IBIS
BOU international journal of avian science
Ibis (2026)
doi: 10.1111/ibi.70101

Review

A systematic review and meta-analysis of variation in nest predation of ground-nesting birds

MARI D. KLAUSSEN,*[1,2] KEVIN A. WOOD,[2] ALEX NICOL-HARPER,[2] ANITA DIAZ ISLA,[1] EMILIE A. HARDOUIN[1] & RICHARD A. STILLMAN[1]
[1]*Bournemouth University, Christchurch House, Talbot Campus, Fern Barrow, Poole, BH12 5BB, UK*
[2]*Conservation Evidence WWT, Bowditch, Slimbridge, Gloucester, GL2 7BT, UK*

Predation and communities of predators of ground-nesting bird nests and fledglings have been studied across multiple groups of ground-nesting birds, such as waders, waterbirds, gamebirds and passerines, and habitats, but differences and similarities between groups are less studied. We synthesized data from 355 studies, mainly from North America and Europe, to investigate variations in predation rates of nests and fledglings of ground-nesting birds. The use of artificial nests to study predation has been a common practice, but the extent to which predation rates are similar to those of real nests has been a topic of discussion since the establishment of the method. Investigating effects on fledgling predation was not possible due to a lack of data. No differences in predation rates were detected for studies with or without invasive species or between waders, waterbirds, gamebirds and passerines, and predation rates were generally high for all groups. Artificial nests did have significantly higher overall predation rates compared to real nests, with an odds-ratio of 0.46 (95% CI: 0.35–0.61) of real nests relative to artificial nests. Mammals were the most frequent predator, being described in 50% of all studies, followed by avian predator species in 35%. Of mammals, the Red Fox *Vulpes vulpes* was described most frequently, in 19% of the studies. Unidentified predators were also prevalent in the literature (10% of studies), highlighting the common problem of not being able to identify predators of nests and fledglings. While the study identified a lack of data for some of the variables and regions, it does suggest that despite the differences in predator communities, predation has similarly high rates across ground-nesting bird groups. Further work is required to better understand predation, especially for fledglings.

Keywords: artificial nests, evidence synthesis, predator community, predator identity, predator–prey interactions.

Many ground-nesting bird species, such as waders (Charadriiformes), passerines (Passeriformes) and gamebirds (Galliformes), are declining rapidly (McMahon *et al.* 2024). Declines have been linked to high rates of nest and fledgling predation (Nicoll & Norris 2010, Roos *et al.* 2018), with wader and gamebird populations potentially being particularly limited by high predation rates (Roos *et al.* 2018). Hence, greater understanding of predation on ground-nesting birds' nests and fledglings is urgently required.

Although it is well established that most predation can be attributed to either mammalian or avian predator species, especially in waders (Macdonald & Bolton 2008, Barton *et al.* 2025), the extent to which different predator species contribute to predation might differ between prey species (Barton *et al.* 2025). The overall predator

*Corresponding author.
Email: mari.dklaussen@gmail.com

community varies between different bird groups and ecosystems (Munkebye *et al.* 2003, Samsonov *et al.* 2022, Parrett *et al.* 2023a, 2023b), which might further influence predation. In some systems, bird eggs and fledglings are an important resource to some predator species (Bêty *et al.* 2001, Aharon-Rotman *et al.* 2015), while in others, eggs may constitute a small fraction of the predators' diets (Lanszki 2005). It is also possible that predation rates are high in certain places because of the disproportionate effect of invasive species on ground-nesting birds. Many ground-nesting bird species are naïve to the threat of invasive predators because they lack the evolutionary history to cope with such introduced species. This has especially been the case for many island-nesting birds being exposed to the new threat of mammalian predators (Arcilla *et al.* 2015). Predation rates are therefore likely to depend on multiple factors, making them complex processes to study in many cases.

The unresolved questions regarding predation of ground-nesting birds, in particular which variables influence predation rates, hinder ongoing attempts by conservation practitioners to reduce predation rates and aid the recovery of threatened populations (Laidlaw *et al.* 2021). Huge efforts are made every year to increase recruitment to ground-nesting bird populations, but often these efforts do not reduce predation enough to meet the fledging numbers needed to avoid further population declines (Fletcher *et al.* 2010, Rickenbach *et al.* 2011, Jellesmark *et al.* 2023).

Many studies have provided estimates of predation rates and predator identities, but how representative these results are might depend on the methods used in the study (Nicoll & Norris 2010). A common method for studying nest predation has been the use of artificial nests. Artificial nests attempt to mimic aspects of real nests to investigate predation rates of eggs, predator communities and drivers for predation (Bocz *et al.* 2017, Arbeiter & Franke 2018). However, the reliability of artificial nests as a way to estimate predation rates of real nests has been a topic of discussion ever since it was established as a method (Ortega *et al.* 1998, Wilson *et al.* 1998, Zanette 2002), with arguments that artificial nests both over- and underestimate predation rates (Willebrand & Marcström 1988, Wilson *et al.* 1998). Many studies have deployed artificial nests but using these studies to compare or inform systems with real nests can be difficult if there are systematic differences in predation rates derived from artificial studies and described predator communities. We therefore wanted to address the question of whether artificial nest studies and real nest studies differed on a multi-study level, not just at a system-specific level. Based on previous studies combining real and artificial nests, we expected artificial nest studies to have higher predation rates globally. We also expected there to be differences in described predator communities between the two.

Ground-nesting is a common strategy in several major bird taxa, but variations exist within and between groups, especially with respect to nest defence and degree of nest concealment (Albrecht & Klvaňa 2004, Brynychová *et al.* 2022). Variations in predation rates could therefore exist between the different ground-nesting bird groups, based on these differences in nesting ecology. Similarities or differences due to nesting ecology could also be extended to the described predator communities between bird groups.

Despite the growing number of studies of nest predation, no attempt has been made to compare predation rates and predator communities between ground-nesting bird groups or real and artificial nests on a multi-study scale to our knowledge. In this study, we conducted a systematic literature review and meta-analysis to investigate if variations in predation rates across studies could be explained by: use of real and artificial nests, groups of birds (waders, waterbirds, gamebirds, passerines) and presence of invasive species. Variations in predator communities between real and artificial nests, and bird groups was also modelled to see if the described predator communities would differ between the methods used and the bird group studied, as this might have implications for how we compare studies on the topic.

METHODS

We used the *Preferred Reporting Items for Systematic reviews and Meta-Analyses* PRISMA (Page *et al.* 2021) flow diagram and checklist (Fig. S1 and Supporting Information) to identify literature and extract information.

Literature search and data extraction

Relevant articles were primarily obtained by searching scientific literature databases. No

temporal or geographical constraints were applied. Only primary articles were included. Material not written in English was excluded from the final dataset. This systematic review is therefore primarily focused on studies from Europe and North America. Literature on the topic probably exists in most languages on all continents, but only literature in the Scandinavian languages, German and French would have been possible to translate within the time limit of the systematic review. Therefore, to avoid the risk of bias towards translation of literature from these geographical regions in our data, we decided to only include literature provided in English.

Two separate searches were carried out in the databases Web of Science (12 December 2024) and Scopus (3 June 2025), using the core collections, resulting in 3164 and 4445 papers (Fig. S1).

Search strings included search terms to allow us to identify relevant literature on predation of ground-nesting bird nests and fledglings: ((‘ground nesting bird*’) OR (‘ground-nesting bird*’) OR wader* OR shorebird* OR waterbird* OR gamebird* OR waterfowl* OR (songbird* AND ground-nesting)) AND ((predat* OR depredat*) OR ‘daily predation rate’ OR (nest* NEAR/5 success*) OR (nest* NEAR/5 surviv*) OR (hatch* NEAR/5 success*) OR (hatch* NEAR/5 fail*) OR (fledg* NEAR/5 success*) OR (fledg* NEAR/5 fail*) OR (breed* NEAR/5 success*) OR (breed* NEAR/5 fail*) OR (predat* NEAR/5 rate*) OR (reproduc* NEAR/5 fail*) OR (reproduc* NEAR/5 success*) OR (egg* NEAR/5 survival) OR (egg* NEAR/5 predation) OR (nest* NEAR/5 predation) OR (egg* NEAR/5 consum*)).

Because the focus of the review was predation of ground nests, four major bird groups where a considerable number of species are ground-nesting were included in the search terms to reduce the number of publications not related to ground-nesting species. Targeted bird groups in the search were therefore waders (Charadriiformes), waterbirds (Anseriformes and Gaviiformes), passerines (Passeriformes) and gamebirds (Galliformes) (Table S1).

Several terms exist to describe the taxonomic groups of interest and some are overlapping, such as ‘wader’ and ‘shorebird’ and ‘waterbird’ and ‘waterfowl’. We therefore included all such terms in the search strings but only used the waterbird and wader terms in the analysis. Many passerines are not ground-nesting, and therefore we included a combined search term (songbird* AND ground-nest*) to narrow down the number of papers related to passerine predation. We also only included studies on passerines if it was explicitly stated in the paper that only ground-nests were considered. Seabirds were not included in our analysis, as many of them are cliff nesting, or inhabit remote islands inaccessible to many predator species, and predation patterns are assumed to differ from those of nests located on the ground. The reference lists of key review articles in the field were checked for additional relevant literature that was not included in the database searches, in a process known as ‘citation chaining’ (Côté *et al.* 2013). Review papers identified by the database searches on similar topics were also checked for relevant literature (Larsen 1991, Macdonald & Bolton 2008, Park *et al.* 2008, Roos *et al.* 2018). The report catalogue of the BTO (https://www.bto.org/our-work/science/publications) and BirdLife International (https://datazone.birdlife.org/publications) were checked for relevant grey literature reports. Duplicates from the two main database searches were removed resulting in 2139 unique publications (Fig. S1). After removing duplicates, these were screened by title and abstract ($n = 2139$). Retained articles ($n = 464$) were then checked to see if they met the inclusion criteria (Table S2), and non-relevant articles were removed, resulting in 355 articles (Fig. S1). We included studies using both real and artificial nests to test the hypothesis that there are differences in predation rates and described predator communities between real and artificial nests.

Data extraction from included literature

For the final set of publications, estimates of predation and survival were extracted together with any reported variance estimates and/or confidence intervals. Several measures of predation and survival exist in the literature, and the specific measure used in each case was recorded. Estimates were extracted together with bird species, sample size (see below), methods of data collection, country of origin and the reported findings of the study. Some of the estimates of predation in the dataset have been manually calculated using the number of nests predated and sample size either from tables or from information provided in the publication, to increase the number of estimates in our analysis. The sample size in the dataset is reported

as the number of nests for studies of egg predation and total number of fledglings for studies focusing on fledgling predation.

Classification of predation events

We defined a predation event as at least one egg being damaged or missing from a nest, or at least one fledgling being confirmed predated. Our study therefore includes events of partial predation. We did not consider trampling as a predation event, and therefore studies reporting predation by ungulates have been excluded ($n = 6$) because in most of the cases, it was difficult to know if trampling was included in estimates of ungulate predation.

