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CONFLICT OF INTEREST

The authors declare that they have no conflict of interest.

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ABSTRACT

Nest predation is the primary cause of nest failure across many bird species. Interventions to support declining or threatened species frequently involve measures to reduce nest predation, through lethal control or non-lethal methods; their efficacy relies on a robust understanding of predator identity. The development of unobtrusive, infrared digital video surveillance now allows the identity of nest predators to be confirmed directly. Here, we collate and analyse nest camera studies from England, Wales, Scotland and the Isle of Man, that are dominated by anthropogenic landscapes and lacking most apex predators, but with a high abundance of mesopredators. We quantify the contribution of predator class and functional groups across groups of prey species, nesting habitats or nest strata. For quantitative analysis we collated 46 nest predation studies, comprising 2088 nests and 609 predation events across 24 avian prey species. Nest predation studies are not yet representative, mostly comprising Waders (Chardriiformes) and a few passerines, in grassland and woodland habitats respectively, with farmland and urban habitats poorly sampled. Wader clutches were predominantly predated by mammals (primarily European Badger *Meles meles*; and Red Fox *Vulpes vulpes*; and particularly on islands European Hedgehog *Erinaceus europaeus*; together 53 % of events), but with non-trivial contributions of ungulates (6 %), predominantly Sheep *Ovis aries*. Passerine clutches were predated by corvids (31 % of events) and mammals (primarily Badger and Fox, 25 % combined). Compared to depredation of passerine clutches, passerine broods were taken by a wider range of predators particularly avian predators, predominantly Eurasian Jay *Garrulus glandarius* (23 % of events, though noting 73% of songbird predation events were in woodland) and raptors (21 %), but also reptiles. Despite the attention given to impacts of Grey Squirrel *Sciurus carolinensis*, its contribution to observed nest predation was negligible. Further work is required to expand understanding of nest predator identity, to improve understanding of changing predator influences across populations, so that, where appropriate for conservation, management strategies can be better informed.

Keywords: nest predation, nest camera, predator control, predator identity, predator management

INTRODUCTION

Nest predation is the primary cause of nest failure across many bird species (Newton, 1998; Ricklefs, 1969; Thompson, 2007), influencing population productivity and demography. Interventions to support declining or threatened bird species frequently involve measures to reduce nest predation, through lethal control (Smith *et al*. 2010) or non-lethal measures (Malpas *et al*. 2013; Garvey *et al*. 2020; Verhoeven *et al.* 2022; Gautschi *et al*. 2024). Lethal control of introduced predators has supported endangered species (Brooke *et al*. 2018), but remains controversial, particularly for native nest predators (van Eeden *et al.* 2017). Nevertheless, in anthropogenic landscapes and regions lacking key apex predators, mesopredators can be abundant (Roos *et al*. 2018) and their management can be an important conservation intervention for threatened bird species (Tapper *et al*. 1996; Moreno-Opo *et al*. 2015; Baines *et al*. 2023). However, any such management should be evidence-based with regards to understanding predator identity, particularly as predator species' contribution to nest predation cannot be predicted from their relative abundance (Fokkema et al. 2024). The development of unobtrusive, infra-red digital video surveillance devices allows nest predator identity to be confirmed (Bolton *et al*. 2007; Thompson, 2007; Cox *et al*. 2012). In contrast to North America (Thompson, 2007; DeGregorio *et al*. 2014; DeGregorio *et al*. 2016), an overview of the relative contribution of different predator species to avian nest predation is lacking for western Europe.

In the UK, populations of many mammalian and avian predator species have increased (Roos *et al*. 2018; 2022). This is perceived to have contributed to declines of many avian prey species, including passerines, waders (Charadriiformes) and Galliformes (Nicoll & Norris, 2010; Roos *et al*. 2018) with particularly strong evidence that seabird, wader and Galliforme populations can be limited by predation (Roos *et al*. 2018). However, without robust evidence, perceptions of predator identity may be unreliable and influenced by the abundance or activity of conspicuous predators, or experience from game management (Galliformes), with uncertain relevance to other prey groups especially passerines. Responses of breeding productivity and population size are greater when a wider range of potential predator species are controlled (Smith *et al*. 2010), but a 'scatter-gun' approach to predator control is not defensible in the absence of evidence supporting the targeting of each predator species. Misplaced predator control could also potentially, through competitor or predator release (Sergio & Hiraldo 2008; Williams *et al*. 2018), increase the abundance of other predator species with greater impacts on nesting productivity. Confirming principal nest predator species also allows species-specific, non-lethal manipulations to be trialled, such as habitat manipulation or diversionary feeding (Laidlaw *et al*. 2019; Mason *et al*. 2021; Bamber et al. 2024).

Nest predator identity has been inferred from signs at depredated nests (Gaston 1973; Rodrigues & Crick, 1997) but this may be unreliable (Larivière 1999; Mallord *et al*. 2012), particularly as adults may remove any remains and other predators may subsequently investigate the depredated nest, including disrupting the lining or leaving scat (Bolton *et al.* 2007). Inferred attribution (e.g. Capstick & Madden 2021) is likely influenced by expectation, adding circularity, with blame often attributed to conspicuous predators. The use of dummy nests cannot resolve predator species, and the relative contribution of mammals and corvids can be biased compared to real nests (Dolman 2012). Temperature loggers can show the timing of predation, with nocturnal events generally attributed to

mammals, although their contribution will be underestimated where these mammals also predate diurnally (Eglington *et al*. 2009), but do not resolve predator species within avian or mammalian guilds. Opportunities for unobtrusive nest monitoring have advanced with compact digital media, infrared light-emitting diodes (LED's) and passive infrared sensors (PIR) (that detect heat and movement) available to trigger image capture. Purpose-built miniature nest camera systems (Bolton *et al*. 2007; Koshkin *et al.* 2016) and some trail cameras (McHenry et al. 2025), allow direct observation studies of nest predator identity.

Despite accumulation of nest camera data, much unpublished, there has been no meta-analysis of nest predator identity conducted to date for Britain or the UK. Here, we collate and analyse published and unpublished nest camera studies from England, Wales, Scotland and the Isle of Man (within the British Islands), to provide evidence for the identity of nest predators. We examine whether the relative contribution of predator classes (mammal, bird and unknown) or finer categories (individual carnivore species and functional groups such as: corvids, raptors, ungulates, domestic mammals and rodents) differed between: bird species groups (passerines, waders, wildfowl, Galliformes); habitats (woodland, arable farmland, grassland or moorland); or nest strata (ground, high-canopy) with model contrasts adapted according to available sample structure. Findings have implications for similar landscapes, particularly in temperate western Europe.

METHODS

Nest camera systems

Many nest camera studies used trail cameras (or 'camera traps'), others used purpose-built miniature nest cameras (incorporating infrared LED's for passive infrared Video Motion Detection, VMD) placed close (e.g. 0.3 – 1 m) to the nest, linked by cable (usually buried) to a digital recording unit incorporating VMD, buried remotely (e.g. 5 m) from the nest. The Royal Society for the Protection of Birds (RSPB) developed an early miniature nest camera (Bolton *et al*. 2007) with LED array, using a security video system to captures images immediately before and after the VMD event, requiring only infrequent (e.g. 5-day) battery and SD card maintenance. Recent miniature nest cameras record continuous digital video (Koshkin *et al.* 2016), and the larger (22 cm x 17 cm) remotely-controlled CamBall system has also occasionally been used at nests. Different nest camera systems may varyingly deter, or attract the attention of, potential nest predators. Most commercial trail-cameras produce audible sounds when photo or video is triggered by the passive infrared array (Meek *et al*. 2014), in contrast to miniature nest cameras in which the recording unit are placed remotely from the nest (Bolton *et al*. 2007). Some trail cameras use shorter-wavelength infrared illumination (i.e. 780–870 nm) within the visual range of some mammalian predators (Meek *et al*. 2014), in contrast to the longer wavelengths (typically 940-950 nm) used in modern trail cameras and miniature nest cameras. Older trail cameras also may perform poorly due to slow trigger speed and limited night vision (McHenry et al. 2025). Therefore, we classified the type of camera use in each study as: far-infrared Miniature Nest Camera; far-infrared Trail Camera; near-infrared Trail Camera; near-infrared CamBall.

