of lapwing *Vanellus vanellus* nests on lowland wet grassland in England and Wales: effects of nest density, habitat and predator abundance. *Journal of Ornithology*, **149**, 555–563.

Nelson, S.H., Evans, A.D. & Bradbury, R.B. (2005) The efficacy of collar-mounted devices in reducing the rate of predation of wildlife by domestic cats. *Applied Animal Behaviour Science*, **94**, 273–285.

Newton, I. (1993) Predation and the limitation of bird numbers. *Current Ornithology*, **11**, 143–198.

Newton, I. (1998) *Population Limitation in Birds*. Academic Press, London.

Newton, I. (2004) The recent declines of farmland bird populations in Britain: an appraisal of causal factors and conservation actions. *Ibis*, **146**, 579–600.

Newton, I., Dale, L. & Rothery, P. (1997) Apparent lack of impact of sparrowhawks on the breeding densities of some woodland songbirds. *Bird Study*, **44**, 129–135.

Oro, D. & Furness, R.W. (2002) Influences of food availability and predation on survival of kittiwakes. *Ecology*, **83**, 2516–2528.

Paradis, E., Baillie, S.R., Sutherland, W.J., Dudley, C., Crick, H.Q.P. & Gregory, R.D. (2000) Large-scale spatial variation in the breeding performance of song thrushes *Turdus philomelos* and blackbirds *T. merula* in Britain. *Journal of Applied Ecology*, **37**, 73–87.

Park, K.J., Calladine, J.R., Graham, K.E., Stephenson, C.M. & Wernham, C.V. (2005) The impacts of predatory birds on waders, songbirds, gamebirds and fisheries. Report to Scotland's Moorland Forum. Available at: http://www.moorlandforum.org.uk/documents/PBRFinal.pdf.

Park, K.J., Graham, K.E., Calladine, J. & Wernham, C.W. (2008) Impacts of birds of prey on gamebirds in the UK: a review. *Ibis*, **150**, 9–26.

Parr, R. (1992) The decline to extinction of a population of Golden Plover in North-East Scotland. *Ornis Scandinavica*, **23**, 152–158.

Parr, R. (1993) Nest predation and numbers of golden plovers *Pluvialis apricaria* and other moorland waders. *Bird Study*, **40**, 223–231.

Petty, S.J., Anderson, D.I.K., Davison, M., Little, B., Sherratt, T.N., Thomas, C.J. & Lambin, X. (2003) The decline of common kestrels *Falco tinnunculus* in a forested area of northern England: the role of predation by northern goshawks *Accipiter gentilis*. *Ibis*, **145**, 472–483.

Quinn, J.L., Reynolds, S.J. & Bradbury, R.B. (2008) Birds as predators and as prey. *Ibis*, **150**, 1–8.

RDCT. (2005) *R: A Language and Environment for Statistical Computing*. R Foundation for Statistical Computing, Vienna.

Redpath, S.M. (1991) The impact of hen harriers on red grouse breeding success. *Journal of Applied Ecology*, **28**, 659–671.

Ruxton, G.D., Thomas, S. & Wright, J.W. (2002) Bells reduce predation of wildlife by domestic cats (*Felis catus*). *Journal of Zoology*, **256**, 81–83.

Sim, I.M.W., Gregory, R.D., Hancock, M.H. & Brown, A.F. (2005) Recent changes in the abundance of British upland breeding birds. *Bird Study*, **52**, 261–275.

Siriwardena, G.M., Baillie, S.R., Buckland, S.T., Fewster, R.M., Marchant, J.H. & Wilson, J.D. (1998) Trends in the abundance of farmland birds: a quantitative comparison of smoothed Common Birds Census indices. *Journal of Applied Ecology*, **35**, 24–43.

Stoate, C. & Szczur, J. (2001) Could game management have a role in the conservation of farmland passerines? *Bird Study*, **48**, 279–292.

Stoate, C. & Szczur, J. (2006) Potential influence of habitat and predation on local breeding success and population in spotted flycatchers *Muscicapa striata*. *Bird Study*, **53**, 328–330.

Summers, R.W., Green, R.E., Proctor, R., Dugan, D., Lambie, D., Moncrieff, R., Moss, R. & Baines, D. (2004) An experimental study of the effects of predation on the breeding productivity of capercaillie and black grouse. *Journal of Applied Ecology*, **41**, 513–525.

Summers-Smith, J.D. (1999) Current status of the house sparrow in Britain. *British Wildlife*, **10**, 381–386.

Tapper, S.C. (1992) *Game Heritage: An Ecological Review from Shooting and Game Keeping Records*. Game Conservancy Trust, Fordingbridge, Hampshire.

Tapper, S.C., Potts, G.R. & Brockless, M.H. (1996) The effect of an experimental reduction in predation pressure on the breeding success and population density of grey partridges *Perdix perdix*. *The Journal of Applied Ecology*, **33**, 965–978.

Tharme, A.P., Green, R.E., Baines, D., Bainbridge, I.P. & O'Brien, M. (2001) The effect of management for red grouse shooting on the population density of breeding birds on heather-dominated moorland. *Journal of Applied Ecology*, **38**, 439–457.

Thirgood, S.J., Redpath, S.M., Rothery, P. & Aebischer, N.J. (2000) Raptor predation and population limitation in red grouse. *Journal of Animal Ecology*, **69**, 504–516.

Thomson, D.L., Green, R.E., Gregory, R.D. & Baillie, S.R. (1998) The widespread declines of songbirds in rural Britain do not correlate with the spread of their avian predators. *Proceedings: Biological Sciences*, **265**, 2057–2062.

UKRWG (2000) *Report of the UK Raptor Working Group*. DETR/JNCC, Bristol.

Valkama, J., Korpimaki, E., Arroyo, B., Beja, P., Bretagnolle, V., Bro, E., Kenward, R., Manosa, S., Redpath, S.M., Thirgood, S. & Vinuela, J. (2005) Birds of prey as limiting factors of gamebird populations in Europe: a review. *Biological Reviews*, **80**, 171–203.

Watson, M., Aebischer, N.J., Potts, G.R. & Ewald, J.A. (2007) The relative effects of raptor predation and shooting on overwinter mortality of grey partridges in the United Kingdom. *Journal of Applied Ecology*, **44**, 972–982.

White, P.J.C., Stoate, C., Szczur, J. & Norris, K.J. (2008) Investigating the effects of predator removal and habitat management on nest success and breeding population size of a farmland passerine: a case study. *Ibis*, **150**, 178–190.

Woods, M., McDonald, R.A. & Harris, S. (2003) Predation of wildlife by domestic cats *Felis catus* in Great Britain. *Mammal Review*, **33**, 174–188.

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Supporting Information

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

Table S1. Common and scientific names of predators and prey.

Table S2. A description of each piece of information extracted from the studies.

Table S3. The predator species included in each of the 32 studies reviewed.

Table S4. The predator species for which data showing a difference in abundance during the study were available (Y).

Table S5. Predator species that were monitored using bespoke census techniques (Y) or generic methodologies (N).

Table S6. Prey-specific information extracted from the 32 studies reviewed, where the studied prey species were (a) game birds, (b) waders, (c) songbirds and (d) others.

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