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RESEARCH

Mapping mammalian meadow bird nest predators in a Dutch dairy farming landscape

Rienk W. Fokkema[1,2] · Egbert van der Velde[1,2] · Marie Stessens[1,2] · Daan Bos[3] · Ondřej Belfín[1,2] · Margje E. de Jong[5,6] · Jos C. E. W. Hooijmeijer[1,2] · Theunis Piersma[1,2,4]

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Abstract

Widespread changes in the European agricultural system have brought about drastic changes in food web interactions, including those between meadow birds and their (nest) predators. Mammals are considered the main nest predators, yet our current knowledge of predator communities in agricultural landscapes is limited. Using camera traps across 11 500 ha of dairy-farming land in Southwest Friesland, The Netherlands, during three spring seasons we monitored: (1) predator presence and (2) actual predation on black-tailed godwit (*Limosa limosa limosa*) nests. During 2021-2023 we detected 11 species of potential mammalian meadow bird predators. The top six, with a daily presence of ≥ 5%, were: domestic cat (*Felis catus*), brown rat (*Rattus norvegicus*), European badger (*Meles meles*), red fox (*Vulpes vulpes*), beech marten (*Martes foina*) and European polecat (*Mustela putorius*). There were marked, and for most species consistent, differences in spatial distribution, with positive co-occurrence of badgers and foxes. Across the three study years, red foxes were the most consistent predators of godwit nests, whereas domestic cats and brown rats predated very few nests despite their high presence. Patterns over the years indicated that as beech marten nest predation diminished, red fox nest predation increased. We suggest that (1) the presence of predator species alone is not an accurate reflection of their actual nest predation, and (2) the presence of single predator species, and their effects on, meadow birds should be assessed in context of the whole predator community.

Keywords Conservation · Ground-nesting · Depredation · Conflict · Food web · Wildlife camera

✉ Rienk W. Fokkema
rienkfokkem@gmail.com

[1] Conservation Ecology Group, Groningen Institute for Evolutionary Life Sciences (GELIFES), University of Groningen, Nijenborgh 7, 9747 AG Groningen, The Netherlands

[2] Centre for Global Ecological Change at the Faculties of Science & Engineering and Campus Fryslân, BirdEyes, University of Groningen, Wirdumerdijk 34, 8911 CE Leeuwarden, The Netherlands

[3] Wildlife Management, van Hall Larenstein, University of Applied Sciences, Agora 1, 8934 CJ Leeuwarden, The Netherlands

[4] Department of Coastal Systems, NIOZ Royal Netherlands Institute for Sea Research, P.O. Box 59, 1790 AB Den Burg, Texel, The Netherlands

[5] Arctic Centre, University of Groningen, PO Box 716, 9700 AS Groningen, the Netherlands

[6] Department of Behavioral and Cognitive Biology, University of Vienna, Djerassiplatz 1, 1030 Vienna, Austria

Introduction

Over the past century, more and more of the Earth's surface has been converted into agricultural land, whilst the use of existing agricultural areas has intensified following technological and chemical innovations (Foley et al. 2005; Bos et al. 2013; Silva-Monteiro et al. 2021). The Netherlands is a clear example of a country where agriculture has intensified fast and comprehensively, especially after the Second World War (Donald et al. 2001; Herzog et al. 2006; Karel 2010; Bos et al. 2013). Initially, in the first half of the 20th century, the level and extent of agriculture gradually intensified and created new opportunities and habitat beneficial for ground-nesting bird species of which the natural breeding grounds were disappearing (Beintema 1991; Bignal and Mccracken 1996; Silva-Monteiro et al. 2021). Simultaneously, predator presence diminished which was associated with intensive persecution and the pesticide DDT lowered avian predator survival and reproduction (Rutz et al. 2006; Freuling et al. 2013; Padayachee et al. 2023). Although it remains unclear

to what extent agricultural landscape changes and a release from predation contributed as a cause, in the 1960s meadow bird species such as black-tailed godwits (*Limosa limosa limosa*) and northern lapwings (*Vanellus vanellus*) reached historical population peaks (Beintema 1991; Groen et al. 2012; Silva-Monteiro et al. 2021). Meadow birds, including egg searching and harvesting, became an integral part of Dutch culture (De Rijk 2015).

In the past decades, however, populations of meadow birds have been in steep decline in Europe (review by Silva-Monteiro et al. 2021). In The Netherlands, the black-tailed godwit, which was elected the country's national bird in 2015, showed a consistent long-term annual population decrease of approximately 5% (Kentie et al. 2016; Sovon 2024). This decline is mainly linked to agricultural land-use having become limited to monocultures, with a high input of slurry manure, the use of pesticides, the implementation of low water tables, earlier and more frequent mowing and frequent reseeding and crop rotation (Beintema 1991; Donald et al. 2001; Kleijn et al. 2010; Groen et al. 2012; Onrust and Piersma 2019; Silva-Monteiro et al. 2021; Craft et al. 2022). Currently, the largest part of the dwindling meadow bird populations takes refuge in fragmented reserves and fields administratively covered by Agri-Environmental Schemes ('AES'; Groen et al. 2012; Kentie et al. 2014; Li et al. 2023; Barba-Escoto et al. 2024). Conservation organizations and farming collectives attempt to safeguard these remaining fragmented populations supported by targeted government funding (Kleijn et al. 2001, 2010; Roodbergen and Teunissen 2014). However, despite these efforts, populations are still in decline and Black-tailed godwits (*Limosa limosa*) are currently listed as near threatened ('NT') on the IUCN red list (Breeuwer et al. 2009; Birdlife International 2017). More and more organisations are calling for nature-inclusive ways of farming and, at the same time, the creation and improvement of larger scale meadow bird reserves to counteract this trend (Newton 2004; Teunissen et al. 2012; Bos et al. 2013).

An important potential side effect is that the clustered distributions of the remaining meadow bird populations could make them more susceptible to predators (Marzluff and Ewing 2001; Chalfoun et al. 2002). Over a period of 40 years, from 1970 to 2010, the predation of nests of meadow birds in The Netherlands steadily increased (Roodbergen et al. 2012). During this time, mammalian predators such as red foxes (*Vulpes vulpes;* hereafter called 'fox'), beech martens (*Martes foina*), and European badgers (*Meles meles;* hereafter called 'badger') became more widespread and numerous (Deinet et al. 2013). Furthermore, invasive alien species such as the raccoon dog (*Nyctereutes procyonoides*) invaded from the east (Kauhala and Kowalczyk 2011; Mulder 2013). Free-ranging domesticated cats (*Felis catus*) are present throughout in urban and agricultural areas (Trouwborst and Somsen 2021). Smaller mammalian predators such as the weasel (*Mustela nivalis*), stoat (*Mustela erminea)* and European polecat (*Mustela putorius;* hereafter called 'polecat') have a more uncertain status, with populations declining due to loss of shelter and breeding places in the increasingly 'organized' landscapes (Hofmeester et al. 2019; Thissen and van Norren 2020; van Uchelen 2021).