We excluded any earlier studies (or part-studies) that used still-frame cameras, mechanical triggers, or active infrared (beam) triggers that may not reliably capture predation events (Sharpe 2006; Bolton *et al*. 2007; Cox *et al*. 2012). Time-lapse VHS video systems were bulky and required frequent maintenance, causing disturbance (Bolton *et al*. 2007), studies that placed these at the nest were, therefore, also excluded. However, we included two studies that used an earlier version of the miniature far-infrared RSPB nest camera, connected by cable to a time-lapse VHS unit buried 30-40 m from the nest (Perkins *et al*. 2005; Summers *et al*. 2009). We also excluded observations made using a miniature GoPro digital camera, as their short battery charge (e.g. < 1 day) is inappropriate for nest monitoring.

Nests at which the camera were reported to fail were omitted. Instances where the predator was unidentified (assumed not to represent equipment failure) were retained as 'unknown'. Identification is relatively assured for larger mammals (hedgehog, fox or larger), corvids or raptors, thus unknown events are more likely to involve small mammals, particularly small mustelids (Least Weasel *Mustela nivalis* and Stoat *Mustela erminea*) and potentially also mice (*Apodemus* spp.) and voles (*Myodes glareolus*). This is especially the case where: there is a longer lag or delay between VMD trigger and image capture; cameras are located in concealing herbaceous vegetation (that can grow during monitoring); the lens orientation is affected by glare; or the camera is set further from the nest (e.g. trail cameras with elevated mount).

Collation of published and unpublished data

We conducted a systematic literature review (in December 2023) across: SCOPUS, Google Scholar, and DART-Europe Etheses Portal. An initial search was performed using general terms: (camera OR video OR "nest camera") AND ("nest predat*" OR depredat*) AND (avian OR aves OR bird* OR passeri* OR wader* OR "ground nest*" OR songbird* OR raptor OR corvid OR mammal OR rodent OR adder). Further searches for specific taxonomic groups were conducted using SCOPUS (up to and including 15 January 2024), by replacing general nesting species terms with terms describing specific taxonomic Families and Genera (listed in Supplementary Material Table S1).

Searches retrieved 3881 articles, which were filtered following PRISMA guidelines (O'Dea *et al*. 2021). Duplicated records (1978 articles), those not written in English (242), and those in an incorrect format (e.g. conference abstracts 407) were removed (Supplementary Materials Fig. S1). The remaining 1254 articles were screened by title and abstract, retained articles were then assessed in detail to ensure methods and reporting met the following criteria for inclusion: 1) the study was conducted in the UK (or Isle of Man); 2) appropriate infrared camera trap or nest cameras were used (see above); 3) natural nests only were considered (no artificial nests, caged or protected nests, or nest boxes - as these can modify vulnerability to different predator species: McCleery et al. 1996; Skwarska et al. 2009); 4) results are reported separately for clutch and (altricial) broods of each prey species. Where published sources re-presented the same data (e.g. Bellamy *et al*. 2018;

Maag *et al*. 2022), only the original publication of the data was included. This resulted in a final library of fourteen articles (Fig. S1). In addition we were aware of several suitable unpublished studies. To ensure the widest representation of species and study systems, we contacted various ringing groups, universities, non-governmental organisations, the British Broadcasting Corporation, and individual (unaffiliated) researchers. Data from these sources were collated following the same criteria for inclusion. Fourteen published and 32 unpublished studies (from 12 research groups) met our criteria for quantitative analyses, together comprising 106 nest-groups (Table 3).

A 'study' described instances where the same methods were employed by an individual or team, to one prey species at one site (the extent of a site was variable, defined by publications or data contributors). For formal quantitative analysis, we limited observations to studies that monitored at least four clutches, or four broods, of the prey species – a compromise between retaining available data while omitting anecdotal observations. The proportion of predation events in which the predator was identified, was 50 % in Langston et al (2007) and at least 65 % in all remaining studies. Of the 46 studies considered, just under half (22, 47.8 %) deployed miniature far-infrared nest cameras; most others used trail cameras (11 far-infrared, 12 near-infrared) and a single study used a CamBall camouflaged within vegetation. Studies varied in the resolution at which data were reported: eight reported nest outcomes pooled across multiple years (Calladine *et al*. 2017), others combined observations from multiple locations (Kirby *et al*. 2018). Sample locations were incompletely reported at varying scales; we were, therefore, unable to formally include geographical covariates in models. However, inclusion of study as a random effect in modelling accounts for some of the spatial variation, see below. Where sample sizes met criteria for inclusion (at least four monitored nests), we used data at the finest resolution available, in unique combinations of prey species, life-stage (clutch or brood), site and year (termed 'nest-groups' hereafter). Thus, a study that reported predation of clutch and broods of two prey species in each of two years, could potentially provide eight unique nest-groups. However, for eight unpublished datasets with low numbers of nests monitored overall, those monitored over multiple years within the same study were pooled to meet the sample-size threshold for inclusion (representing 7 % of all nest-groups, and 14 % of all predated nests). Amongst these nest-groups, the number of years varied from two to six, with a median of 3.5.

For each nest-group, within each study, we extracted information describing: 1) the prey species, 2) the number of nests monitored by cameras, 3) the total number of depredated nests and 4) the number of nests depredated by each predator species (including 'unknown'). We also extracted information for potential covariates: 5) year(s) of data collection, 6) broad habitat type (Table 1). We did not differentiate between partial and complete-predation events, as this information was not always available in studies. Predation during egg-laying was combined with predation of clutches, but events for which it was unclear whether predation occurred at egg or chick life-history stage were excluded from analysis. Instances where a camera was deployed but malfunctioned ('camera failure') were excluded from analyses. Overall, 81 nests were omitted from the study due to nest camera failure (3.9 % of the total monitored nests). Eighteen studies had fewer than five nest camera failures; 11 failures reported by Sharpe (2006) occurred during experimental tests of different camera setups; thirteen studies reported no camera failures, information concerning camera failures was not available for the remaining 14 studies. Information on nest-success rate

(Mayfield, 1975) was not available for most studies. However, we report the proportion of monitored nests in each nest-group that were observed to be predated.

Analyses

We treated nest-groups as replicate observations in tests of whether the relative contribution of different categories of predator (taxonomic class, or key species and functional types) differed between groups of prey species (taxonomic group, habitat, nesting strata). The relative contribution of each predator category was analysed as the number of predation events attributed to it (a multinomial dependent variable), for each replicate nest-group, using Bayesian multinomial mixed effects models employed with Stan, a probabilistic programming language (see: https://mc-stan.org/), through the *brms* package (Bürkner, 2017) in R (version 4.3.1, R Core Team, 2023). Default un-informed priors were used in all models, and the recommended 2000 iterations (of which the first 1000 were 'warm-up' draws) with four chains, were sufficient for model convergence (Bürkner, 2017). Model performance was checked with *Rhat* scores (between 1.0 and 1.1) and effective sample size values ('bulk' and 'tail' ESS >1000). To generate meaningful biological values from the parameter estimates, models were then used to predict the proportion of predation events attributed to predator response variables, drawn from the posterior predictive distribution. Pairwise-comparisons between predator categories (class/type), for each category of the fixed-effects were then performed, comparing differences in estimated marginal means (EMM). Comparisons were considered significant where the 95 % confidence intervals of the EMM differences did not span zero.

In all cases, 'study' was included as a random effect and, for year-specific nest-groups, sample year was nested as a unique factor within study to account for possible stochastic variation in predation patterns among years within each study-site (this does not assume year affects are similar among studies/sites). It was not necessary to weight nest-groups by the numbers of predation events observed, as the dependent variable (probability of predation by predator class/type) was defined at the level of the monitored nest, so that studies with more nests contributed more than those with fewer nests. Note that sample sizes in the models varied, depending on which prey and predator categories were considered in the analysis (Table 1).

Predation of clutches of different prey groups

The relative contribution of predator categories to the predation of clutches, was compared among different bird prey categories (broods could not be considered in these models as waders are precocial), assessed with two models (Table 1). The first model compared the relative contribution of predator classes (mammals; birds; and unknown predators, Table 1) to predation of clutches of: ground-nesting passerines (all species built open nests); waders; and 'other' prey (pooling three ground-nesting waterfowl, one Galliform, and two seabird species, but excluding Black-legged Kittiwake *Rissa tridactyla*, which as the only cliff-nesting species was expected to differ to ground-nesting species in predator exposure). The second model was limited to ground-nesting passerine and wader clutches, this allowed predators to be refined into 12 finer categories that *a priori* considered those individual mammalian carnivore species that are widespread and relatively abundant (Fox; Badger; Hedgehog; Stoat), plus pooled functional groups (see Table 2). Only one clutch was depredated by a reptile, and this observation was excluded from these analyses.

