

A review of predation as a limiting factor for bird populations in mesopredator-rich landscapes: a case study of the UK

Staffan Roos^{1*} , Jennifer Smart^{2,3}, David W. Gibbons² and Jeremy D. Wilson¹

¹*RSPB Centre for Conservation Science, Edinburgh, EH12 9DH, U.K.*

²*RSPB Centre for Conservation Science, Sandy, SG19 2DL, U.K.*

³*School of Biological Science, University of East Anglia, Norwich, NR4 7TJ, U.K.*

ABSTRACT

The impact of increasing vertebrate predator numbers on bird populations is widely debated among the general public, game managers and conservationists across Europe. However, there are few systematic reviews of whether predation limits the population sizes of European bird species. Views on the impacts of predation are particularly polarised in the UK, probably because the UK has a globally exceptional culture of intensive, high-yield gamebird management where predator removal is the norm. In addition, most apex predators have been exterminated or much depleted in numbers, contributing to a widely held perception that the UK has high numbers of mesopredators. This has resulted in many high-quality studies of mesopredator impacts over several decades. Here we present results from a systematic review of predator trends and abundance, and assess whether predation limits the population sizes of 90 bird species in the UK. Our results confirm that the generalist predators Red Fox (*Vulpes vulpes*) and Crows (*Corvus corone* and *C. cornix*) occur at high densities in the UK compared with other European countries. In addition, some avian and mammalian predators have increased numerically in the UK during recent decades. Despite these high and increasing densities of predators, we found little evidence that predation limits populations of pigeons, woodpeckers and passerines, whereas evidence suggests that ground-nesting seabirds, waders and gamebirds can be limited by predation. Using life-history characteristics of prey species, we found that mainly long-lived species with high adult survival and late onset of breeding were limited by predation. Single-brooded species were also more likely to be limited by predation than multi-brooded species. Predators that depredate prey species during all life stages (i.e. from nest to adult stages) limited prey numbers more than predators that depredated only specific life stages (e.g. solely during the nest phase). The Red Fox and non-native mammals (e.g. the American Mink *Neovison vison*) were frequently identified as numerically limiting their prey species. Our review has identified predator–prey interactions that are particularly likely to result in population declines of prey species. In the short term, traditional predator-management techniques (e.g. lethal control or fencing to reduce predation by a small number of predator species) could be used to protect these vulnerable species. However, as these techniques are costly and time-consuming, we advocate that future research should identify land-use practices and landscape configurations that would reduce predator numbers and predation rates.

Key words: trophic cascades, intra-guild predation, landscape of fear, land-use, predator avoidance, top-down control, life-history traits, nest predation.

CONTENTS

I. Introduction	2
II. Methods	3
(1) Are the densities of generalist predators higher in the UK than in other European countries?	3
(2) Have predator numbers increased in the UK?	4
(3) Does predation limit individual bird species or groups of species?	4

* Author for correspondence (Tel: ++44 1313 174151; E-mail: staffan.roos@rspb.org.uk)

(a) Selection of relevant literature	4
(b) Categorisation of results from the literature	4
(4) Do species or groups of species limited by predation share certain nest-site characteristics, migratory strategies or life-history traits?	5
(5) Data analysis	5
III. Results	6
(1) Are the densities of generalist predators higher in the UK than in other European countries?	6
(2) Have predator numbers increased in the UK?	6
(a) Avian predators	6
(b) Mammalian predators	6
(3) Does predation limit individual bird species or groups of species?	9
(a) Literature review	9
(b) Evidence that predation limits bird populations	9
(4) Do species or groups of species limited by predation share certain nest-site characteristics, migratory strategies or life-history traits?	10
(5) What predator species and at what life stage can predation limit prey populations?	11
(a) Predator species	11
(b) Predation at various life stages	12
IV. Discussion	12
(1) Generalist predator densities	12
(2) Trends in predator numbers	12
(3) Species groups limited by predation	13
(4) Proximate and ultimate causes of high predation	16
(5) What can be done to alleviate predation pressure?	17
V. Conclusions	18
VI. Acknowledgments	18
VII. References	18
VIII. Supporting Information	22

I. INTRODUCTION

There have been widespread population declines of many bird species across northwest Europe and North America (Donald, Green, & Heath, 2001; North American Bird Conservation Initiative, 2016; Pan-European Common Bird Monitoring Scheme, 2016), principally due to intensification of agricultural and forestry practices (Chamberlain *et al.*, 2000; Wretenberg *et al.*, 2006; Gregory *et al.*, 2007). However, there are growing concerns that predation may have contributed to these population declines across Europe and North America, because populations of many predators have increased (Deinet *et al.*, 2013; Marra & Santella, 2016; Newton, 2017). Reasons for the increases in predator numbers may include improved opportunities for foraging on human-associated waste (Eggers *et al.*, 2005; Marzluff & Neatherlin, 2006), mesopredator release as a result of anthropogenic removal of top predators (Crooks & Soulé, 1999; Ritchie *et al.*, 2012), increased numbers of free-ranging Domestic Cats *Felis catus* (Beckerman, Boots, & Gaston, 2007; Baker *et al.*, 2008; Thomas, Fellowes, & Baker, 2012; Marra & Santella, 2016) and changes in land-use patterns, landscape composition and landscape fragmentation that have favoured generalist predators (e.g. Robinson *et al.*, 1995; Oehler & Litvaitis, 1996; Hannon & Cotterill, 1998; Douglas *et al.*, 2013; Lees, Newton, & Balmford, 2013; Wilson *et al.*, 2014). In addition, populations of predatory

mammals and birds have recovered following reductions in secondary pesticide poisoning and illegal persecution (Newton, 1998, 2017; Burfield, 2008) and through successful reintroductions (Seddon, Armstrong, & Maloney, 2007). However, contrasting population trends of predators and prey species may not necessarily reflect cause and effect (e.g. Newton, 1998; Newson *et al.*, 2010a, 2010b). Furthermore, where predator management occurs (e.g. *via* lethal predator control or fencing to exclude predators), overall predation rate may not change, because of compensatory predation by other predator species (Newton, 1998; Bodey *et al.*, 2011). Accordingly, a review of corvid impacts on productivity and population size of other bird species revealed that removing corvids was significantly less effective than removing both corvids and other predators (Madden, Arroyo, & Amar, 2015). The lethal control of predators also attracts opposition on ethical grounds (Messmer *et al.*, 1999; Reiter, Brunson, & Schmidt, 1999; Warburton & Norton, 2009), and may have low effectiveness and high costs, especially if total eradication is attempted (Doherty & Ritchie, 2017).

The observed range expansion and numerical increase of top predators in many parts of North America and Europe (Lensink, 1997; Breitenmoser, 1998; Deinet *et al.*, 2013; Newsome & Ripple, 2015) may not necessarily result in increased predation rates of birds. Interactions between predator species (e.g. intra-guild predation) may influence the total abundance of predators in an area, with sometimes unexpected trophic cascades (e.g. Pimm, 1991; Polis & Holt,

1992; Holt & Polis, 1997). For example, the return of large predatory mammals and birds can reduce the population size of mesopredators upon which they prey (Petty *et al.*, 2003; McDonald, O'Hara, & Morrish, 2007; Berger, Gese, & Berger, 2008; Sergio & Hiraldo, 2008; Carlsson *et al.*, 2010; Pasanen-Mortensen, Pyykönen, & Elmhagen, 2013), or change their movement and foraging patterns (Salo *et al.*, 2008). Both the numerical and behavioural impacts may reduce the mesopredators' predation rates of species at lower trophic levels (Sovada, Sargeant, & Grier, 1995; Berger *et al.*, 2008). Ritchie & Johnson (2009) found that in seven of eight examples involving avian prey, there was evidence that the presence of an apex predator suppressed the population size or behaviour of mesopredators, which in turn resulted in higher breeding success and population size of the prey species.

It is important to understand whether predation is driving bird population declines because there is a growing global conservation conflict between those who consider that lethal predator control should be a routine part of conservation management (e.g. Reynolds & Tapper, 1996) and those who argue that it should be used either not at all or as a last rather than a first option when managing predation (Treves & Naughton-Treves, 2005; Warburton & Norton, 2009). This conflict is particularly polarised in the UK because the UK has the most high-yield gamebird management in the world, but set in weak regulatory frameworks (Mustin *et al.*, 2011; Pillai & Turner, 2017). This intensive gamebird management is associated with widespread illegal killing of protected predators (Etheridge, Summers, & Green, 1997; Whitfield *et al.*, 2004; Whitfield, Fielding, & Whitehead, 2008; Smart *et al.*, 2010; Amar *et al.*, 2012; Whitfield & Fielding, 2017). In addition, there is a prevalent perception by land managers in the UK that populations of generalist predators, particularly Red Fox *Vulpes vulpes*, Magpie *Pica pica*, Carrion Crow *Corvus corone* and Hooded Crow *C. comix* are high and increasing relative to other parts of Europe (Ainsworth *et al.*, 2016). As a result, there have been a large number of high-quality studies of predator impacts in the UK.

This combination of intensive gamebird management, arguably abundant mesopredators and a rich literature of scientific studies of predation impacts makes the UK an important case study which could help to resolve conflicts over the role of predator control in conservation and land management. We therefore carried out a systematic review (Pullin & Stewart, 2006) of the effects of predation on population sizes of bird species, focusing on the UK as a case study. There is evidence that the effects of predators on avian prey species are similar in temperate regions, which makes our study relevant elsewhere. For example, Madden *et al.* (2015) showed that the effects of corvids on the productivity of their avian prey did not differ between the UK, France and the USA, which represent different geographical and ecological contexts, with different predator and prey communities. In addition, the effects of non-native predators, particularly rats, Feral Cats (*Felis catus*) and mustelids such as Stoat *Mustela erminea*, Polecat *M. putorius* (and its domesticated form Ferret *M. p. furo*) and American Mink *Neovison vison*, on

avian prey on islands are similar across different geographical areas with different prey species (Moore, Roy, & Helyar, 2003; Nordström *et al.*, 2003; Towns & Broome, 2003; Ratcliffe *et al.*, 2010; Jones *et al.*, 2011), supporting the notion that conclusions from this study regarding non-native predators are likely to be of wider relevance.

For the purposes of this review, we consider predation that reduces the number of breeding individuals to levels below those that would occur in the absence of that predation as having a limiting effect on the bird species. Specifically, we examined four questions: (i) are densities of foxes and corvids higher in the UK than in other European countries?; (ii) Have predator numbers increased in the UK?; (iii) Does predation limit individual bird species or groups of species and if it does, which predator species is responsible and at what life stage do they depredate the prey species?; and (iv) Do species or groups of species limited by predation share certain nest-site characteristics, migratory strategies or life-history traits?

II. METHODS

(1) Are the densities of generalist predators higher in the UK than in other European countries?

We compiled information on Red Fox densities across Europe using existing literature, summarised by Harris & Yalden (2008) and Pasanen-Mortensen *et al.* (2013), and references therein). We restricted the records from Russia to those west of longitude 60° East (i.e. European records) and, following Pasanen-Mortensen *et al.* (2013), we excluded density estimates from urban environments. We also excluded countries for which we only had one density estimate (i.e. Lithuania, France, Czech Republic, Hungary and the Republic of Ireland). The Red Fox estimates came from several different methods (e.g. nocturnal spotlight counts, hunting bag records, snow tracks and den counts). We followed the approach of Pasanen-Mortensen *et al.* (2013) to transform den density to Red Fox density by multiplying each den by two (i.e. one male and one female Red Fox per den). This underestimates the true Red Fox density because each den, at least in the UK, can host a group of foxes (e.g. the breeding pair plus offspring from the previous year; Harris & Yalden, 2008). In addition, in high-density areas, there are non-breeding foxes that are not associated with a specific den (Harris & Yalden, 2008). We also used a recent estimate of 430515 individuals for the UK Red Fox population (The Mammal Society, 2013) to provide an approximate national density estimate for the UK (number of foxes/land area of the UK ≈ 1.75 foxes km⁻²).

We extracted the estimated population sizes (number of pairs) of corvids in each European country from BirdLife International (2015). We summed the number of Hooded and Carrion Crow pairs for countries where both species occur to generate a total crow population estimate. For countries where only one of the two species occurs, we used that number as the total Crow estimate. We divided

the country-specific numbers of pairs of Crows by the area of the country to estimate density (i.e. pairs km⁻²), and did the same for Magpie. These simple density estimates provided a conservative estimate of true densities, because in most countries there are habitats with almost no breeding Crows and Magpies (e.g. Balmer *et al.*, 2013), whereas these species occur at much higher densities in other habitats. In addition, both Magpie and Crow populations contain a large proportion of non-breeding individuals (Loman, 1980; Birkhead, 1991). Thus, the estimates provided here are likely to be lower than the actual number of individuals in each country.

(2) Have predator numbers increased in the UK?

We quantified population trends of mammalian and avian predator species using published data from the UK-wide BTO/RSPB/JNCC Breeding Bird Survey (BBS; Harris *et al.*, 2017), in which mammals are also counted, and the National Gamebag Census (NGC; Aebischer, Davey, & Kingdon, 2011). We recognise that both the BBS and the NGC have weaknesses as indices of mammal trends. The BBS is a bespoke bird-monitoring scheme, and because most mammals are nocturnal, the BBS most likely under-records the density of the Red Fox and other medium-sized predators, potentially affecting the robustness of trends. The NGC does not record catching effort, so the trends in predators killed are not corrected for variation in effort among years. For scarce and protected predators (i.e. legislation prevents NGC data to be collected for Otter *Lutra lutra*, Pine Marten *Martes martes* and Badger *Meles meles*), neither the BBS nor the NBC can provide any trends. Nevertheless, these schemes together provide the most up-to-date measure of mammal trends in the UK. For long-term trends for common bird species in the UK, we used the combined trend from the BBS and its predecessor, the Common Bird Census [CBC; see Robinson *et al.*, 2016 for survey and analytical methods]. For scarce raptors, we used results from bespoke national surveys (e.g. Ewing *et al.*, 2008; Hayhow *et al.*, 2017b; Wotton *et al.*, in press), annual monitoring data collated by the Rare Breeding Bird Panel (RBBP; summarised in Hayhow *et al.*, 2017a) and the Scottish Raptor Monitoring Scheme (SRMS; Challis *et al.*, 2016). Finally, for gulls and skuas, we used results from the bespoke national Seabird Monitoring Program (JNCC, 2015).

(3) Does predation limit individual bird species or groups of species?

(a) Selection of relevant literature

Following the guidelines of Pullin & Stewart (2006), we carried out a systematic review to answer questions 3 and 4. We conducted a literature review by searching *Web of Science* and *Google Scholar* for relevant literature (the search phrases and method used to determine the relevance of each publication are provided as online Supporting Information in Appendix S1), and then searching relevant references in these

publications. We also used several previous reviews and books on similar and related topics to identify additional literature (e.g. Newton, 1979, 1998, 2013; Baille, Gooch, & Birkhead, 1992; Andr n, 1994; Redpath & Thirgood, 1997; Valkama *et al.*, 2005; Gibbons *et al.*, 2007; Holt *et al.*, 2008; MacDonald & Bolton, 2008; Park *et al.*, 2008; Sergio & Hiraldo, 2008; Nicoll & Norris, 2010; Smith *et al.*, 2010, 2011; Madden *et al.*, 2015; Ainsworth *et al.*, 2016). Finally, we asked colleagues at universities, non-governmental organisations (NGOs) and statutory agencies to identify relevant peer-reviewed papers, MSc and PhD theses as well as ‘grey’ literature (e.g. reports from NGOs, statutory agencies and universities).

(b) Categorisation of results from the literature

We focused on changes in abundance of individual prey species (i.e. numerical changes). Surrogates for abundance included density (e.g. pairs or nests km⁻²), number of encounters per line transect and number of territorial males. Most studies focused on abundance during the breeding season, but two studies used changes in abundance of resident species during the non-breeding season, which could reflect changes in breeding abundance (e.g. Chamberlain, Glue, & Toms, 2009; Bell *et al.*, 2010).

Many published studies examined the effect of predation on several prey species simultaneously, and to separate the species-specific responses, we use the word ‘case’ to refer to the response of one prey species to one or more predator species. We only included cases where species-specific prey responses to predators were quantified. Wherever possible, we used results that included the effect of changing abundance of one predator species on a single prey species. However, in many cases involving predator management (e.g. by lethal control or fencing), multiple predator species were managed simultaneously. In these cases, we used the response of one prey species to the changing densities of the group of managed predator species as the response.

We categorised the correlation between predators and prey abundance for each case as ‘Negative correlation’, ‘No correlation’ or ‘Positive correlation’, using the original studies’ reported parameter estimates and significance of statistical tests as guideline, with $P \geq 0.05$ as a threshold between no correlation and either positive or negative correlations. We also classified the studies into three groups, based on their scientific quality. These groups were: ‘Fair’ – *observational studies* mainly from one study area which focused mainly on correlation between predation rates and prey abundance and provided further evidence (e.g. statistical modelling) to examine whether or not those predation levels were likely to limit bird prey populations numerically; ‘Good’ – *comparative studies* which contrasted prey trends, numbers or densities between places or times when predators were present *versus* absent, or at higher *versus* lower abundance, to examine the evidence that predation limits bird populations; and ‘Best’ – *experimental studies* comparing prey trends, numbers or densities between areas or times in which predators were experimentally removed or excluded, *versus* those in which predators were

not manipulated. For studies in the categories ‘Good’ and ‘Best’, predation levels were often reported and we used those results to support our categorisation. Occasionally, two or more studies from the same study area on the same prey species were used to support the categorisation (Appendix S2, Table S2.1).