To study the interaction between the ground-nesting birds and the different mammalian species potentially predating meadow bird nests, camera traps at nests are widely used to survey nests and their fate (Teunissen et al. 2006; Krüger et al. 2018; Salewski and Schmidt 2022). While this documents which species are emptying nests, nest photos do not show the spatial and temporal distribution patterns of the predators concerned. This limits our understanding of the actual role of predators in observed rates of nest predation relative to their presence. Furthermore, the mere presence of predators may also exert indirect, nonconsumptive effects, for instance by affecting the decisions of meadow birds where to breed (Lima 2009; Abbey-Lee et al. 2016).

To address the knowledge gap about predator distributions, we developed a study design to monitor the spatial and temporal presence of the elusive nocturnal mammalian predators in an agricultural landscape managed for dairy farming, using the customary nest monitoring in combination with a stratified randomized grid of camera traps. By employing the grid at similar locations three springs in a row, we set out to explore: (1) which mammalian predator species were present in our study area, (2) the consistency and correlations in the spatial distribution of the different predators over the study years and (3) the relation between the presence of mammalian predator species and the actual observed rates of photo-captured predation of black-tailed godwit nests, and specifically how this relation varied over the study years.

Material and methods

Study area and species

Our study took place during the springs of 2021–2023 in an area of dairy farming in southwest Friesland, The Netherlands (52°57'N, 5°27'E). The study area of 11 486 ha was subdivided into 3218 individual fields, a mosaic with different land-use intensities (Howison et al. 2018). Large parts of the study area are highly productive monocultures interspersed with smaller areas consisting of meadow bird reserves managed by conservation organizations, as well as AES parcels managed by farming collectives (Barba-Escoto et al. 2024.). In terms of predator species control during the study years, foxes, free-roaming domestic cats, brown rats and beech martens were allowed to be culled with certain restrictions. For domestic cats, brown rats and foxes culling occurred throughout the area, while beech martens were

killed specifically in only two sub-areas with high meadow bird densities (see discussion for further details). Meadow bird populations in the study area have been monitored since 2004, with a focus on black-tailed godwits (hereafter called 'godwits'; Groen et al. 2012; Kentie et al. 2018; Verhoeven et al. 2022). During the years of our study, we estimated the godwit breeding population in our study area at around 1800 individuals (Hooijmeijer et al. 2024). Godwits are ground-nesting birds with cryptic nests and nesting behaviour. They commonly lay four eggs and have precocial chicks that are guided by both parents until fledging at 3.5–4 weeks of age (Beintema et al. 1995). Godwits winter in western Africa and Iberia and migrate back to north-western Europe to breed in spring (Verhoeven et al. 2021), with about 87% of the NW-European population breeding in The Netherlands (Kentie et al. 2016).

Monitoring relative predator presence

To obtain an index of predator presence in our study area, to make comparisons over space and time, we deployed a fixed camera grid during the springs of 2021–2023. In March 2021, we set up 60 camera locations, which were maintained at the same location during the other study years, with some minor adjustments (see further below). We used Browning 2018 Dark Ops Pro XD (Model type BTC-6PXD). These camera traps had a 0.2s reaction time when an animal first appeared in the camera's detection range. When triggered the camera traps took a burst of eight pictures with a 0.3 s recovery time between pictures. After the burst of eight pictures, the camera waited 1s before being responsive again. The camera traps had no infrared glow with a 28 m range of flash, 24 m range of detection, an image angle of 42°, and they were soundless. We set the traps to Central European Time (CET).

We deployed the camera traps at fixed locations based on a structured randomized grid to reduce the dependency of our sampling points on variation within the landscape. To assign the 60 locations, a grid of locations which were at least 500 meters from one another was overlaid on the study area. From these locations, 467 suitable locations were chosen based on the following criteria: (1) they had to be on land (a portion of our study area consists of waterbodies) and (2) they had to be at least 100 m from villages/buildings and not on or very close to main roads (to prevent theft and too many people and domestic animals on the pictures). We chose 120 of the 467 locations using a randomized number with the rand() function in Excel (Microsoft 2021). The fields in our study area are typically bordered by water-filled ditches and can be accessed by one or more field entrances. From GPS-tracking studies we know that predator species commonly use these field entrances to traverse the area (Jonge Poerink and Dekker 2020). Therefore, for each of the 120 selected random sampling points, we allocated the nearest field entrance as the actual camera trap location using Google Earth (Google inc.). The first 60 of these locations were the primary locations and the next 60 locations were backup locations in case one of the primary locations could not be used.

Overall, we realized 42 of the primary locations within 250 m of the assigned GPS point and seven of the secondary locations within 250 m of the assigned GPS point (total: 82% realized). In 11 cases we placed the camera trap >250 m from the primary or the secondary assigned GPS point (on average at 514 m distance, range 264–1003 m from the assigned location). After placement, the average distance between camera traps and their closest neighbouring camera trap was 1051 m (range 609 – 1957 m). Reasons for not being able to place the camera at the primary location were: (1) no permission from the landowner, (2) cattle grazing on either side of the field entrance and thus a too large risk of damage to the camera and data overflow, (3) the field entrance being unsuitable as no predators could go across, i.e. impermeable gate and (4) practical reasons such as maintenance logistics.

We placed the camera traps at one side of the field entrance facing a northwest-northeast direction to prevent the glare of the sun from causing false triggers and to make sure they were safe from agricultural activities. We painted the camera traps 'meadow-green' and fitted them on specially designed poles in the same colour on which the camera was attached 50 cm from the ground to the base of the camera trap. On top of the pole, anti-pigeon pins were mounted to prevent birds using it as a perch. By using the option 'motion test' on the camera and adjusting the direction, we checked whether the camera detected movement across the entire field entrance. We placed camera traps as such that they had a diagonal view of the field entrance to see approaching animals already from further away and to get both pictures from the front as well as the side of the animal. We used no bait at the locations. This setup was suitable to quantify the occurrence of larger predators, smaller species such as stoats and weasels may have been partly missed (Rowcliffe et al. 2011; Hofmeester et al. 2017), especially when vegetation was higher.

Every 3–4 weeks we changed the SD card and every six weeks the batteries. Every period between an SD card swap is termed 'a deployment'. Near the end of the camera period in May, we trimmed vegetation in front of the camera traps to prevent false triggers and blocked view. Due to local circumstances, we moved four camera locations to a nearby field entrance in 2022 (average ± SD: 172 ± 114 m) and one in 2023 (317 m).