Invasive species

Invasive species were included in the analysis to test whether predator communities where invasive species were included would have a disproportionate effect on predation rates. We classified six species or families of invasive species: Red Fox if the study originated from countries where the red fox is described as an invasive species, such as Australia or New Zealand, rodents (Rodentia) if they originated from studies of island communities or if the study described the rodent as invasive, Raccoon Dog *Nyctereutes procyonoides* or American Mink *Neogale vison* if the study originated outside the natural distribution of either of these species, and all instances of domestic cats *Felis catus* and dog *Canis familiaris* predation as this is not expected to be natural in any location.

Standardization of predation estimates

Several measurements of predation were in the primary literature, such as daily predation rate (DPR), percent predated, predation rate, daily survival rate (DSR) and hatching success, and estimates were therefore standardized to one common measurement of predation for our analysis. We used proportion of nests experiencing predation of at least one egg (note, not proportion of all eggs predated) of the total study population as the standard measurement of nest predation. Classifying a predation event after confirming predation of at least one egg was the most common practice across studies, because complete predation or abandonment was assumed to take place after partial predation. It was therefore not possible to categorize proportions of nests from individual studies as partial or completely predated. For fledgling predation, proportion of fledglings (note, individuals not broods) predated across the total study population was used as the standard measurement.

The proportion of the population of nests or fledglings predated was used as the standard measurement as this was the most common unit of measurement and the most informative for this review. For nest predation, only estimates of egg predation were used. For altricial species, this means that predation of young still in the nest bowl (nestlings) was not regarded as nest predation because we assumed that predation of eggs and hatched nestlings could be quite different based on begging calls from nestlings and parental investment in defending nestlings from predators. For fledgling predation, fledglings were defined as offspring that had left the nest bowl but were still dependent on parents and had not fledged.

For studies reporting predation rates, we checked the publication for descriptions of how rates were calculated. In most of the publications, rates were defined as the number of nests with eggs predated divided by the total sample size, and therefore also reflect the proportion of nests predated, and these estimates were therefore directly included in the analysis without any transformation. Estimates of DPR were transformed into proportion of nests predated where possible. DPR can be defined as $-\frac{\ln PR}{T}$ where PR is the proportion of predated nests and T is the total exposure time, or days of incubation, of the study species (Ricklefs 1969). The proportion predated nests can therefore be defined as $PR = e^{DPR \cdot T}$. Several studies used measurements of survival when investigating predation, assuming that survival is the inverse measure of predation (Mayfield 1961). These measurements were not transformed or included in this analysis because survival cannot be assumed to be the inverse of predation. Several other causes of failure exist such as abandonment, trampling, flooding and starvation (Espie *et al.* 1998, Roche *et al.* 2010, Mandema *et al.* 2013), and including these estimates could lead to overestimating predation rates.

Data analysis

Factors affecting predation rates of ground-nests

Generalized mixed models (GLMMs) with a binomial distribution were fitted using the *glmmTMB* R

package (Brookes *et al.* 2017) to explore variations in overall predation rates for ground-nesting birds. We separated estimates of nest and fledging predation and modelled them separately. Variation in predation as a cause of failure was the main interest of the analysis, and therefore only a subset of the data where estimates of predation were provided (351 estimates from 182 studies) was used for the statistical analysis. Forty-three studies had more than one estimate of predation, and *Study ID* was therefore fitted as a random factor to account for non-independence between estimates derived from the same study. Low estimates of egg-stage predation do not necessarily reflect high hatching success because nests can be lost due to other causes. The relationship between predation rates and total failure rate was therefore checked to see if low estimates of predation would still be an accurate estimate of failure in those populations. For studies which experimentally reduced predation, for example by fencing nests, we only included estimates before any experiments were performed (controls) to only include natural rates of predation in the models ($n = 319$).

We first fitted a model with monitoring type (binary: real nests and artificial nests, Table 1) as the predictor to investigate the effect of nest monitoring used on predation rates, and one with invasive species to investigate the effect that presence of invasive species might have on predation rates. Based on the results of the monitoring type model, we decided to remove estimates based on artificial nest experiments when fitting the model for bird groups. We then fitted a model with bird taxa from studies using real nests (categorical, four levels: wader, waterbird, gamebird, passerine, Table 1).

The R package *DHARMa* (Hartig 2024) was used to check that model assumptions were met and to inspect model residuals. The R package *performance* (Lüdecke et al. 2021) was used to check collinearity between the predictor variables and to estimate explanatory power of each model.

Table 1. Descriptions of covariates used in the GLMM looking at predation rates.

Predictors	Types	Levels
Bird type	Categorical	Wader, waterbird, passerine, gamebird
Monitoring type	Categorical	Artificial nests, real nests
Invasive species	Binary	1 = present, 0 = absent

Difference in mean proportion of unidentified predators between studies using camera traps and physical evidence of predation was checked using a two-sided Welch *t*-test. Statistically significant relationships were inferred where $P < 0.05$.

Differences in predator communities

We used generalized linear latent variable models (GLLVMs) to investigate predator community composition for our included studies. GLLVM is an extension of the basic GLMM modelling multivariate data that uses a factor analytical approach (Niku *et al.* 2019). It can therefore be used as a statistical approach to study predator communities of ground-nesting birds based on the predictor variables used in the GLMMs discussed in the previous section.

We modelled predator communities for each estimate of predation in our dataset as the multivariate response using the *gllvm* package in R (Niku *et al.* 2019). Many studies only reported presence or absence of predators, and we therefore used this as the measurement in our response variable to be able to include as much data as possible in the analysis. For studies reporting proportions predated by different predators, we assigned presence when an estimate was provided and absence when no estimate was provided for each predator in our dataset. Therefore, the analysis of predator communities for our predictors should be interpreted as how often or not a predator has been reported in contributing to nest predation in different studies. Based on trials to balance computing time and model selection power, we ran the model over 10 trials to find the best fit.

Monitoring type and bird group were used as the predictor variables in the model to investigate potential differences in predator communities for real or artificial nests, or between different bird groups. Bird groups were combined in the same way as in the GLMM described above. Two categories in the bird group predictor, *other* and *not specified*, were removed from the analysis as being too vague to be useful. Predators with fewer than 10 total observations were removed to improve estimation of the latent variables. We also combined species of mustelids into one category named *mustelid* and all corvid species into one category named *corvid* to facilitate model convergence. A second model was fitted where all canids (fox species, domestic dog, Wolf *Canis lupus* and Coyote *Canis latrans*) were grouped into the

category *canids* to investigate differences in predator communities on a broader scale. Additionally, we removed the predators *hedgehog* (Erinaceinae) ($n = 12$) and *domestic cat* ($n = 19$) as they only appeared in studies on real nests, and on further inspection the study areas of these studies had never conducted artificial nest studies and the influence of these predators on artificial nests have never been tested and could lead to false results in the model. All modelling was done under R version 4.4.1 (R Core Team 2025).

RESULTS

Literature search and data extraction

Of the 355 included studies, most originated from Europe and North America (Fig. 1). North America made up 38.4% of all studies, while studies from Northern Europe and Great Britain made up 23% and 7% of the studies, respectively. There were particularly few studies from Asia and South America (two and seven, respectively; Fig. 1). Artificial nests were used as a method to study predation in 141 studies. In total, 124 of these only included artificial nests while 17 included both artificial and real nests. In total, 209 studies included only real nests.

Assessment of multiple types of evidence from around and inside the nest was the most common method to identify predator species ($n = 93$, Fig. 2). Evidence included bitemarks on plasticine eggs, eggshell remains and tracks in substrates around the nest. The second most common method of identification was the use of cameras to capture predation events ($n = 71$). In some cases, a combination of multiple identification methods was used (10 studies using evidence and camera traps and six using a combination of other methods; Fig. 2). Studies using camera traps had a smaller proportion of unidentified predators on average compared to studies only relying on physical evidence, but the difference was not significant (two-sided Welch t-test $P = 0.1$).

Waders were the most often studied bird group in the primary literature, followed by waterbirds and gamebirds (143, 89 and 49 studies, respectively). Forty-six studies did not specify what bird group they were focusing on, and half ($n = 28$) of these were artificial nest studies not attempting to mimic the nests of any real ground-nesting species.

There were some differences in main predators for each of the bird groups. For both waterbirds

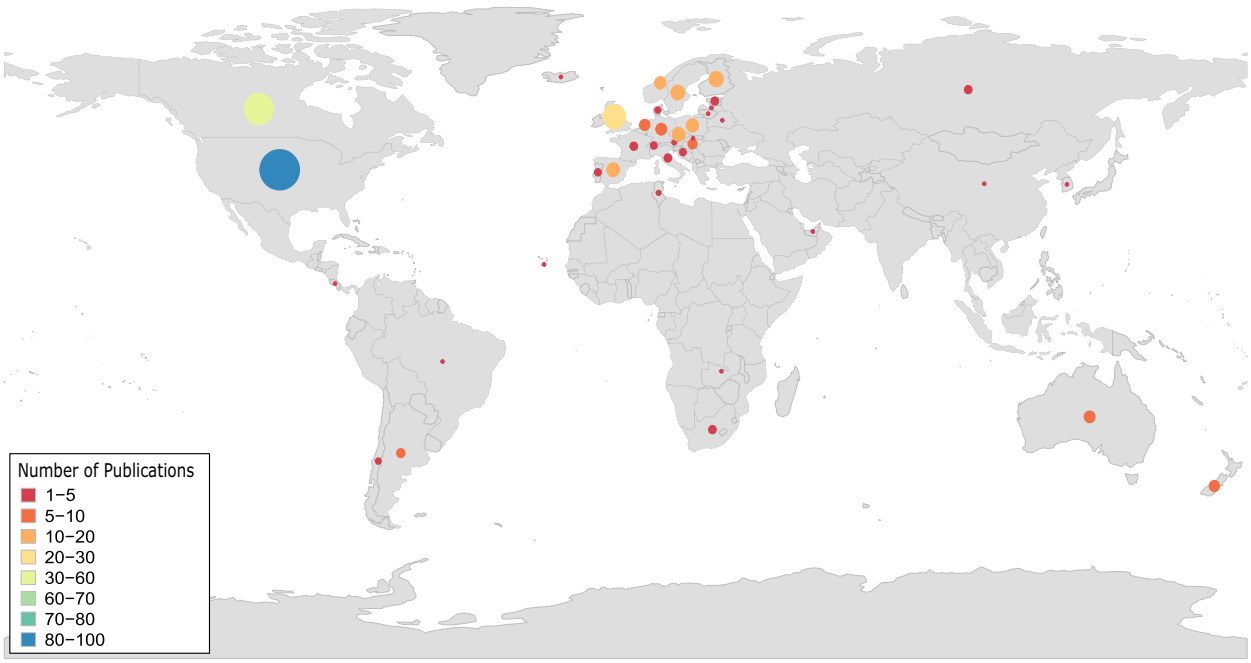

Figure 1. Number of studies originating from different countries. Most studies originated from North America and Europe, with very few studies from Africa, Asia and South America.