We amalgamated the direction of the correlation and the scientific quality of each case into a new variable (‘Evidence’) measured on an ordinal scale between -3 and $+3$. Thus, -3 indicated a negative correlation between predators and prey estimated from a formal experiment (i.e. from a study classified as ‘Best’), -2 indicated a negative correlation between predators and their prey from a study classified as ‘Good’, and so on through to $+3$, which indicated a positive correlation between predators and prey determined from a study with formal experiments (see Appendix S2, Table S2.2). For cases with ‘No correlation’, the scientific quality of the study (i.e. Fair, Good and Best) was incorporated into a zero score with three levels (i.e. 0F, 0G and 0B; Appendix S2, Table S2.2).

For each case, we used the information provided in the published study to identify at what stage in the life of the prey species (e.g. ‘Nest’, ‘Nest & juvenile’, ‘Juvenile’, ‘Juvenile & adult’ and ‘All stages’) that the predator–prey interaction occurred. We also recorded which predator species were identified in each case. For the purposes of data analysis, we pooled predator species into nine categories: ‘Raptors’, ‘Skuas and gulls’, ‘Corvids’, ‘Fox’, ‘Corvids & fox’, ‘Corvids, fox & others’ (the latter two when corvids, Red Fox and sometimes other predators were managed simultaneously, so that the relative importance of each predator could not be ascertained), ‘Native mammals’, ‘Non-native mammals’ and ‘Others’ (which contained woodpeckers, and infrequently reported predators, such as Green Woodpecker *Picus viridis*, Common Coot *Fulica atra* and Common Moorhen *Gallinula chloropus*).

(4) Do species or groups of species limited by predation share certain nest-site characteristics, migratory strategies or life-history traits?

For life-history traits, we used longevity (i.e. the maximum age from UK ringing records), expected reproductive lifespan (estimated from UK ringing records; this is the life expectancy of individuals reaching breeding age), age at first breeding, mean clutch size, mean annual juvenile survival, mean annual adult survival and the number of broods per year. Data were taken mainly from Robinson *et al.* (2016), but also from Martin & Clobert (1996) for clutch size and the mean number of broods per year for passerines. For the few instances where parameters could not be found in these sources, we used species-specific literature (see Appendix S2, Table S2.1 for references used for the different species). Information on nest-site location and migratory strategy were taken from Cramp (1992) and Robinson *et al.* (2016), respectively. We found information on nest site, migratory strategy, longevity, average lifespan, age at first breeding and clutch size for all species. However, for 15 species, we were

unable to find estimates of juvenile survival and for four species we were unable to find estimates of adult survival (Appendix S2, Table S2.3). Consequently, we had complete records of 833 predator–prey interactions across 75 species (cases; Table S2.3).

(5) Data analysis

To analyse the ordinal categories of evidence, we used ordinal logistic models (OLMs; also known as ordinal logistic regressions (OLRs) or cumulative link models (CLMs); McCullagh, 1980; Thomson, Furness, & Monaghan, 1998a).

We found many examples of a single study contributing many individual predator–prey cases. We therefore included ‘Study ID’ as a random effect in our analyses. To account for phylogenetic non-independence of species, we fitted ‘Prey family’ [i.e. the taxonomic listing recommended by the British Ornithologists’ Union (BOU) in its British List] as another random effect in all analyses. We also included ‘Prey group’ as a fixed factor in our models. For this variable, we pooled species with similar biology to form seven main groups: ‘Seabirds’ (shearwaters, storm petrels, gulls, skuas, terns and auks), ‘Raptors and owls’, ‘Waders’ (oystercatchers, avocets, plovers, and sandpipers), ‘Gamebirds’ (pheasants, partridges and grouse), ‘Pigeons’ (pigeons and doves), ‘Woodpeckers’ and ‘Passerines’. Another group, ‘Waterfowl’ (ducks; $N = 2$ cases, and grebes; $N = 1$ case) contained too few cases and was excluded from further analyses. In summary, when analysing whether prey species were limited numerically by predation, we fitted ordinal logistic mixed models (OLMMs) with ‘Evidence’ as the response variable, ‘Prey group’ as a categorical explanatory variable, and with ‘Study ID’ and ‘Prey family’ as random effects. We specified a logit link and, because we used two random effects, a Laplace approximation (Christensen, 2015). We used post-hoc Tukey’s test to identify significant differences between prey groups.

Once we had identified species groups limited numerically by predation, we examined whether these groups shared certain nest-site characteristics (i.e. ground, shrub, tree, cavity and generalist; the latter was used for species that readily use several of the previous categories, such as Common Kestrel *Falco tinnunculus* and Spotted Flycatcher *Muscicapa striata*) and migratory predisposition (resident, migratory and mixed resident/migratory strategy) using χ^2 -tests. Secondly, we explored whether the life-history traits were correlated. The results showed that there were strong and mainly positive correlations between some of the life-history traits; longevity was positively related to reproductive lifespan, age at first breeding and adult survival ($r \geq 0.79$). Similarly, reproductive lifespan was positively related to age at first breeding and adult survival ($r \geq 0.82$). Age at first breeding was correlated with adult survival ($r \geq 0.71$). All other correlations were less strong (i.e. $-0.57 \geq r \leq 0.51$). Because of these correlations, we used a principal component analysis (PCA) to reduce the number of life-history variables into meaningful axes. However, since we lacked estimates for juvenile survival for 15 species (see Appendix S2, Table S2.3), we omitted this variable. We added a dummy variable for

whether a species was ground-nesting (coded '1') or not (coded '0') to the PCA, because initial analyses revealed that ground-nesting was a very strong predictor for a species being limited by predation. The initial analyses also revealed that no single migratory strategy was linked to being limited by predation. We therefore omitted migratory strategy from the PCA. Thus, for the PCA, we had a data set of 84 species and seven variables. Because of the strongly correlated variables in the PCA, we used an oblique rotation (see e.g. Legendre & Legendre, 2012) using the R command 'Promax'. We regarded a variable as loading on a given PCA axis if the (absolute) factor loading was ≥ 0.35 for that PCA axis, and was < 0.35 for the other, or regarded it as mixed if the variable had a factor loading of > 0.35 for both axes.

To evaluate how the PCA axes were related to the evidence that a species was limited numerically by predation, we calculated the species-specific mean of the 'Evidence' for each species and regressed that against the PCA axes with an eigenvalue of > 1.0 (i.e. PC1 and PC2; see Section III.4). Whilst the use of arithmetic means is not strictly correct in terms of the ordinal 'Evidence' classification (Thomson *et al.*, 1998a), it indicates the slope and provides a visualisation of the relationship.

To examine if different predator groups had different ability to limit prey species numerically, we fitted an OLMM with 'Evidence' as response variable and 'Predator group' (i.e. the nine groups summarised in Section II.3b) as explanatory variable. To control for the phylogenetic non-independence of prey species as well as the non-independence of cases, which sometimes came from the same study, we specified 'Prey species', nested within 'Prey family', and 'Study ID' as random variables. We specified a logit link and, because we used two random effects, a Laplace approximation (Christensen, 2015). We used a post-hoc Tukey's test to identify significant differences between predator groups.

Finally, to examine at what stage predation was most likely to limit prey numbers, we fitted an OLMM with 'Evidence' as response variable and 'Stage' (with the five stages summarised in Section II.3b) as explanatory variable. Again, to control for the phylogenetic non-independence of prey species as well as the non-independence of cases, we specified 'Prey species', nested within 'Prey family', and 'Study ID' as random variables. We specified a logit link and, because we used two random effects, a Laplace approximation (Christensen, 2015). We used a post-hoc Tukey's test to identify significant differences between stages.

For all analyses, we used R (R Core Team, 2015), and for the OLMMs we used the R package 'ordinal' (Christensen, 2015).

III. RESULTS

(1) Are the densities of generalist predators higher in the UK than in other European countries?

The Red Fox density was higher in the UK than all other European countries except Italy and Spain (Fig. 1A). The

most recent population estimate of Red Fox in the UK (The Mammal Society, 2013) suggested that there were 1.75 Red Foxes km^{-2} , and earlier estimates from England and Wales suggested mean (\pm S.E.) densities of around 1.65 ± 0.19 and 1.33 ± 0.68 Red Foxes km^{-2} , respectively. Red Fox densities were lower in Northern Ireland ($0.32 \pm 0.06 \text{ km}^{-2}$) and in Scotland ($0.15 \pm 0.06 \text{ km}^{-2}$).

The density of Crows was higher in the UK than in any other European country ($5.15 \text{ pairs km}^{-2}$; Fig. 1B). However, the density of Magpies in the UK was intermediate compared to other European countries ($2.45 \text{ pairs km}^{-2}$; Fig. 1C).

(2) Have predator numbers increased in the UK?

(a) Avian predators

The most recent data suggest that half of the common and widespread avian predator species monitored by the BBS (i.e. eight of 16 species) increased significantly in numbers in the UK between 1995 and 2015 (Table 1; see also Appendix S3 for supporting information regarding these trends). Widespread species that could potentially limit the numbers of their avian prey species which showed significant population increases during the period 1995–2015 included Red Kite *Milvus milvus* (+1,231%), Common Buzzard *Buteo buteo* (+84%), Barn Owl *Tyto alba* (+217), Great Spotted Woodpecker *Dendrocopos major* (+130%), Jay *Garrulus glandarius* (+19%), Jackdaw *Corvus monedula* (+54%), Carrion Crow (+18%) and Raven *Corvus corax*; +46%). Stable populations were recorded for Peregrine *Falco peregrinus*, Hobby *Falco subbuteo*, Magpie and Hooded Crow (Table 1). Significant declines were recorded for Eurasian Sparrowhawk *Accipiter nisus* (−16%), Common Kestrel (−38%), Little Owl *Athene noctua* (−57%) and Tawny Owl *Strix aluco* (−28%). Scarce raptors monitored by periodic surveys (i.e. Golden Eagle *Aquila chrysaetos*, Hen Harrier *Circus cyaneus* and Merlin *Falco columbarius*) have mainly shown stable or increasing population trends, with Hen Harrier being the only exception with a significant 29% decline between 2004 and 2016 (Table 2). Also rare raptors monitored by annual surveys (i.e. White-tailed Eagle *Haliaeetus albicilla*, Montagu's Harrier *Circus pygargus*, Marsh Harrier *C. aeruginosus*) and Goshawk *Accipiter gentilis* have mainly shown increasing trends in the last decades, with only Montagu's Harrier showing a 15% population decline (Table 2). The population trends of skuas and gulls were mixed. Two species showed both long- and short-term population increases and two species showed both long- and short-term declines. One species increased in the 1980s, but has declined since, and for one species the current trend is unknown (Table 3, see Appendix S3 for more information regarding these trends).

(b) Mammalian predators

For species where gamebag data were available, the long-term NGC trends (1961–2009) suggested significant increases of four of the eight mammalian predators: Red Fox, Stoat, the introduced, non-native American Mink

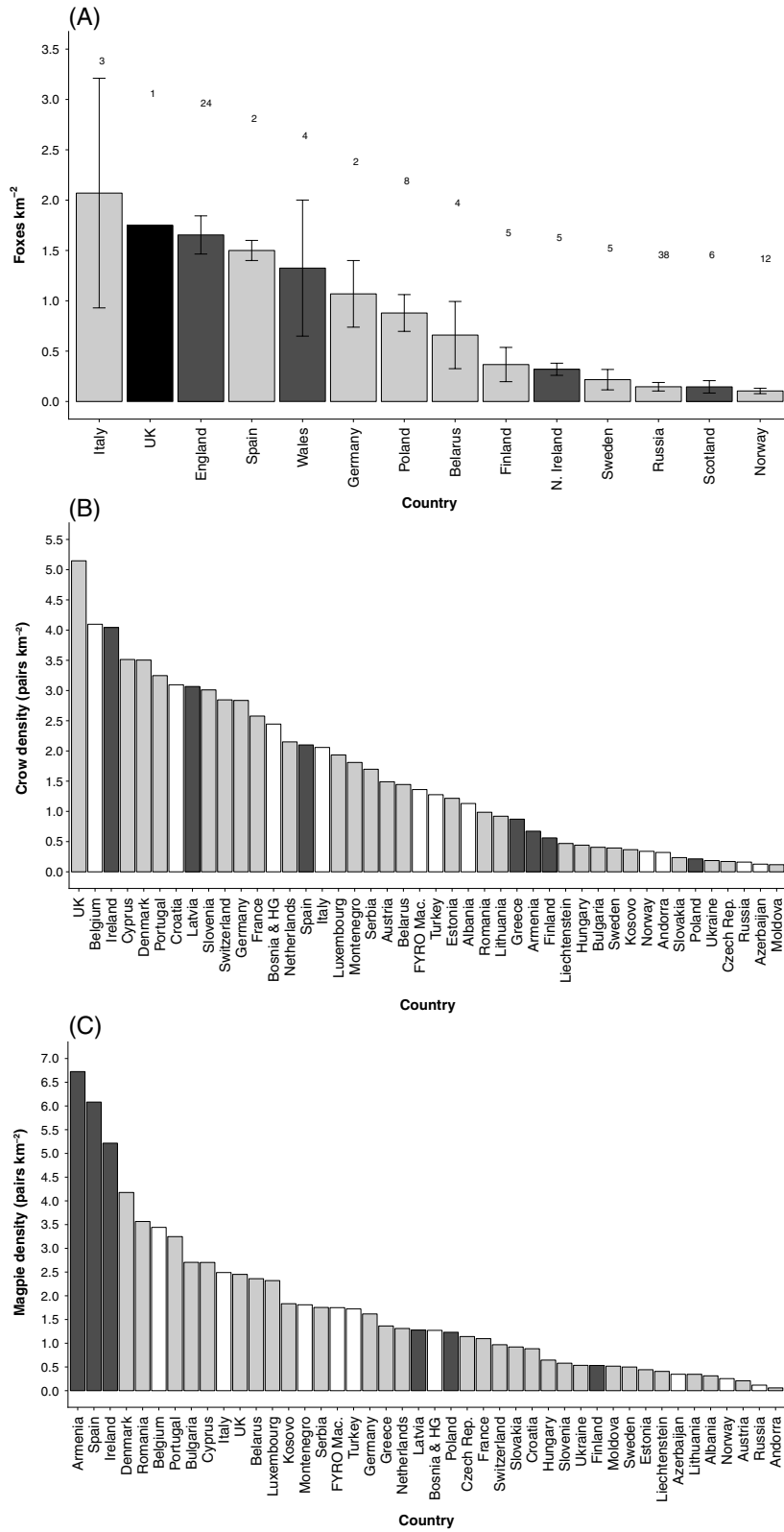


Fig. 1. Densities of (A) Red Fox, (B) Crows (Carrion and Hooded Crows combined) and (C) Magpie in European countries. For Red Fox, the four countries within the UK are denoted in dark grey, and the most recent density estimate for the entire UK is shown in black. The bars show mean, standard errors and sample size for each estimate. Most data on Red Fox densities are from Pasanen-Mortensen *et al.* (2013). For Crows and Magpie, countries with highly accurate population estimates are shown in dark grey, intermediate accuracy with light grey and poor accuracy in white (data from BirdLife International, 2015).

Table 1. Population trends of predatory birds in the UK given as a percentage change from the start year. Both long-term trends from the combined Common Bird Census (CBC) and the Breeding Bird Survey (BBS) for the period 1970–2014 (Hayhow *et al.*, 2017a) as well as the shorter-term BBS trend for the period 1995–2015 (Harris *et al.*, 2017) are shown. The signs + and – indicate whether the trend is positive or negative. Figures in bold indicate that the population trend is significantly different from zero. There are no significance tests available for the UK long-term trends 1970–2014

Species Survey Years	UK CBC/ BBS 1970–2014	UK BBS 1995–2015	England BBS 1995–2015	Scotland BBS 1995–2015	Wales BBS 1995–2015	N. Ireland BBS 1995–2015
Red Kite		+1,231	>10,000			
Sparrowhawk	+74	–16	–21			
Buzzard	+454	+84	+194	+22	–2	>10,000
Kestrel	–48	–38	–24	–69		
Hobby		–12	–9			
Peregrine		–13	+45			
Barn Owl		+217	+238			
Little Owl	–65	–57	–57			
Tawny Owl	–32	–28	–29			
Great Spotted Woodpecker	+360	+130	+105	+413	+180	
Jay	+14	+19	+6		+38	
Magpie	+100	–2	±0	+39	–21	+6
Jackdaw	+152	+54	+65	+23	+27	+98
Carrion Crow	+99	+18	+27	–6	+14	
Hooded Crow		+17		–27		+179
Raven		+46	+130	+35	+34	

Table 2. Population trends and most recent estimate of the number of breeding pairs for rare breeding raptors from national species-specific surveys under the Statutory Conservation Agency and RSPB Annual Breeding Bird Scheme (SCARABBS) or collated by the Rare Breeding Bird Panel (RBBP). The signs + and – indicate whether the trend is positive or negative. Figures in bold indicate that the population trend is significantly different from zero. There are no significance tests available for the RBBP trends

Species	Trend	Period	Pairs in the UK	Survey type	Reference
White-tailed Eagle	+902	1985–2016	102	Annual surveys RSPB	Hayhow <i>et al.</i> (2017a)
Golden Eagle	+16	1982–2015	508	SCARRABS	Hayhow <i>et al.</i> (2017b)
Merlin ^a	+94	1993/94–2008	1162	SCARRABS	Ewing <i>et al.</i> (2008)
Montagu's Harrier	–15	1985/89–2011/15	10	Annual surveys RBBP	Hayhow <i>et al.</i> (2017a)
Marsh Harrier	+479	1985/89–2011/15	365	Annual surveys RBBP	Hayhow <i>et al.</i> (2017b)
Hen Harrier ^b	–24	2004–2016	575	SCARRABS	Wotton <i>et al.</i> (in press)
Goshawk	+274	1985/89–2011/15	542	Annual surveys RBBP	Hayhow <i>et al.</i> (2017a)

^aThe 95% CI for the Merlin population estimate was 891–1462 (Ewing *et al.*, 2008).