To annotate the pictures, we grouped them per deployment in sequences of two minutes. We processed all pictures using artificial intelligence (AI) in the program Agouti

(v1-v4a, Liefting et al. 2022). Next, all sequences with mammalian predators identified by the AI were manually checked (for an overview of the classified and unclassified sequences per year see Table S1). For the 2021 dataset, we formally evaluated the accuracy of the identification algorithm of Agouti using confusion matrices (for more details see: Bos et al. 2022). The accuracy was high for the detected mammalian predator species (range 87–98% correct), though manual corrections were necessary. As a random check of 1619 unclassified sequences in 2021 revealed that 15% contained detections of our target predators, we checked all sequences that were not classified by the AI and corrected the classification manually when required. Due to logistical constraints, we focused on the time of day of which we knew from the camera trapping data that most additional predator data could be gained, as that was when they were predominantly active (between 17h00 and 08h00 CET; 96% of all predator detections in this period in the springs of 2021 and 2022). For the spring data of 2023 we further narrowed this time period down to minimize the processing time (between 18h00 and 05h00 CET; 91% of all predator detections in this period in spring 2021–2022). For all three study years, we restricted the analyses of the camera grid data to between 15 March and 31 May, a period when vegetation was low enough to not cause many false triggers, or obscure passing species.

Monitoring nest predation

In addition to measuring the presence of predators in our study area, we also aimed to quantify the contribution of various species to nest predation rates. To this end, during April, May and the first half of June we searched the fields in our study area for godwit nests (for protocol see: Kentie et al. 2015; Hooijmeijer et al. 2024). Each year, we monitored nearly a quarter of all found nests using camera traps (2021: 22%, 2022: 25%, 2023: 24%; for a complete overview see Table S2) distributed across godwit breeding sites in our study area (Fig. S3). Camera traps (mostly Browning 2018 Dark Ops Pro XD and some Browning 2020 Patriot and Reconyx HF2X Hyperfire 2 & HC600) were placed, preferably in a NW/NE direction (to prevent sun glare), at a 2–3 m distance from incubated nests, to minimize chances of abandonment of the brood. Nests were visited weekly or, if possible, checked from a distance using binoculars or a telescope to determine their fate.

A nest was deemed potentially predated when remains of eggs or unhatched chicks were found or when the nest was suddenly empty before the expected time of hatching (determined by an egg flotation method: Liebezeit et al. 2007). The exact fate of camera monitored nests was determined by assessing the pictures collected using the camera traps in detail from the last picture to the moment of predation to determine the predator species responsible for the predation event. We took care to also look further back in the sequence to see if multiple predators were responsible and/or to determine whether the birds had already abandoned the brood before predation.

Statistics

We performed all data analyses in R version 4.3.2 (R Core Team 2023). We focused all analyses on six species which were overall detected ≥ 5% of the days during which the camera traps were deployed, namely fox, badger, beech marten, polecat, domestic cat and brown rat (see section "Mammalian predator species in the study area and spatial distribution" of Results and Fig. 1).

To analyse variation in the site-specific daily presence of the six focal species over the years we used generalized linear mixed-effects models (GLMM, R package lme4, Bates et al. 2015), with the number of days a species was seen and not seen per camera location as a combined response variable and using a binomial distribution (Crawley 2012). We added species and year and their interaction as predictors, and camera site as a random effect to account for non-independence in the dataset. In addition, we fitted an observer level random effect to account for overdispersion, which became apparent after we first fitted our full model (Harrison 2015). We analysed the differences in the number of camera sites where species were observed between the study years using a generalized linear model (GLM, R package stats, R Core Team 2023) with the number of locations each species was seen as a response variable and a Poisson distribution. We fitted species and year as predictor, but not their interaction as the dataset proved too small (N=18 records) for such a complex model. We assessed the predictability in the presence of species over the camera grid during the study years using a GLM with a binomial distribution, and the probability that species were seen at each location in 2021 as a predictor for the probability that the species was seen in 2022. We included species as a factor as well as the interaction between the probability to be seen in 2021 and species to allow for species specific effects. We used an equivalent model to test how well the observed distribution of species in 2021 still explained their observed distribution in 2023. For all models, we performed model selection based on the Akaike Information Criterion with a correction for small sample sizes (AICc), using the cumulative Akaike weight ≤ 0.95 to select the best fitting model(s) (Symonds and Moussalli 2011). In all cases there was one clear best fitting model based on the cumulative Akaike weight. We performed post hoc contrasts of main effects or interactions within the selected model(s) using the emmeans package (Lenth 2024).

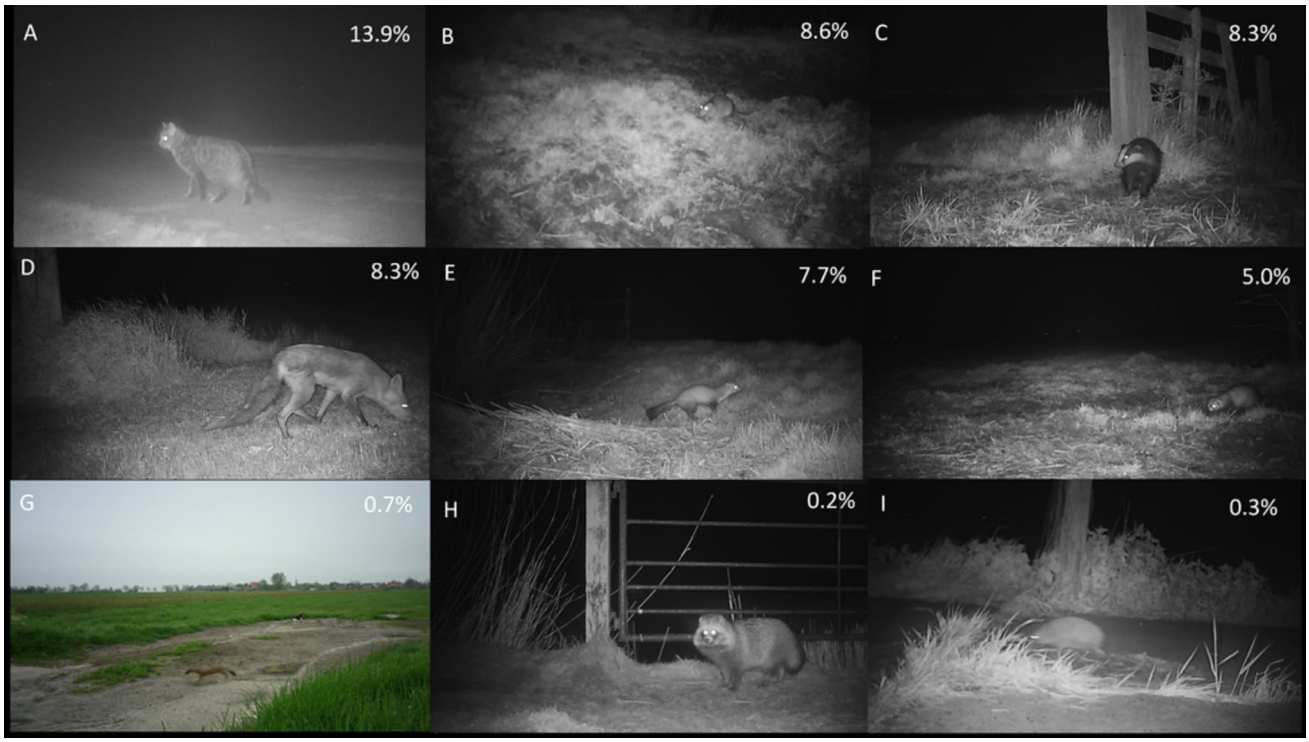

Fig. 1 Collage of known mammalian egg and/or chick predator species of black-tailed godwits captured on our camera grid. The percentage represents the overall number of days each species was detected across all sites, divided by the total of camera trapping days in 2021–2023 (11189 days). **A**=domestic cat, **B**=brown rat, **C**=European badger, **D**=red fox, **E**= beech marten, **F**=European polecat, **G**=stoat/weasel, **H**=raccoon dog, **I**=hedgehog