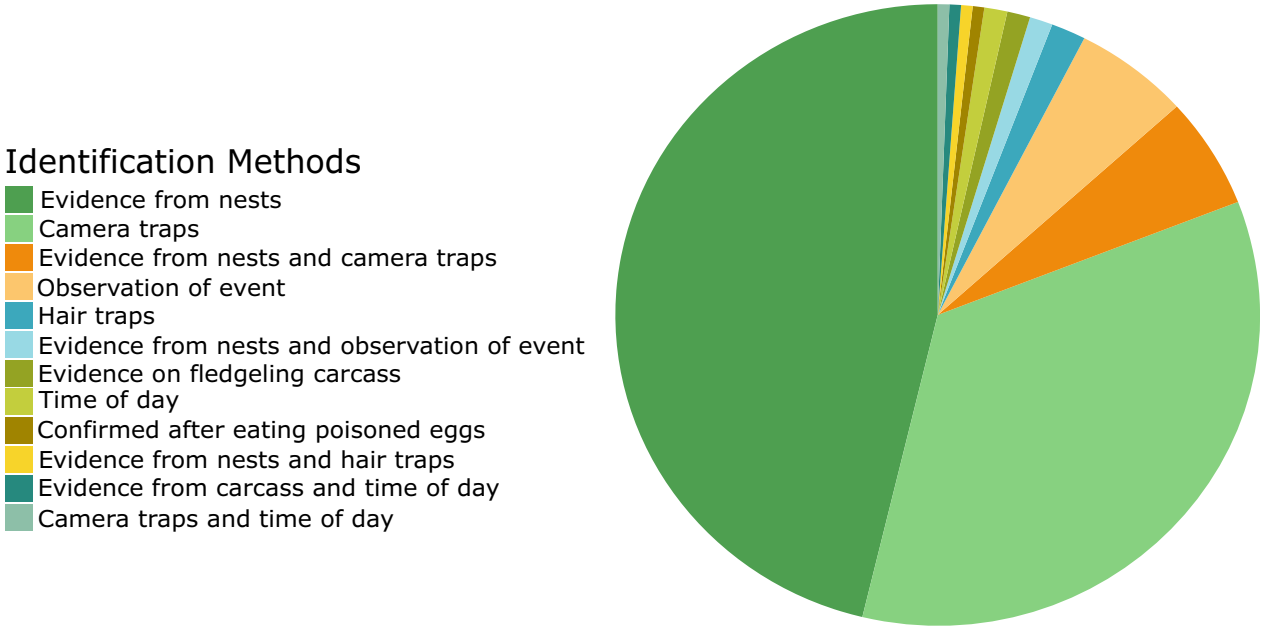

Figure 2. Identification methods used to identify predator species of ground-nesting bird nests and fledgelings. Evidence from nests includes bitemarks on plasticine eggs, eggshell remains, tracks in substrate, fledgeling remains and general signs of disturbance around the nest bowl.

and gamebirds, predators were most often unidentified across studies, with this being the second most frequent predator category for waders (26%, 69% and 33% of studies, respectively; Fig. 3). For waders, the main identified predator was Red Fox (34% of studies), but corvids and gulls were also described frequently (32% and 25% of studies). Red Fox was also an important predator for gamebirds and waterbirds, being the second and third most common predator described for these groups (63% and 24%, respectively). For passerines, rodents were most often identified (47% of studies). Waders and waterbirds had an overlapping predator community, with four of five of the most frequently described predators being the same groups (unidentified predators, Red Fox, gulls and unidentified avian predators). However, corvids seemed to be more important for waders, while American Mink was more important for waterbirds. American Mink was classified as an invasive species in 77% of all papers where the species was identified as a predator of waterbird nests.

Of all predator taxa, mammals were most often described in the literature (50.6% of all papers; Fig. 4). Avian predators were described in 35.8% of all papers, while unknown predators made up 10.1% (Fig. 4). Reptiles were described in just under 2.0% of all papers, while non-placental mammals, such as marsupials, and arthropods were described in <1.0%. Of the identified mammalian predators, Red Fox was the most common predator to be identified (19.8% of all studies; Fig. 4). Unidentified mammal species was the second most common predator category (16.5% of all studies; Fig. 4). For avian predators, unidentified bird species was the most frequent category, with corvids almost as frequent (23.5% and 18.1%, respectively, Fig. 4).

Variation in predation rates

GLMMs could only be fitted for nest predation. We only had 15 observations of fledgling predation, and we could therefore not proceed to fit a model for this response variable.

Predation rates and total failure rates had a positive covariance, and a correlation of 0.7. The mean predation rate across studies was 0.47 (sd: 0.25, CI: 0.44–0.50). The model with monitoring type (real vs artificial nests) as the predictor suggested that the type of monitoring used in a study affects predation rate of nests ($P < 0.01$, Table 2, Fig. 5). The model suggested that predation rate is lower overall for real nests compared to that of

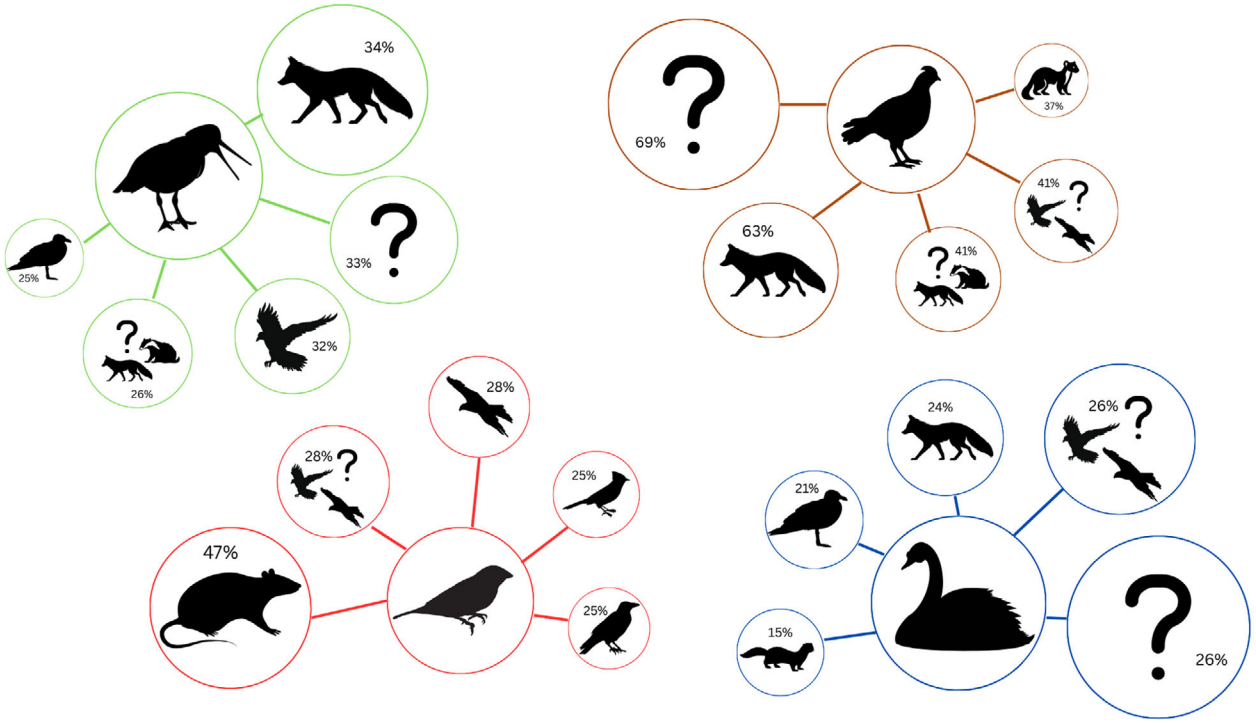

Figure 3. Bird groups included in the literature and their five most commonly described predators. Top-left waders, top-right gamebirds, bottom-left passerines and bottom-right waterbirds. The five most described predators for waders were Red Fox 34%, unidentified predators 33%, corvids 32%, unknown mammal 26% and gulls 25%. For gamebirds, the five most described predators were unidentified predators 69%, Red Fox 63%, unknown mammal 41%, unknown bird 41% and marten species 37%. For passerines, the five most identified predators were rodents 47%, unknown bird 28%, birds of prey 28%, jays 25% and crow species 25%. The five most described predators for waterbirds were unidentified predators 26%, unknown bird 26%, Red Fox 24%, gulls 21% and American Mink 15%.

artificial nests, with an odds-ratio of 0.46 (95% CI: 0.35–0.61) of real nests relative to artificial nests. The invasive species model did not find any detectable differences in overall predation rates ($P = 0.5$, Fig. 5). However, this could be due to a small sample size for invasive species ($n = 31$). There was no detectable difference in predation rates between bird groups (Table 2, Fig. 5).

Differences in predator communities

The GLLVM indicated that there were some differences in described predator communities between the different monitoring types, and bird groups (Fig. 6, Table S4). Passerines lacked sufficient data to be included in this analysis. Natural nest studies had less predation from corvids and unidentified avian predators, but slightly more predation from birds of prey, gulls, Raccoons (*Procyon lotor*) and Coyotes, compared to artificial nests (Fig. 6). Waders and waterbirds had significantly more predation from gulls, Arctic Fox *Vulpes lagopus* and birds of prey compared to the reference group, gamebirds (Fig. 6). Waterbirds also had slightly more predation from skuas *Stercorarius* sp. and Raccoon Dogs. Gamebirds had more predation from reptiles, Boar *Sus scrofa*, rodents and mustelids compared to waders and waterbirds. Gamebirds also had more predation from Coyotes and Raccoons compared to waders, and more predation from Red Fox than did waterbirds.

Proposed factors for reducing predation rates

The most common method tested for reducing predation was the use of barriers around the nests to hinder predator access (Fig. 7). Barriers included nest fencing, restricting ground predators and cages which restrict access to all predators.