^bThe 95% CI for the Hen Harrier population estimate was 477–694 (Wotton *et al.*, in press).

Table 3. Population trends for gulls and skuas for targeted seabird monitoring programmes JNCC (2015). + and – signs indicate whether the trend is positive or negative. There are no significance tests available for these trends

Species	UK	UK	UK
	1969/70– 1985/88	1985/88– 1998/2002	2000– 2014
Arctic Skua	+226	–37	–71
Great Skua	+148	+26	+19
Black-headed Gull	+5	0	+102
Lesser Black-backed Gull	+29	+40	NA
Herring Gull	–48	–13	–38
Greater Black-backed Gull	–7	–4	–6

and Grey Squirrel *Sciurus carolinensis* (Table 4). Similarly, short-term NGC data (1995–2009) showed that four of the eight mammalian predators have increased in numbers. However, for two species the population trends differed between the long-term and short-term trends; the population trend for Weasel *Mustela nivalis* showed a long-term decline but a short-term increase, whereas the reverse was true for American Mink (Table 4).

For two species, Red Fox and Grey Squirrel, trends were available from both the NGC and BBS for the years 1995–2009, but for the BBS more recent updated trends for the years 1996–2015 were available. Between 1995 and 2009, when BBS data suggested that Red Fox populations were stable, NGC data showed a significant 11% increase (Table 4). However, the recent BBS trend for Red Fox suggested that numbers have fallen by 39% between 1996

Table 4. Population trends of mammalian predators, given as a percentage increase or decrease from the start year to the end year for the whole of the UK and for three of the countries within the UK (no trends for mammalian predators are available for Northern Ireland). The National Gamebag Census (NGC) is from Aebischer *et al.* (2011). The Breeding Bird Survey (BBS) trends are from Risely *et al.* (2011), which has the same end year as the NGC, and Harris *et al.* (2017) for the most up-to-date trends. There are no BBS trends for any mammalian predators from Scotland and Northern Ireland. Figures in bold indicate that the population trend is significantly different from zero. + and – signs indicates whether the trend is positive or negative. Empty cells indicate that no trend was available. Exceptions to the start year of NGC trends are 1962^a, 1976^b, 1977^c and 1984^d

Species	UK				England				Scotland			Wales			
	Survey	NGC	NGC	BBS	BBS	NGC	NGC	BBS	BBS	NGC	NGC	BBS	NGC	NGC	BBS
Start year	1961	1995	1995	1996	1961	1995	1995	1996	1961	1995	1996	1961	1995	1995	1996
End year	2009	2009	2009	2015	2009	2009	2009	2015	2009	2009	2015	2009	2009	2009	2015
Red Fox	+203	+11	–1	–39	+258	+26	+13	–44	+150	–15		+24	+33		
Grey Squirrel	+97	+59	+31	–9	+97	+58	+26	–10	+311^c	+100		+87	+88	+53	+9
Hedgehog	–52	–33			–53	–28			–19	–37		–84	–68		
Feral Cat	–39	–15			–45	–15			–29	–12		–64	7		
Stoat	+117	+28			+150	+42			+49	+11		–48	–35		
Weasel	–37	+51			–37	+73			–16	+23		–93	–67		
Polecat	+176	+6			+43 ^b	+53			–32 ^d	–27		+51 ^b	+11		
American Mink	+163^a	–41			+226^a	–30			+61^b	–51			–14		

and 2015 (Table 4). The UK-wide, English and Welsh BBS trends for Grey Squirrels between 1995 and 2009 suggested a significant increase in numbers. However, the most up-to-date BBS trends (1996–2015) for these regions showed significant declines for the UK and England, and a small but significant increase in numbers of Grey Squirrels in Wales (Table 4).

(3) Does predation limit individual bird species or groups of species?

(a) Literature review

We found 81 studies between 1958 and 2016 that examined whether predation may limit UK bird populations numerically. Together, these studies examined the effects of predation on 90 prey species covering 908 cases (Table S2.3). The most frequently studied species was Lapwing *Vanellus vanellus* with 46 cases, followed by 18 passerine species with 20 or more cases each, as well as Curlew *Numenius arquata* and Red Grouse (*Lagopus lagopus scotica*) with 24 and 22 cases, respectively (Table S2.1). The most frequently studied predators were Eurasian Sparrowhawk (112 cases), Magpie (104), Grey Squirrel (100), and Carrion Crow (92). Four studies (i.e. Thomson *et al.*, 1998b; Amar *et al.*, 2006; Newson *et al.*, 2010a,b) that included correlative tests of the effect of Eurasian Sparrowhawk, Common Buzzard, Common Kestrel, several species of corvids and Grey Squirrel on a large number of prey species based on national bird-monitoring data sets contributed to the large number of cases. Accordingly, by far the most common scientific quality category was ‘Good’ ($N = 741$). In addition, there were 116 cases in the ‘Fair’ category and 51 cases in the ‘Best’ category. Full information regarding cases, studies, prey and predator species and evidence categories are provided in Table S2.1.

(b) Evidence that predation limits bird populations

Overall, 138 of the 908 cases (15.2%) were categorised as predation having a limiting effect on prey numbers (i.e. categories –3, –2 and –1; Table 5). Between 1958 and 2016, there was no significant temporal trend in the score for ‘Evidence’ (OLMM, LR $\chi^2 = 0.01$, $df = 1$, $P = 0.91$).

There was a significant association between the scientific quality of studies (i.e. ‘Best’, ‘Good’ and ‘Fair’) and the relationship between predator and prey numbers (i.e. negative correlation, no correlation or positive correlation; χ^2 -test, $\chi^2 = 90.593$, $df = 4$, $P < 0.0001$). Examination of the contribution that each cell in this 3×3 contingency table made to the total χ^2 value showed that studies using a formal experimental approach to remove predators (i.e. categorised as ‘Best’) were more likely to produce a negative correlation between predator and prey numbers than expected by chance (i.e. 27 observed cases *versus* 7.57 expected, which is 55.1% of the total χ^2 value). The second largest contribution to the total χ^2 value was the ‘Fair’ and ‘negative correlation’ cell, which contributed 16.1% (i.e. 33 observed *versus* 17.26 expected). In the subset of studies that had removed predators experimentally ($N = 68$ cases), there was no significant difference between prey groups in terms of an effect on the prey population size following predator removal (χ^2 -test, $\chi^2 = 7.646$, $df = 4$, $P = 0.105$; Table 6). After an experimental removal of predators, the majority of cases involving Gamebirds (81.33% of cases) and Seabirds (80.00% of cases) found an increase in the population size of the prey species, whereas this effect was smaller for Waders (44.83% of cases), Passerines (40.00%) and Raptors and owls (33.33%; Table 6).

Overall, there was a significant difference among prey groups in the evidence for population limitation by predation (OLMM, LR $\chi^2 = 19.32$, $df = 6$, $P = 0.004$; Fig. 2 and Appendix S4, Fig. S4.1A). There was no

Table 5. Summary of the evidence for predation limiting populations of various prey species groups. The evidence of a limiting effect of predators was summarised as an ordinal response variable [from a strongly negative effect (−3), to no effect (0), to a strongly positive effect (+3)] based on the scientific strength of the study (see Section II.3). In the analyses, the only case with an evidence level of +3 was converted to +2

Prey group	Negative correlation			No effect 0	Positive correlation			Total	% cases with a negative correlation
	−3	−2	−1		1	2	3		
Seabirds	4	4	5	3	0	0	0	16	81.25
Gamebirds	6	15	5	30	2	2	0	60	43.33
Ducks	0	0	1	2	0	0	0	3	33.33
Waders	12	9	12	92	1	3	1	130	25.38
Raptors and owls	1	1	1	7	0	1	0	11	27.27
Pigeons	0	1	0	6	1	4	0	12	8.33
Woodpeckers	0	2	0	17	0	4	0	23	8.70
Passerines	4	45	10	521	8	65	0	653	9.04
Total	27	77	34	678	12	79	1	908	15.20

Table 6. The number of cases where experimental removal of predators resulted in an increase or no change in prey population size for different prey groups. There were no cases of experimental predator removal involving the prey groups Ducks, Pigeons or Woodpeckers

Prey group	Change in prey population size after predator removal		Total	% cases with increase
	Increase	No change		
Seabirds	4	1	5	80.00
Gamebirds	9	2	11	81.33
Raptors & owls	1	2	3	33.33
Waders	13	16	29	44.83
Passerines	8	12	20	40.00
Total	35	33	68	51.47

evidence for Pigeons, Woodpeckers and Passerines being limited numerically by predators (Table 5, Fig. 2). Although a relatively high percentage of cases of Raptors and owls showed a negative association with their predators (27.3%; Table 5), the statistical modelling, which took the non-independence of many results from the same study and results on the same taxonomic family into account, showed that Raptors and owls were in general not limited numerically by their predators (Fig. 2). However, there was strong evidence that Seabirds (81.3% of all cases), Gamebirds (43.3%) and Waders (25.4%) were limited in this way (i.e. categories −3, −2 and −1; Table 5, Fig. 2, Fig. S4.1). Post-hoc Tukey's tests revealed that Seabirds were significantly more limited by predation than Pigeons ($P = 0.002$), Woodpeckers ($P = 0.036$) and Passerines ($P = 0.029$; Fig. 2). Also Gamebirds and Waders were significantly more limited by predation than Pigeons ($P = 0.028$ and $P = 0.0418$, respectively; Fig. 2).

Among the cases showing no correlation between prey and predator trends, most studies for all prey groups apart from Seabirds were classified as 'Good' (Fig. S4.1B). This was

especially true for Woodpeckers and Passerines, where most cases (i.e. $\geq 73\%$) fell into this category (Fig. S4.1), suggesting that the lack of an effect of predators on prey was not caused by poor study design.

(4) Do species or groups of species limited by predation share certain nest-site characteristics, migratory strategies or life-history traits?

There was a significant difference in nest-site characteristics between the various species groups (χ^2 test, $\chi^2 = 58.47$, $df = 24$, $P = 0.0001$). In particular, the species groups identified to be most limited by predation (Seabirds, Gamebirds and Waders), were more often ground-nesters than expected by chance ($\chi^2 = 38.89$, $df = 1$, $P < 0.0001$; Fig. S4.2A). Similarly, there was a significant difference in migratory status between species groups ($\chi^2 = 42.00$, $df = 12$, $P < 0.0001$). However, the species groups identified to be limited by predation did not share the same migratory strategy. Gamebirds were more often residents, Seabirds were more often migratory and Waders were more often categorised as having a mixed resident/migratory strategy than would be expected by chance (Fig. S4.2B). Overall, species groups identified as not being limited by predation were more often residents than expected by chance ($\chi^2 = 10.29$, $df = 2$, $P = 0.006$; Fig. S4.2B).

The PCA of life-history traits showed that only the first two axes had eigenvalues > 1.0 (i.e. they explained more variation than the underlying variables) and together explained 78.4% of the variation (Table S4.1). A scree plot confirmed that only PC1 and PC2 were meaningful in explaining variation in the data set and therefore only these axes were retained for a rotation.

The first axis, PC1, explained 61.2% of the variation (Table S4.1) and was strongly negatively correlated with longevity, lifespan, age at first breeding, and adult survival as well as being positively related to clutch size (Fig. 3, Table S4.2). Thus, PC1 explained variation along the r - K

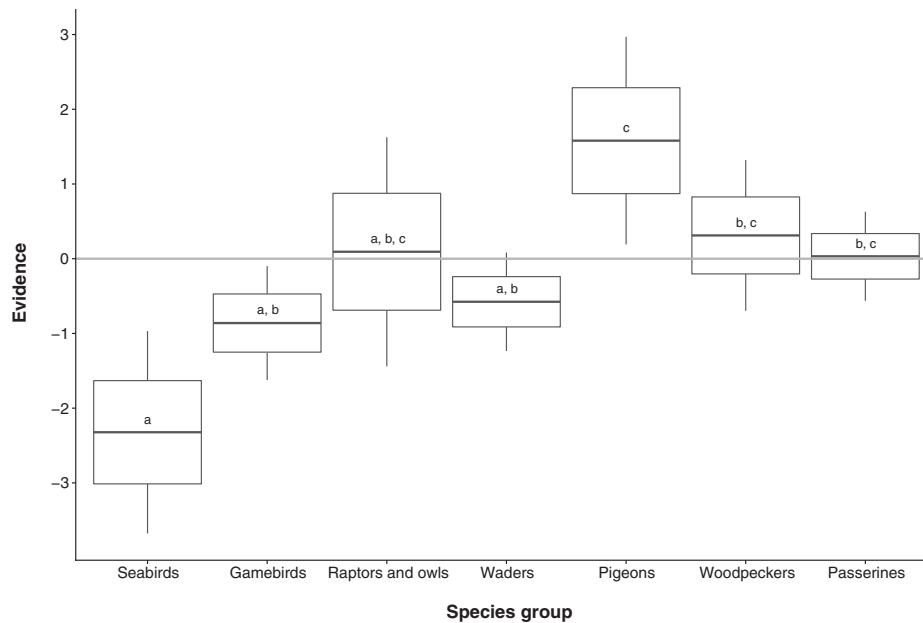


Fig. 2. Modified box plot showing the variation in evidence that different species groups are limited by predation. The horizontal lines in the boxes show the least-square mean (i.e. the mean when taking random terms of the statistical model into account), the boxes show ± 1 standard error and the whiskers show the upper and lower 95% confidence intervals. Different lower-case letters denote significant differences between groups revealed by a post-hoc Tukey's test.

gradient, with positive PC1 values related to r strategies (short lifespan, low adult survival, early start of breeding and large clutch sizes), and negative PC1 values related to K strategies (long lifespan, high adult survival, late start of breeding and low clutch sizes). There was a significant positive relationship between PC1 and the 'Evidence' that a species was limited by predation (linear regression: estimate: 0.24 ± 0.04 , $F_{82,1} = 37.40$, $P < 0.0001$; $r^2_{\text{adj}} = 0.30$; Fig. S4.3A).

The second axis, PC2, explained 17.3% of the variation (Table S4.1). This axis was strongly positively correlated with the number of broods, but negatively related to clutch size and ground-nesting propensity. Thus, PC2 mainly explained variation in reproductive strategies, i.e. whether a species laid several small clutches in one season (i.e. high PC2 scores, e.g. pigeons), or a single large clutch (i.e. low PC2 scores, e.g. gamebirds; Fig. 3). There was a significant positive relationship between PC2 and the 'Evidence' that a species was limited by predation (linear regression: estimate: 0.31 ± 0.08 , $F_{82,1} = 14.79$, $P = 0.0002$; $r^2_{\text{adj}} = 0.14$; Fig. S4.3B).

In summary, species reported to be limited by predation tended to be single-brooded, long-lived, begin breeding later in life and, to a lesser extent, ground-nesting.

(5) What predator species and at what life stage can predation limit prey populations?

(a) Predator species

There was a significant difference between predator groups in the probability that they limited their avian prey (OLMM,

LR $\chi^2 = 24.05$, $df = 8$, $P = 0.002$). Post-hoc Tukey's tests revealed that the predator group 'Corvid, Fox & other' were more often reported to limit their prey populations numerically than the predator groups 'Corvids' ($P = 0.004$), 'Raptors' ($P = 0.011$) and 'Others' ($P = 0.008$; Fig. 4).

The number of cases that identified one or several predators as having a limiting effect on prey populations is summarised in Table 7. Native mammals were frequently reported as having a limiting effect on their prey (61.1% of cases). Most of these included Red Fox (i.e. 45 of 72 cases; 62.5%), either alone ($N = 18$ cases) or as part of a guild of controlled predators ($N = 27$).

Of the non-native mammals, American Mink (71.4% of the cases), Hedgehog *Erinaceus europaeus* [66.7%; all cases involved studies conducted on a Scottish island where the Hedgehog is an invasive non-native species (Jackson, 2001; Jackson, Fuller, & Campbell, 2004)] and Brown Rat *Rattus norvegicus* (75.0%) were frequently reported as limiting their prey (Table 7). However, most cases of non-native mammals involved Grey Squirrels (100 of 141 cases; 70.9%), which were rarely reported as having a negative association with their potential prey (11.0% of cases). Overall, non-native mammals were reported as limiting their prey numerically in 28 of 141 cases (9.9%).