Life-history stage and nest strata

For passerine species only, we tested whether the relative contribution of predator categories differed between clutch and brood stages, and between species nesting on the ground or in the low-canopy (combined) to those located in the high-canopy (no species were listed as nesting in the 'mid-canopy'). All species of passerine considered build open nests, so whether predator contributions vary between different types of nests could not be assessed. We conducted two analyses (Table 1), the first considered predator classes (mammals; birds; unknown), the second considered 13 finer predator categories (12 listed above, plus reptiles that depredated passerine broods: Table 2). However, as observations of predation were imbalanced across nesting strata (only 31 nests were located in the high-canopy), results should be interpreted with caution.

Broad habitat

Wader and passerine nests in our sample differed in habitat representation (five habitat types in total – Table 1), therefore, whether predator contributions differed among habitats was examined separately for these two prey groups. In each model, contributions were compared between the three predator classes; for passerines two and waders three habitats were considered (Table 1). We acknowledge that classification of habitat is to an extent subjective, and consideration of scale may differ among studies. Studies that reported sites comprised of habitat mosaics, or that pooled data across samples from multiple habitat types (e.g. Stevens et al. 2008), were coded as 'mixed'.

RESULTS

Collated data

Across the 106 nest-groups analysed, no predation events were observed in 14, among the remaining 92 nest-groups (34 published, 58 unpublished, where a 'nest-group' comprises a set of nests of the same species, life-history stage, site and year, Table 3) 2088 nests were monitored by nest cameras, across 24 bird prey species, with 609 (29.2 %) predated on nest-camera (Table 3). The observed frequency of nest predation varied with prey type and life-history stage: across 55 wader nest-groups, 356 (33.5 %) of 1062 monitored nests were predated; in contrast although only 21 seabird nests were monitored, 20 of these were predated (Fig. S2). The rate of unidentified predators was similar between the three most common nest camera types (far-IR miniature nest camera, far-IR trail; near-IR trail: $\chi^2 = 2.82$, df = 2, p= 0.25, see Table S2).

Identification of nest predators

Across the entire dataset, 42 prey and 34 predator species were considered (see summary in Fig. 1, further detail in Fig. S3). The 92 nest-groups that met criteria for quantitative analysis sampled 24 prey and identified 32 predator species; additional anecdotal observations (36 nest-groups of which most, 35, observed a single nest of one prey species) spanned a further 18 prey species (including 15 passerines) but identified only two additional predators (Little Owl *Athene Noctua*; Grass Snake *Natrix natrix*, Table S3).

Predators of clutches in nests on the ground

For predation of wader clutches, mammals (predicted percentage: 88.1, 95% CI 76.0 - 96.3) contributed more than avian (10.5, 95 %, CI 3.2 - 21.3) predators (difference between estimated marginal means, EMM: 77.3 %, 95% CI: 55.1-93.8 %), or 'unknown' predators (EMM: 84.6 %, 95% CI: 73.1-96.3 %, Fig. 2a, Table S4). For passerine clutches, predation was more evenly spread between mammalian (predicted percentage: 68.5, 95 % CI 22.0 - 94.4) and avian (18.3, 2.91-57.8 %) predators. The percentage of instances where the predator could not be identified appeared lower for wader clutches (1.16, 0.2-4.5 %), than passerine (9.18, 0.5-47.5 %) or 'other' (7.89, 0.53-43.9 %) nests (Fig. 2a).

The high percentage of mammalian predation on waders (Fig. 2b) was predominantly due to Badger (41.7 %, 29.0-55.6 %) and Fox (23.0 %, 8.9-40.5 %), and to a lesser extent ungulates (6.3 %, 1.1-17.6 %, Table S5, Fig. 2b) comprising 23 and one predation events by Sheep *Ovis aries* and deer (species not recorded), respectively. While Hedgehog depredated 69 wader nests (19% of 356 events), 65 of these were in one island study (Calladine *et al.* 2017), and thus their relative contribution was lower in models (0.46 %, 0.004-6.02 %) that accounted for random effects of study. The exclusion of studies from islands where predator assemblages differ substantially (The Hebrides, n =281 predated nests; Isle of Man; n =15; Isle of Skye, n = 9), did not alter results (Table S10 and S11). Most mammalian predation of passerine clutches was by Badger (26.0 %, 5.10-58.8 %) while ungulates (Fallow Deer, *Dama dama*; Muntjac *Muntiacus reevesi*) took only three passerine clutches (1.10 %, 0.01-15.28 %). Rodents, Stoat and other mustelids did not commonly predate on either prey group (all contributed less than 5 % to predation, Fig. 2b), but may disproportionately contribute to unidentified events (see methods).

Of the identified avian predators of ground-nests, corvids were responsible for 4.9 % (0.06-56.6 %) and 4.0 % (0.4-17.2 %, Table S5, Fig. 2b) of passerine and wader predation respectively, while raptors and 'other' avian species (including gulls and woodpeckers) were rarely identified predating clutches (each predatory group responsible for less than 3.5 % of predation, Fig. 2b).

Nests of 'other' prey species were more commonly predated by mammalian (predicted proportion: 76.4 % 29.2-96.5 %) than avian species (12.8 % 1.7-47.3%), although this comparison was not statistically significant. For other prey, Fox were responsible for all predation events of raptors (Hen Harrier *Circus cyaneus*); Hedgehog were the most common predator of seabirds, Galliformes were predated by Pine Marten *Martes martes*, and waterfowl by Eurasian Otter *Lutra lutra*, Stoat and Brown Rat *Rattus norvegicus* (Fig. S3).

Passerine clutches, broods and nest strata

Analysis of predator classes examined 193 predation events (Fig. 3a). For passerine nests in the high-canopy, avian predators contributed more to predation than mammals, for both clutches (80.7%, 19.3-99.2 %) and broods (89.5%, 29.2-99.6 %, Fig 5a, Table S6). For ground-nesting passerines, the contribution of avian predators to predation of both clutches and broods was substantial, but less than that of mammals (Fig. 3a). For ground nesting passerines 14.3 % (2.1-42.9 %) and 9.5 % (2.3-26.2 %) of clutch and brood predation events were 'unknown' predators, respectively; for high-canopy nests there were no 'unknown' predators (Fig 5a), although these were represented by only 31 nests of Hawfinch *Coccothraustes coccothraustes* and Spotted Flycatcher *Muscicapa striata* (from three studies).

Analysis of predator species and functional groups examined 203 predation events (Fig. 3b). Fox (20.9%, 4.2-53.4%) and corvids (14.5%, 4.7-27.0%) contributed most to predation of ground-nesting passerine broods (Fig. 3b), but raptors were responsible for 20.9% (4.3-53.4%) of brood predation (more than ungulates, Table S7, Fig. 3). Reptiles were also more likely to predate on broods than clutches of ground-nesting species (nine of ten reptilian predation events by Adder *Vipera berus* were on broods of Wood Warbler *Phylloscopus sibilatrix* and Woodlark *Lullula arborea*).

Four of the thirteen categories of predator were represented in the high-canopy dataset (reptiles and 'unknown' predators were absent, Cat *Felis catus* was the only mammalian predator), of which only corvids were observed more than five times, this complicated model fitting and interpretation (note large confidence intervals in Fig. 3b). While patterns for avian predators followed those observed for ground-nesting species (i.e. clutches were depredated by corvids, broods by both corvids and raptors), more data are required to draw robust conclusions for the high-canopy.

Broad habitat

Most monitored passerine nests were in woodland, some were in mixed habitats (Fig. 4a), but predation of passerine nests was excluded for: farmland (eight events, all mammalian) and heath/montane habitat (two events only, one avian and one unknown). Predator identity was identified in 80.8 % of events in woodland (117 of 147, Fig. 4a) and in all events in mixed habitats (n = 27). Predation in woodlands was evenly spread between avian and mammalian predators and in mixed habitats, avian predators appeared to contribute more to predation, although not significantly (Fig. 4a, Table S8).

Wader nest-groups spanned a different suite of habitats, including: grassland (n = 291), farmland (n = 21), coastal (n=29), and mixed habitats (n = 10); an additional two events in wetland habitat were omitted from analysis to facilitate model convergence. Mammals were the dominant predators of wader clutches, responsible for significantly more events than avian predators in all habitat types (Fig. 4b, Table S9). This pattern remained consistent when nests from islands were excluded from analyses (281 nests from The Hebrides in grassland habitat and 15 nests from the Isle of Man in coastal habitat).