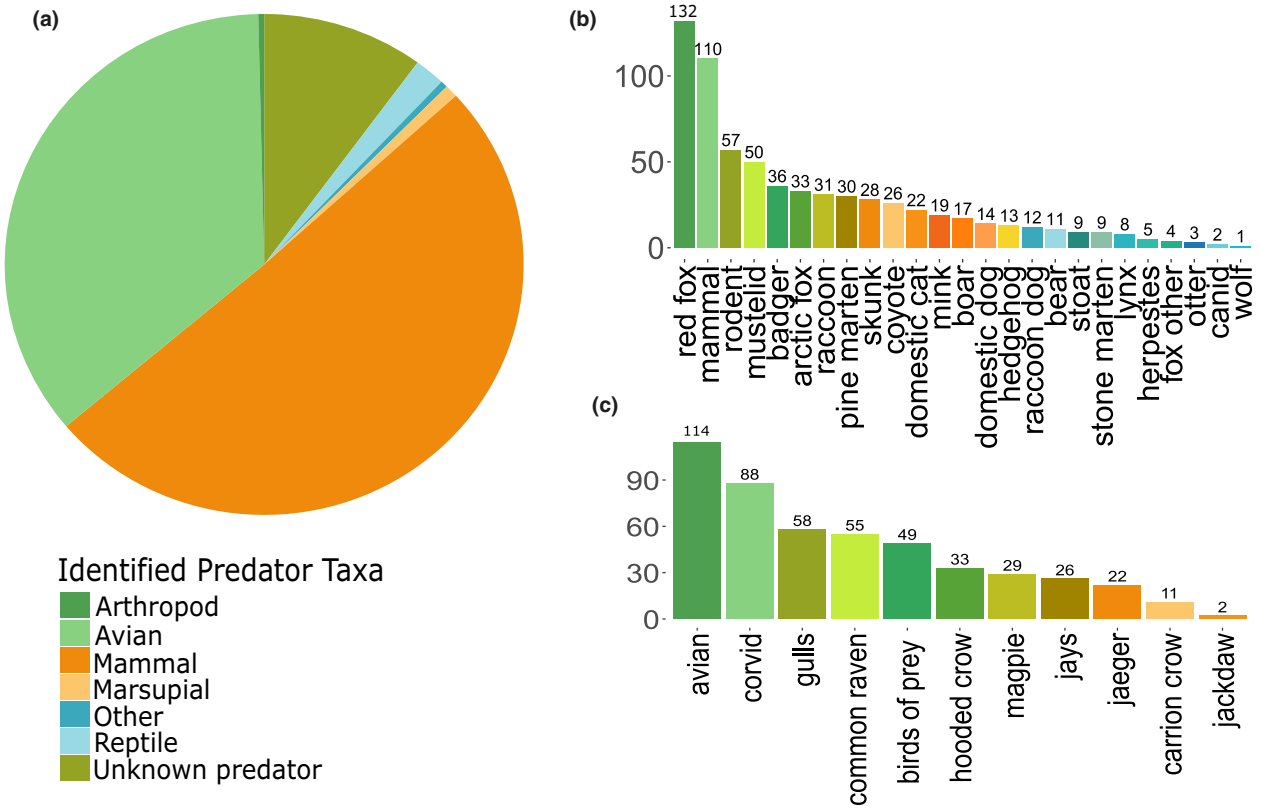

Figure 4. (a) Identified predator taxa in the literature. Avian predators were described in 35.8% of papers, mammals in 50.6% of papers, reptiles in 1.9% of papers, marsupials in 0.8% of papers and arthropods in 0.4% of papers. Other species, such as livestock, were described in 0.4% of papers. In total, 10.1% of papers reported not being able to identify some or all of the predators. (b) Identified mammals described in studies. (c) Identified avian predators described in studies. The *y*-axis on bar-plots show number of papers describing predation of predator species. Numbers above bars indicate total number of papers where predators were identified.

Table 2. Predation rate (odds-ratio), lower confidence limit (2.5%), upper confidence limit (97.5%), *P*-value, R^2 conditional and R^2 marginal for all three GLMM's.

Models	Covariate	Odds ratio	2.50%	97.50%	*P*-value	R^2c	R^2m
Predation rate ~ monitoring type	Intercept	1.5	1.21	1.87	0.004		
	Real nests	0.46	0.35	0.61	>>0.01	0.83	0.17
Predation rate ~ invasive species	Intercept	0.96	0.82	1.14	0.92		
	Invasive species	1.17	0.74	1.84	0.5	0.8	0.003
Predation rate ~ bird type	Intercept	0.91	0.5	1.66	0.78	0.8	0.03
	Passerine	0.73	0.33	1.58	0.42		
	Wader	0.75	0.39	1.43	0.38		
	Waterbird	0.56	0.27	1.16	0.12		

The use of barriers in experiments to reduce predation was almost exclusively used in wader studies. Reducing predator density was almost as common an experiment to reduce predation as barriers and was more evenly distributed among studies of different bird groups. Most experiments used lethal control as a method to manipulate predator densities. Only one study tested predator aversion as a method to reduce predation. The experiment consisted of supplying predators with

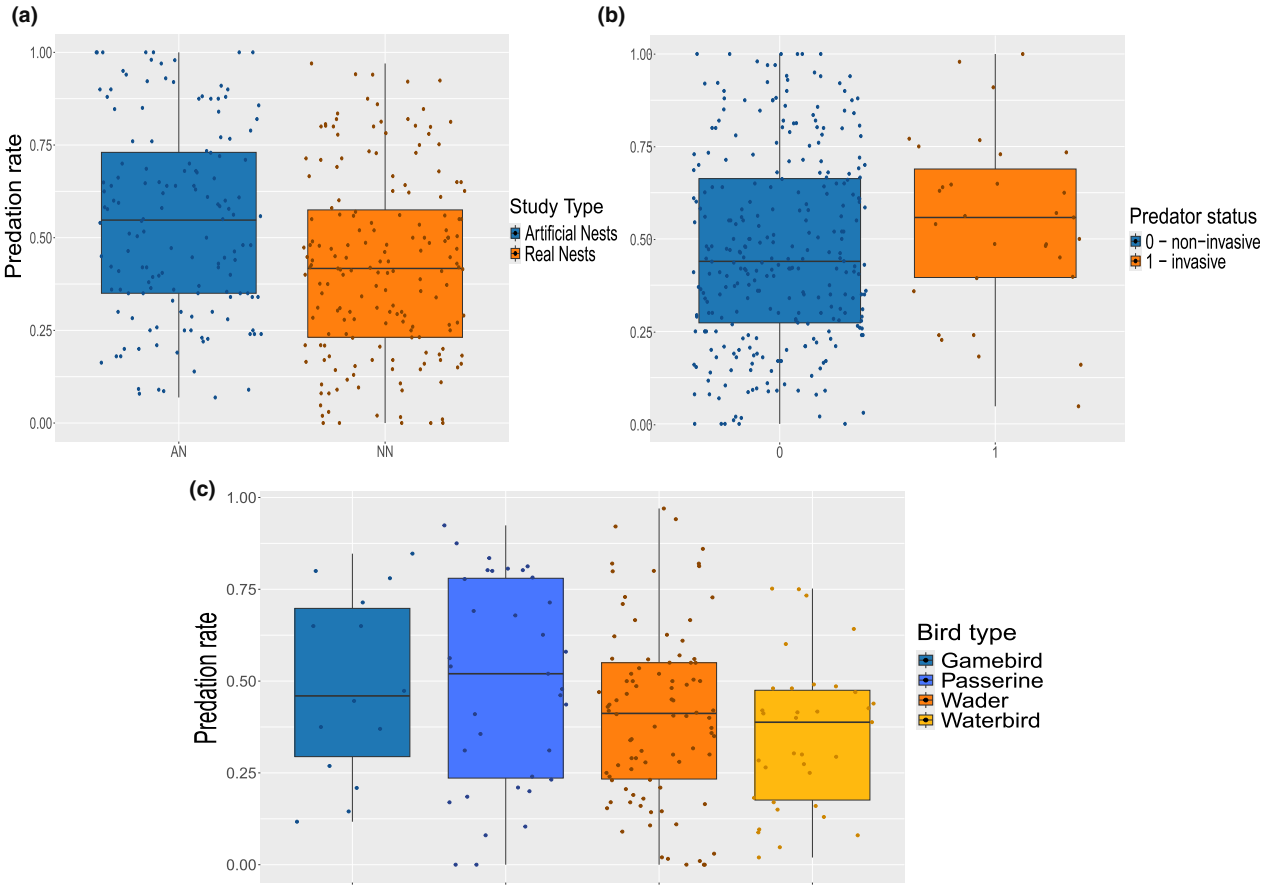

Figure 5. Results from the GLMMs. Predation rate was fitted as the response in all models. (a) Variation in predation rates between studies using real and artificial nests. (b) Variation in predation rates between studies with and without invasive species. (c) Variation in predation rates between bird groups: gamebirds, passerines, waders and waterbirds.

eggs injected with foul tasting substances to train them to avoid eggs.

DISCUSSION

Predation is a common but challenging focus of study of ground-nesting birds because methodological variations can affect results, especially due to differences between studies using real and artificial nests. This is even true for the predator communities, where differences existed depending on the monitoring (real vs artificial nests) or the identification method (camera traps, nest evidence) used. Even though we could not find any differences in overall predation rates between bird groups, there were differences and similarities in predator communities across studies that potentially reflect similarities in nesting ecology for some of the bird groups.

Identifying predators of ground-nesting birds

'Unidentified predators' were most often described for both gamebirds and waterbirds, and second most often for waders, highlighting the prevailing problem of identifying nest predators for ground-nesting birds. Of all the identification methods used, cameras had the lowest proportion of unidentified predators, although the mean difference in unidentified predators between studies using camera traps and physical evidence was not significant. Live cameras and camera traps record predators at the nest and therefore capture the event of predation (barring any malfunction). A recent review of predator identity of nest predators in the UK using only camera studies to identify predators found that as little as 1.6% of predators were unidentified for waders (Barton *et al.* 2025). Most