We examined correlations in the site-specific daily presence, i.e. fraction of unique days on which a predator was detected divided by the total of days the camera was active at the location, of the different species using a correlation matrix using the package 'corrplot' (Wei and Simko 2021). Significance tests in this package were at $p = 0.05$ and based on Kendall correlation tests.

For our analysis of nest predation by the six focal species, we had two cases in our dataset where two species of predator were responsible for nest loss. In this case we only used the first predator in the analysis, as the second one may have followed the first or the scent left after the predation (Holopainen et al. 2020). We furthermore focused our analysis only on predation which happened before hatching, excluding one case where a beech marten predated the hatchlings. This led to a total dataset of 134 predated nests by the focal species, all of which failed completely after predation. In most cases the broods failed directly after predation, 129 nests were completely emptied. Five nests were partially depredated; in two cases the eggs were abandoned and in the three others incubation was re-commenced, but the same species of nest predator came again. In the latter three cases the species of predator was only counted once.

To examine the relation between our acquired index of predator presence and our index of predator predation rates, we interpreted the recorded share of each focal predator species in the total nest predation by all focal species in relation to their share in the overall number of days each focal predator was detected (for maps on the spatial occurrence of nest predation, see Figs. S4-S6). We used two-sided binomial tests at a 95% confidence level to evaluate, for the total dataset as well as for each study year, whether the six focal predator species were predating nests relatively less, more or equal to the index of their overall presence as revealed by our camera grid.

Results

Mammalian predator species in the study area and spatial distribution

We observed 11 potential mammalian meadow bird predator species (based on: Teunissen et al. 2008; Krüger et al. 2018) in our study area (Fig. 1). Six species were detected ≥ 5% of the camera trapping days combined across 2021–2023: the domestic cat, brown rat, European badger, red fox, beech marten and the European polecat (from highest occurrence to lowest, see Fig. 1). These constitute our six focal species in subsequent analyses. Domestic

dogs (*Canis lupus familiaris*) were also detected (1.2% of the days) in all years; however, this was mostly when they were under control by their owners and not roaming alone and are therefore not listed in Figure 1. Weasel, stoat, raccoon dog and hedgehog (*Erinaceus europaeus*) were also observed in our study area but detected far less often (Fig 1; observations of weasel or stoat are combined).

Overall, there were marked spatial differences in the presence of the six focal species over the study area (Figs. 2 and 3). The number of sites visited was different per species (top model: Tables S3 and S6). Badgers were less widespread, i.e. detected at fewer camera sites, than domestic cats (estimate: −0.55, z-ratio: −3.79, $p<0.01$), beech martens (estimate: −0.50, z-ratio: −3.44, $p<0.01$) and polecats (estimate: −0.45, z-ratio: −3.07, $p<0.05$). Foxes and brown rats did not differ in how widespread they were from any of the other species.

In terms of the overall presence in the study area from 2021–2023, domestic cats were observed most days relative to the total number of days all camera traps were deployed, followed by brown rats, badgers, red foxes, beech martens and polecats (Fig. 1). We examined these patterns in detail at the level of the camera sites for each year. We found that site specific daily predator presence differed between species (top model: Tables S4 and S7). In terms of species differences, domestic cats had a higher site specific daily presence than the other species (cat mean presence relative to: beech marten, estimate: 0.79, z-ratio: 3.305, $p<0.05$; fox, estimate: 1.04, z-ratio: 4.226, $p<0.01$; polecat, estimate: 1.11, z-ratio: 4.581, $p<0.01$; brown rat, estimate: 1.35, z-ratio: 5.403, $p<0.001$; badger, estimate: 1.57, z-ratio: 6.177, $p<0.001$). Beech marten, fox, polecat and brown rat did not differ from each other in their site-specific daily presence. Badgers, however, had a lower site-specific daily presence than beech