A total of 324 cases involved raptors, but only 33 (10.2%) cases showed that raptors limited their prey (Table 7). The raptors most frequently reported to do so were Hen Harrier (32.0% of cases) and Peregrine (16.7% of cases). Sparrowhawks, Common Buzzards, Common Kestrels and Merlins were rarely reported to limit their prey populations (i.e. $\leq 10.7\%$ of cases involving these species). Similarly, of

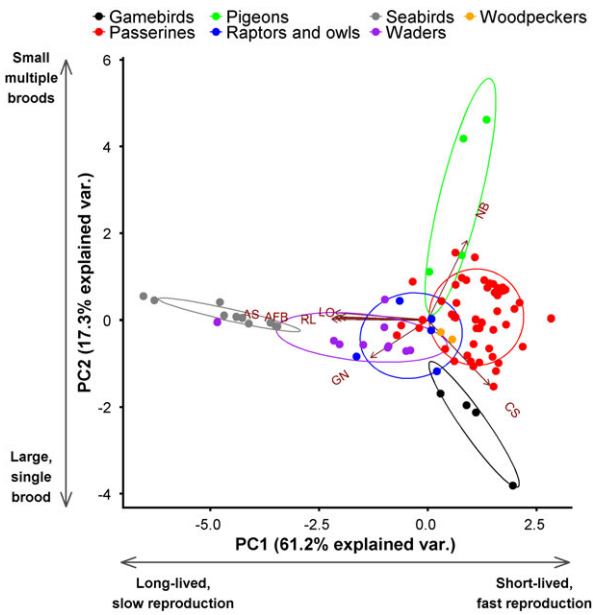


Fig. 3. Ordination of the 84 species of birds obtained from a principal component analysis (PCA) on their life-history and nest-site characteristics (see also Tables S4.1 and S4.2). The 68% confidence ellipses are shown for each prey group. The PC1 axis explains variation from long-lived, slow-reproducing (negative values) to short-lived, fast-reproducing species (positive values). The PC2 axis explains variation from single-brooded species with large clutches (negative values) to multi-brooded species with small clutches (positive values). The variables are shown by arrows (pointing in the direction of increasing values) and their abbreviated names: LO, Longevity; RL, Reproductive lifespan; AFB = Age at first breeding; CS, Clutch size; AS, Adult survival; NB, Number of annual broods; GN, Ground-nesting.

the 376 cases involving corvids, few (13.6%) suggested that corvids limited prey populations, with this percentage being highest for Hooded and Carrion Crow (28.6 and 17.4%, respectively).

Finally, 17 of 118 cases (i.e. 14.4%) involving other predatory bird species (e.g. gulls, skuas and woodpeckers) showed that they limited prey numbers (Table 7). Most cases involved the Great Spotted Woodpecker ($N = 63$ cases), of which only two (3.2%) showed that they limited prey numbers. All other predators in this group involved fewer than 10 cases.

(b) Predation at various life stages

There was a significant difference among the life stages at which predation occurred and the 'Evidence' that predation limited prey populations (OLMM, LR $\chi^2 = 23.34$, $df = 4$, $P = 0.0001$; Fig. 5). Post-hoc Tukey's tests showed that predation that occurred across all prey life stages was more likely to limit prey than predation that was restricted to specific life stages ($P \leq 0.002$; Fig. 5). Of the 53 cases where predation was reported to occur at all life stages, Non-native mammals were the predator in 19 of cases (35.8%), foxes and corvids in combination in another 19 cases (35.8%;

i.e. the predator management focused on corvids and foxes simultaneously, and their relative importance as predators could not be disentangled), and Red Fox in 15 cases (28.3%). The predator groups Raptors, Native mammals and Corvids were not classified as depreeding prey at all life stages. Of 261 cases where predation was classified as occurring at both the juvenile and adult stages, Raptors were responsible for almost all (i.e. 255 cases, 97.7%). Finally, of 492 cases where predation was classified as occurring at the nest stage, Corvids were responsible for most (292 cases, 59.3%).

IV. DISCUSSION

(1) Generalist predator densities

We have shown that the densities of the Red Fox and Crows (i.e. the combined densities of Hooded and Carrion Crows), but not Magpies, are high in the UK compared to many other European countries (Fig. 1). Studies from the USA, Finland, Sweden and the UK suggest that highest Red Fox densities occur in urban areas and in intensive agricultural landscapes and semi-natural uplands where woodlands and conifer plantations provide suitable sites for dens, and where there is high primary production and a lack of apex mammalian predators such as Wolf *Canis lupus* and Lynx *lynx lynx* (Kurki *et al.*, 1998; Elmhagen & Rushton, 2007; Elmhagen *et al.*, 2010; Pasanen-Mortensen *et al.*, 2013; Newsome & Ripple, 2015). The landscapes of Great Britain provide these conditions, and in combination with high food supplementation in the form of approximately 50 million released gamebirds annually (Aebischer, 2013), the high Red Fox densities in the UK compared to other European countries (Fig. 1A) are unsurprising. Crows have most likely benefitted from similar land-use patterns to foxes, including agricultural landscapes with high food availability in improved grasslands (Barnett *et al.*, 2004), suitable nesting sites in scattered woodlands and plantations, high abundance of a protein-rich food supply in the form of road-killed Common Pheasants *Phasianus colchicus* (i.e. 5–13% of released Pheasants are killed in vehicle collisions, particularly between September and March; Turner & Sage, 2003; Lees *et al.*, 2013; Madden & Perkins, 2017) and low population size of apex predators such as Goshawk and Golden Eagle (Table 2), which would otherwise limit Crow numbers and distribution (Ellenberg, Gast, & Dietrich, 1984). We also note that several studies have reported lower breeding success and lower population density of Magpies in areas with high Crow abundance (Baeyens, 1981; Møller, 1982; Birkhead, 1991). High Crow abundance in the UK may therefore, in combination with high legal control of Magpies using traps (Aebischer, 2016), contribute to the moderate abundance of Magpies here compared to other European countries (Fig. 1C).

(2) Trends in predator numbers

Many avian predators, including Carrion Crows, have increased in recent decades (Table 1). For mammalian

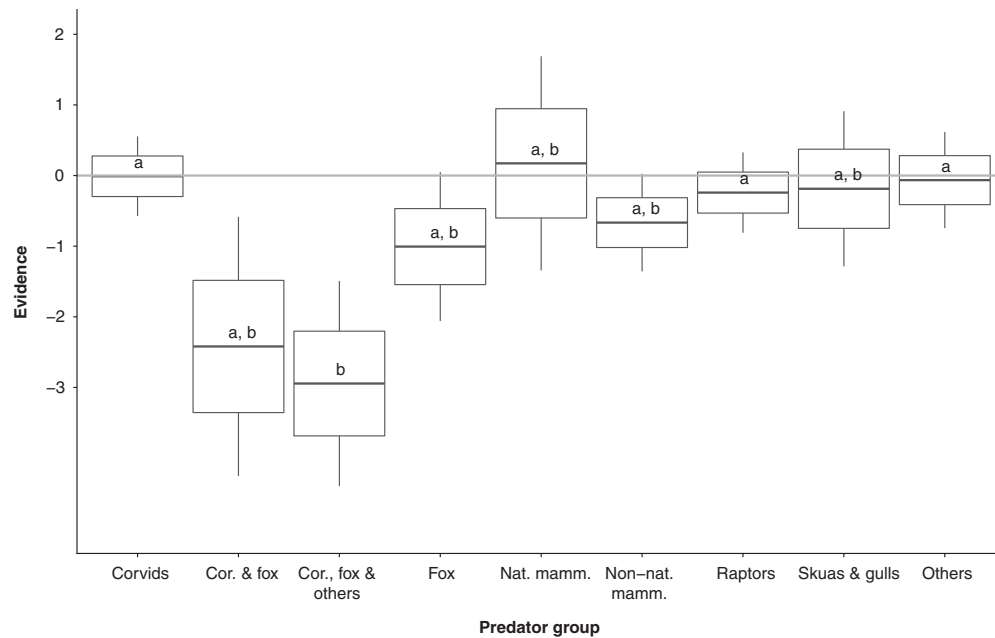


Fig. 4. Modified box plot showing the variation in evidence that different predator groups can limit their prey numerically. The horizontal lines in the boxes show the least-square mean (i.e. the mean when taking random terms of the statistical model into account), the boxes show ± 1 standard error and the whiskers show the upper and lower 95% confidence intervals. Different lower-case letters denote significant differences between groups revealed by a post-hoc Tukey's test. Abbreviations: Cor. & fox, Corvids and foxes; Cor., fox & others, Corvids, foxes and others; Nat. mamm., Native mammals; Non-nat. mamm., Non-native mammals.

predators, the lack of a bespoke national mammal survey is problematic for the estimation of robust trends. Given the different count methods of the BBS and NGC, it is perhaps not surprising that Red Fox trends from these two sources show opposing patterns in recent years (Aebischer, 2014; Harris *et al.*, 2017). The lack of survey effort and the unknown changes in lethal control techniques (e.g. increasing use of shooting at night using spotlights) may have contributed to the increased number of culled foxes reported by the NGC (Aebischer *et al.*, 2011; Aebischer, 2014). However, overall the NGC trends suggest that half of the monitored species, including the Red Fox (Aebischer, 2014), have increased in numbers. From an international perspective, the UK has a high density of generalist predators and the continued national increase of foxes and Carrion Crows suggests that it should be possible to detect any limiting effects of these species on populations of their avian prey. For some other species, notably Badger, there are anecdotal reports of high and increasing numbers (Ainsworth *et al.*, 2016). This is supported by one of the few scientific attempts to estimate changes in the British Badger population, which reported a 77% increase in Badger numbers and a 43% increase in the number of Badger setts between 1988 and 1997 (Wilson, Harris, & McLaren, 1997).

(3) Species groups limited by predation

Despite significant increases of many predators in the UK (Tables 1–3), there is no strong evidence that most species

of pigeons, raptors and owls, woodpeckers and passerines are limited by predation (Table 5, Fig. 2). However, there is good evidence that seabirds, gamebirds and waders are limited by predation in many circumstances (Table 5, Fig. 2). Further examination of our results suggests that it is generalist predators (Foxes and Crows; MacDonald & Bolton, 2008; Fletcher *et al.*, 2010) and introduced non-native predators (Brown Rat, American Mink and Hedgehog; the latter introduced to some Scottish islands; Craik, 1997; Jackson, 2001; Jackson *et al.*, 2004; Ratcliffe *et al.*, 2009) that limit these prey species (Fig. 4). Our results for non-native predators and seabirds accord with studies that have shown that seabirds nesting on oceanic islands are limited numerically and sometimes even driven to extinction by non-native predators (reviewed in e.g. Atkinson, 1996; Jones *et al.*, 2011). However, seabirds often re-colonise these islands if the non-native predators are eradicated (Townes & Broome, 2003; Ratcliffe *et al.*, 2009, 2010). Two experimental studies explicitly showed that lethal removal of generalist predators increased breeding success and population size in both autumn and the following spring of Grey Partridge *Perdix perdix* as well as Red Grouse and several wader species (Tapper, Potts, & Brockless, 1996; Fletcher *et al.*, 2010). In accordance with Valkama *et al.* (2005), we found little evidence that raptors limited gamebird populations. However, one exception came from the well-studied Langholm Moor in south-west Scotland, where Hen Harriers and Peregrines limited Red Grouse numbers and restricted population recovery following a decline in Red Grouse numbers caused by a long-term loss of

Table 7. The number of cases where the evidence that predators can limit prey species has been assessed. The table is sorted in descending order of the number of cases of the main predator. Cases involving the main predator and other predators (e.g. when predator control simultaneously reduced the abundance of several predatory species) are presented in italics after each main predator. Non-native predators include tests involving hedgehogs (all from the Outer Hebrides, where hedgehogs are non-native). The category 'Raptor' was used when the exact species of raptor could not be identified to species level

Predator group	Predator species	Evidence						N cases	Negative association	
		-3	-2	-1	0	1	2		N	%
Native mammal	Total	22	13	9	25	1	2	72	44	61.11
	Red Fox	2	4	3	9	0	0	18	9	50.00
	<i>Red Fox and other species</i>	<i>10</i>	<i>6</i>	<i>2</i>	<i>8</i>	<i>0</i>	<i>1</i>	<i>27</i>	<i>18</i>	<i>66.67</i>
	Weasel	2	0	0	1	0	0	3	2	66.67
	<i>Weasel and other species</i>	<i>5</i>	<i>1</i>	<i>1</i>	<i>4</i>	<i>0</i>	<i>1</i>	<i>12</i>	<i>7</i>	<i>58.33</i>
	Stoat	0	0	0	0	1	0	1	0	0.00
	<i>Stoat and other species</i>	<i>2</i>	<i>2</i>	<i>1</i>	<i>0</i>	<i>0</i>	<i>0</i>	<i>5</i>	<i>5</i>	<i>100.00</i>
	Pine Marten	0	0	2	3	0	0	5	2	40.00
	Badger	0	0	0	0	0	0	0	0	0.00
	<i>Badger and other species</i>	<i>1</i>	<i>0</i>	<i>0</i>	<i>0</i>	<i>0</i>	<i>0</i>	<i>1</i>	<i>1</i>	<i>100.00</i>
Non-native mammals	Total	10	18	0	99	0	14	141	28	19.86
	Grey Squirrel	0	11	0	80	0	9	100	11	11.00
	Feral Cat	0	3	0	12	0	5	20	3	15.00
	American Mink	2	3	0	2	0	0	7	5	71.43
	<i>American Mink and other species</i>	<i>1</i>	<i>0</i>	<i>0</i>	<i>0</i>	<i>0</i>	<i>0</i>	<i>1</i>	<i>1</i>	<i>100.00</i>
	Hedgehog	4	0	0	2	0	0	6	4	66.67
	<i>Hedgehog and other species</i>	<i>0</i>	<i>0</i>	<i>0</i>	<i>1</i>	<i>0</i>	<i>0</i>	<i>1</i>	<i>0</i>	<i>0.00</i>
	Brown Rat	2	1	0	1	0	0	4	3	75.00
	<i>Brown Rat and other species</i>	<i>1</i>	<i>0</i>	<i>0</i>	<i>0</i>	<i>0</i>	<i>0</i>	<i>1</i>	<i>1</i>	<i>100.00</i>
	Ferret	0	0	0	1	0	0	1	0	0.00
Raptors	Total	0	29	4	266	5	20	324	33	10.19
	Sparrowhawk	0	9	3	91	5	4	112	12	10.71
	Buzzard	0	4	0	60	0	7	71	4	5.63
	<i>Buzzard and other species</i>	<i>0</i>	<i>0</i>	<i>0</i>	<i>7</i>	<i>0</i>	<i>0</i>	<i>7</i>	<i>0</i>	<i>0.00</i>
	Kestrel	0	5	0	49	0	4	58	5	8.62
	Hen Harrier	0	8	0	16	0	1	25	8	32.00
	<i>Hen Harrier and other species</i>	<i>0</i>	<i>0</i>	<i>0</i>	<i>7</i>	<i>0</i>	<i>0</i>	<i>7</i>	<i>0</i>	<i>0.00</i>
	Peregrine	0	1	1	8	0	2	12	2	16.67
	<i>Peregrine and other species</i>	<i>0</i>	<i>0</i>	<i>0</i>	<i>7</i>	<i>0</i>	<i>0</i>	<i>7</i>	<i>0</i>	<i>0.00</i>
	Merlin	0	0	0	9	0	1	10	0	0.00
	Goshawk	0	1	0	3	0	1	5	1	20.00
	<i>Goshawk and other species</i>	<i>0</i>	<i>0</i>	<i>0</i>	<i>7</i>	<i>0</i>	<i>0</i>	<i>7</i>	<i>0</i>	<i>0.00</i>
	Raptor	0	1	0	1	0	0	2	1	50.00
	Golden Eagle	0	0	0	1	0	0	1	0	0.00
	Corvids	Total	13	24	14	280	6	39	376	51
Magpie		0	4	2	82	4	12	104	6	5.77
<i>Magpie and other species</i>		<i>1</i>	<i>2</i>	<i>0</i>	<i>21</i>	<i>0</i>	<i>1</i>	<i>25</i>	<i>3</i>	<i>12.00</i>
Carrion Crow		3	8	5	66	1	9	92	16	17.39
Hooded Crow		0	0	2	5	0	0	7	2	28.57
<i>Carrion/Hooded Crow and other species</i>		<i>9</i>	<i>7</i>	<i>2</i>	<i>27</i>	<i>0</i>	<i>1</i>	<i>46</i>	<i>18</i>	<i>97.83</i>
Jay		0	3	0	43	0	13	59	3	5.08
<i>Jay and other species</i>	<i>0</i>	<i>0</i>	<i>0</i>	<i>23</i>	<i>0</i>	<i>1</i>	<i>24</i>	<i>0</i>	<i>0.00</i>	
Raven	0	0	3	13	1	2	19	3	15.79	
Other bird species	Total	2	5	10	92	0	9	118	17	14.41
	Great Spotted Woodpecker	0	2	0	53	0	8	63	2	3.17
	<i>Great Spotted Woodpecker and other species</i>	<i>0</i>	<i>0</i>	<i>0</i>	<i>3</i>	<i>0</i>	<i>0</i>	<i>3</i>	<i>0</i>	<i>0.00</i>
	Great Skua	0	0	5	3	0	0	8	5	62.50
	Black-headed Gull	1	0	1	4	0	0	6	2	33.33
	Common Gull	0	0	3	2	0	0	5	3	60.00
	<i>Common Gull and other species</i>	<i>0</i>	<i>1</i>	<i>0</i>	<i>5</i>	<i>0</i>	<i>0</i>	<i>6</i>	<i>1</i>	<i>16.67</i>
	Arctic Skua	0	0	0	4	0	0	4	0	0.00
	Great Black-backed Gull	0	0	0	4	0	0	4	0	0.00
	Herring Gull	0	0	0	4	0	0	4	0	0.00
	Lesser Black-backed Gull	0	0	0	4	0	0	4	0	0.00
	<i>Lesser B-backed gull and other species</i>	<i>0</i>	<i>0</i>	<i>1</i>	<i>0</i>	<i>0</i>	<i>0</i>	<i>1</i>	<i>1</i>	<i>100.00</i>
	Green Woodpecker	0	1	0	0	0	0	1	1	100.00
<i>Coot and Moorhen and other species</i>	<i>1</i>	<i>0</i>	<i>0</i>	<i>0</i>	<i>0</i>	<i>0</i>	<i>1</i>	<i>1</i>	<i>100.00</i>	
Unknown	Unknown	0	0	2	0	0	0	2	2	100.00