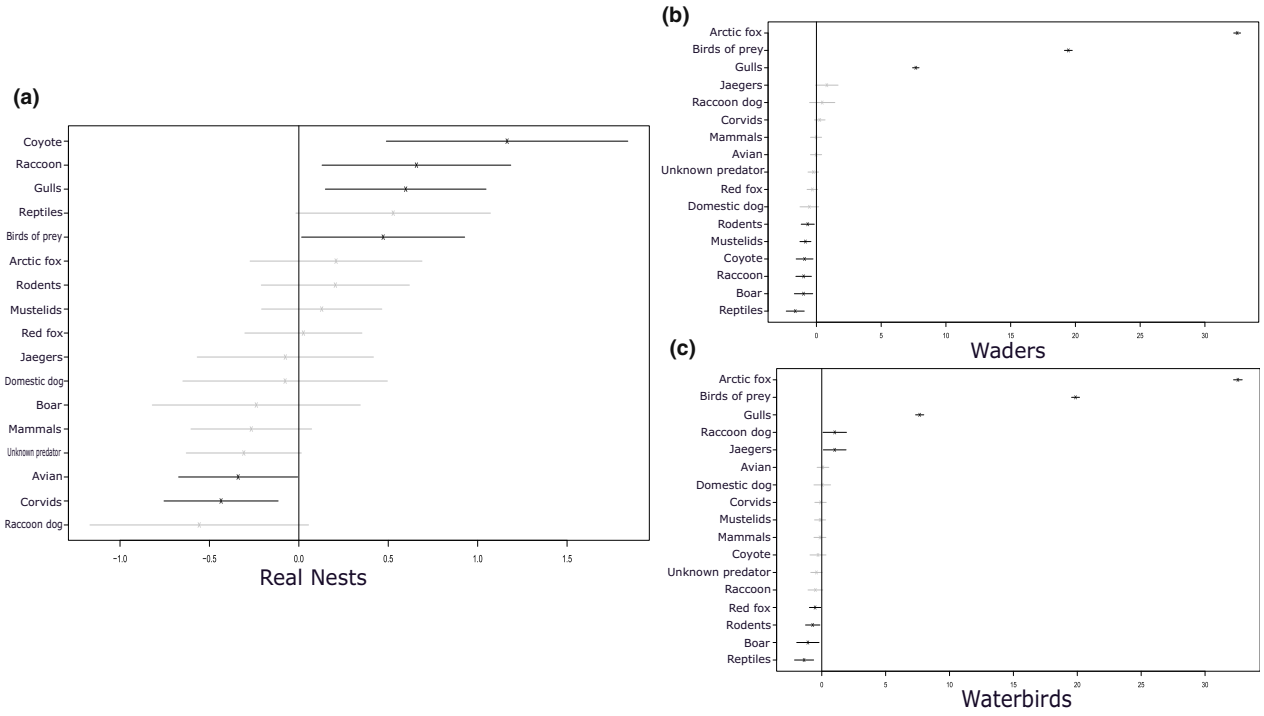

Figure 6. Coefficient plots showing results from GLLVM. Results from the coefficient plots should be interpreted as the differences between the reference category and the other category of the predictor. Statistically significant results are highlighted as black estimates and confidence intervals, grey estimates indicate non-significant result. Predator species are represented on the *y*-axis. The *x*-axis is shown in units of standard deviations. (a) Differences in described predators for studies using real and artificial nests. To produce the coefficient plot, artificial nests from the monitoring type predictor were used as reference. (b) Differences in described predators for waders and reference group gamebirds. (c) Differences in described predators for waterbirds and reference group gamebirds.

instances where predation was unknown were due to camera failure, and so the method seems reliable as long as equipment is functional.

The large proportion of unidentified predators (‘*unknown*’, ‘*avian*’, ‘*mammal*’) in all the bird groups might be due to the use of physical evidence as an identification method alone. Avian predators in particular had a high proportion of records described as simply ‘avian predation’, or records only describing general categories such as ‘*corvid*’. This could be due to avian predators leaving fewer and less distinct signs of predation. Specific metrics of bitemarks are commonly used to classify mammalian predation (Lyver 2000). However, such metrics are more uncertain for bird species as they only leave incisions on wax and plasticine eggs (Moller 1989, Purger *et al.* 2004). Hair traps can be used to identify mammals, but none of the studies using this identification method mentioned also collecting feathers or other physical traces of birds (Pasitschniak-Arts & Messier 1996, Cooper & Ginnett 2000). Track boards and similar methods for recording tracks again seem more common as an identification method for mammals as they will have to access nests on the ground, while avian predators might simply fly directly to the nests, potentially not leaving any tracks. There might therefore be a bias in the literature towards identifying mammals because of the greater number of established methods for identifying this group. In many cases, the magnitude of avian predation is similar to that of mammal predation, and correctly identifying the species of avian predators is therefore important to better understand how they affect ground-nesting bird populations.

In the absence of camera traps, physical evidence remains useful when identifying predators. In many cases it is not feasible to use camera traps because of the costs of covering each nest with a camera, or because the camera causes disturbance to incubating parents. Cameras cannot be easily

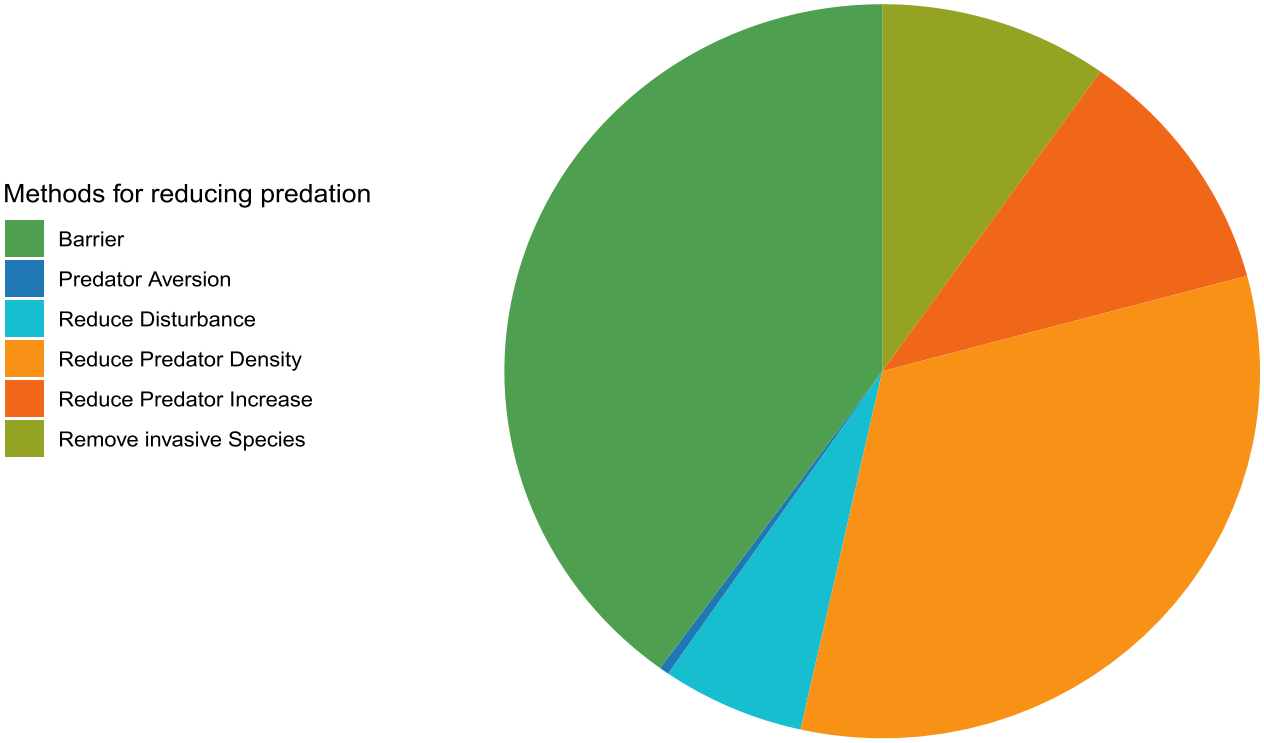

Figure 7. Proposed methods for reducing predation for ground-nesting birds. Most methods were explored in studies relating to waders, waterbirds and gamebirds. The most common method described for reducing predation involved reducing predator density or increasing it through various methods (41%). The second most common method described was the use of physical barriers to restrict predator access to nests (40%). Removing invasive species was described in 11%. Reducing disturbance was used as a method in 8% of papers, and predator aversion in just one study.

used for identification of predators on fledglings since they move around in the landscape. If the remains of fledglings are recovered fast enough, identification of predators may be narrowed down (Klaussen, pers. observ.). There is also a potential for using DNA analysis of fledgling remains to identify predators (Hopken *et al.* 2016). Some DNA, from saliva, skin, fur or feathers, is likely to be left on remains and can be used to identify predators if enough DNA can be recovered.

Variation in predation rates

Predation rates and total failure rates had a positive covariance and a moderate correlation. Nests can be lost to other causes, such as flooding and trampling, and it is therefore possible that studies reporting low predation rates lost nests to other causes. However, our results suggest that the predation rate is reflective of the total failure rate and that in instances of low predation rates, nest success might usually be higher.

Artificial versus real nest studies

The model indicated that artificial nests experience significantly more predation compared to real nests, supporting the findings of studies examining the use of artificial nests in local systems (Ortega *et al.* 1998, Burke *et al.* 2004).

An important consideration is whether increased predation rates of artificial nests could be explained by nest properties, such as absence of adult birds and poorer nest crypsis than real nests. These nest properties cannot be simulated for artificial nests, and predators are therefore presumably more likely to detect and predate artificial nests. However, not all predator species can be successfully deterred by defending adults. Larger mammal species impose too great a risk to the incubating adult, causing the adults to leave the nest when approached (Parrett *et al.* 2023a, 2023b). It is therefore possible that predation of artificial nests is more realistic for some predator groups. The results from the GLLVM indicated that some avian predators including corvids were observed more often as predators of

artificial nests than real nests, while there was no significant difference for most of the common mammalian nest predators.

It is possible that the higher avian predation is a result of artificial nests being a more available food source when defending parents are not present. Many corvid species cache food and can remember locations of food supplies and often revisit the same areas when foraging (Fjeld & Sonerud 1988, Bennett 1993). Artificial nests are often placed along transects or in clusters to help with relocation (Sargent *et al.* 1998, Klausen *et al.* 2010) and, as a result, corvids may be able to readily locate and revisit such nests.

It is also possible that artificial nests are more readily predated by corvids because these predators often explore novel objects in their environment (Miller *et al.* 2022). Objects associated with placement of artificial nests, such as camera traps and nest markers, might attract corvids and alert them to the high density of artificial nests (Henden *et al.* 2025).

Some predator species and groups were identified more often in real nest studies. In contrast to corvids, raptors and gulls were significantly more mentioned in real nest studies. Gulls and birds of prey have been described predating nests of waders and waterbirds, potentially because they nest in similar habitats to these predators or in proximity to the feeding sites of the predators (Bêty *et al.* 2001, Jackson 2001, Bentzen *et al.* 2017). Gulls and birds of prey might be less interested in human activity associated with artificial nest studies compared to that of corvids and therefore do not visit artificial nest sites as often. If artificial nests are being used to investigate the predator community in a system, the experimental design and its potential impact on the predators attracted to the nests should be accounted for. Using artificial nests can be useful for studying patterns and mechanisms of predation in general but should not be used to describe these patterns for real species.

The effect of bird group on ground-nest predation rates

Type of nest monitoring was the only significant predictor in any of the models; we did not find any effects of bird group on predation rates. It is possible that no pattern was detected because of the broad categories used in the model. Differences in size and the degree of aggressive nest defence exists within groups, especially for waders and waterfowl, where larger birds such as geese, swans and larger bodied waders such as curlews and lapwing, often chase or mob predators (Kis *et al.* 2000, Anderson *et al.* 2019, Calvert *et al.* 2019). It is therefore possible that differences in predation rates are better described by the size of the species or the nest defence tactic it uses. This is apparent when comparing passerines to the other groups with larger average sizes. For passerines, smaller predators such as rodents, smaller corvids such as jays and reptiles were more common predators, potentially suggesting that smaller predators have better access to nests.

Main predators of ground-nesting birds

We could not fit models to investigate predation of fledglings. Predation rates and patterns of predation on fledglings are much less studied than nest predation. Investigating causes for mortality and number of predation events is generally more difficult for fledglings because they are mobile and can be hard to relocate. It can also be difficult to obtain accurate estimates of predation because many individuals are never resighted, and the cause of death cannot be confirmed. This is usually because not all individuals can be fitted with transmitters to aid relocation, and because predators often leave few, if any, remains, making it difficult to determine the cause of death.