DISCUSSION

Our dataset represents the most comprehensive collation of British nest camera studies to date. However, although 609 predation events were analysed, evidence is not yet representative across prey species, landscapes and habitats, with Galliformes, and cavity and canopy-nesting passerines poorly represented. Among passerines, only seven (predominantly ground-nesting) of the 83 passerine species that regularly breed in the UK have been the focus of a systematic nest camera study. Studies were biased towards semi-natural habitats, with 76 % of passerine predation events from woodlands (including plantation clear-fells) and 81 % of wader events from grassland. Urban habitats were poorly represented, and one study reported predator identity by pooling across habitats (Stevens et al. 2008) although clutch- and brood-survival were greater in rural gardens than in farmland or woodland (Stevens et al. 2007). Few predation events were attributed to domestic species (Cat and Dog *Canis familiaris*, six and three nests, respectively), potentially reflecting the low

representation of urban nests despite the potentially substantial impacts of Cat on urban and peri-urban nesting productivity (Sims *et al*. 2008) while Dog can exert high rates of recreational disturbance in peri-urban contexts (Thomas et al. 2024). Despite the importance of farmland to many birds of conservation concern (Gregory *et al*. 2004), few nest-camera studies were conducted in arable farmland (29 predation events), reflecting a wider paucity of wildlife camera studies from farmland (Rolio et al. 2024). We also found no nest camera studies from hedgerows despite their importance to numerous small passerines. Opportunistic observations (excluded from quantitative models) covered an additional fifteen passerine prey species, some in urban or farmland habitats; appropriate systematic nest-camera studies would expand understanding of predators within such habitats.

An important consideration is whether nest cameras influence predator behaviour, either by deterring neophobic or by attracting inquisitive predators, thereby biasing predation rates and relative species' contributions. Previous meta-analysis found camera surveillance reduced rates of nest predation in more than half the studies reviewed (Richardson *et al.* 2009) but included earlier studies that potentially used bulky or analogue equipment. However, across a wide range of species, rates of nest success are similar between nests with and without cameras (e.g. Bolton *et al*. 2007; Koshkin *et al.* 2016), particularly for ground-nesting species of open-habitats (waders; terns) primarily exposed to mammalian carnivores (e.g. Sanders & Maloney 2002; McKinnon & Bêty 2009; Burns *et al*. 2013; Salewski & Schmidt 2022). Nevertheless, common concerns are that: visitation during monitoring or camera installation exposes nests to predation by vigilant corvids or by mammalian predators alert to scent cues; conversely, that obvious cameras reduce nest predation by neophobic corvids; and that corvid wariness varies with local control intensity. We urge caution in deploying nest cameras, particularly in dense and concealing herbaceous vegetation where disruption during camera installation may provide cues to predators, although miniature nest cameras may be less obtrusive than trail cameras. In all intensive species- or site-specific studies, nest success rates should be monitored for samples of nests with and without cameras.

Within any nest camera study, recording of nest-groups should include: location of each nest (e.g. using hand-held GPS); landscape context including local predator management activities – and ideally local monitoring of predator abundance; time taken setting-up; camera type(s) (still, video, trail camera or nest camera, single unit or separate recorder-unit/battery) and model; sleep interval or continuous recording; sensor type (near- or far-infrared); trigger lag; camera height above ground and distance from nest; and should distinguish any predation (or nest outcome) events missed due to camera failure from events where predators could not be identified.

Identity of nest predators in Britain

Mammals were responsible for the majority of nest predation events recorded, particularly of wader clutches, while a mix of mammals, corvids, and some raptors were responsible for predation of passerine clutches and broods. Although predation of precocial chicks could not be included in this analysis of nest camera observations, wader chicks are also known to be predated by a wider range of predators than wader clutches, with greater contribution by diurnal avian predators including raptors (Mason *et al*. 2018). A notable finding was the extremely broad range of nest predator species, that included species of conservation concern such as Adder (UK BAP, England S41; Gardner

et al. 2019) and Common Kestrel *Falco tinnunculus* (UK BoCC Amber, national IUCN Vulnerable; Stanbury et al., 2021). We also confirm non-trivial levels of nest predation by herbivorous ungulates (mainly Sheep, also deer), particularly on wader clutches. While acknowledging sample limitations, the contributions of Eurasian Magpie *Pica pica* and crows (Carrion Crow *Corvus corone* and Hooded Crow *C. cornix*) to predation of passerine nests was negligible: only one and two predation events respectively and one (crow) in opportunistic data. Whether observations of crow predation were influenced by avoidance in some sites with lethal control is unknown. Rook *Corvus frugilegus* and Western Jackdaw *Coloeus monedula* were recorded predating only five and nine wader nests, respectively, fewer than were predated by ungulates. In contrast, Eurasian Jay *Garrulus glandarius* depredated 49 passerine nests (24 % of all predation of passerine nests), and were the most frequent predator among opportunistic observations (seven, 30% of passerine prey events). Based on signs, Jay were considered the primary nest predator of Long-tailed Tits A*egithalos caudatus* (Gaston 1973) and were found to be the primary predator in a nest camera study of Eurasian Blackcap *Sylvia atricapilla* (Schaeffer 2004). Our results broadly accord with previous reviews that found: predominantly mammalian predation of wader clutches (MacDonald & Bolton 2008); no evidence that Grey Squirrel are important nest predators (Broughton 2020); infrequent responses of avian (mainly wader, Galliforme and passerine) productivity to corvid density and a limited response to Eurasian Magpie compared to crows (Madden *et al*. 2015); weaker responses to corvid removal than to removal of broader suites of predators (Madden *et al*. 2015); and stronger evidence for the role of guilds that included Fox than for corvids alone, in limiting populations (Roos *et al*. 2018).

Further nest camera studies across a wider range of nesting species, habitats and landscapes are needed to inform predator management, with current evidence incomplete in terms of prey species, habitats, landscapes and management context. That mammalian carnivores predominated across a range of ground-nesting waders, passerines and wildfowl, reinforces the potential of fencing (of individual nests, or key sites: Malpas et al. 2013; Gautschi *et al*. 2024) and lethal control measures for those species that can be legally controlled (Tapper et al. 1996; Smith et al. 2010) to mitigate nest predation. However, the potential for compensatory release of predators to control of their competitors is poorly understood. Control of Grey Squirrel is advocated by many land managers to protect wild bird nests, but our data indicate they likely have minimal impacts on avian nest success (see also: Broughton 2020), in contrast to the role of American Red Squirrel *Tamiasciurus hudsonicus* as an important nest predator in North American conifer forests (DeGregorio *et al*. 2016). Again, we note the limited sample canopy-nesting species.

While risks of nest trampling by livestock are recognised (e.g. Sharps et al. 2015), the non-trivial level of nest predation by Sheep may be important for ground-nesting birds. That deer and Sheep predate clutches and even broods is long-established (Furness 1988; Vazquez et al. 2023), but often overlooked. If associated with mineral nutrition (Furness 1988) ungulate nest predation may be greater in areas of acidic soil. Nest predation risk may be alleviated by changes in timing of grazing, while for some ground-nesting bird species that nest in sparse vegetation most commonly created by heavy grazing (Green & Griffiths 1994) physical ground-disturbance can create suitable nesting conditions at a lower grazing intensity (Zielonka et al. 2019; Hawkes et al. 2021).