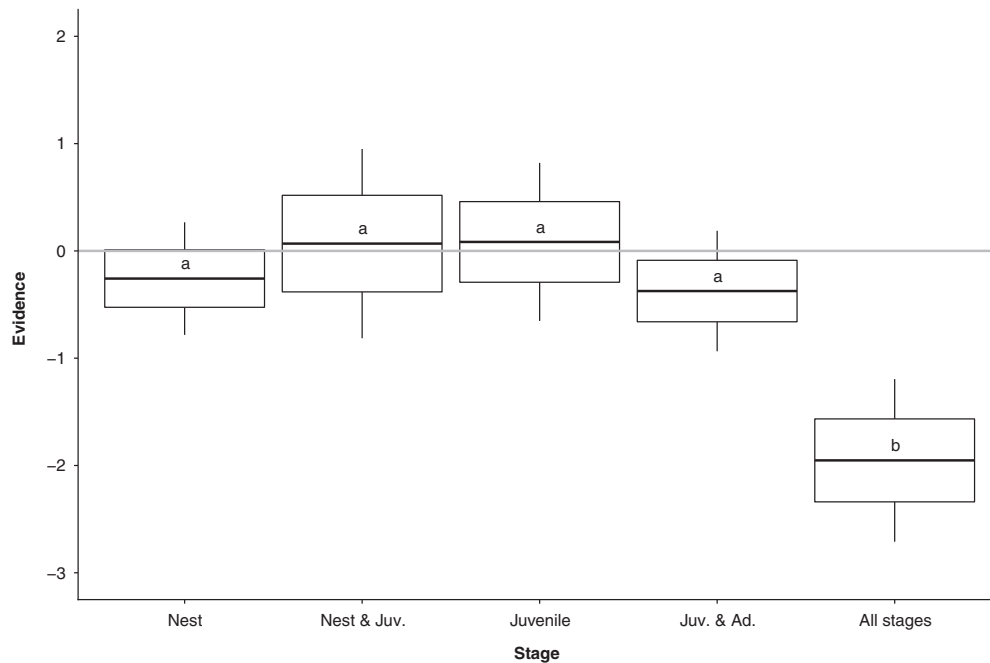


Fig. 5. Modified box plot showing the variation in evidence that predation at different life stages of the prey can limit their populations numerically. The horizontal lines in the boxes show the least-square mean (i.e. the mean when taking random terms of the statistical model into account), the boxes show ± 1 standard error and the whiskers show the upper and lower 95% confidence intervals. Different lower-case letters denote significant differences between groups revealed by a post-hoc Tukey's test. Abbreviations: Juv., juvenile; Ad., adult.

suitable Heather *Calluna vulgaris* habitat in combination with continued hunting of the grouse population (e.g. Redpath & Thirgood, 1999; Thirgood *et al.*, 2000a, 2000b). Also, Hen Harriers have been shown to limit populations of Skylarks *Alauda arvensis*, Meadow Pipits *Anthus pratensis* and Stonechats *Saxicola rubicola* (Amar *et al.*, 2008; Baines *et al.*, 2008) in studies carried out in the same Scottish study area. By contrast, we found little evidence that another raptor with a high proportion of passerines in its diet, the Eurasian Sparrowhawk, limits the population size of their passerine prey species. This result is supported by many spatially independent studies in the UK and in Europe (Geer, 1978; Perrins & Geer, 1980; Newton, Dale, & Rothery, 1997; Thomson *et al.*, 1998b; Newson *et al.*, 2010b).

We found only a few cases of intra-guild predation where the numbers of raptors and owls in the UK were limited by other predators (e.g. Petty *et al.*, 2003). However, studies elsewhere have shown that intra-guild predation by large avian predators can limit the numbers of smaller avian predators (reviewed by Sergio & Hiraldo, 2008; Newton, 2017). In particular, Goshawk, Eurasian Eagle Owl *Bubo bubo* and Golden Eagle have been shown to limit the number of seven, six and two different raptor and owl species, respectively (Newton, 2017). It is likely that the impoverished raptor community in parts of the UK (i.e. with the near-absence of Eurasian Eagle Owls and restricted ranges of Goshawks and Golden Eagles) would limit intra-guild predation effects compared to those observed elsewhere. The lack of apex avian predators in the UK

could also have contributed to the relatively rapid increase in small avian predators (e.g. Eurasian Sparrowhawk and Common Kestrels) when organo-chlorine pesticides were phased out (Newton, 1986, 2017). In addition, the recent population increases of large mammal and bird predators in many European countries caused by declines in persecution and successful reintroduction programs (Deinet *et al.*, 2013), suggest that the effects of intra-guild predation will be more visible in the future. This will provide exciting opportunities for intra-guild predation studies.

We used a novel approach to examine how life-history characteristics influenced the probability that a species was limited numerically by predation. Our results from the PCA showed that prey species could be ordered along a gradient describing variation from long-lived species with high adult survival and late onset of breeding (*K* strategy) to short-lived species with low adult survival and early onset of breeding (*r* strategy). In addition, the PCA suggested that prey species could be ordered along a second axis that described variation in reproductive strategies, from species laying one large clutch per year to species laying several, small clutches per year. It is however important to notice that many species can re-lay after a nest failure, and that this ability is not restricted to multi-brooded species. Long-lived species (e.g. Seabirds and Waders) and ground-nesting species with a single large clutch (i.e. Gamebirds) were most likely to be limited by predation (Figs 2 and 3).

Several reviews from across the world have shown that breeding success and post-breeding densities of birds

increased when predators were removed (Côté & Sutherland, 1997; Newton, 1998; Smith *et al.*, 2010). Côté & Sutherland (1997) found little evidence that the number of breeding birds increased following predator removal, whereas subsequent reviews, which were able to incorporate many more recent studies, found that removal of predators increased breeding success as well as breeding population size (Newton, 1998; Smith *et al.*, 2010). However, these reviews included studies from oceanic islands, inhabited by predator-naïve and flightless prey which suffered heavy predation by non-native predators (Jones *et al.*, 2011), alongside mainland predator–prey interactions, which have evolved over long timescales. Our review focused on predator–prey interactions in a smaller geographical area dominated by predator–prey interactions that have probably evolved over a long time period, with only a few relatively novel interactions caused by deliberate or accidental introductions of non-native species (Craik, 1997; Jackson *et al.*, 2004; Ratcliffe *et al.*, 2009). Our results confirm that formal experimental studies that removed predators often resulted in higher breeding numbers of seabirds and gamebirds, and to some extent also waders (Fig. 2, Table 6). For passerines, our study found that only eight of the 20 cases in which one or several predators were experimentally removed led to breeding population size increases (Table 6). In addition, four of these cases came from the same location that simultaneously introduced predator removal and habitat management to benefit prey species (Stoate & Szczur, 2001; White *et al.*, 2008), making the relative importance of predation and habitat difficult to interpret.

Several reviews have found that removing multiple predator species is more likely to lead to a detectable increase in prey numbers than removal of a single predator species (Holt *et al.*, 2008; Nicoll & Norris, 2010; Smith *et al.*, 2010). The lack of a detectable effect when only a single species is removed is probably due to a compensatory increase in predation by the remaining predator species (Newton, 1998). Our results support this conclusion in that the predator group ‘Corvids’ was rarely reported to limit prey species, whilst the predator group ‘Corvids, fox and others’ (i.e. cases where the predator management focused on all these groups simultaneously) was significantly more likely to increase prey populations than when only corvids were managed (Fig. 4). A previous review suggested that the Red Fox rather than corvids are associated with reduced prey breeding success and low population growth rates (Madden *et al.*, 2015). Our results do not fully support this, because the management (i.e. any combination of lethal removal or exclusion using fences) of foxes alone was not more likely to result in increased prey numbers than when just corvids were managed (Fig. 4).

(4) Proximate and ultimate causes of high predation

When predation has been identified as a proximate cause of limitation of population growth of a species, it is important to understand why one or several predator species is sufficiently abundant that its predation can have this impact. In

North America and continental Europe, many studies have identified the ultimate cause of forest bird declines as habitat loss and fragmentation of pristine and semi-natural forest ecosystems (Robinson *et al.*, 1995; Ludwig, Storch, & Graf, 2009). This has led to higher depredation rates of birds’ nests by generalist predators penetrating the forest fragments from surrounding farmed areas (Andrén, 1992; Eggers *et al.*, 2005). In the UK, such studies are rare, probably because the UK has few continuous forested landscapes, but is dominated by open landscapes (i.e. agricultural land and open ‘moorland’, the latter consisting of mixed grassland and dwarf-shrub heaths). Here, generalist predators inhabiting woodland and forestry plantations may depredate nests of ground-nesting birds breeding in the surrounding open landscape. This can increase the perceived risk of nest predation (i.e. the plantations create ‘landscapes of fear’; *cf.* Norrdahl & Korpimäki, 1998; Sergio, Marchesi, & Pedrini, 2003; Roos & Pärt, 2004; Bertholdt *et al.*, 2017). Consequently, the abundance of ground-nesting gamebirds and waders on moorland, bogs and lowland wet grasslands is lower in areas up to 1 km from forest plantations than further away from these plantations (Lavers & Haines-Young, 1997; Hancock, Grant, & Wilson, 2009; Douglas *et al.*, 2013; Wilson *et al.*, 2014; Bertholdt *et al.*, 2017).

Another potential ultimate cause of unsustainably high predation is anthropogenic increases of food resources for generalist predators, which may then increase in numbers. For example, the intensification of agricultural systems, particularly the conversion of unimproved, semi-natural grasslands to improved grasslands, may have benefitted generalist predators, such as corvids, by an increased density and nutritional content of grass roots which results in an increased population of herbivorous soil invertebrates such as leatherjackets (Barnett *et al.*, 2004). Furthermore, increased livestock numbers and poor husbandry may benefit scavengers (e.g. foxes and corvids) in the form of increased carrion availability (Fuller & Gough, 1999). In addition, human-associated waste (Eggers *et al.*, 2005; Marzluff & Neatherlin, 2006) and feeding of feral but free-roaming cats (Beckerman *et al.*, 2007; Baker *et al.*, 2008; Marra & Santella, 2016) may increase some predator numbers. Moreover, releases of large numbers of gamebirds for shooting purposes, which reached a combined total of over 50 million Common Pheasants and Red-legged Partridges *Alectoris rufa*, both non-native species, in the UK in 2011 (Aebischer, 2013) may provide generalist predators with increased food supplies. For example, many Common Pheasants are killed by predators, mainly foxes (i.e. ca. 36% of 325 released and radio-tagged pheasants; Turner & Sage, 2003), or are killed in vehicle collisions, particularly when dispersing from release pens between September and November and in February and March when supplementary feeding ceases (Madden & Perkins, 2017), are wounded by shots (and not retrieved by the hunters) and thereby become easy prey, or are scavenged when dead (the ratio wounded: killed Pheasants is unknown, but is between 0.10 and 1.0 for Pink-footed Geese *Anser brachyrhynchus* in Denmark; Noer, Madsen, &

Hartmann, 2007; Clausen *et al.*, 2017). Corvids may also feed on the grain provided as supplementary food to released Common Pheasants, particularly in the late winter months when more natural food may be limited (Sánchez-García, Buner, & Aebischer, 2015). Released gamebirds and their supplementary food may therefore provide a reliable food source for many generalist predators, hence increasing their numbers (Lees *et al.*, 2013). The number of predators may then increase predation pressure, or reduce the extent of refuge areas for prey (Norrdahl & Korpimäki, 1998; Roos & Pärt, 2004). In such circumstances, predator control is merely treating the symptoms, not the cause, of the unsustainably high predation rates.

(5) What can be done to alleviate predation pressure?

To reduce predation pressure on prey groups identified by this review as limited by predation (i.e. seabirds, waders and gamebirds), the short-term remedy might be to continue to manage predators (e.g. by lethal control and fencing). Whereas the lethal control of non-native invasive species (e.g. Grey Squirrel on mainland Britain, as well as American Mink and rats on seabird islands) is supported by most stakeholders, the lethal control of native predators is more controversial both in Europe and North America (Reynolds & Tapper, 1996; Reiter *et al.*, 1999; Smith *et al.*, 2010; Doherty & Ritchie, 2017). For example, the widespread illegal killing of raptors, notably Red Kites *Milvus milvus*, Hen Harriers, Peregrines and Golden Eagles (Smart *et al.*, 2010; Fielding *et al.*, 2011; Amar *et al.*, 2012; Whitfield & Fielding, 2017) is strongly opposed by the general public, conservation NGOs and animal welfare organisations. However, the intensive legal predator control of foxes, corvids and certain mustelid species in combination with large-scale habitat management on land used for shooting of Red Grouse in northern England and Scotland is also contentious (Thompson *et al.*, 2016; Sotherton, Baines, & Aebischer, 2017). This type of land management has resulted in extremely high densities of Red Grouse (means of 110 and 327 birds km⁻² during pre- and post-breeding counts across 25 English Grouse moors in 2016; Newborn *et al.*, 2017), which is 5–10 times higher than densities of the nominate race (i.e. Willow Grouse) in Scandinavia where no habitat management and predator control takes place (Sandercock *et al.*, 2011). The near-absence of predators on moors managed for Red Grouse has benefitted some wader species of conservation concern, notably Curlews (Fletcher *et al.*, 2010; Douglas *et al.*, 2013). However, the intensity of lethal predator control to benefit a few quarry species has led to a debate in North America and Europe regarding the ethical aspects of such land management (Messmer *et al.*, 1999; Treves & Naughton-Treves, 2005; Warburton & Norton, 2009). A survey of a random sample of USA households revealed that, when given specific predator control scenarios, respondents supported control to enhance avian productivity, except when controlling raptors to protect upland gamebirds (Messmer *et al.*, 1999). Respondents also

showed greater support for predator control when prey species were of conservation concern and when the predator species were less charismatic (Messmer *et al.*, 1999). Few, if any, similar European studies have been undertaken. Apart from any ethical considerations, lethal predator control, as well as some non-lethal methods to manage predation, such as fencing, are costly and time-consuming tasks with uncertain efficacy over the longer term (Malpas *et al.*, 2013; Doherty & Ritchie, 2017). Also diversionary feeding, in which a predator is offered alternative prey to divert it from depredating species of conservation concern or quarry species, is time consuming and may not always result in higher numbers of the prey species (Redpath, Thirgood, & Leckie, 2001; Kubasiewicz *et al.*, 2016; C.S. Ludwig, A. McCluskie, P. Keane, C. Barlow, R.M., Francksen, D. Bubb, S. Roos, N.J. Aebischer & D. Baines, in preparation). An alternative approach, reducing the number of gamebird carcasses available to scavenging generalist predators, would likely lead to reductions in the numbers of generalist predators (Lees *et al.*, 2013). Finally, re-introductions or facilitation of natural re-colonisation of apex predators may also suppress meso-predators *via* intra-guild predation (Sergio & Hiraldo, 2008; Pasanen-Mortensen *et al.*, 2013), with a likely net benefit for some prey species (Ritchie *et al.*, 2012).

It might therefore be a cost-effective long-term solution to consider land-use changes that make whole landscapes less predator-friendly. Such changes would probably be most successful if they incorporated a combination of factors. Creating habitats known to improve the abundance of prey species (e.g. Peach *et al.*, 2001; Aebischer & Ewald, 2010; Aebischer *et al.*, 2016) is a good starting point. For example, in a landscape dominated by Red Fox predation, Lapwing nests had a significantly higher predation risk when located in or near areas of taller grassy vegetation, which is the preferred habitat for the foxes' main prey (small mammals) (Laidlaw *et al.*, 2015). Thus, by managing grazing pressure, suitable areas for Lapwing could be located away from the preferred foraging areas of foxes (Laidlaw *et al.*, 2015, 2017). Furthermore, by creating more 'natural' habitat along field margins in agricultural landscapes, the resulting denser vegetation cover would make it more difficult for predators to find their avian prey (Evans, 2004). Such measures are likely to increase both the nest survival rates of a range of ground- and shrub-nesting species (Bradbury *et al.*, 2000; Hinsley & Bellamy, 2000; Dunn *et al.*, 2016) and can, together with the provision of seed-rich stubble fields over winter, increase the over-winter survival of granivorous birds (Peach, Siriwardena, & Gregory, 1999; Siriwardena *et al.*, 2007; Potts, 2012). At a wider landscape scale, it is likely that removal of forest plantations on peat bogs (primarily to restore blanket bog ecosystems and associated ecosystem services, such as carbon storage) and near lowland wet grasslands may reduce predator numbers and increase habitat available for waders and gamebirds. However, recent land-use policies in the UK are advocating increased forest cover. For example, the Scottish Government is aiming to

increase the total woodland cover in Scotland from 17.1 to 25% over the next century (Scottish Executive, 2006; Sing, Towers, & Ellis, 2013). It is likely that moorland wader species, such as the globally near-threatened Curlew, will be more deleteriously affected by such forest expansion than the loss of moorland alone would predict (Douglas *et al.*, 2013; Wilson *et al.*, 2014). It is therefore important that new woodland expansion schemes should avoid locating new plantations in open landscapes near known concentrations of gamebirds and waders.