An effort should therefore be made to advance the methods for identifying and quantifying fledgling predation. An alternative to using manual radiotelemetry to locate tagged chicks is the use of automatic radiotracking stations (ARTS) which continuously record locations and can therefore provide more accurate movement patterns and timings of predation for chicks (Mason *et al.* 2018). However, ARTS can be costly compared to the traditional manual chick finding, which makes it less accessible to smaller projects. An alternative manual tracking method is the use of trained dogs. Trained dogs are being used to locate vulnerable bird species in New Zealand and to locate bumblebee nests (Robertson & Fraser 2009, Liczner *et al.* 2021). Using trained dogs to locate chicks would require access to trained dogs and ethical considerations around using dogs in habitats with vulnerable wader species.

Compared to gamebirds, waders and waterbirds had significantly more predation from Arctic

Foxes, gulls and birds of prey. However, only gulls were described as one of the top five predators in the literature for waders and waterbirds (Fig. 3). This indicates that Arctic Fox and birds of prey are not one of the main predators for these bird groups overall but are more important predators for these birds compared to gamebirds. In contrast, gulls were one of the main predators described for waders and waterbirds but not for gamebirds. Many waterbirds and waders nest in similar habitats to several gull species, and gulls are often observed visiting nesting grounds of waders and waterfowl (Jackson 2001, Andersson & Waldeck 2006, Parrett *et al.* 2023a, 2023b). The significantly higher occurrences of Arctic Fox and bird of prey predation could be due to these predators often visiting areas of high wader and waterfowl nest densities in arctic environments. Indeed, many of the studies mentioned alternative prey hypotheses as one of the explanations for high predation rates of arctic wader and waterfowl systems (Stickney 1991, Ebbinge & Spaans 2002, Eide *et al.* 2005, Reiter & Andersen 2011). Significantly, more predation from skuas/jaegers according to the GLLVM further supports this.

We did not find any suggestions that birds of prey are an important predator for gamebird nests. The importance of birds of prey as a predator of adult gamebird populations has long been discussed, especially in Europe (Valkama *et al.* 2005, Park *et al.* 2008). We found that mammals were the most important nest predators of gamebirds, especially mustelids which were significantly more common as nest predators for gamebirds than for the other groups (Fig. 6). Boar, Raccoons and Coyotes were also significantly more common predators of gamebirds, noting that many gamebird studies originated from grassland systems in North America, where these species are common nest predators. The lack of evidence of birds of prey as an important nest predator to gamebirds in this study could be due to studies to a large extent focusing on adult predation, while egg and fledgling predation is less studied.

Red Fox was described as a common predator for all bird groups, and this species was also the mammal most often identified as a nest predator. Waders and gamebirds especially had high levels of Red Fox predation, for which the species was the most and second most described predator respectively. Our results therefore confirm previous findings (Green & Etheridge 1999, Harding *et al.* 2001, Barton *et al.* 2025) that the Red Fox is an important contributor to nest predation, not just at a local scale but across ground-nesting bird groups covering a large geographical range, thus highlighting Red Fox predation as a global issue for ground-nesting birds.

For passerines, four of the five most described predators were avian. Jays (Eurasian Jay *Garrulus glandarius*, Blue Jay *Cyanocitta cristata* and Steller's Jay *Cyanocitta stelleri*) were described as a predator of passerine nests in 25% of all cases, which is a similar rate to that reported by Barton *et al.* (2025), suggesting that jays substantially contribute to predation of passerine nests across Europe and North America. Rodents were also frequently described as a predator of passerine nests. High levels of rodent predation could be due to passerine eggs being more available to small rodents, both because of small egg sizes and adult passerines being too small to deter certain rodents. Indeed, both waterbirds and waders had significantly less predation from rodents compared to gamebirds in the GLLVM, suggesting that nests of these bird groups are not suitable food sources for rodents. We were, however, not able to include passerines in the GLLVM due to lack of data and could therefore not examine differences in predator communities statistically for this bird group. Studies of nest predation in passerines are common, but these studies identify the predator community less often than studies of the other bird groups. Not reporting the predator community could be due to passerine studies not being able to identify predators of nests and fledglings as often as studies focusing on other groups (Barton *et al.* 2025).

For all bird groups, the predators described were typically generalist meso-predators. Many generalist predator species have increased over recent decades, attributed to a range of potential drivers including meso-predator release, increased urbanization and intensification of agriculture, and gamebird releases (Andren 1992, Prugh *et al.* 2009, Gordon *et al.* 2017, Benmazouz *et al.* 2021, Madden *et al.* 2023). It is therefore likely that high predation rates are linked to high densities of these predators (Niemczynowicz *et al.* 2017, Bravo *et al.* 2022, Baines *et al.* 2023). Comparing systems with varying degrees of urbanization and intensified agriculture to investigate to what degree these factors influence predation rates and predator communities globally would therefore be useful.

Invasive species did not contribute to higher predation rates according to our models. Ground-nesting birds not being able to adapt to the increased threat of invasive predator species caused by high levels of naivety because of a lack of co-evolutionary history has been a serious threat to many species of ground-nesting birds (Clode & Macdonald 2002, Schuettler *et al.* 2009, Arcilla *et al.* 2015). This has especially been an issue when mammalian predators have been introduced to island bird populations. We also found that the American Mink was one of the most commonly described predators for waterbirds, and in most studies, this was outside the species' native range, highlighting the importance of this invasive species as a predator of ground nests. It is, however, possible that this lack of effect is dependent on the native predator community of the ground-nesting birds being studied. Many ground-nesting birds, other than those on isolated islands, naturally experience predation from mammals. These species might therefore more easily adapt to predation from new mammalian predators relative to more naïve populations. A stronger effect of invasive species on predation rates might therefore be more obvious if studies on isolated populations with no or few natural mammalian predators and those naturally experiencing mammalian predation were separated. Several of the invasive species accounted for different percentages of total predation in many of the studies. Red Fox and rodents were identified as predators on isolated islands to a greater extent than American Mink and Raccoon Dog in Europe, suggesting that invasive predators account for a greater proportion of total predation in isolated island populations. Invasive predators might also compete with native predators and therefore reduce predation from native predators without changing the overall predation rate (Henry 1969). There is also the possibility that the studies could not identify predation from invasive species because of the problems with identifying predators from evidence at the nests alone, as discussed above. It is therefore possible that the non-significant effect of invasive predators is caused by studies being misclassified as not having invasive predators present. There were also very few studies that reported invasive species, and so the result might also be influenced by small sample sizes ($n = 31$). A few studies that described invasive species did not provide estimates of predation and could therefore not be included in the model.

Proposed methods to reduce nest predation

Several methods are being explored in the attempt to decrease predation rates of nests and fledglings (Fig. 7). The most common experimental methods included physically restricting predator access using fencing and cages and reducing predator densities or rates of predator population increase. Studies examining the effect of physical barriers were most common for waders, reflecting the ongoing effort to reduce wader nest predation (Estelle *et al.* 1996, Barber *et al.* 2010, Black *et al.* 2023). Many studies reported reduced nest predation when fencing and cages were deployed. However, the use of barriers did not, in most cases, increase fledging rate. It is therefore possible that the use of barriers only delays predation.

Some studies also considered the effect of reducing human disturbance, especially in coastal breeding species. Human use of nesting habitats during the breeding season can have a negative impact on nest survival because increased human activity increases the time adult birds spend away from the nest and fledglings (Ruhlen *et al.* 2003, Faillace & Smith 2016). Most studies suggested that restrictions to human use of nesting habitats during the nesting season would be favourable, but this is often difficult to implement as nesting areas overlap with areas of high recreational or commercial value.

The removal of predators through organized predator control was most common for waders and gamebirds. Many wader and gamebird species nest in habitats and regions where predator densities have increased drastically (Andren 1992, Roos *et al.* 2018). In particular, meso-predators such as the Red Fox and corvids have increased and were also described most frequently as nest predators of these birds. However, many of these studies only reported a temporary decrease in nest predation, and predator densities and predation rates increased if predator control ceased. This suggests that predator control, especially of generalist predators, is not a long-term solution. Researching and identifying long-term solutions should therefore be prioritized in future studies of ground-nesting bird nest predation. Understanding why predator densities sustain themselves at high levels, and how they behave and move in favourable habitats such as urbanized and agricultural areas would be helpful for identifying long-term solutions in ground-nesting bird conservation.

Recommendations for future studies

Several literature limitations constrained our meta-analysis. Many artificial nest studies did not attempt to mimic real nests or gave very vague descriptions of what species they were mimicking, making it impossible to use these estimates to compare differences within bird groups. To properly assess the difference between real and artificial nests, trials with both methods should be carried out in the same systems over the same time periods to have comparable data. However, how closely artificial nests can resemble real nests is likely to be different for different bird groups. It is, for example, possible to use duck eggs or pheasant eggs to closely mimic certain waterfowl and gamebirds, but similar readily available alternatives are less common for waders or passerines. How predation was assessed differed between studies, which also restricted the number of samples used in the meta-analysis. Many studies used direct measurements of predation, such as total predation rates, daily predation rates or percentage of nests predated, which all reflect similar measurements and can therefore be transformed and compared. However, many studies used estimates of survival of nests when discussing predation. Since survival estimates cannot be taken to be the inverse of predation estimates, we were not able to include these studies in our analysis. Direct measurements of predation together with nest survival estimates should be provided whenever possible.

Many studies also failed to identify predators or the relative contribution of each predator to nest predation. Predation due to mammals and birds could be explained by quite different mechanisms, and so knowing the identity of the predators is helpful for understanding what is causing nest predation. Focusing more on understanding the ecology of predators in the system rather than just monitoring nests and trying to identify the predators should therefore be considered for future studies.

We thank Bournemouth University and WWT for funding this project. We also thank Audun Rugstad for the helpful advice with the GLLVM. We also thank the reviewers and the editor who provided valuable feedback to the systematic review.

AUTHOR CONTRIBUTIONS

Kevin A. Wood: Writing – review and editing; supervision; methodology. **Emilie A. Hardouin:** Writing – review and editing; supervision. **Mari D. Klaussen:** Writing – original draft; formal analysis; conceptualization; data curation; methodology; visualization; software; writing – review and editing. **Alex Nicol-Harper:** Writing – review and editing; supervision; methodology. **Anita Diaz Isla:** Supervision; writing – review and editing. **Richard A. Stillman:** Supervision; writing – review and editing; conceptualization.

FUNDING

This study was supported by Bournemouth University and Wildfowl and Wetlands Trust.

CONFLICT OF INTEREST

The authors declare that they have no conflicts of interest.

ETHICAL NOTE

None.

DATA AVAILABILITY STATEMENT

All data and code used in our analyses can be accessed via Figshare (10.6084/m9.figshare.30601796).

REFERENCES

Aharon-Rotman, Y., Soloviev, M., Minton, C., Tomkovich, P., Hassell, C. & Klaassen, M. 2015. Loss of periodicity in breeding success of waders links to changes in lemming cycles in Arctic ecosystems. *Oikos* **124**: 861–870.