Predator assemblages are changing, driven by recovery from historic persecution, climatic change, habitat modification, and re-introductions. Mammalian predator populations are poorly monitored

in the UK, but occupancy trends (1970-2016; Coomber *et al.* 2021) show that: Least Weasel strongly decreased; Stoat decreased; Fox showed no change in occupancy but declined in abundance (1996-2014; Harris et al. 2016); while Badger increased in both occupancy and abundance (Mathews et al. 2018). Recovering Eurasian Otter populations consolidated across most of England by 2009-10 (Crawford 2010). Otter frequently feed on birds, including wildfowl, waders and passerines (Webb 1975; Jenkins et al. 1980), but our sample of wildfowl nests was limited. European Polecat *Mustela putorius* have now recovered much of their historic range (Mathews et al. 2018), but their role in nest predation is unclear. Re-introduced Red Kite *Milvus milvus* have increased predation of Northern Lapwing *Vanellus vanellus* clutches and reduced their breeding abundance in southern England (Mason *et al*. 2021). Re-establishment of apex raptors such as White-tailed Eagle *Haliaeetus albicilla* and Eurasian Goshawk *Accipiter gentilis*, has potential to reduce abundance of smaller nest predators, while re-introduction of additional mesopredators such as Pine Marten and European Wildcat *Felis silvestris* is further altering predator assemblage composition. How such changes will affect rates of avian nest failure is unclear. The extent to which predation is additive, or compensatory (Fokkema, et al. 2024) is unknown, as is the degree to which intra-guild competition may constrain overall nest-predation rates by altering the abundance and or spatio-temporal activity of smaller predators (Sergio & Hiraldo 2008; Williams *et al*. 2018). As predator impacts can depend on their breeding and provisioning phenology relative to breeding of potential prey (e.g. Upcott *et al.* 2024), climatic change may also alter the relative contribution of different predator species. Ongoing monitoring of predator composition, species-specific abundance, and contributions to nest predation, are required to understand such interactions. Understanding of predator impacts can be linked to their local abundance and functional responses to landscape features, through nest camera studies paired with wider surveillance across study landscapes, that is particularly lacking in farmland (Roilo *et al.* 2024).

Nest predation reduces breeding productivity, including for multi-brooded species (Mallord et al. 2008); but consequences for population abundance, trends and dynamics depend on an interplay with other factors across life stages (Perrins & Greer 1980; Newton 1998). Although meta-analysis of predator removal experiments shows effects on avian population abundance as well as breeding productivity (Smith *et al*. 2010), it is not clear which life history stages underpin these. Notably, historic baselines for the abundance and distribution of waders and other ground-nesting birds, reflect greater landscape and habitat suitability, as well as greater levels of predator control (Reynolds & Tapper 1996). An acceptance that restoration of diverse predator assemblages will lead to changes in prey populations may be appropriate in many instances. Even where nest predation has consequences for population abundance, demography of vulnerable species can also be managed through enhancements to habitat quality and resource availability; integrative management strategies are therefore required (Newton 2004; Roos *et al*. 2018). However, for threatened and declining species, information from nest camera studies can inform potential management. We found few studies of: Galliformes, tree-nesting passerines, birds in farmland contexts and few observations from an urban setting; further work with a focus on these species and habitats, would help to expand understanding of nest predation of birds across Britain.

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Tables:

Figures

Supplementary Online Material (SOM):

Table S5b Pairwise comparison of estimated marginal means (EMM) of each category, on the response scale.

Table S6a Results of Bayesian multinomial regression analysis, comparing predators of passerine clutches (CL) and broods (BR), for ground and canopy-nesting species.

Table S6b Pairwise comparison of estimated marginal means (EMM) of each category, on the response scale.

Table S7a Results of Bayesian multinomial regression analysis, comparing predators of passerine clutches (CL) and broods (BR), between ground/low canopy and high-canopy nesting species**.**

Table S7b Pairwise comparison of estimated marginal means (EMM) of each category, on the response scale.

Table S8a Results of Bayesian multinomial regression analysis, comparing predators of passerine nests between three broad habitats: mixed, woodland and farmland.

Table S8b Pairwise comparison of estimated marginal means (EMM) of each category, on the response scale.

Table S9a Results of Bayesian multinomial regression analysis, comparing predators of wader clutches between three broad habitats: grassland, mixed and wetlands.

Table S9b Pairwise comparison of estimated marginal means (EMM) of each category, on the response scale.

Table S10a Results of Bayesian multinomial regression analysis, comparing predators of clutches of ground-nesting passerine, wader, and 'other' species'. Data from island sites removed.

Table S10b Pairwise comparison of estimated marginal means (EMM) of each category, on the response scale. Data from island sites removed.

Table S11a Results of Bayesian multinomial regression analysis, comparing predators of passerine and wader clutches only. Data from island sites removed.

Table S11b Pairwise comparison of estimated marginal means (EMM) of each category, on the response scale. Data from island sites removed.

Table S12a Results of Bayesian multinomial regression analysis, comparing predators of wader clutches between three broad habitats: grassland, mixed and wetlands. Data from island sites removed.

Table S12b Pairwise comparison of estimated marginal means (EMM) of each category, on the response scale. Data from island sites removed.

889 **Table 1.** Models examined the number of nests depredated by each predator category (multinomial,
890 categorical). For each model, we show classification of: predators and avian prey; nest strata; and
891 habitat; in Model 1, prey type 'other' pools Raptor; Seabird; Galliformes; and Waterfowl. Life stage:
892 CL, clutch; BR, brood; *n*, sample size, number of predated nests; *n2* excluding island studies of
893 waders; habitat: F, Farmland; Wd, woodland; G, grassland; Mx, Mixed or mosaic habitats; C, Coastal.
894 For nest strata (Storchová & Hořák, 2018), 'Ground' combines ground (n = 169) and low-canopy (n =
895 3) nests, *versus* high-canopy. For details of predator categories and prey species identity, see Table 2.
896 Random categorical effects of year of data collection and study (may contain more than one nest-
897 group, see text) are included in all models.

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Model	**Predator groups**	**Prey groups**	**Life stage**	**Nest strata**	**Habitat**	***Year, Study***	***n***	***n2***
Prey groups model 1	3 classes (Bird, Mammal, Unknown)	Waders; Passerines; other	CL	Ground	All	+, +	419	294
Prey groups model 2	12 categories (excluding reptiles)	Waders; Passerines	CL	Ground	All	+, +	389	275
Life stage and nest strata 1	3 classes	Passerines	CL *vs*. BR	Ground *vs*. high-canopy	All	+, +	193	
Life stage and nest strata 2	13 categories (including reptiles)	Passerines	CL *vs*. BR	Ground *vs*. high-canopy	All	+, +	203	
Passerine habitat	3 classes	Passerines	All	All	Wd, Mx	+, +	174	
Wader habitat	3 classes	Waders	CL	Ground (all)	F, G, Mx, C	+, +	351	237

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Table 2. Species considered in predator and avian prey categories of statistical models (see Table 1). For each prey species, number of predated clutches and broods in the analysed dataset are given in parentheses (these may differ from sample sizes contributing to each statistical model).

	Class	Type	Species
Predator	Bird	Corvid	Carrion & Hooded Crows *Corvus corone & C. cornix* Western Jackdaw *Coloeus monedula* Eurasian Jay *Garrulus glandarius* Eurasian Magpie *Pica pica* Northern Raven *Corvus corax* Rook *Corvus frugilegus*
	Bird	Raptor	Common Buzzard *Buteo buteo* Eurasian Goshawk *Accipiter gentilis* Common Kestrel *Falco tinnunculus* Western Marsh Harrier *Circus aeruginosus* Peregrine Falcon *Falco peregrinus* Eurasian Sparrowhawk *Accipiter nisus* Tawny Owl *Strix aluco*
	Bird	Other Birds	Common Crane *Grus grus* Great Spotted Woodpecker *Dendrocopos major* gulls Common Pheasant *Phasianus colchicus*
	-	Reptile	Adder *Vipera berus*
	Mammal	Ungulate	deer (including *Dama dama, Muntiacus reevesi*) Domestic Sheep *Ovis aries*
	Mammal	Domestic Mammal	Cat *Felis catus* Dog *Canis familiaris*
	Mammal	Badger	European Badger *Meles meles*
	Mammal	Fox	Red Fox *Vulpes vulpes*
	Mammal	Hedgehog	European Hedgehog *Erinaceus europaeus*
	Mammal	Stoat	Stoat *Mustela erminea*
	Mammal	Other Mustelids	Eurasian Otter *Lutra lutra* Pine Marten *Martes martes* Least Weasel *Mustela nivalis*
	Mammal	Rodents	Brown Rat *Rattus norvegicus* Grey Squirrel *Sciurus carolinensis* other rodent (mouse *Apodemus* sp. or vole)
	Unknown		Predators that could not be identified
Prey		Passerine	Hawfinch *Coccothraustes coccothraustes (*2,2) European Nightjar[$] *Caprimulgus europaeus* (9,7) Eurasian Skylark *Alauda arvensis* (4,4) Spotted Flycatcher *Muscicapa striata* (15,12) Song Thrush *Turdus philomelos* (0, 3) Woodlark *Lullula arborea* (9, 48) Wood Warbler *Phylloscopus sibilatrix* (12, 76)
		Galliform	Western Capercaillie *Tetrao urogallus* (11)
		Seabird	Arctic Tern *Sterna paradisaea* (4) Little Tern *Sternula albifrons* (7)