V. CONCLUSIONS

(1) Debate around the importance of predation and the significance of predator control as a conservation management tool is highly topical in the UK, where the abundance of mesopredators are higher than in many other countries and many high-quality studies on the effects of predation on prey species have been undertaken. Here we have shown that contrary to the beliefs of many stakeholders (e.g. Ainsworth *et al.*, 2016), there is little evidence that predation limits the numbers of pigeons, raptors, owls, woodpeckers and passerines, even in landscapes with abundant and increasing populations of many generalist mammalian and avian predators. However, our results showed that predation, mainly by foxes and non-native mammals can limit the numbers of ground-nesting species, such as waders, gamebirds, and seabirds.

(2) Our results also suggest that predator management aimed at foxes and corvids simultaneously is more likely to result in stable or increasing prey populations.

(3) Management interventions have to date tended to focus on lethal predator control or highly localised and intensive non-lethal measures such as fencing (Malpas *et al.*, 2013) and diversionary feeding of predators (Redpath *et al.*, 2001). Much more attention needs to be paid in future to landscape-scale measures to reduce predation impacts, such as changes in land-use configurations (e.g. removal of commercial forest plantations; Douglas *et al.*, 2013; Wilson *et al.*, 2014; Bertholdt *et al.*, 2017), habitat management (Eglington *et al.*, 2009; Laidlaw *et al.*, 2017) and the re-establishment of populations of apex predators (Ritchie *et al.*, 2012; Pasanen-Mortensen *et al.*, 2013), as well as a critical test of the environmental sustainability of intensive gamebird releasing that may cause trophic cascades (Lees *et al.*, 2013).

(4) A life-history approach was used to quantify and visualise predator–prey relationships in a novel way. Our approach identified prey groups where predator management might be an important conservation tool.

(5) Our results could be a useful starting point for discussions between stakeholders with contrasting views on lethal predator control to benefit individual species groups.

VI. ACKNOWLEDGMENTS

We thank Jeff Knott and Dave Hoccom who were instrumental in setting up this study. We also thank two anonymous referees, Tim Benton and Alison Cooper for providing constructive criticism on an earlier version of this paper.

VII. REFERENCES

- References marked with asterisk have been cited within the supporting information*
- AEBISCHER, N. (2013). *National Gamebag Census: Released Game Species*. The Game & Wildlife Conservation Trust, Fordingbridge.
- AEBISCHER, N. (2014). *National Gamebag Census: Rabbits, Foxes and Mustelids*. Game & Wildlife Conservation Trust, Fordingbridge.
- AEBISCHER, N. (2016). *National Gamebag Census: Woodcock, Woodpigeon and Pests*. Game & Wildlife Conservation Trust, Fordingbridge.
- AEBISCHER, N. J., BAILEY, C. M., GIBBONS, D. W., MORRIS, A. J., PEACH, W. J. & STOATE, C. (2016). Twenty years of local farmland bird conservation: the effects of management on avian abundance at two UK demonstration sites. *Bird Study* **63**, 10–30.
- AEBISCHER, N. J., DAVEY, P. G. & KINGDON, N. G. (2011). *National Gamebag Census: Mammal Trends to 2009*. Game & Wildlife Conservation Trust, Fordingbridge.
- AEBISCHER, N. J. & EWALD, J. A. (2010). Grey partridge *Perdix perdix* in the UK: recovery status, set-aside and shooting. *Ibis* **152**, 530–542.
- AINSWORTH, G., CALLADINE, J., MARTAY, B., PARK, K., REDPATH, S., WERNHAM, C., WILSON, M. & YOUNG, J. (2016). *Understanding Predation: A Review Bringing Together Natural Science and Local Knowledge of Recent Wild Bird Population Changes and their Drivers in Scotland*, p. 62. Edinburgh, Scotland.
- AMAR, A., COURT, I. R., DAVISON, M., DOWNING, S., GRIMSHAW, T., PICKFORD, T. & RAW, D. (2012). Linking nest histories, remotely sensed land use data and wildlife crime records to explore the impact of grouse moor management on peregrine falcon populations. *Biological Conservation* **145**, 86–94.
- *AMAR, A., GRANT, M., BUCHANAN, G., SIM, I., WILSON, J., PEARCE-HIGGINS, J. W. & REDPATH, S. (2011). Exploring the relationships between wader declines and current land-use in the British uplands. *Bird Study* **58**, 13–26.
- AMAR, A., HEWSON, C. M., THEWLIS, R. M., SMITH, K. W., FULLER, R. J., LINDSELL, J. A., CONWAY, G., BUTLER, S. & MACDONALD, M. A. (2006). *What's Happening to our Woodland Birds? Long-Term Changes in the Populations of Woodland Birds*, 238pp. RSPB and BTO, Sandy, Thetford.
- *AMAR, A., REDPATH, S., SIM, I. & BUCHANAN, G. (2010). Spatial and temporal associations between recovering populations of common raven *Corvus corax* and British upland wader populations. *Journal of Applied Ecology* **47**, 253–262.
- *AMAR, A. & REDPATH, S. M. (2002). Determining the cause of the hen harrier decline on the Orkney Islands: an experimental test of two hypotheses. *Animal Conservation* **5**, 21–28.
- 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.
- ANDRÉN, H. (1992). Corvid density and nest predation in relation to forest fragmentation: a landscape perspective. *Ecology* **73**, 794–804.
- ANDRÉN, H. (1994). Effects of habitat fragmentation on birds and mammals in landscapes with different proportions of suitable habitat: a review. *Oikos* **71**, 355–366.
- ATKINSON, I. A. E. (1996). Introductions of wildlife as a cause of species extinctions. *Wildlife Biology* **2**, 135–141.
- *BADYAEV, A. V. (1997). Avian life history variation along altitudinal gradients: an example with Cardueline finches. *Oecologia* **111**, 365–374.
- BAEYENS, G. (1981). Magpie breeding success and carrion crow interference. *Ardea* **69**, 125–139.
- BAILE, S., GOOCH, S. & BIRKHEAD, T. (1992). The effects of magpie predation on songbird populations. In *Britain's birds in 1990–1991: the conservation and monitoring review* (eds J. ANDREWS and S. CARTER), pp. 68–73. British Trust for Ornithology, London.
- *BAINES, D. (1991). Factors contributing to local and regional variation in black grouse breeding success in northern Britain. *Ornis Scandinavica* **22**, 264–269.
- *BAINES, D. (1996). The implications of grazing and predator management on the habitats and breeding success of black grouse *Tetrao tetrix*. *Journal of Applied Ecology* **33**, 54–62.
- *BAINES, D., AEBISCHER, N., MACLEOD, A. & WOODS, J. (2011). *Assessing the Activity of Predators in Relation to Capercaillie Hen Densities and Breeding Performance*, 40 pp. Scottish Natural Heritage, Inverness.
- *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**, S27–S36.
- *BAINES, D. & RICHARDSON, M. (2013). Hen harriers on a Scottish grouse moor: multiple factors predict breeding density and productivity. *Journal of Applied Ecology* **50**, 1397–1405.
- 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**, S86–S99.
- *BALDASSARRE, G. (2014). *Ducks, Geese, and Swans of North America*. John Hopkins University Press, Baltimore.
- BALMER, D. E., GILLINGS, S., CAFFREY, B. J., SWANN, R. L., DOWNIE, I. S. & FULLER, R. J. (2013). *Bird Atlas 2007–2011: The Breeding and Wintering Birds of Britain and Ireland*. BTO Books, Thetford.
- BARNETT, P. R., WHITTINGHAM, M. J., BRADBURY, R. B. & WILSON, J. D. (2004). Use of unimproved and improved lowland grassland by wintering birds in the UK. *Agriculture, Ecosystems & Environment* **102**, 49–60.
- BECKERMAN, A. P., BOOTS, M. & GASTON, K. J. (2007). Urban bird declines and the fear of cats. *Animal Conservation* **10**, 320–325.
- BELL, C. P., BAKER, S. W., PARKES, N. G., BROOKE, M. D. & CHAMBERLAIN, D. E. (2010). The role of the Eurasian Sparrowhawk (*Accipiter nisus*) in the decline of the house sparrow (*Passer domesticus*) in Britain. *The Auk* **127**, 411–420.
- BERGER, K. M., GESE, E. M. & BERGER, J. (2008). Indirect effects and traditional trophic cascades: a test involving wolves, coyotes, and pronghorn. *Ecology* **89**, 818–828.
- BERTHOLDT, N. P., GILL, J. A., LAIDLAW, R. A. & SMART, J. (2017). Landscape effects on nest site selection and nest success of northern lapwing *Vanellus vanellus* in lowland wet grasslands. *Bird Study* **64**, 30–36.
- Birdlife International (2015). *European Red List of Birds*. Office for Official Publications of the European Communities, Luxembourg.
- BIRKHEAD, T. (1991). *The Magpies: The Ecology and Behaviour of Black-Billed and Yellow-Billed Magpies*. Poyser, London.
- BODEY, T. W., MCDONALD, R. A., SHELDON, R. D. & BEARHOP, S. (2011). Absence of effects of predator control on nesting success of northern Lapwings *Vanellus vanellus*: implications for conservation. *Ibis* **153**, 543–555.
- *BOLTON, M., TYLER, G., SMITH, K. & BAMFORD, R. (2007). The impact of predator control on lapwing *Vanellus vanellus* breeding success on wet grassland nature reserves. *Journal of Applied Ecology* **44**, 534–544.
- *BOWKER, G., BOWKER, C. & BAINES, D. (2007). Survival rates and causes of mortality in black grouse *Tetrao tetrix* at Lake Vyrnwy, North Wales, UK. *Wildlife Biology* **13**, 231–237.
- *BOYD, H. (1962). Mortality and fertility of European Charadrii. *Ibis* **104**, 368–387.
- BRADBURY, R. B., KYRKOS, A., MORRIS, A. J., CLARK, S. C., PERKINS, A. J. & WILSON, J. D. (2000). Habitat associations and breeding success of yellowhammers on lowland farmland. *Journal of Applied Ecology* **37**, 789–805.
- BREITENMOSE, U. (1998). Large predators in the alps: the fall and rise of man's competitors. *Biological Conservation* **83**, 279–289.
- *BROUGHTON, R. K., HILL, R. A., BELLAMY, P. E. & HINSLEY, S. A. (2011). Nest-sites, breeding failure, and causes of non-breeding in a population of British marsh tits *Poecile palustris*. *Bird Study* **58**, 229–237.
- BURFIELD, I. J. (2008). The conservation status and trends of raptors and owls in Europe. *Ambio* **37**, 401–407.
- *BUXTON, J. (1950). *The Redstart*. Collins, London.
- CARLSSON, N. O. L., JESCHKE, J. M., HOLMQVIST, N. & KINDBERG, J. (2010). Long-term data on invaders: when the fox is away, the mink will play. *Biological Invasions* **12**, 633–641.
- CHALLIS, A., WILSON, M. W., HOLLING, M., ROOS, S., STEVENSON, A. & STIRLING-AIRD, P. (2016). Scottish raptor monitoring scheme, 2015. Stirling, UK, pp. 49.
- 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., GLUE, D. E. & TOMS, M. P. (2009). Sparrowhawk *Accipiter nisus* presence and winter bird abundance. *Journal of Ornithology* **150**, 247–254.
- *CHARMAN, E. C., SMITH, K. W., DILLON, I. A., DODD, S., GRUAR, D. J., CRISTINACCE, A., GRICE, P. V. & GREGORY, R. D. (2012). Drivers of low breeding success in the lesser spotted woodpecker *Dendrocopos minor* in England: testing hypotheses for the decline. *Bird Study* **59**, 255–265.
- *CHARMAN, E. C., SMITH, K. W., GRUAR, D. J., DODD, S. & GRICE, P. V. (2010). Characteristics of woods used recently and historically by lesser spotted woodpeckers *Dendrocopos minor* in England. *Ibis* **152**, 543–555.
- CHRISTENSEN, R. H. B. (2015). Ordinal - Regression Models for Ordinal Data.
- CLAUSEN, K. K., HOLM, T. E., HAUGAARD, L. & MADSEN, J. (2017). Crippling ratio: a novel approach to assess hunting-induced wounding of wild animals. *Ecological Indicators* **80**, 242–246.
- CÔTÉ, I. M. & SUTHERLAND, W. J. (1997). The effectiveness of removing predators to protect bird populations. *Conservation Biology* **11**, 395–405.
- CRAIK, C. (1997). Long-term effects of north American Mink *Mustela vison* on seabirds in western Scotland. *Bird Study* **44**, 303–309.
- *CRAMP, S. (1985). In *Handbook of the Birds of Europe, the Middle East and North Africa The Birds of the Western Palearctic* (Volume 4, ed. S. CRAMP), p. 966. Oxford University Press, Oxford.
- CRAMP, S. (1992). In *Handbook of the Birds of Europe, the Middle East and North Africa The Birds of the Western Palearctic* (Volume 6, ed. S. CRAMP), p. 728. Oxford University Press, Oxford.
- CROOKS, K. R. & SOULÉ, M. E. (1999). Mesopredator release and avifaunal extinctions in a fragmented system. *Nature* **400**, 563–566.
- *DAWSON, N. M., MACLEOD, C. D., SMITH, M. & RATCLIFFE, N. (2011). Interactions with Great Skuas *Stercorarius skua* as a factor in the long-term decline of an Arctic Skua *Stercorarius parasiticus* population. *Ibis* **153**, 143–153.
- *DE LEON, A., MINGUEZ, E., HARVEY, P., MEEK, E., CRANE, J. E. & FURNESS, R. W. (2006). Factors affecting breeding distribution of storm-petrels *Hydrobates pelagicus* in Orkney and Shetland. *Bird Study* **53**, 64–72.
- DEINET, S., IERONYMIDOU, C., MCRAE, L., BURFIELD, I. J., FOPPEN, R. P., COLLEN, B. & BÖHM, M. (2013). Wildlife comeback in Europe: the recovery of selected mammal and bird species. Final report to Rewilding Europe by ZSL, BirdLife International and the European Bird Census Council, 308 pp. Rewilding Europe, London.
- *DIETRICH, V. C. J., SCHMOLL, T., WINKEL, W. & LUBJUH, T. (2003). Survival to first breeding is not sex-specific in the coal tit (*Parus ater*). *Journal für Ornithologie* **144**, 148–156.
- DOHERTY, T. S. & RITCHIE, E. G. (2017). Stop jumping the gun: a call for evidence-based invasive predator management. *Conservation Letters* **10**, 15–22.
- *DONALD, P. F. (2004). *The Skylark*. T & A D Poyser, London.
- *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.
- DONALD, P. F., GREEN, R. E. & HEATH, M. F. (2001). Agricultural intensification and the collapse of Europe's farmland bird populations. *Proceedings of the Royal Society of London Series B-Biological Sciences* **268**, 25–29.
- DOUGLAS, D. J. T., BELLAMY, P. E., STEPHEN, L. S., PEARCE-HIGGINS, J. W., WILSON, J. D. & GRANT, M. C. (2013). Upland land use predicts population decline in a globally near-threatened wader. *Journal of Applied Ecology* **51**, 194–203.
- DUNN, J. C., GRUAR, D., STOATE, C., SZCZUR, J. & PEACH, W. J. (2016). Can hedgerow management mitigate the impacts of predation on songbird nest survival? *Journal of Environmental Management* **184**, 535–544.
- EGGERS, S., GRIESSER, M., ANDERSSON, T. & EKMAN, J. (2005). Nest predation and habitat change interact to influence Siberian jay numbers. *Oikos* **111**, 150–158.
- EGLINGTON, S. M., GILL, J. A., SMART, M. A., SUTHERLAND, W. J., WATKINSON, A. R. & BOLTON, M. (2009). Habitat management and patterns of predation of northern lapwings on wet grasslands: the influence of linear habitat structures at different spatial scales. *Biological Conservation* **142**, 314–324.
- ELLENBERG, H., GAST, F. & DIETRICH, J. (1984). Elster, Krähe und Habicht ein Beziehungsgefüge aus Territorialität, Konkurrenz und Prädation. *Verhandlungen der Gesellschaft für Ökologie* **12**, 319–330.
- ELMHAGEN, B., LUDWIG, G., RUSHTON, S. P., HELLE, P. & LINDÉN, H. (2010). Top predators, mesopredators and their prey: interference ecosystems along bioclimatic productivity gradients. *Journal of Animal Ecology* **79**, 785–794.
- ELMHAGEN, B. & RUSHTON, S. P. (2007). Trophic control of mesopredators in terrestrial ecosystems: top-down or bottom-up? *Ecology Letters* **10**, 197–206.
- ETHERIDGE, B., SUMMERS, R. W. & GREEN, R. E. (1997). The effects of illegal killing and destruction of nests by humans on the population dynamics of the hen harrier *Circus cyaneus* in Scotland. *Journal of Applied Ecology* **34**, 1081–1105.
- EVANS, K. L. (2004). The potential for interactions between predation and habitat change to cause population declines of farmland birds. *Ibis* **146**, 1–13.
- EWING, S. R., REBECCA, G. W., HEAVISIDES, A., COURT, I., LINDLEY, P., RUDDOCK, M., COHEN, S. & EATON, M. A. (2008). Breeding status of Merlins *Falco columbarius* in the UK in 2008. *Bird Study* **58**, 379–389.
- FIELDING, A., HAWORTH, P., WHITFIELD, P., MCLEOD, D. & RILEY, H. (2011). *A Conservation Framework for Hen Harriers in the United Kingdom*, p. 90. JNCC, Peterborough.
- FLETCHER, K., AEBISCHER, N. J., BAINES, D., FOSTER, R. & HOODLESS, A. N. (2010). Changes in breeding success and abundance of ground-nesting moorland birds in relation to the experimental deployment of legal predator control. *Journal of Applied Ecology* **47**, 263–272.
- *FLETCHER, K., HOODLESS, A. N. & BAINES, D. (2013). Impacts of predator abundance on red grouse *Lagopus lagopus scotica* during a period of experimental predator control. *Wildlife Biology* **19**, 248–256.
- *FRANSSON, T., KOLEHMAINEN, T., KROON, C., JANSSON, L. & WENNINGER, T. (2010). EURING list of longevity records for European birds. <http://www.euring.org/data-and-codes/longevity-list>
- FULLER, R. J. & GOUGH, S. J. (1999). Changes in sheep numbers in Britain: implications for bird populations. *Biological Conservation* **91**, 73–89.
- GEER, T. A. (1978). Effects of nesting sparrowhawks on nesting tits. *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. RSPB Research Report No. 23 RSPB, Sandy.
- *GOOCH, S., BAILLE, S. R. & BIRKHEAD, T. R. (1991). Magpie *Pica pica* and songbird populations. Retrospective investigation of trends in population density and breeding success. *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.
- *GREEN, R. E. & ETHERIDGE, B. (1999). Breeding success of the hen harrier *Circus cyaneus* in relation to the distribution of grouse moors and the red fox *Vulpes vulpes*. *Journal of Applied Ecology* **36**, 472–483.
- GREGORY, R. D., VORISEK, P., VAN STRIEN, A., MEYLING, A. W. G., JIGUET, F., FORNASARI, L., REIF, J., CHYLARECKI, P. & BURFIELD, I. J. (2007). Population trends of widespread woodland birds in Europe. *Ibis* **149**, 78–97.
- *GROOM, D. W. (1993). Magpie *Pica pica* predation on blackbird *Turdus merula* nests in urban areas. *Bird Study* **40**, 55–62.
- *GULICKX, M. M. C. & KEMP, J. B. (2007). Provision of nest cages to reduce little ringed plover *Charadrius dubius* nest predation at Welney, Norfolk, England. *Conservation Evidence* **4**, 30–32.
- HANCOCK, M. H., GRANT, M. C. & WILSON, J. D. (2009). Associations between distance to forest and spatial and temporal variation in abundance of key peatland breeding bird species. *Bird Study* **56**, 53–64.
- HANNON, S. J. & COTTERILL, S. E. (1998). Nest predation in aspen woodlots in an agricultural area in Alberta: the enemy from within. *The Auk* **115**, 16–25.
- *HARDING, N. J., GREEN, R. E. & SUMMERS, R. W. (1994). *The Effects of Future Changes in Land Use on Upland Birds in Britain*. Royal Society for the Protection of Birds, Sandy.
- HARRIS, S., MASSIMINO, D., GILLINGS, S., EATON, M. A., NOBLE, D., BALMER, D. E., PROCTER, D. & PEARCE-HIGGINS, J. W. (2017). *The Breeding Bird Survey 2016*, 35pp. British Trust for Ornithology, Thetford.
- HARRIS, S. & YALDEN, D. W. (2008). *Mammals of the British Isles: Handbook*, Fourth Edition (). Mammal Society.
- HAYHOW, D. B., AUSDEN, M. A., BRADbury, R. B., BURNELL, D., COPELAND, A. I., CRICK, H. Q. P., EATON, M. A., FROST, T., GRICE, P. V., HALL, C., HARRIS, S. J., MORECROFT, M. D., NOBLE, D. G., PEARCE-HIGGINS, J. W., WATTS, O. & WILLIAMS, J. M. (2017a). *The State of the UK's Birds 2017*. Sandy.
- HAYHOW, D. B., BENN, S., STEVENSON, A., STIRLING-AIRD, P. K. & EATON, M. A. (2017b). Status of golden eagle *Aquila chrysaetos* in Britain in 2015. *Bird Study* **64**, 281–294.
- *HEUBECK, M., MELLOR, R. M. & HARVEY, P. V. (1997). Changes in the breeding distribution and numbers of kittiwakes *Rissa tridactyla* around Unst, Shetland, and the presumed role of predation by great skuas *Stercorarius skua*. *Seabird* **19**, 12–21.
- *HILL, D. (1988). Population dynamics of the avocet (*Recurvirostra avosetta*) breeding in Britain. *Journal of Animal Ecology* **57**, 669–683.
- HINSLEY, S. A. & BELLAMY, P. E. (2000). The influence of hedge structure, management and landscape context on the value of hedgerows to birds: a review. *Journal of Environmental Management* **60**, 33–49.
- 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.
- HOLT, R. D. & POLIS, G. A. (1997). A theoretical framework for intraguild predation. *American Naturalist* **149**, 745–764.
- *HÖTKER, H. (1988). Lifetime reproductive output of male and female meadow pipits *Anthus pratensis*. *Journal of Animal Ecology* **57**, 109–117.
- *HOY, S. R., PETTY, S. J., MILLON, A., WHITFIELD, D. P., MARQUISS, M., DAVISON, M. & LAMBIN, X. (2015). Age and sex-selective predation moderate the overall impact of predators. *Journal of Animal Ecology* **84**, 692–701.
- *HUDSON, P. J. (1992). *Grouse in Space and Time*, 225pp. Game Conservancy Limited, Fordingbridge.
- 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.
- *JACKSON, D. B. & GREEN, R. E. (2000). The importance of the introduced hedgehog (*Erinaceus europaeus*) as a predator of the eggs of waders (Charadrii) on machair in south Uist, Scotland. *Biological Conservation* **93**, 333–348.
- *JENKINS, D., WATSON, A. & MILLER, G. R. (1964). Predation and red grouse populations. *Journal of Applied Ecology* **1**, 183–195.
- JNCC (2015). Seabird population trends and causes of change: 1986–2014. Report, Peterborough, UK.
- JONES, H. P., TERSHY, B. R., ZAVALA, E. S., CROLL, D. A., KEITT, B. S., FINKELSTEIN, M. E. & HOWALD, G. R. (2011). Severity of the effects of invasive rats on seabirds: a global review. *Conservation Biology* **22**, 16–26.
- KUBASIEWICZ, L. M., BUNNEFELD, N., TULLOCH, A. I. T., QUINE, C. P. & PARK, K. J. (2016). Diversionary feeding: an effective management strategy for conservation conflict? *Biodiversity and Conservation* **25**, 1–22.
- KURKI, S., NIKULA, A., HELLE, P. & LINDEN, H. (1998). Abundances of red fox and pine marten in relation to the composition of boreal forest landscapes. *Journal of Animal Ecology* **67**, 874–886.
- *LACK, D. (1947). The significance of clutch-size. *Ibis* **89**, 302–352.
- *LAIDLAW, R. A., SMART, J., SMART, M. A. & GILL, J. A. (2015). The influence of landscape features on nest predation rates of grassland-breeding waders. *Ibis* **157**, 700–712.
- LAIDLAW, R. A., SMART, J., SMART, M. A. & GILL, J. A. (2017). Scenarios of habitat management options to reduce predator impacts on nesting waders. *Journal of Applied Ecology* **54**, 1219–1229.
- LAVERS, C. P. & HAINES-YOUNG, R. H. (1997). Displacement of dunlin *Calidris alpina schinzii* by forestry in the flow country and an estimate of the value of moorland adjacent to plantations. *Biological Conservation* **79**, 87–90.
- LEES, A. C., NEWTON, I. & BALMFORD, A. (2013). Pheasants, buzzards, and trophic cascades. *Conservation Letters* **6**, 141–144.
- LEGENDE, P. & LEGENDRE, L. (2012). *Numerical Ecology*, Third Edition (). Elsevier, Amsterdam.
- LENSINK, R. (1997). Range expansion of raptors in Britain and the Netherlands since the 1960s: testing an individual-based diffusion model. *Journal of Animal Ecology* **66**, 811–826.
- LOMAN, J. (1980). Reproduction in a population of the hooded crow *Corvus cornix*. *Holarctic Ecology* **3**, 26–35.
- LUDWIG, T., STORCH, I. & GRAF, R. F. (2009). Historic landscape change and habitat loss: the case of black grouse in lower Saxony, Germany. *Landscape Ecology* **24**, 533–546.
- MACDONALD, M. A. & BOLTON, M. (2008). Predation on wader nests in Europe. *Ibis* **150**, 54–73.
- MADDEN, C. F., ARROYO, B. & AMAR, A. (2015). A review of the impacts of corvids on bird productivity and abundance. *Ibis* **157**, 1–16.
- MADDEN, J. R. & PERKINS, S. E. (2017). Why did the pheasant cross the road? Long-term road mortality patterns in relation to management changes. *Royal Society Open Science* **4**, 170617.
- MALPAS, L. R., KENNERLEY, R. J., HIRONS, G. J. M., SHELDON, R. D., AUSDEN, M., GILBERT, J. C. & SMART, J. (2013). The use of predator-exclusion fencing as a management tool improves the breeding success of waders on lowland wet grassland. *Journal for Nature Conservation* **21**, 37–47.
- MARRA, P. P. & SANTELLA, C. (2016). *Cat Wars: The Devastating Consequences of a Cuddly Killer*. Princeton University Press, Princeton.
- MARTIN, T. E. & CLOBERT, J. (1996). Nest predation and avian life-history evolution in Europe versus North America: a possible role of humans? *The American Naturalist* **147**, 1028–1046.
- MARZLUFF, J. M. & NEATHERLIN, E. (2006). Corvid response to human settlements and campgrounds: causes, consequences, and challenges for conservation. *Biological Conservation* **130**, 301–314.
- *MATTHYSEN, E. (1989). Nuthatch *Sitta europaea* demography, beech mast, and territoriality. *Ornis Scandinavica* **20**, 278–282.
- *MCCLEERY, R. H., CLOBERT, J., JULLIARD, R. & PERRINS, C. M. (1996). Nest predation and delayed cost of reproduction in the great tit. *Journal of Animal Ecology* **65**, 96–104.
- *MCCLEERY, R. H. & PERRINS, C. M. (1991). Effects of predation on the number of great tits *Parus major*. In *Bird Population Studies. Relevance to Conservation and Management* (eds C. M. PERRINS, J.-D. LEBRETON and G. M. H. HIRONS), pp. 129–147. Oxford University Press, Oxford.
- MCCULLAGH, P. (1980). Regression models for ordinal data. *Journal of the Royal Statistical Society, Series B* **42**, 109–142.
- MCDONALD, R. A., O'HARA, K. & MORRISH, D. J. (2007). Decline of invasive alien mink (*Mustela vison*) is concurrent with recovery of native otters (*Lutra lutra*). *Diversity and Distributions* **13**, 92–98.
- *MCMILLAN, R. L. (2014). Hen harriers on Skye, 2000–12: nest failures and predation. *Scottish Birds* **34**, 30–39.
- MESSMER, T. A., BRUNSON, M. W., REITER, D. & HEWITT, D. G. (1999). United States public attitudes regarding predators and their management to enhance avian recruitment. *Wildlife Society Bulletin* **27**, 75–85.
- MØLLER, A. P. (1982). Characteristics of magpie *Pica pica* territories of varying duration. *Ornis Scandinavica* **13**, 94–100.
- MOORE, N. P., ROY, S. S. & HELYAR, A. (2003). Mink (*Mustela vison*) eradication to protect ground-nesting birds in the western isles, Scotland, United Kingdom. *New Zealand Journal of Zoology* **30**, 443–452.
- *MURTON, R. K. (1958). The breeding of woodpigeon populations. *Bird Study* **5**, 157–183.
- *MURTON, R. K. & ISAACSON, A. J. (1964). Productivity and egg predation in the woodpigeon. *Ardea* **52**, 30–47.
- MUSTIN, K., NEWBY, S., IRVINE, J., ARROYO, B. & REDPATH, S. (2011). *Biodiversity Impacts of Game Bird Hunting and Associated Management Practices in Europe and North America*, 72 Pp. The James Hutton Institute, Craigiebuckler, Aberdeen.