Albrecht, T. & Klvaňa, P. 2004. Nest crypsis, reproductive value of a clutch and escape decisions in incubating female mallards *Anas platyrhynchos*. *Ethology* **110**: 603–613.

Anderson, H.B., Fuglei, E., Madsen, J. & van der Wal, R. 2019. High-Arctic nesting geese occupying less favourable nest sites are more vulnerable to predation. *Polar Res.* **38**. https://doi.org/10.33265/polar.v38.3352

Andersson, M. & Waldeck, P. 2006. Reproductive tactics under severe egg predation: An Eider's dilemma. *Oecologia* **148**: 350–355. https://doi.org/10.1007/s00442-006-0374-7

Andren, H. 1992. Corvid density and nest predation in relation to forest fragmentation: A landscape perspective. *Ecology* **73**: 794–804.

Arbeiter, S. & Franke, E. 2018. Predation risk of artificial ground nests in managed floodplain meadows. *Acta Oecol.* **86**: 17–22.

Arcilla, N., Choi, C.-Y., Ozaki, K. & Lepczyk, C.A. 2015. Invasive species and Pacific Island bird conservation: A selective review of recent research featuring case studies of

Swinhoe's storm petrel and the Okinawa and Guam rail. *J. Ornithol.* **156**: 199–207.

Baines, D., Fletcher, K., Hesford, N., Newborn, D. & Richardson, M. 2023. Lethal predator control on UK moorland is associated with high breeding success of curlew, a globally near-threatened wader. *Eur. J. Wildl. Res.* **69**: 6. https://doi.org/10.1007/s10344-022-01631-5

Barber, C., Nowak, A., Tulk, K. & Thomas, L. 2010. Predator Exclosures enhance reproductive success but increase adult mortality of piping plovers (*Charadrius melodus*). *Avian Conserv. Ecol.* **5**: 6. https://doi.org/10.5751/ACE-00419-050206

Barton, M.G., Conway, G.J., Henderson, I.G., Baddams, J., Balchin, C.S., Brides, K., Butcher, N., Cameron, T.C., Davis, T., Eyre, J., Foster, R., Gornall, D., Kallamballi, N.K., Laurie, P., Nixon, A., Noyes, P., Parish, D.M.B., Samson, L., Smart, J., Wilde, N., Wright, M.A. & Dolman, P.M. 2025. Meta-analysis of predator identity in nest-camera studies in the British Islands. *Ibis* **168**: 42–62.

Benmazouz, I., Jokimäki, J., Lengyel, S., Juhász, L., Kaisanlahti-Jokimäki, M.-L., Kardos, G., Paládi, P. & Kövér, L. 2021. Corvids in urban environments: A systematic global literature review. *Animals* **11**: 3226. https://doi.org/10.3390/ani11113226

Bennett, A.T.D. 1993. Spatial memory in a food storing corvid. *J. Comp. Physiol. A Neuroethol. Sens. Neural Behav. Physiol.* **173**: 193–207.

Bentzen, R., Dinsmore, S., Liebezeit, J., Robards, M., Streever, B. & Zack, S. 2017. Assessing development impacts on Arctic nesting birds using real and artificial nests. *Polar Biol.* **40**: 1527–1536.

Bêty, J., Gauthier, G., Giroux, J.-F. & Korpimäki, E. 2001. Are goose nesting success and lemming cycles linked? Interplay between nest density and predators. *Oikos* **93**: 388–400.

Black, K.M., Karpanty, S.M., Robinson, S.G., Bellman, H.A., Walker, K.M., Catlin, D.H. & Fraser, J.D. 2023. Using GPS location data to assess red fox responses to predator Exclosure setup and hatching at shorebird nests. *Wildl. Soc. Bull* **47**: e4120. https://doi.org/10.1002/wsb.1420

Bocz, R., Szep, D., Witz, D., Ronczyk, L., Kurucz, K. & Purger, J.J. 2017. Human disturbances and predation on artificial ground nests across an urban gradient. *Anim. Biodivers. Conserv.* **40**: 153–157. https://doi.org/10.32800/abc.2017.40.0153

Bravo, C., Sarasa, M., Bretagnolle, V. & Pays, O. 2022. Detectability and predator strategy affect egg depredation rates: Implications for mitigating nest depredation in farmlands. *Sci. Total Environ.* **829**. https://doi.org/10.1016/j.scitotenv.2022.154558

Brookes, M.E., Kristensen, K., van Benthem, K.J., Magnusson, A., Berg, C.W., Nielsen, A., Skaug, H.J., Mächler, M. & Bolker, B.M. 2017. glmmTMB balances speed and flexibility among packages for zero-inflated generalized linear mixed modeling. *R J.* **9**: 378–400.

Brynychová, K., Sládeček, M., Pešková, L., Chajma, P., Firlová, V., Elhassan, E., Vozabulová, E., Janatová, V., Almuhery, A. & Šálek, M. 2022. Aggressiveness in a subtropical shorebird's nest defense is adjusted to the predator species and shared by conspecifics. *Aggress. Behav.* **48**: 475–486.

Burke, D.M., Elliott, K., Moore, L., Elliott, K., Moore, L., Dunford, W., Nol, E., Phillips, J., Holmes, S. & Freemark, K. 2004. Patterns of nest predation on artificial and natural nests in forests. *Conserv. Biol.* **18**: 381–388.

Calvert, A.M., Alisauskas, R.T. & Kellett, D.K. 2019. Fitness heterogeneity in adult snow and Ross's geese: Survival is higher in females with brood patches. *Auk* **136**(3). https://doi.org/10.1093/auk/ukz027

Clode, D. & Macdonald, D.W. 2002. Invasive predators and the conservation of island birds: The case of American mink *Mustela vison* and terns *Sterna* spp. in the Western isles, Scotland. *Bird Study* **49**: 118–123.

Cooper, S.M. & Ginnett, T.F. 2000. Potential effects of supplemental feeding of deer on nest predation. *Wildl. Soc. Bull.* **28**: 660–666.

Côté, I.M., Curtis, P.S., Rothstein, H.R. & Stewart, G.B. 2013. Gathering Data: Searching Literature and Selection Criteria. In *Handbook of Meta-Analysis in Ecology and Evolution*. Princeton, NJ: Princeton University Press. https://doi.org/10.23943/princeton/9780691137285.003.0004

Ebbinge, B.S. & Spaans, B. 2002. How do Brent geese (*Branta b. bernicla*) cope with evil? Complex relationships between predators and prey; [Wie Gehen Ringelgänse (*Branta b. bernicla*) Mit Feinden um? Komplexe Räuber-Beute-Beziehungen]. *J. Ornithol.* **143**: 33–42. https://doi.org/10.1007/BF02465456

Eide, N.E., Eid, P.M., Prestrud, P. & Swenson, J.E. 2005. Dietary responses of Arctic foxes *Alopex lagopus* to changing prey availability across an Arctic landscape. *Wildl. Biol.* **11**: 6. https://doi.org/10.2981/0909-6396(2005)11%5B109:DROAFA%5D2.0.CO;2

Espie, R.H.M., James, P.C. & Brigham, R.M. 1998. The effects of flooding on piping plover *Charadrius melodus* reproductive success at Lake Diefenbaker, Saskatchewan, Canada. *Biol. Conserv.* **86**: 215–222.

Estelle, V.B., Mabee, T.J. & Farmer, A.H. 1996. Effectiveness of predator exclosures for pectoral sandpiper nests in Alaska. *J. Field Ornithol.* **67**: 447–452.

Faillace, C.A. & Smith, B.W. 2016. Incubating snowy plovers (*Charadrius nivosus*) exhibit site-specific patterns of disturbance from human activities. *Wildl. Res.* **43**: 288–297.

Fjeld, P.E. & Sonerud, G.A. 1988. Food caching, cache recovery, and the use of an egg Shell dump in hooded crows *Corvus corone cornix*. *Ornis Scand. (Scand. J. Ornithol.)* **19**: 268–274.

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. *J. Appl. Ecol.* **47**: 263–272.

Gordon, C.E., Moore, B.D. & Letnic, M. 2017. Temporal and spatial trends in the abundances of an apex predator, introduced mesopredator and ground-nesting bird are consistent with the mesopredator release hypothesis. *Biodivers. Conserv.* **26**: 1445–1462.

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*. *J. Appl. Ecol.* **36**: 472–483.

Harding, E.K., Doak, D.F. & Albertson, J.D. 2001. Evaluating the effectiveness of predator control: The non-native red fox as a case study. *Conserv. Biol.* **15**: 1114–1122.

Hartig, F. 2024. *DHARMa: Residual Diagnostics for Hierarchical (Multi-Level/Mixed) Regression Models*. V. R package verion 0.4.7. Released. https://CRAN.R-project.org/package=DHARMa.

Henden, J.-A., Ims, R.A. & Strømeng, M.A. 2025. Trail cameras can greatly inflate nest predation rates. *J. Wildl. Manage.* **89**: e22684.

Henry, V. 1969. Predation on dummy nests of ground-nesting birds in southern Appalachians. *J. Wildl. Manage.* **33**: 169–172. https://doi.org/10.2307/3799666

Hopken, M.W., Orning, E.K., Young, J.K. & Piaggio, A.J. 2016. Molecular forensics in avian conservation: A DNA-based approach for identifying mammalian predators of ground-nesting birds and eggs ecology. *BMC. Res. Notes* **9**: 14. https://doi.org/10.1186/s13104-015-1797-1

Jackson, D.B. 2001. Experimental removal of introduced hedgehogs improves wader nest success in the Western isles, Scotland. *J. Appl. Ecol.* **38**: 802–812.

Jellesmark, S., Ausden, M., Blackburn, T.M., Hoffmann, M., McRae, L., Visconti, P. & Gregory, R.D. 2023. The effect of conservation interventions on the abundance of breeding waders within nature reserves in the United Kingdom. *Ibis* **165**: 69–81.

Kis, J., Liker, A. & Szekely, T. 2000. Nest defence by lapwings: Observations on natural behaviour and an experiment. *Ardea* **88**: 155–163.

Klausen, K.B., Pedersen, Å.Ø., Yoccoz, N.G. & Ims, R.A. 2010. Prevalence of nest predators in a sub-Arctic ecosystem. *Eur. J. Wildl. Res.* **56**: 221–232.

Laidlaw, R.A., Smart, J., Ewing, H., Franks, S.E., Belting, H., Donaldson, L., Hilton, G.M., Hiscock, N., Hoodless, A.N., Hughes, B., Jarrett, N.S., Kentie, R., Kleyheeg, E., Lee, R., Roodbergen, M., Scott, D.M., Short, M.J., Syroechkovskiy, E.E., Teunissen, W., Ward, H., White, G. & Gill, J.A. 2021. Predator management for breeding waders: A review of current evidence and priority knowledge gaps. *Wader Study* **128**: 44–55. https://doi.org/10.18194/ws.00220

Lanszki, J. 2005. Diet composition of red fox during rearing in a moor: A case study. *Folia Zool.* **54**: 213–216.