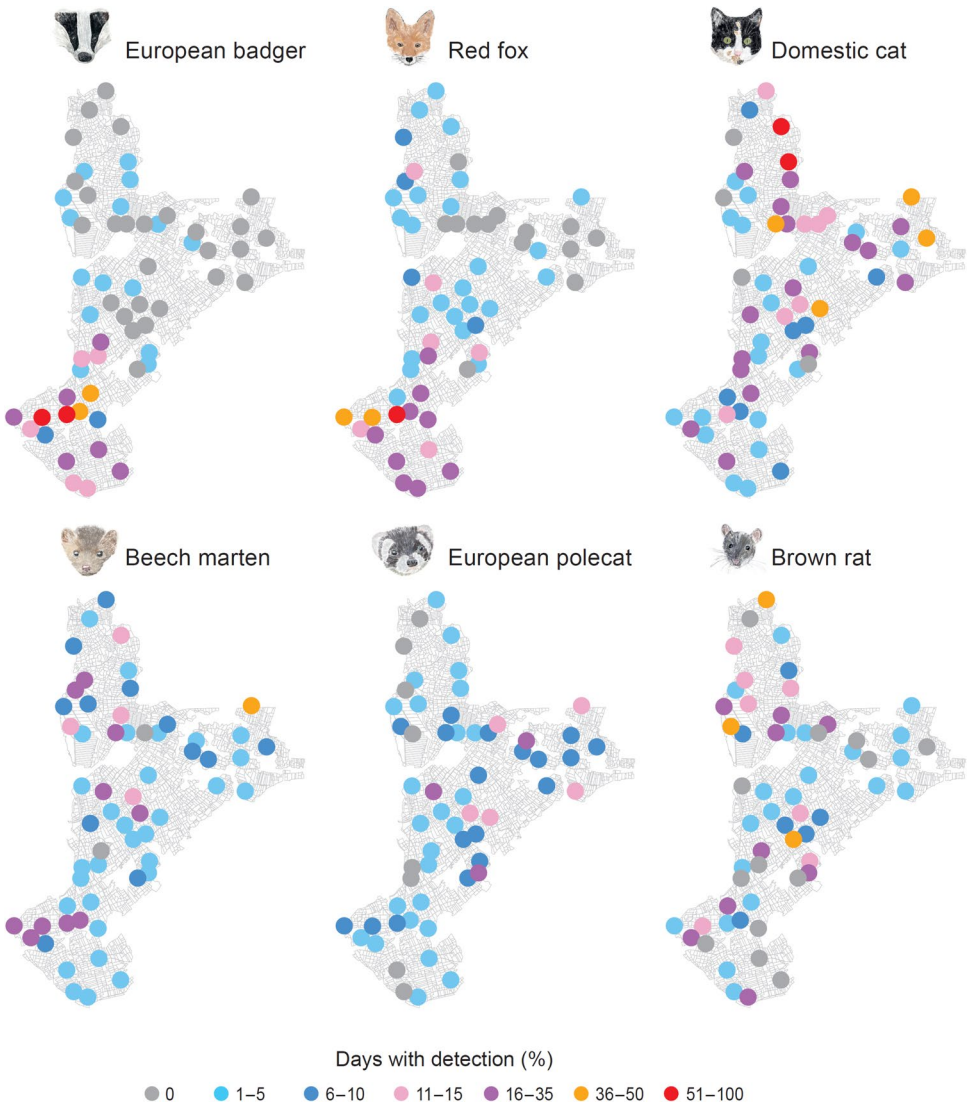

Fig. 2 The spatial distribution of the six focal mammalian meadow bird predators monitored by the camera grid in our study area. The dots depict the percentage of days a certain predator was detected at a location (site specific daily presence) over the three study years (2021–2023)

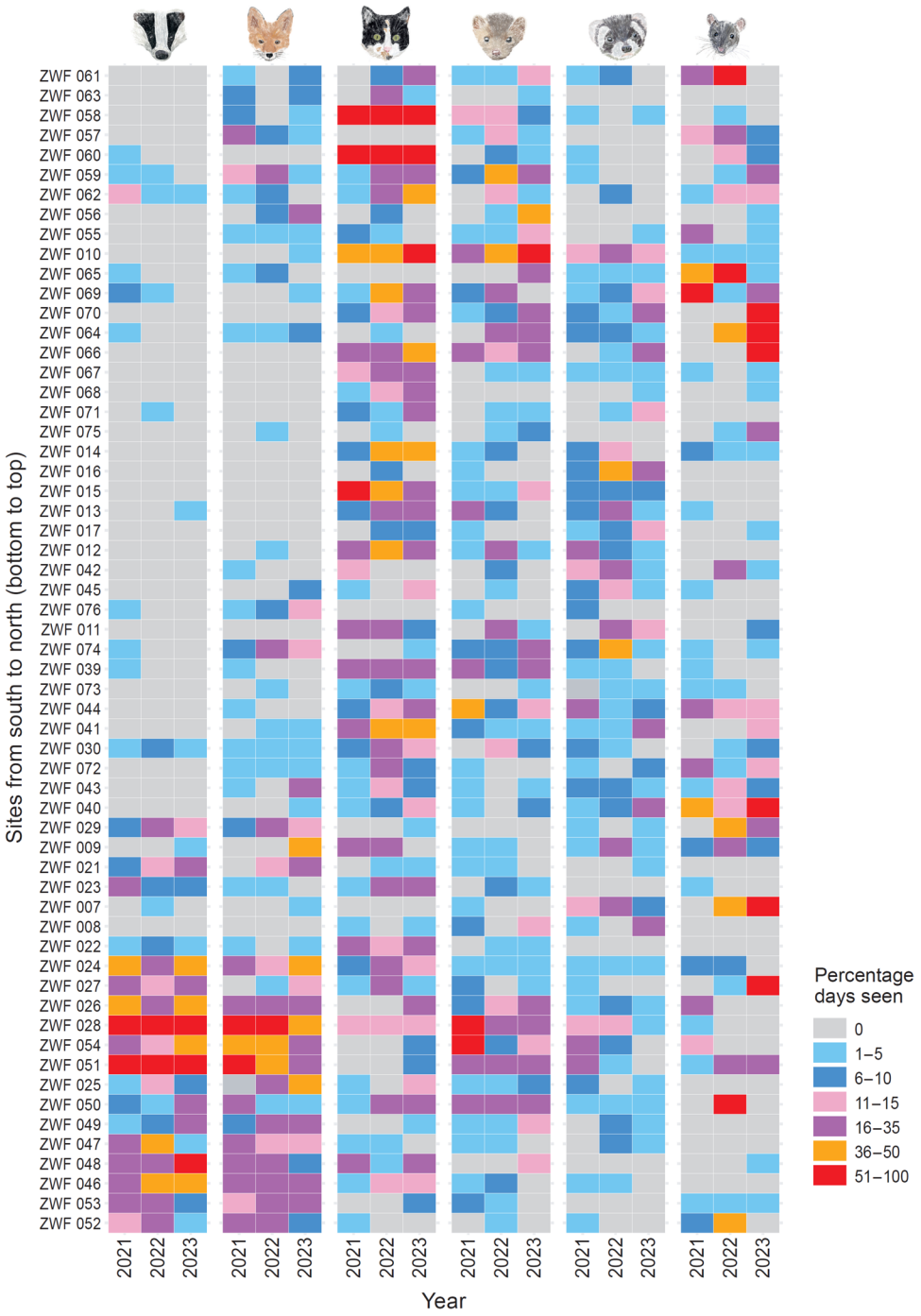

Fig. 3 The percentage of days each species was detected at each grid camera location (site specific daily presence) for each study year. The camera sites are ordered from south to north (bottom to top). Drawings refer to the different focal species (see Fig. 2 for species names)

martens (estimate: −0.78, z-ratio: −3.021, $p<0.05$); this was likely because badgers were overall less widespread than beech martens. There was no clear evidence for differences in the site-specific daily presence of the six focal predator species between the study years (included in top model, but not significant in post hoc test). Also, site-specific daily presence did not differ between the species over the years (interaction not in the top model, see Table S4).

Over the three spring seasons, we found a strong positive correlation in the site-specific daily presence of fox and badgers (0.87), whereas fox and badger presence correlated negatively with the presence of polecats (−0.16 for both; Fig. 4). Fox site-specific daily presence further also correlated negatively with the presence of domestic cats (−0.26), whereas cat presence correlated positively with that of beech martens (0.44).