- NEWBORN, D., HOWARTH, D., RICHARDSON, M., WARREN, P. & BAINES, D. (2017). *Uplands Monitoring in 2016*. The Game and Wildlife Conservation Trust, Fordingbridge.
- NEWSOME, T. M. & RIPPLE, W. J. (2015). A continental scale trophic cascade from wolves through coyotes to foxes. *Journal of Animal Ecology* **84**, 49–59.
- NEWSON, S. E., LEECH, D. I., HEWSON, C. M., CRICK, H. Q. P. & GRICE, P. V. (2010a). Potential impact of grey squirrels *Sciurus carolinensis* on woodland bird populations in England. *Journal of Ornithology* **151**, 211–218.
- NEWSON, S. E., REXSTAD, E. A., BAILLIE, S. R., BUCKLAND, S. T. & AEBISCHER, N. J. (2010b). Population change of avian predators and grey squirrels in England: is there evidence for an impact on avian prey populations? *Journal of Applied Ecology* **47**, 244–252.
- NEWTON, I. (1979). *Population Ecology of Raptors*. T & AD Poyser Ltd., Berkhamsted.
- NEWTON, I. (1986). *The Sparrowhawk*. T & AD Poyser Ltd., London.
- NEWTON, I. (1998). *Population Limitations in Birds*. Academic Press, Amsterdam.
- NEWTON, I. (2013). *Bird Populations*. HarperCollins Publishers, London.
- NEWTON, I. (2017). Invited commentary: fifty years of raptor research. *Journal of Raptor Research* **51**, 95–106.
- 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.
- NICOLL, M. & NORRIS, K. (2010). Detecting an impact of predation on bird populations depends on the methods used to assess the predators. *Methods in Ecology and Evolution* **1**, 300–310.
- NOER, H., MADSEN, J. & HARTMANN, P. (2007). Reducing wounding of game by shotgun hunting: effects of a Danish action plan on pink-footed geese. *Journal of Applied Ecology* **44**, 653–662.
- NORDSTRÖM, M., HÖGMANDER, J., LAINE, J., NUMMELIN, J., LAANETU, N. & KORPIMÄKI, E. (2003). Effects of feral mink removal on seabirds, waders and passerines on small islands in the Baltic Sea. *Biological Conservation* **109**, 359–368.
- NORRDAHL, K. & KORPIMÄKI, E. (1998). Fear in farmlands: how much does predator avoidance affect bird community structure? *Journal of Avian Biology* **29**, 79–85.
- North American Bird Conservation Initiative (2016). *The State of North America's Birds 2016*. Environment and Climate Change Canada, Ottawa.
- OEHLER, J. D. & LITVAITIS, J. A. (1996). The role of spatial scale in understanding responses of medium-sized carnivores to forest fragmentation. *Canadian Journal of Zoology* **74**, 2070–2079.
- *ORO, D. & FURNESS, R. W. (2002). Influences of food availability and predation on survival of kittiwakes. *Ecology* **83**, 2516–2528.
- Pan-European Common Bird Monitoring Scheme (2016). *Trends of Common Birds in Europe, 2016 Update*. European Bird Census Council, Prague.
- *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., 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.
- PASANEN-MORTENSEN, M., PYYKÖNEN, M. & ELMHAGEN, B. (2013). Where lynx prevail, foxes will fail – limitation of a mesopredator in Eurasia. *Global Ecology and Biogeography* **22**, 868–877.
- PEACH, W. J., LOVETT, L. J., WOTTON, S. R. & JEFFS, C. (2001). Countryside stewardship delivers curlew bunting (*Emberiza hortulana*) in Devon, UK. *Biological Conservation* **101**, 361–373.
- PEACH, W. J., SIRIWARDENA, G. M. & GREGORY, R. D. (1999). Long-term changes in over-winter survival rates explain the decline of reed buntings *Emberiza schoeniclus* in Britain. *Journal of Applied Ecology* **36**, 798–811.
- PERRINS, C. M. & GEER, T. A. (1980). The effect of Sparrowhawks on tit populations. *Ardea* **68**, 133–142.
- 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.
- PILLAI, A. & TURNER, A. (2017). *A Review of Game Bird Law and Licensing in Selected European Countries, 77 Pp*. Scottish Natural Heritage, Edinburgh.
- PIMM, S. L. (1991). *The Balance of Nature? Ecological Issues in the Conservation of Species and Communities*. The University of Chicago Press, Chicago.
- POLIS, G. A. & HOLT, R. D. (1992). Intraguild predation: the dynamics of complex trophic interactions. *Trends in Ecology and Evolution* **7**, 151–154.
- *POTTS, G. R. (1980). The effects of modern agriculture, nest predation and game management on the population ecology of partridges (*Perdix perdix* and *Alectoris rufa*). *Advances in Ecological Research* **11**, 1–79.
- *POTTS, G. R. (1986). *The Partridge: Pesticides, Predation and Conservation*. Collins, London.
- POTTS, G. R. (2012). *The Partridges*. Collins, London.
- PULLIN, A. S. & STEWART, G. B. (2006). Guidelines for systematic review in conservation and environmental management. *Conservation Biology* **20**, 1647–1656.
- R Core Team (2015). *R: A Language and Environment for Statistical Computing*. R Foundation for Statistical Computing, Vienna.
- *RATCLIFFE, N. (2004). Little terns in Britain and Ireland: estimation and diagnosis of population trends. In RSPB Research Report No. 8, RSPB, Sandy, pp. 3–17.
- RATCLIFFE, N., BELL, M., PELEMBE, T., BOYLE, D., BENJAMIN, R., WHITE, R., GODLEY, B., STEVENSON, J. & SANDERS, S. (2010). The eradication of feral cats from Ascension Island and its subsequent recolonization by seabirds. *Oryx* **44**, 20–29.
- *RATCLIFFE, N., CRAIK, C., HELYAR, A., ROY, S. & SCOTT, M. (2008). Modelling the benefits of American mink *Mustela vison* management options for terns in West Scotland. *Ibis* **150**, 114–121.
- *RATCLIFFE, N., HOUGHTON, D., MAYO, A., SMITH, T. & SCOTT, M. (2006). The breeding biology of terns on the western Isles in relation to mink eradication. *Atlantic Seabirds* **8**, 127–135.
- RATCLIFFE, N., MITCHELL, I., VARNHAM, K., VERBOVEN, N. & HIGSON, P. (2009). How to prioritize rat management for the benefit of petrels: a case study of the UK, Channel Islands and Isle of Man. *Ibis* **151**, 699–708.
- REDPATH, S. M. & THIRGOOD, S. J. (1997). In *Birds of Prey and Red Grouse* (ed. I. Newton, 148 pp). Centre for Ecology and Hydrology, Norwich.
- REDPATH, S. M. & THIRGOOD, S. J. (1999). Numerical and functional responses in generalist predators: hen harriers and peregrines on Scottish grouse moors. *Journal of Animal Ecology* **68**, 879–892.
- REDPATH, S. M., THIRGOOD, S. J. & LECKIE, F. M. (2001). Does supplementary feeding reduce predation of red grouse by hen harriers? *Journal of Applied Ecology* **38**, 1157–1168.
- REITER, D. K., BRUNSON, M. W. & SCHMIDT, R. H. (1999). Public attitudes toward wildlife damage management and policy. *Wildlife Society Bulletin* **27**, 746–758.
- REYNOLDS, J. C. & TAPPER, S. C. (1996). Control of mammalian predators in game management and conservation. *Mammal Review* **26**, 127–155.
- RISELY, K., RENWICK, A. R., DADAM, D., EATON, M. A., JOHNSTON, A., BAILLIE, S. R., MUSGROVE, A. J. & NOBLE, D. G. (2011). *The Breeding Bird Survey 2010*. British Trust for Ornithology, 24pp, Thetford.
- RITCHIE, E. G., ELMHAGEN, B., GLEN, A. S., LETNIC, M., LUDWIG, G. & McDONALD, R. A. (2012). Ecosystem restoration with teeth: what role for predators? *Trends in Ecology & Evolution* **27**, 265–271.
- RITCHIE, E. G. & JOHNSON, C. N. (2009). Predator interactions, mesopredator release and biodiversity conservation. *Ecology Letters* **12**, 982–998.
- ROBINSON, R. A., LEECH, D. I., MASSIMINO, D., WOODWARD, I., HAMMOND, M. J., HARRIS, S. J., NOBLE, D. G., WALKER, R. H., EGLINGTON, S. M., MARCHANT, J. H., SULLIVAN, M. J. P. & BAILLIE, S. R. (2016). *BirdTrends 2016: Trends in Numbers, Breeding Success and Survival for UK Breeding Birds*. BTO, Thetford.
- ROBINSON, S. K., THOMPSON, F. R. III, DONOVAN, T. M., WHITEHEAD, D. R. & FAABORG, J. (1995). Regional forest fragmentation and the nesting success of migratory birds. *Science* **267**, 1987–1990.
- ROOS, S. & PÄRT, T. (2004). Nest predators affect spatial dynamics of breeding red-backed shrikes (*Lanius collurio*). *Journal of Animal Ecology* **73**, 117–127.
- SALO, P., NORDSTRÖM, M., THOMSON, R. L. & KORPIMÄKI, E. (2008). Risk induced by a native top predator reduces alien mink movements. *Journal of Animal Ecology* **77**, 1092–1098.
- SÁNCHEZ-GARCÍA, C., BUNER, F. D. & AEBISCHER, N. J. (2015). Supplementary winter food for gamebirds through feeders: which species actually benefit? *The Journal of Wildlife Management* **79**, 832–845.
- SANDERCOCK, B. K., NILSEN, E. B., BROSETH, H. & PEDERSEN, H. C. (2011). Is hunting mortality additive or compensatory to natural mortality? Effects of experimental harvest on the survival and cause-specific mortality of willow ptarmigan. *Journal of Animal Ecology* **80**, 244–258.
- *SANDVIK, H., ERIKSTAD, K. E., FAUCHALD, P. E. R. & TVERAA, T. (2008). High survival of immatures in a long-lived seabird: insights from a long-term study of the Atlantic puffin (*Fratercula arctica*). *The Auk* **125**, 723–730.
- Scottish Executive (2006). *The Scottish Forestry Strategy*, 88pp. Edinburgh.
- SEDDON, P. J., ARMSTRONG, D. P. & MALONEY, R. F. (2007). Developing the science of reintroduction biology. *Conservation Biology* **21**, 303–312.
- SERGIO, F. & HIRALDO, F. (2008). Intraguild predation in raptor assemblages: a review. *Ibis* **150**, 132–145.
- SERGIO, F., MARCHESI, L. & PEDRINI, P. (2003). Spatial refugia and the coexistence of a diurnal raptor with its intraguild owl predator. *Journal of Animal Ecology* **72**, 232–245.
- *SIMS, V., EVANS, K. L., NEWSON, S. E., TRATALOS, J. A. & GASTON, K. J. (2008). Avian assemblage structure and domestic cat densities in urban environments. *Diversity and Distributions* **14**, 387–399.
- SING, L., TOWERS, W. & ELLIS, J. (2013). Woodland expansion in Scotland: an assessment of the opportunities and constraints using GIS. *Scottish Forestry* **67**, 18–25.
- *SIRIWARDENA, G. M. (2004). Possible roles of habitat, competition and avian nest predation in the decline of the willow tit *Parus montanus* in Britain. *Bird Study* **51**, 193–202.
- *SIRIWARDENA, G. M. (2006). Avian nest predation, competition and the decline of British marsh tits *Parus palustris*. *Ibis* **148**, 255–265.
- SIRIWARDENA, G. M., STEVENS, D. K., ANDERSON, G. Q. A., VICKERY, J. A., CALBRADE, N. A. & DODD, S. (2007). The effect of supplementary winter seed food on breeding populations of farmland birds: evidence from two large-scale experiments. *Journal of Applied Ecology* **44**, 920–932.