Larsen, T. 1991. Anti-predator behaviour and mating systems in waders: Aggressive nest defence selects for monogamy. *Anim. Behav.* **41**: 1057–1062.

Liczner, A.R., MacPhail, V.J., Woollett, D.A., Richards, N.L. & Colla, S.R. 2021. Training and usage of detection dogs to better understand bumble bee nesting habitat: Challenges and opportunities. *PLoS One* **16**: 1–18.

Lüdecke, D., Ben-Shachar, M., Patil, I., Waggoner, P. & Makowski, D. 2021. Performance: An R package for assessment, comparison and testing of statistical models. *J. Open Source Softw.* **6**: 31–39.

Lyver, P.O'B. 2000. Identifying mammalian predators from bite Marks: A tool for focusing wildlife protection. *Mammal Rev.* **30**: 31–44.

Macdonald, M.A. & Bolton, M. 2008. Predation on wader nests in Europe. *Ibis* **150**(Suppl. 1): 54–73.

Madden, J.R., Buckley, R. & Ratcliffe, S. 2023. Large-scale correlations between gamebird release and management and animal biodiversity metrics in lowland Great Britain. *Ecol. Evol.* **13**: e10059. https://doi.org/10.1002/ece3.10059

Mandema, F.S., Tinbergen, J.M., Ens, B.J. & Bakker, J.P. 2013. Livestock grazing and trampling of birds' nests: An experiment using artificial nests. *J. Coast. Conserv.* **17**: 409–416.

Mason, L.R., Smart, J. & Drewitt, A.L. 2018. Tracking day and night provides insights into the relative importance of different wader chick predators. *Ibis* **160**: 71–88.

Mayfield, H. 1961. Nesting success calculated from exposure. *Wilson Bull.* **73**: 255–261.

McMahon, B.J., Doyle, S., Mougeot, F. & Arroyo, B. 2024. The decline of ground nesting birds in Europe: Do we need to manage predation in addition to habitat? *Glob. Ecol. Conserv.* **55**: e03213. https://doi.org/10.1016/j.gecco.2024.e03213

Miller, R., Lambert, M.L., Frohnwieser, A., Brecht, K.F., Bugnyar, T., Crampton, I., Garcia-Pelegrin, E., Gould, K., Greggor, A.L., Izawa, E.-I., Kelly, D.M., Li, Z., Luo, Y., Luong, L.B., Massen, J.J.M., Nieder, A., Reber, S.A., Schiestl, M., Seguchi, A., Sepehri, P., Stevens, J.R., Taylor, A.H., Wang, L., Wolff, L.M., Zhang, Y. & Clayton, N.S. 2022. Socio-ecological correlates of neophobia in corvids. *Curr. Biol.* **32**: 74–85.e4.

Moller, A.P. 1989. Nest site selection across field-woodland ecotones: The effect of nest predation. *Oikos* **56**: 240.

Munkebye, E., Pedersen, H.C., Steen, J.B. & Brøseth, H. 2003. Predation of eggs and incubating females in willow ptarmigan *Lagopus l. lagopus*. *Fauna Norv.* **23**: 1–8.

Nicoll, M. & Norris, K. 2010. Detecting an impact of predation on bird populations depends on the methods used to assess the predators. *Methods Ecol. Evol.* **1**: 300–310.

Niemczynowicz, A., Świętochowski, P., Brzeziński, M. & Zalewski, A. 2017. Non-native predator control increases the nesting success of birds: American mink preying on wader nests. *Biol. Conserv.* **212**: 86–95.

Niku, J., Hui, F.K.C., Taskinen, S. & Warton, D.I. 2019. Gllvm: Fast analysis of multivariate abundance data with generalized linear latent variable models in r. *Methods Ecol. Evol.* **10**: 2173–2182.

Ortega, C.P., Ortega, J.C., Rapp, C.A. & Backensto, S.A. 1998. Validating the use of artificial nests in predation experiments. *J. Wildl. Manage.* **62**: 925.

Page, M.J., McKenzie, J.E., Bossuyt, P.M., Boutron, I., Hoffmann, T.C., Mulrow, C.D., Shamseer, L., Tetzlaff, J.M., Akl, E.A., Brennan, S.E., Chou, R., Glanville, J., Grimshaw, J.M., Hróbjartsson, A., Lalu, M.M., Li, T., Loder, E.W., Mayo-Wilson, E., McDonald, S., McGuinness, L.A., Stewart, L.A., Thomas, J., Tricco, A.C., Welch, V.A., Whiting, P. & Moher, D. 2021. The PRISMA 2020 statement: An updated guideline for reporting systematic reviews. *BMJ (Clinical Research Ed.) (England)* **372**: n71.

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**(Suppl. 1): 9–26.

Parrett, J.P., Johnson, C.B., Gall, A.E. & Prichard, A.K. 2023a. Factors influencing incubation behavior and nesting success of yellow-billed loons in Arctic Alaska. *J. Wildl. Manage.* **87**: e22406. https://doi.org/10.1002/jwmg.22406

Parrett, J.P., Prichard, A.K.K., Johnson, C.B. & Lawhead, B.E. 2023b. An ongoing shift in mammalian nest predators of yellow-billed loons in Arctic Alaska. *Arctic* **76**: 14–25.

Pasitschniak-Arts, M. & Messier, F. 1996. Predation on artificial duck nests in a fragmented prairie landscape. *Ecosci.* **3**: 436–441. https://doi.org/10.1080/11956860.1996.11682361

Prugh, L.R., Stoner, C.J., Epps, C.W., Bean, W.T., Ripple, W.J., Laliberte, A.S. & Brashares, J.S. 2009. The rise of the mesopredator. *Bioscience* **59**: 779–791.

Purger, J.J., Mészáros, L.A. & Purger, D. 2004. Ground nesting in recultivated forest habitats: A study with artificial nests. *Acta Ornithol.* **39**: 141–145. https://doi.org/10.3161/068.039.0211

R Core Team. 2025. *R: A Language and Environment for Statistical Computing*. Vienna: R Foundation for Statistical Computing. https://www.R-project.org/.

Reiter, M.E. & Andersen, D.E. 2011. Arctic foxes, lemmings, and Canada goose nest survival at Cape Churchill, Manitoba. *Wilson J. Ornithol.* **123**: 266–276.

Rickenbach, O., Grüebler, M.U., Schaub, M., Koller, A., Naef-Daenzer, B. & Schifferli, L. 2011. Exclusion of ground predators improves northern lapwing *Vanellus vanellus* chick survival. *Ibis* **153**: 531–542. https://doi.org/10.1111/j.1474-919X.2011.01136.x

Ricklefs, R.E. 1969. An analysis of nesting mortality in birds. *Smithson. Contrib. Zool.* **9**: 1–48. https://repository.si.edu/server/api/core/bitstreams/a75610ea-bcea-47a0-8d96-bd81a44cbb6d/content

Robertson, H.A. & Fraser, J.R. 2009. Use of trained dogs to determine the age structure and conservation status of kiwi *Apteryx* spp. populations. *Bird Conserv. Int.* **19**: 121–129.

Roche, E.A., Arnold, T.W. & Cuthbert, F.J. 2010. Apparent Nest abandonment as evidence of breeding-season mortality in Great Lakes piping plovers (*Charadrius melodus*). *Auk* **127**: 402–410.

Roos, S., Smart, J., Gibbons, D.W. & Wilson, J.D. 2018. A review of predation as a limiting factor for bird populations in mesopredator-rich landscapes: A case study of the UK. *Biol. Rev. Camb. Philos. Soc.* **93**: 1915–1937.

Ruhlen, T.D., Abbott, S., Stenzel, L.E. & Page, G.W. 2003. Evidence that human disturbance reduces snowy plover chick survival. *J. Field Ornithol.* **74**: 300–304.

Samsonov, S., Grudinskaya, V., Grabovsky, A., Makarova, T. & Shitikov, D. 2022. A hidden threat in abandoned fields: Frequent nest predation by common adder on ground-nesting passerines. *Eur. J. Wildl. Res.* **68**: 11. https://doi.org/10.1007/s10344-022-01559-w

Sargent, R.A., Kilgo, J.C., Chapman, B.R. & Miller, K.V. 1998. Predation of artificial nests in hardwood fragments enclosed by pine and agricultural habitats. *J. Wildl. Manage.* **62**: 1438–1442. https://doi.org/10.2307/3802010

Schuettler, E., Klenke, R., McGehee, S., Rozzi, R. & Jax, K. 2009. Vulnerability of ground-nesting Waterbirds to predation by invasive American mink in the Cape Horn biosphere reserve, Chile. *Biol. Conserv.* **142**: 1450–1460. https://doi.org/10.1016/j.biocon.2009.02.013

Stickney, A. 1991. Seasonal patterns of prey availability and the foraging behavior of Arctic foxes (*Alopex lagopus*) in a waterfowl nesting area. *Can. J. Zool.* **69**: 2853–2859.

Valkama, J., Korpimäki, E., Arroyo, B., Beja, P., Bretagnolle, V., Bro, E., Kenward, R., Mañosa, S., Redpath, S.M., Thirgood, S. & Viñuela, J. 2005. Birds of prey as limiting factors of gamebird populations in Europe: A review. *Biol. Rev. Camb. Philos. Soc.* **80**: 171–203.

Willebrand, T. & Marcström, V. 1988. On the danger of using dummy nests to study predation. *Auk* **105**: 31. https://digitalcommons.usf.edu/auk/vol105/iss2/31

Wilson, G.R., Brittingham, M.C. & Goodrich, L.J. 1998. How well do artificial nests estimate success of real nests? *Condor* **100**: 357–364.

Zanette, L. 2002. What do artificial nests tells us about nest predation? *Biol. Conserv.* **103**: 323–329.

Received 14 November 2025;
Revision 30 June 2026;
revision accepted 14 July 2026.
Associate Editor: Alexandre Millon

SUPPORTING INFORMATION

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

Figure S1. Flow chart illustrating the process of identifying and screening literature to include in the review. Two literature databases, WebOfScience and Scopus, and two report registers, BTO and BirdLife International, were checked for relevant literature. Five exclusion criteria were used to filter out irrelevant literature. Not focusing on predation, focusing on non-ground-nesting bird species, not including estimates, not being a primary article or not being written in English. Based on PRISMA flowchart. Source: Page MJ, et al. BMJ 2021;372:n71. doi: 10.1136/bmj.n71. This work is licensed under CC BY 4.0. To view a copy of this licence, visit https://creativecommons.org/licenses/by/4.0/

Table S1. Number of studies of each species of each bird group type included in the review.

Table S2. Exclusion criteria used to select literature for the review.

Table S3. Occurrences of different bird groups in different habitats.

Table S4. Estimates of predator communities from the GLLVM.

Figure S2. Changes in use of camera trap studies and artificial nest studies over time. Camera trap-based studies have increased since the early 2000s. Artificial nest studies have been frequently used since the 1970's.