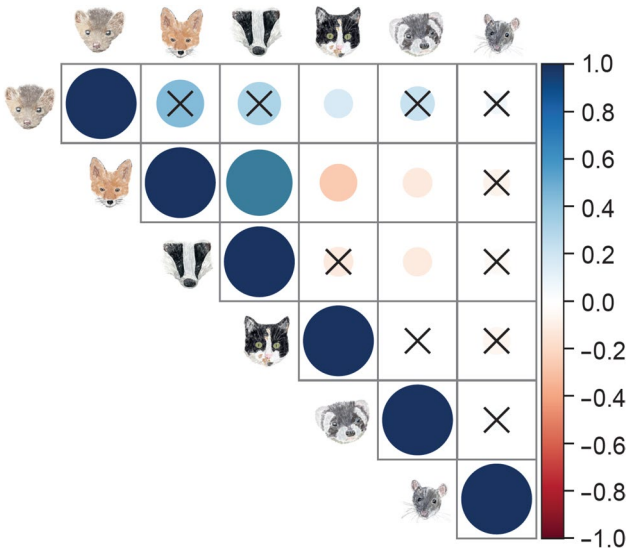

Fig. 4 Correlation matrix of the site-specific daily presence of the six focal predator species, based on the camera trapping data over all three study years (2021–2023). The crosses represent non-significant relationships based on Kendall correlation tests. If not crossed-out the correlation was significant ($p<0.05$). Drawings refer to the different focal species (see Fig. 2 for names)

Badgers, despite visiting the least sites overall and having the lowest overall site-specific presence, were most consistent in their presence at the camera sites they did occur at. They visited 73% of the sites where they occurred 2 years in a row and 66% of the sites 3 year in a row. This was followed by the domestic cat with 63% of the sites where they occurred 2 years in a row and 57% of the sites 3 years in a row. Polecats (60% 2-years in a row; 46% 3-years in a row) and red foxes (51% 2-years in a row; 45% 3-years in a row) had a more intermediate presence, while beech martens (53% 2-years in a row; 39% 3-years in a row) as well as brown rats (37% 2-years in a row; 28% 3-years in a row) had a less predictable presence.

When the consistency of species presence was analysed in detail, we found that a model with the factors species, year and their interaction best fitted the dataset (Tables S5 and S8). The observed presence of the six predators on all sites in 2021 was a positive predictor for their presence in 2022. This was especially so for the badger (slope: 3.97) and least so for the beech marten with only a small positive slope (slope: 0.36). The consistency in badger presence between the years was significantly higher than that of the beech marten (estimate: 3.61, z-ratio: 3.40, $p<0.01$; Fig. S1). The positive slopes in the effect for all other species did not differ from one another, although there was a trend that the slope of the effect for badgers also differed from that of brown rats (slope: 1.18; estimate: 2.80, z-ratio: 2.74, p = 0.07). These patterns still held two years later in 2023. In addition, the slope of badgers in comparison with brown rats then went from a trend to significant, i.e. the consistency in badger presence was higher than brown rat presence (slope badger 3.59, brown rat: 0.25; estimate: 3.34, z-ratio: 3.36, $p<0.05$; Fig. S2).

Nest predation index in relation to predator presence index

All of the six focal mammalian predator species that were detected on the camera grid predated godwit nests. From 2021–2023, these species were responsible for 64% of the 211 photo-captured nest predation events at 677 godwit nests (Fig. 5; see Table S2). The remaining 36% was due to avian predators (20%), other or unidentified mammalian species (8%) and unknown species (8%) (for exact numbers see Table S9).

Overall, for the full dataset of 2021–2023 combined, red foxes clearly predated nests more than their share in the daily presence based on the camera grid data ('Total': Fig. 6, Table 1, see Table S10 for absolute numbers). For the badger, the difference was less pronounced, but their share in nest predation was also higher than their share in daily presence. For beech martens and polecats their share in nest predation matched with their share in the local daily presence. Despite a high daily presence, brown rats and domestic cats predated very few nests. When examined at a yearly level we found that beech martens went from predating more nests relative to their share in the daily presence in 2021, to equal to in 2022 and less than in 2023 (Fig. 6, Table 1, Table S10). Foxes on the other hand went from an equal number of nests in relation to their share in the daily presence in 2021, to more nests relative to their share in the daily presence in 2022 and 2023. For polecats and badgers the pattern varied with year with polecats predating nests equal to their share in the local daily presence in 2021 and 2023, but higher than their share in 2022. For badgers a similar pattern emerged, except they peaked in 2023. In all study years, domestic cats predated a low share of the godwit nests despite their high presence as shown by our camera grid index. Brown rats exhibited a similar pattern as cats, however, in 2023 their level of nest predation went slightly up.

Discussion

We discovered a large and dynamic community of mammalian species potentially predating meadow bird nests, six of which were detected relatively frequent (for full list see: Fig. 1). The relative role of these predators in the actual documented nest predation of godwit nests varied over space and time.

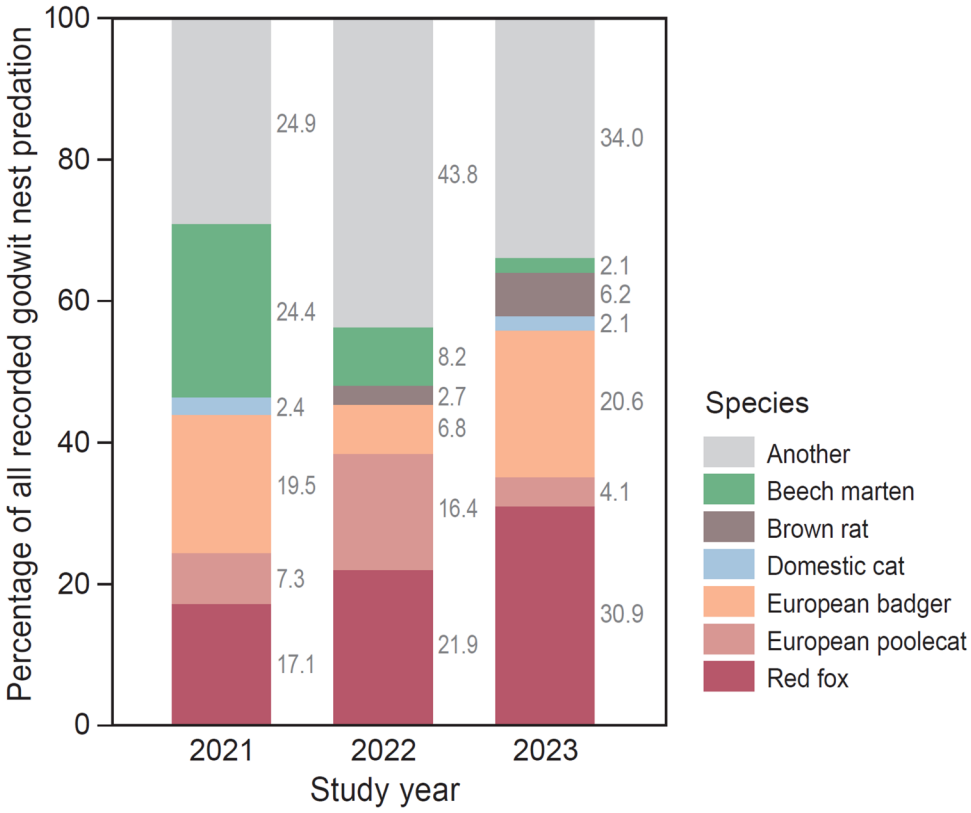

Fig. 5 Overview of the recorded percentage of predation of black-tailed godwit nests by the six most commonly occurring mammalian predators during the breeding seasons of 2021–2023 using camera traps. The specific percentages of recorded predation by each species are depicted in the stacked bars. The category 'Other' depicts nest predation caused by avian predators as well as non-identified or non-focal mammalian predators. Numbers on top depict the number of nests that were predated in that year divided by the total number of nests followed using camera traps. Drawings refer to the different focal species (see Fig. 2 for names)