- SMART, J., AMAR, A., SIM, I. M. W., ETHERIDGE, B., CAMERON, D., CHRISTIE, G. & WILSON, J. D. (2010). Illegal killing slows population recovery of a re-introduced raptor of high conservation concern - the red kite *Milvus milvus*. *Biological Conservation* **143**, 1278–1286.
- SMITH, R. K., PULLIN, A. S., STEWART, G. B. & SUTHERLAND, W. J. (2010). Effectiveness of predator removal for enhancing bird populations. *Conservation Biology* **24**, 820–829.
- SMITH, R. K., PULLIN, A. S., STEWART, G. B. & SUTHERLAND, W. J. (2011). Is nest predator exclusion an effective strategy for enhancing bird populations? *Biological Conservation* **144**, 1–10.
- SOTHERTON, N., BAINES, D. & AEBISCHER, N. J. (2017). An alternative view of moorland management for red grouse *Lagopus lagopus scoticus*. *Ibis* **159**, 693–698.
- SOVADA, M. A., SARGEANT, A. B. & GRIER, J. W. (1995). Differential effects of coyotes and red foxes on duck nest success. *Journal of Wildlife Management* **59**, 1–9.
- *STEWART, F. (2010). *Ecology and conservation of the willow tit (Poecile montanus) in Britain*. Unpublished PhD Thesis: University of Nottingham.
- STOATE, C. & SZCZUR, J. (2001). Could game management have a role in the conservation of farmland passerines? A case study from a Leicestershire farm. *Bird Study* **48**, 279–292.
- *STOATE, C. & SZCZUR, J. (2006a). Potential influence of habitat and predation on local breeding success and population in spotted flycatchers *Muscicapa striata*. *Bird Study* **53**, 328–330.
- *STOATE, C. & SZCZUR, J. (2006b). *Spotted Flycatchers at Loddington*. The Game Conservancy Trust, Fordingbridge.
- *SUMMERS, R. W., DUGAN, D. & PROCTOR, R. (2010). Numbers and breeding success of Capercaillies *Tetrao urogallus* and black Grouse *T. tetrix* at Abernethy Forest, Scotland. *Bird Study* **57**, 437–446.
- *SUMMERS, R. W., GOLDER, P., WALLACE, N., IASON, G. & WILSON, J. (2015). *Correlates of Capercaillie Productivity in Scots Pinewoods in Strathspey*, 42pp. Inverness.
- *SUMMERS, R. W., GREEN, R. E., PROCTOR, R., DUGAN, D., LAMBE, 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, R. W., WILLI, J. & SELVIDGE, J. (2009). Capercaillie *Tetrao urogallus* nest loss and attendance at Abernethy Forest, Scotland. *Wildlife Biology* **15**, 319–327.
- 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*. *Journal of Applied Ecology* **33**, 965–978.
- *TAYLOR, W. G., ETHERIDGE, B. & SUMMERS, R. W. (2016). The role of predation in the decline in the breeding success of Scottish crested tits in a coastal pine plantation. *Scottish Birds* **36**, 121–134.
- *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.
- The Mammal Society (2013). *Red Fox (Vulpes vulpes)*. The Mammal Society.
- THIRGOOD, S. J., REDPATH, S. M., HAYDON, D. T., ROTHERY, P., NEWTON, I. & HUDSON, P. J. (2000a). Habitat loss and raptor predation: disentangling long- and short-term causes of red grouse declines. *Proceedings of the Royal Society B-Biological Sciences* **267**, 651–656.
- THIRGOOD, S. J., REDPATH, S. M., ROTHERY, P. & AEBISCHER, N. J. (2000b). Raptor predation and population limitation in red grouse. *Journal of Animal Ecology* **69**, 504–516.
- THOMAS, R. L., FELLOWES, M. D. E. & BAKER, P. J. (2012). Spatio-temporal variation in predation by urban domestic cats (*Felis catus*) and the acceptability of possible management actions in the UK. *PLoS One* **7**, e49369.
- *THOMPSON, P. S., BAINES, D., COULSON, J. C. & LONGRIGG, G. (1994). Age at first breeding, philopatry and breeding site-fidelity in the lapwing *Vanellus vanellus*. *Ibis* **136**, 474–484.
- THOMPSON, P. S., DOUGLAS, D. J. T., HOCOCOM, D., KNOTT, J., ROOS, S. & WILSON, J. D. (2016). Environmental impacts of high-output driven shooting of red grouse *Lagopus lagopus scoticus*. *Ibis* **158**, 446–452.
- THOMSON, D. L., FURNESS, R. W. & MONAGHAN, P. (1998a). The analysis of ordinal response data in the behavioural sciences. *Animal Behaviour* **56**, 1041–1043.
- THOMSON, D. L., GREEN, R. E., GREGORY, R. D. & BAILLIE, S. R. (1998b). The widespread declines of songbirds in rural Britain do not correlate with the spread of their avian predators. *Proceedings of the Royal Society in London, Serie B*. **265**, 2057–2062.
- TOWNS, D. R. & BROOME, K. G. (2003). From small Maria to massive Campbell: forty years of rat eradications from New Zealand islands. *New Zealand Journal of Zoology* **30**, 377–398.
- TREVES, A. & NAUGHTON-TREVES, L. (2005). Evaluating lethal control in the management of human-wildlife conflict. In *People and Wildlife: Conflict or Coexistence?* (eds R. WOODROFFE, S. THIRGOOD and A. RABINOWITZ), pp. 86–106. Cambridge University Press, London.
- TURNER, C. & SAGE, R. B. (2003). *Fate of Released Pheasants*. The Game Conservancy Trust, Fordingbridge.
- VALKAMA, J., KORPIMÄKI, 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.
- *VAN DER WAL, R. & PALMER, S. C. F. (2008). Is breeding of farmland wading birds depressed by a combination of predator abundance and grazing? *Biology Letters* **4**, 256–258.
- *VAN HECKE, P. (1981). Ortstreue, Altersaufbau und Mortalität einer Population des Baumpiepers (*Anthus t. trivialis*). *Journal für Ornithologie* **122**, 23–35.
- *VOTIER, S. C., HEUBECK, M. & FURNESS, R. W. (2008). Using inter-colony variation in demographic parameters to assess the impact of skua predation on seabird populations. *Ibis* **150**, 45–53.
- WARBURTON, B. & NORTON, B. G. (2009). Towards a knowledge-based ethic for lethal control of nuisance wildlife. *Journal of Wildlife Management* **73**, 158–164.
- *WATSON, M. (2004). *The effects of raptor predation on Grey Partridges Perdix perdix*. Unpublished DPhil. Thesis.
- *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. (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.
- WHITFIELD, D. P. & FIELDING, A. H. (2017). *Analyses of the Fates of Satellite Tracked Golden Eagles in Scotland*, 285pp. Edinburgh.
- WHITFIELD, D. P., FIELDING, A. H., MCLEOD, D. R. A. & HAWORTH, P. F. (2004). The effects of persecution on age of breeding and territory occupation in golden eagles in Scotland. *Biological Conservation* **118**, 249–259.
- WHITFIELD, D. P., FIELDING, A. H. & WHITEHEAD, S. (2008). Long-term increase in the fecundity of hen harriers in Wales is explained by reduced human interference and warmer weather. *Animal Conservation* **11**, 144–152.
- WILSON, G., HARRIS, S. & MCLAREN, G. (1997). *Changes in the British Badger Population 1988–1997*. People's Trust for Endangered Species, London.
- WILSON, J. D., ANDERSON, R., BAILEY, S., CHETCUIT, J., COWIE, N. R., HANCOCK, M. H., QUINE, C. P., RUSSELL, N., STEPHEN, L. & THOMPSON, D. B. A. (2014). Modelling edge effects of mature forest plantations on peatland waders informs landscape-scale conservation. *Journal of Applied Ecology* **51**, 204–213.
- WOTTON, S. R., BLADWELL, S., MATTINGLEY, W., MORRIS, N. G., RAW, D., RUDDOCK, M., STEVENSON, A. & EATON, M. A. (in press). The status of the hen harrier *Circus cyaneus* in the UK and Isle of Man in 2016. *Bird Study*.
- WRETFENBERG, J., LINDSTRÖM, Å., SVENSSON, S., THIERFELDER, T. & PÄRT, T. (2006). Population trends of farmland birds in Sweden and England: similar trends but different patterns of agricultural intensification. *Journal of Applied Ecology* **43**, 1110–1120.
- *WRIGHT, L. J., HOBLYN, R. A., GREEN, R. E., BOWDEN, C. G. R., MALLORD, J. W., SUTHERLAND, W. J. & DOLMAN, P. M. (2009). Importance of climatic and environmental change in the demography of a multi-brooded passerine, the woodlark *Lullula arborea*. *Journal of Animal Ecology* **78**, 1191–1202.

VIII. SUPPORTING INFORMATION

Additional supporting information may be found online in the Supporting Information section at the end of the article.

Appendix S1. Search phrases used in web of science and google scholar searches.

Appendix S2. The predator–prey interactions identified in the literature review.

Table S2.1. All predator–prey interactions (cases) used in the analyses.

Table S2.2. The amalgamated response variable ‘Evidence’ used to describe the combination of prey response to predators and the scientific strength of the study.

Table S2.3. The number of studies and predator–prey interaction cases per prey group found in the literature review.

Appendix S3. Detailed explanation of the population trends of avian and mammalian predators in the UK.

Appendix S4. Additional information regarding the effects of predators on prey species as well as additional results from the Principal Component Analysis (PCA).

Fig. S4.1. The effect of predators on seven different groups of prey species categorised by the scientific strength of the study and the strength of evidence.

Fig. S4.2. Association plots showing the relationship between prey groups and nest-site characteristics and migratory strategy.

Table S4.1. Eigenvalues, standard deviations, and percentage variance explained of the principal component analysis axes.

Table S4.2. Rotated loadings for the principal component analysis.

Fig. S4.3. Plots showing the relationship between evidence and PC1 and PC2 scores for individual species.

(Received 31 July 2017; revised 19 April 2018; accepted 25 April 2018)