		Wader	Common Snipe *Gallinago gallinago* (3) Common Redshank *Tringa totanus* (27) Common Ringed Plover *Charadrius hiaticula* (39) Eurasian Oystercatcher *Haematopus ostralegus* (31) Northern Lapwing *Vanellus vanellus* (167) Pied Avocet *Recurvirostra avosetta* (1) Black-tailed Godwit *Limosa limosa* (16) Eurasian Curlew *Numenius arquata* (48) Dunlin *Calidris alpina* (14) Eurasian Stone-curlew *Burhinus oedicnemus* (10)
		Waterfowl	Common Shelduck *Tadorna tadorna* (8) Horned Grebe *Podiceps auritus* (4)

$European Nightjar is a 'near-passerine', but has been included with passerines for analysis due to similar nesting ecology

Table 3. Nest camera data included in analysis, after screening out failed cameras, those not meeting the threshold number of monitored nests and uncertainty over timing of predation with regards to the life-history stage (clutch or brood). Studies are ordered by prey type (passerines and European Nightjar; raptors; seabirds; waterfowl; and waders). NG is the number of nest-groups within each study. For each nest-group, separately for clutch or brood stages, the number of nests predated: n_{pr}, and total monitored by nest cameras: n_t is shown as n_{pr} /n_t while [-] denotes no nests were monitored. Where numbers of nests monitored at clutch and brood stage were not given separately, the number of predation events reported separately for clutch and brood n_{pr}, is shown relative to the total of monitored nests across clutch and brood combined, n_T as {n_{pr} /n_T}. Unpublished sources are grouped by contributor; numbers in parentheses after the source (or research group) indicate separate sets of data each treated as a discrete 'study' (see Table 1). The spatial and temporal resolution at which nest predation was reported varied: studies that pooled across multiple years are shown as (…); multiple locations as (…). Habitat codes: F, Farmland; Mx, Mixed or mosaic habitats; Wd, woodland; G, grassland; HM, Heath/Montane; C, coastal; Wt, Wetlands; Ms, missing data. Camera types: Nest camera, far infrared miniature nest camera (Bolton et al. 2007); Trail NIR, near infrared trail camera; Trail FIR, far infrared trail camera; CAMBALL, near infrared Bradley CamBall 3. Data from Working for Waders has been published in Noyes et al. (2024).

Source	NG	Years	County/Region	Habitat	Prey	Clutch, n_{pr} /n_T	Brood, n_{pr} /n_T	Camera Type
Kirby *et al*. 2018	2	(2013-17)	(Welsh borders; N Wales)	Wd	Hawfinch	{2/19}	{2/19}	Nest camera
Langston *et al*. 2007	2	2003	S England	HM	European Nightjar	{2/8}	{0/8}	Nest camera
Dolman 2009	4	2008, 2009	East Anglia	Wd	European Nightjar	{2/18, 5/26}	{4/18, 3/26}	Nest camera
Morris & Gilroy 2008	2	2006	(England, 9 locations)	F	Eurasian Skylark	{4/29}	{4/29}	Nest camera
RSPB (1)	2	2007	Hampshire	Wd	Song Thrush	0/4	3/4	Nest camera
Bolton 2007	2	2005	Devon	Mx	Spotted Flycatcher	7/12	0/17	Nest camera
Stevens *et al*. 2008	2	(2005-06)	(SW England, East Anglia)	Mx	Spotted Flycatcher	8/48	12/53	Nest camera
Dolman 2009	4	2008, 2009	East Anglia	Wd	Woodlark	{4/66, 5/81}	{16/66, 22/81}	Nest camera
Eyre & Baldwin* (unpublished)	6	2010-2012	SE England	HM	Woodlark	0/13, 0/21, 0/14	5/19, 4/23, 1/17	Nest camera
Bellamy *et al*. 2018	4	(2009-13)	Wales, S England	Wd	Wood Warbler	{3/33, 2/65}	{27/33, 25/65}	Nest camera
Davis (unpublished)	2	2012	Hampshire	Wd	Wood Warbler	7/20	10/21	Nest camera
Davis (unpublished)	2	2013	Hampshire	Wd	Wood Warbler	0/13	14/22	Nest camera
McMillan *et al*. 2014	1	(2009-12)	Isle of Skye	Ms	Hen Harrier	[-]	9/19	Nest camera
Summers *et al*. 2009	1	(2003-07)	Scotland	Wd	Western Capercaillie	11/20	[-]	Nest camera
Isle of Man[$] (1)	1	(2014-15)	Isle of Man	C	Arctic Tern	4/4	[-]	Trail NIR
Isle of Man[$] (2)	1	(2014-17)	Isle of Man	C	Little Tern	7/7	[-]	Trail NIR
WWT (1)	2	2021	Lancashire	Wt	Common Shelduck	4/8	[4]	Trail NIR

Source	NG	Years	County/Region	Habitat	Prey	Clutch, n_{pr} /n_T	Brood, n_{pr} /n_T	Camera Type
Perkins, *et al*. 2005	2	2001	N Scotland	Wt	Horned Grebe	1/7	0/7	Nest camera
Perkins, *et al*. 2005	2	2002	N Scotland	Wt	Horned Grebe	3/15	2/15	Nest camera
BBC	1	2021	Norfolk	G	Pied Avocet	1/10	[-]	CAMBALL
RSPB (2)	2	2016, 2017	Cambridgeshire	G	Black-tailed Godwit	3/14, 6/12	[-]	Nest camera
RSPB (2)	1	(2019, 2022-23)	Cambridgeshire	G	Black-tailed Godwit	7/9	[-]	Nest camera
Calladine, *et al*. 2017	1	(2012-14)	(Outer Hebrides, 2 locations)	G	Common Snipe	3/6	[-]	Trail NIR
Zielonka, *et al*. 2019	1	2018	East Anglia	G	Eurasian Curlew	6/10	(-)	Nest camera
GWCT (1)	1	(2018-23)	Aberdeenshire	G	Eurasian Curlew	3/15	[-]	Trail NIR
RSPB (3)	1	2021	East Ayrshire	G	Eurasian Curlew	4/7	[-]	Trail FIR
RSPB (4)	3	2021-23	Highland	Mx	Eurasian Curlew	0/7, 3/16, 7/28	[-]	Trail NIR
RSPB (5)	1	2023	Northumberland_1	G	Eurasian Curlew	1/5	[-]	Trail NIR
RSPB (5)	1	2023	Northumberland_2	G	Eurasian Curlew	1/5	[-]	Trail NIR
RSPB (6)	1	2023	Lancashire	G	Eurasian Curlew	4/17	[-]	Trail NIR
Working for Waders (1)	2	2022, 2023	Perthshire	F	Eurasian Curlew	6/19, 1/11	[-]	Trail NIR
Curlew Recovery	1	2023	Yorkshire	Ms	Eurasian Curlew	3/7	[-]	Trail NIR
WWT (2)	2	2022, 2023	Gloucestershire	G	Eurasian Curlew	3/15, 1/15	[-]	Trail NIR
Grosvenor Estate	3	2021-23	Lancashire	G	Eurasian Curlew	0/6, 1/13, 4/12	[-]	Trail FIR
Calladine, *et al*. 2017	1	(2012-14)	(Outer Hebrides, 2 locations)	G	Dunlin	14/62	[-]	Trail NIR
Sharpe 2006	1	2004	(N Wales, 3 locations)	G	Northern Lapwing	9/33	[-]	Nest camera
GWCT (2)	6	2018-23	Aberdeenshire	G	Northern Lapwing	2/18, 3/22, 3/31, 21/54, 16/56, 14/49	[-]	Trail FIR
RSPB (7)	1	2010	Somerset	G	Northern Lapwing	1/8	[-]	Nest camera
RSPB (7)	1	2011	Somerset	G	Northern Lapwing	5/12	[-]	Nest camera
RSPB (8)	4	2011-14	Oxfordshire	G	Northern Lapwing	6/20, 3/9, 5/15, 3/5	[-]	Nest camera
RSPB (8)	1	(2015-17)	Oxfordshire	G	Northern Lapwing	8/8	[-]	Nest camera
RSPB (9)	1	(2015-19)	Cambridgeshire	G	Northern Lapwing	2/16	[-]	Nest camera
RSPB (10)	1	2023	Lancashire	F	Northern Lapwing	1/4	[-]	Trail NIR
RSPB (11)	2	2019, 2021	S Lanarkshire	G	Northern Lapwing	2/8, 8/16	[-]	Nest camera
Working for Waders (2)	1	2022	Perthshire	F	Northern Lapwing	4/18	[-]	Trail FIR
Calladine, *et al*. 2017	1	(2012-14)	(Outer Hebrides, 2 locations)	G	Northern Lapwing	51/93	[-]	Trail NIR
Working for Waders (3)	1	2022	Perthshire	F	Eurasian Oystercatcher	9/23	[-]	Trail FIR