Patterns of predator presence in context of the ecology of the species

The presence of the six focal species was found to be consistent over the years. Badgers were the least widespread of all species, as they were mostly present in the south of our study area, but at the locations where they were detected they had a high and consistent presence. Overall, the high daily presence of the typically forest-dwelling badger in this open intensely managed meadow landscape was unexpected since also earlier work predicted their absence in the habitats of our study area (Piza-Roca et al. 2018). From work in Ireland, Scotland, England and Italy it is known that badgers occur in the agricultural landscape (Kruuk 1978; Kruuk and Parish 1981, 1985; Remonti et al. 2006; Gaughran et al. 2018; Redpath et al. 2023), but the meadow landscape in the North of the Netherlands is very open with large waterbodies and with little cover available in the form of woodlots, shrubbery or hedges. The badgers most likely moved in from nearby forested areas where they were reintroduced in the 1960s (area of Gaasterland, southeast of our study area; van Moll 2002; Piza-Roca et al. 2018). In our study area, observations of badgers were already made in the period 1989–2012, but no settlements were recorded in this period (Broekhuizen et al. 2016). The badgers were presumably roaming around in this period, which is in line with GPS tracking work in England which revealed that badgers can have home ranges up to max 7 km^2 (Gaughran et al. 2018). However, in recent years, it has become apparent that badgers settled in our study area and actively dug burrows in sand ridges, railway embankments, high ditch sides and sand deposits (similar to observations in Essex, England by Skinner et al. 1991) and produced offspring too (personal communication with local hunters).

Badger presence was strongly positively correlated with that of foxes over all study years. Although badgers and foxes are known to compete with one another (e.g. over shared food resources), with the badger competitively superior to the fox (Macdonald et al. 2004; Trewby et al. 2008), in our study area badgers and foxes did not seem to avoid one another in space (consistent with Zalewska et al. 2021). Foxes, like badgers, may have colonized our study area coming in from nearby forested areas around the 1990s (Broekhuizen et al. 2016) and may have a highly correlated presence with badgers due to a shared habitat preference. Foxes and badgers may both prefer sandier soils, suitable for constructing their burrows (Remonti et al. 2006). It has been shown that badgers and foxes can sometimes even co-inhabit the same burrows (Kowalczyk et al. 2008; Mori et al. 2015; Nowakowski et al. 2020). Badgers are seen as the facilitating species by digging burrows which can also be beneficial for foxes (Nowakowski et al. 2020).

Badger, as well as fox presence, correlated negatively with the presence of polecats. Polecats are known to select water-rich areas (Rondinini et al. 2006; Harrington and

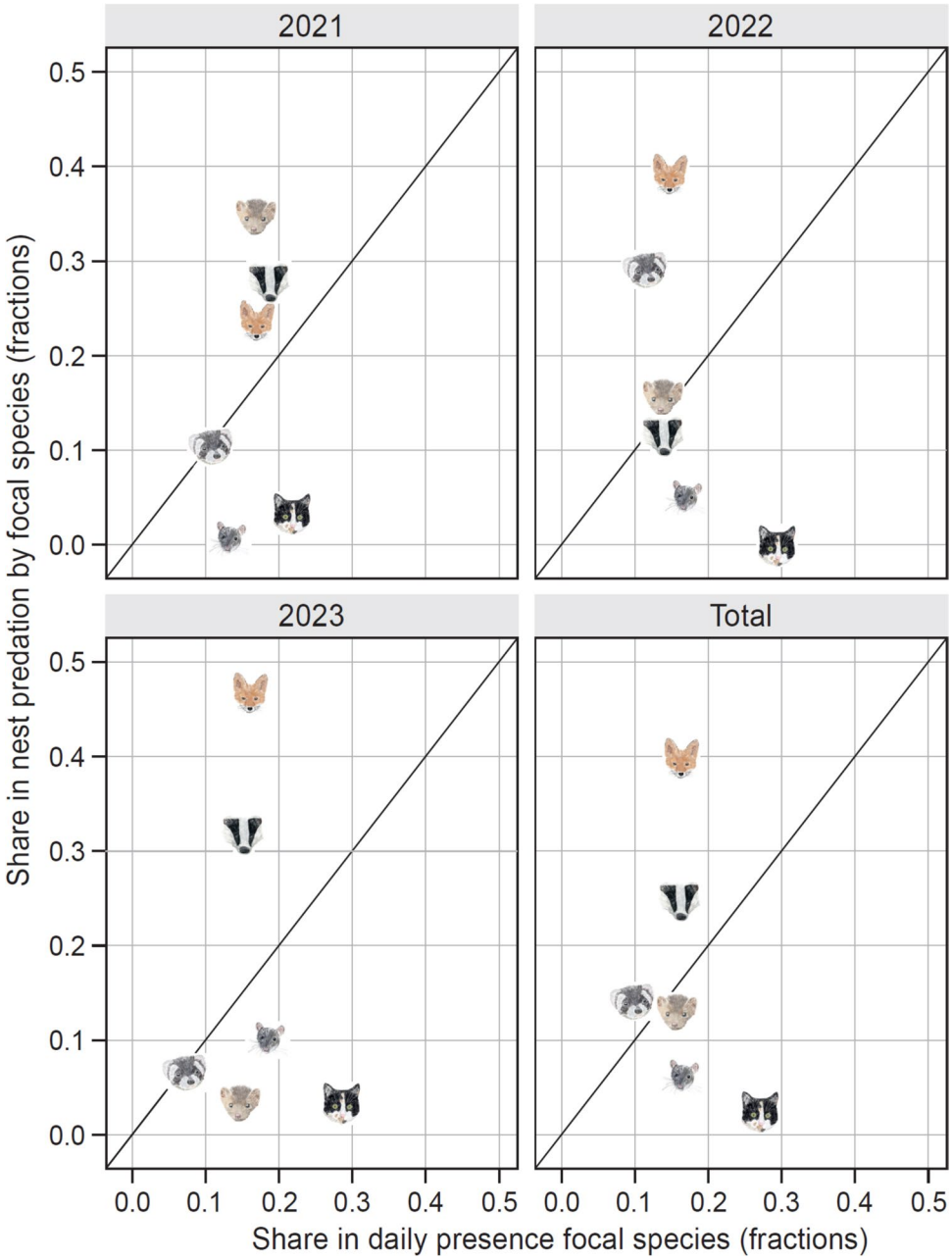

Fig. 6 The relationship between the photo-captured relative share in the daily presence of mammalian meadow bird predators (x-axis) and their share in the actual photo-captured predation by the six focal species of godwit nests for each study year (y-axis) and the total over all study years. If points are above the x = y line species predated a higher share of the godwit nests relative to their share in the daily presence as determined by our camera grid (for tests of significance see Table 1). When below the line, it is lower. For this comparison, the shares (fractions) in the daily presence and the nest predation for each species were calculated within the set of our six focal species only. Drawings refer to the different focal species (see Fig. 2 for names).