Source	NG	Years	County/Region	Habitat	Prey	Clutch, n_{pr} /n_T	Brood, n_{pr} /n_T	Camera Type
GWCT (3)	6	2018-23	Aberdeenshire	G	Eurasian Oystercatcher	0/5, 1/7, 3/17, 2/6, 3/7, 4/19	[-]	Trail FIR
RSPB (12)	1	2023	Lancashire	G	Eurasian Oystercatcher	2/4	[-]	Trail NIR
Essex Wildlife Trust (1)	1	2023	Essex	C	Eurasian Oystercatcher	7/7	[-]	Trail FIR
RSPB (13)	1	2011	Oxfordshire	G	Common Redshank	2/6	[-]	Nest camera
Calladine, *et al*. 2017	1	(2012-14)	(Outer Hebrides, 2 locations)	G	Common Redshank	25/56	[-]	Trail NIR
Calladine, *et al*. 2017	1	(2012-14)	(Outer Hebrides, 2 locations)	G	Common Ringed Plover	17/64	[-]	Trail NIR
Isle of Man[$] (3)	1	(2015, 2017-18, 2020)	Isle of Man	C	Common Ringed Plover	4/4	[-]	Trail NIR
Essex Wildlife Trust (2)	1	2023	Essex	C	Common Ringed Plover	18/18	[-]	Trail FIR
BTO	1	(2011-12)	Wiltshire	G	Eurasian Stone-curlew	10/21	(-)	Nest camera

[$]Isle of Man Government, Department for Environment, Food, and Agriculture. *subset of data published in Eyre and Baldwin (2014) who also reported two additional predation events of clutches by Carrion Crow in 2010 and 2012; these were excluded from analysis due to initial uncertainty regarding nest stage.

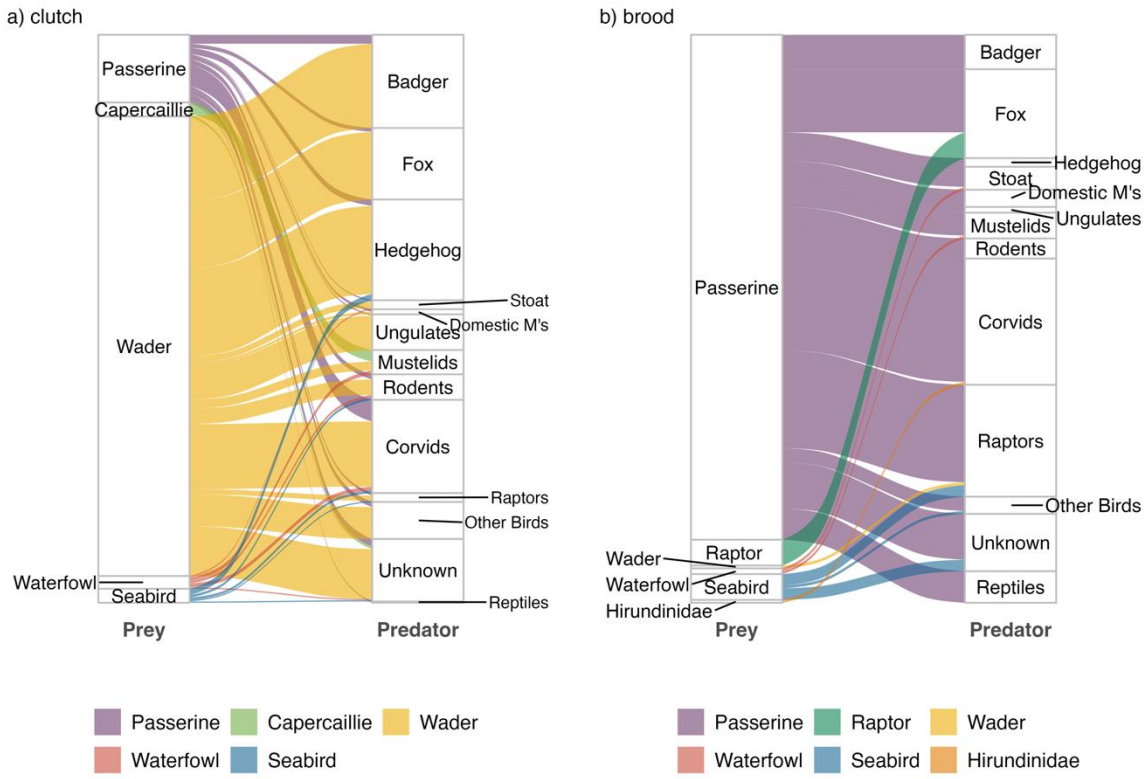

Figure 1. Schematic showing relations between categories of avian nest prey species and predators, separately for (a) clutch and (b) brood. All data, including opportunistic records, are included. The height of the axis panels and width of bars indicates the corresponding proportions of all predated clutches or broods. Domestic M's are Cat and Dog.

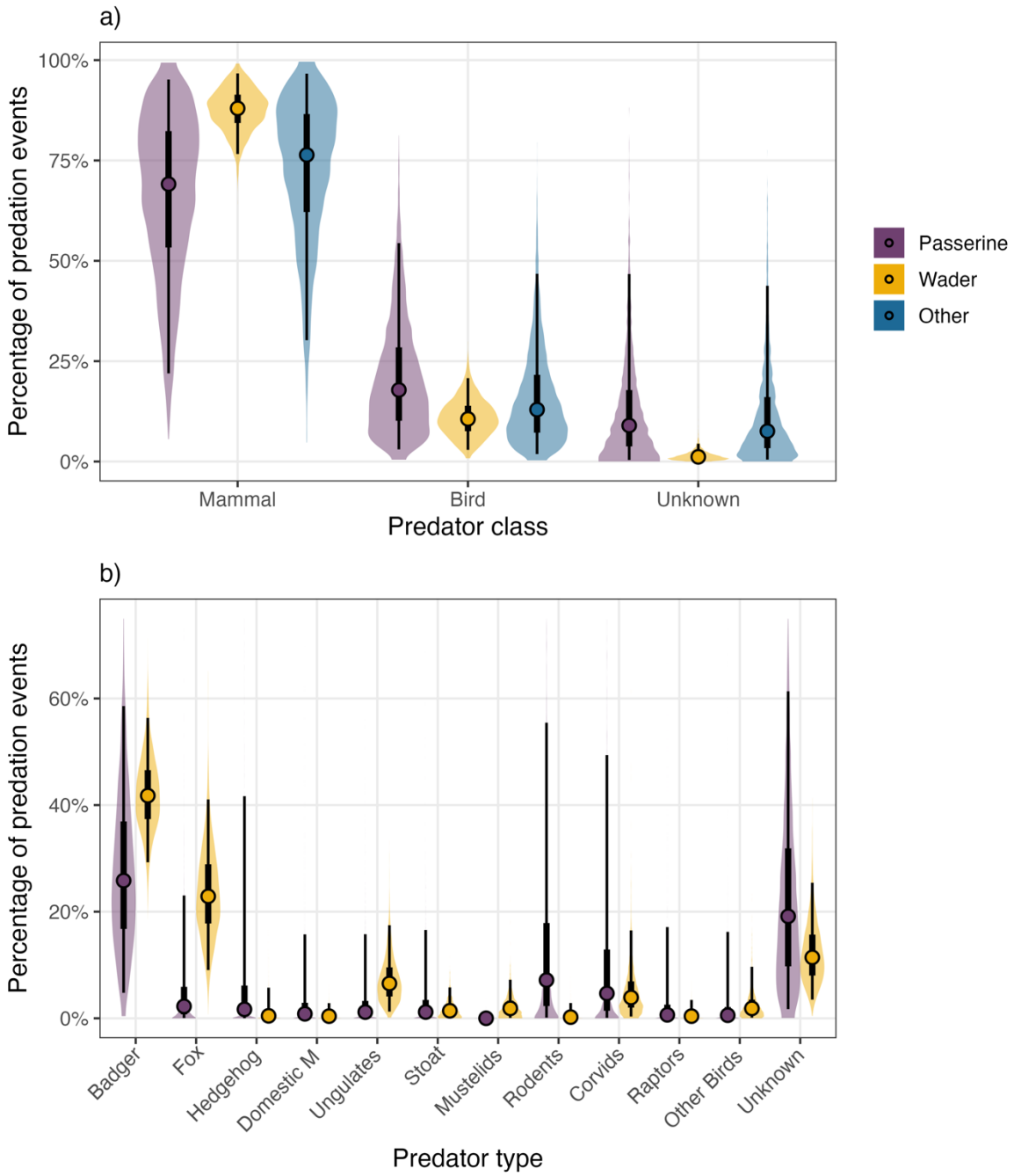

Figure 2. Contribution of predator categories to predation of clutches of (a) passerines, waders and other species (considering predator classes), and (b) passerines and waders only (considering 12 predator categories). Shown are predictions drawn from the posterior distribution of the models: points are the median values from the posterior draws, thick bars the 50% credible intervals, thin bars 95% credible intervals and violin shading the spread of data, from 200 draws of the posterior distribution.

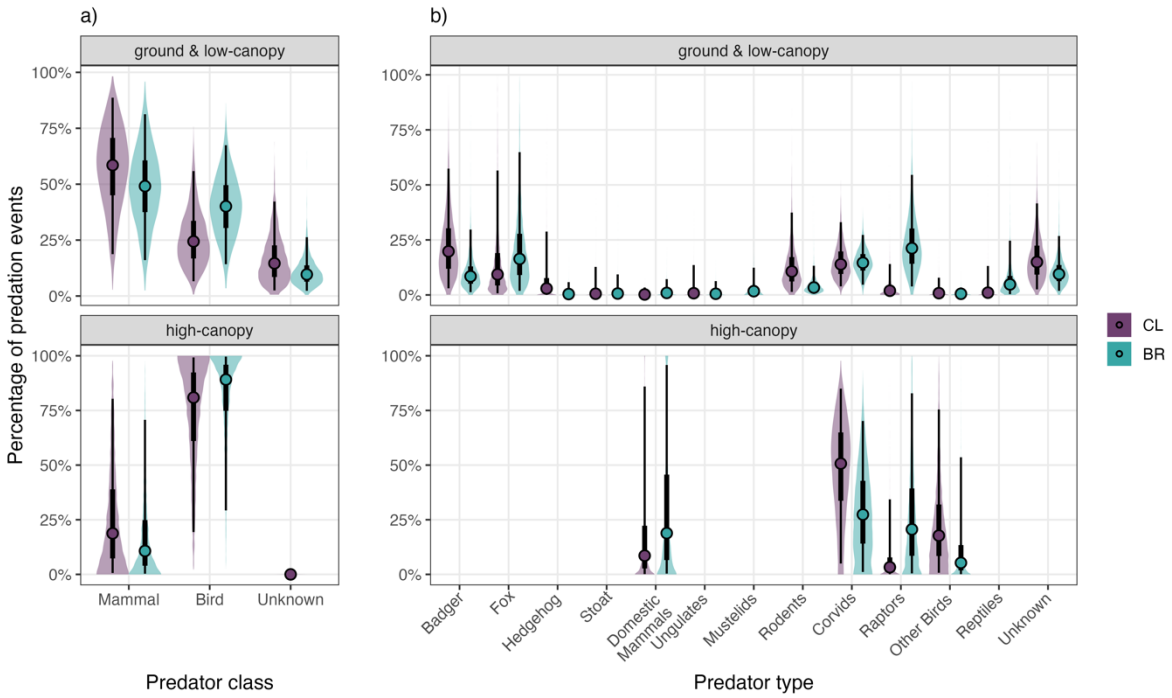

Figure 3. Contribution of (a) predator classes (b) 13 finer predator categories, to predation of passerine clutches (CL) or broods (BR), shown separately for nesting strata (ground and/or low-canopy, *versus* high-canopy). Shown are predictions drawn from the posterior distribution of the models: points are the median values from the posterior draws, thick bars the 50% credible intervals, thin bars 95% credible intervals and violin shading the spread of data, from 200 draws of the posterior distribution, with percentages calculated for each life-stage:nest strata group. Note that missing points reflect instances where no predation events were captured.

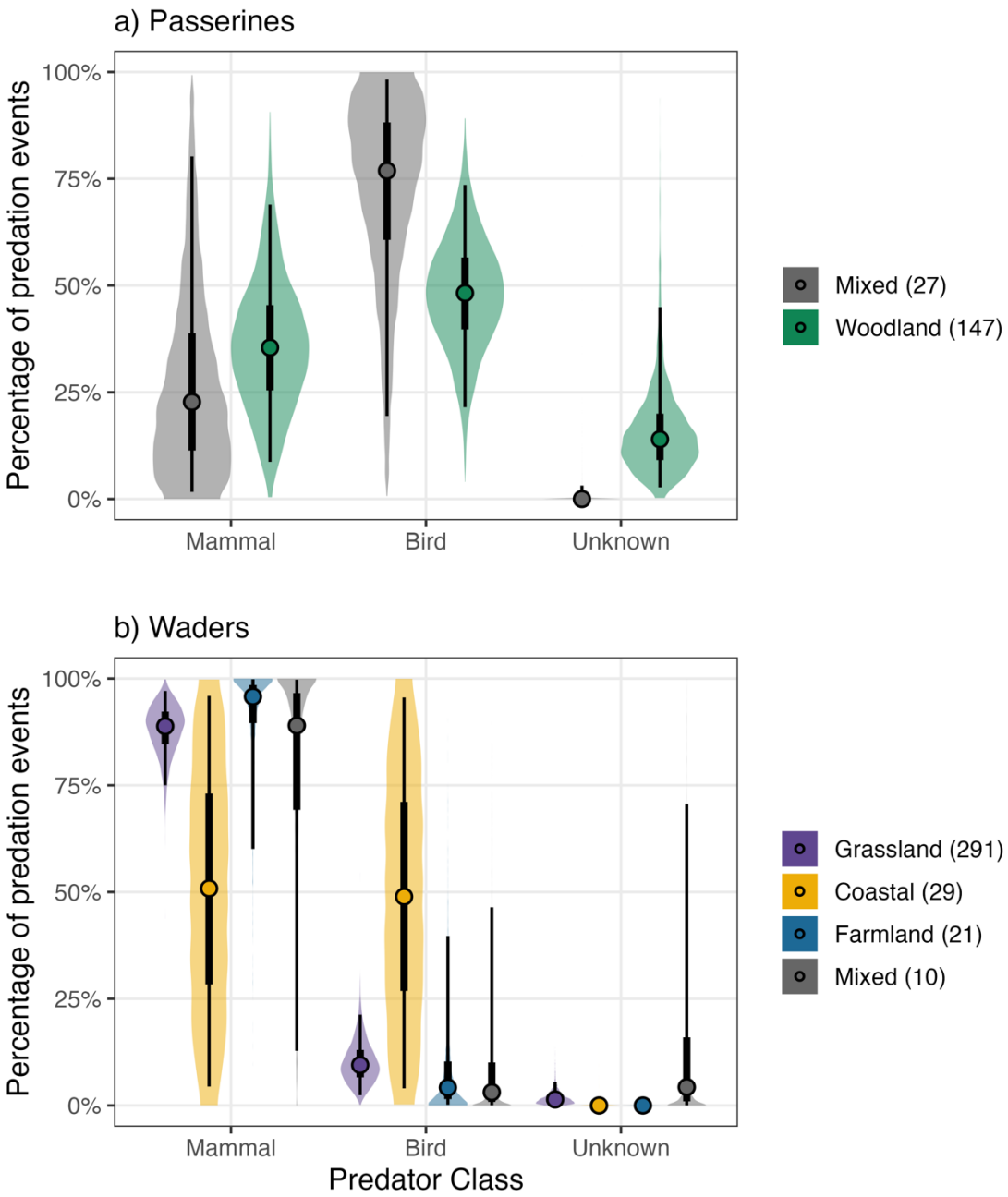

Figure 4. Contribution of predator classes to predation of clutches of (a) passerines and (b) waders, compared among broad habitat categories (with number of predated nests in parentheses). Shown are predictions drawn from the posterior distribution of the models: points are the median values from the posterior draws, thick bars the 50% credible intervals, thin bars 95% credible intervals and violin shading the spread of data, from 200 draws of the posterior distribution.