MacDonald 2008; Lodé 2011) and this may explain their relatively higher presence at camera sites in the east of the study area, a region characterized by many water bodies, high-water tables and peat soils (Howison et al. 2018). Polecats have been placed on the red list in The Netherlands and are labelled as 'vulnerable' (Costa et al. 2014; Croose et al. 2018; Hofmeester et al. 2019; Thissen and van Norren 2020).

Fox presence had a negative correlation with domestic cat presence, while beech marten presence had a positive correlation with cat presence. Logically, domestic cat presence will be higher closer to villages and farms, and beech martens are well known to frequent farms and inhabit urban areas as well (Rondinini and Boitani 2002). Red foxes from rural populations on the other hand are known to avoid human settlements possibly because they are culled (see further below; Díaz-Ruiz et al. 2016), thus potentially explaining the observed correlations. Alternatively, domestic cats could be directly avoiding foxes, as foxes are a potential lethal predator to them (Sogliani and Mori 2019; Rees et al. 2023).

Table 1 Binomial tests of the share (fraction) in photo-captured nest predation by each of the six focal species during the study years relative to what would be expected given their photo-captured share in the total number of days on which all focal predators were detected at field entrances in the whole study area. Significant values indicate if a species predated nests more or less than expected

Species	Year	Probability success	95% Confidence interval	Probability true	*P* value
BEECH MARTEN	2021	0.34	0.18 – 0.54	0.17	<0.05
BEECH MARTEN	2022	0.15	0.06 – 0.29	0.13	0.65
BEECH MARTEN	2023	0.03	0.00 – 0.11	0.14	<0.01
BEECH MARTEN	Total	0.13	0.08 – 0.20	0.15	0.72
RED FOX	2021	0.24	0.10 – 0.44	0.17	0.32
RED FOX	2022	0.42	0.26 – 0.59	0.14	<0.001
RED FOX	2023	0.47	0.34 – 0.60	0.16	<0.001
RED FOX	Total	0.40	0.31 – 0.48	0.16	<0.001
POLECAT	2021	0.1	0.02 – 0.27	0.1	1
POLECAT	2022	0.29	0.16 – 0.46	0.11	<0.01
POLECAT	2023	0.06	0.02 – 0.15	0.08	0.82
POLECAT	Total	0.14	0.09 – 0.21	0.10	0.11
BADGER	2021	0.28	0.13 – 0.47	0.2	0.35
BADGER	2022	0.13	0.04 – 0.28	0.13	1
BADGER	2023	0.31	0.20 – 0.44	0.15	<0.01
BADGER	Total	0.24	0.18 – 0.33	0.16	<0.01
DOMESTIC CAT	2021	0.03	0.00 – 0.18	0.22	<0.05
DOMESTIC CAT	2022	0	0.00 – 0.09	0.3	<0.001
DOMESTIC CAT	2023	0.03	0.00 – 0.11	0.29	<0.001
DOMESTIC CAT	Total	0.02	0.00 – 0.06	0.27	<0.001
BROWN RAT	2021	0	0.00 – 0.12	0.13	<0.05
BROWN RAT	2022	0.05	0.00 – 0.17	0.18	<0.05
BROWN RAT	2023	0.09	0.04 – 0.19	0.18	0.07
BROWN RAT	Total	0.06	0.03 – 0.11	0.17	<0.001

Linking predator presence to their share in nest predation

Overall, across the springs of 2021–2023 combined, the red fox was the most consistent predator of godwit nests, also taking a higher proportion of nests relative to their share in the daily presence in the field, as determined from our camera grid index. Red foxes are known from previous work to be a relatively important meadow bird nest predator (Teunissen et al. 2006, 2008; Laidlaw et al. 2019; Laux et al. 2022). As a meadow bird protection measure, red foxes are culled in our study area (e.g. local permissions for 'lamping'; 360 foxes culled from 2020–2023 in the three management units of which our study area is part; de Vries 2023). Earlier work on the culling of foxes in Great Britain and in Germany indicates that it needs to be intensive and suitably timed in order to have any benefit for prey populations as its influence is short-term, likely due to high rates of replacement of culled foxes which can already happen after one week (Kämmerle et al. 2019; Porteus et al. 2019) or even overnight (Porteus et al. 2024). In order to be able to evaluate the effects of culling predators as a meadow bird conservation strategy a more in-depth study is required. Besides more detailed information on the culling itself, the numbers culled, the timing and how it is organised, it is important to take changes in the full predator community into account, as targeted culling of one species may open up opportunities for other predator species (Courchamp et al. 1999; Beggs et al. 2019; Ellis et al. 2020).

We detected that badgers also predated a higher proportion of nests compared to their share in daily presence, although this was less pronounced than for the fox. Beech martens and polecats predated godwits nests equal to their presence, but their influence varied between the sampling years. Beech martens are relative newcomers as a nest predator in the agricultural meadow landscape of The Netherlands, with the first reports of their presence in 2014 based on incidental camera trapping in our study area (unpublished data). In 2021, beech martens were observed to be a main nest predator across our study area (Fig. 5, Fig. S4). In 2022 and 2023, this diminished and predation was only reported at some locations, despite beech martens still being present throughout the area (Figs. 3 and 5, Figs. S5 and S6). In evaluating these yearly patterns, and considering that we follow about a quarter of all nests each year over all known breeding spots in the study area, we assume that the distribution of the predators we observed on our nest cameras is an accurate reflection which of the predators were responsible for the nest predation.

However, especially for the first year of study (2021) we should be careful. In this year a lower percentage of the camera monitored nests were predated (20%, Table S2) compared to the non-camera monitored nests (33% predated). From literature it is known that predator species may at first need to get used to camera traps at nests (i.e. they represent novel objects) and may avoid them (Meek et al. 2016). This could have affected the patterns we have seen in the first year if the avoidance was species specific. In the later years the avoidance of the camera traps could have turned into attraction (for detailed investigations of such effects see: Richardson et al. 2009; Meek et al. 2016; Caravaggi et al. 2020; Salewski and Schmidt 2022). For now, we have no indication that this is the case for the camera monitoring, with a similar probability to be predated for camera monitored nests (33%, Table S2) vs non-camera monitored nests (31%) in 2022 as well as in 2023 (38% vs 42%). This calculation was done on a positive selection of nests, i.e. we only started monitoring nests with camera traps which had reached the incubation stage, while non-camera monitored could also already have been predated in the laying stage. However, a lack of camera effect was also found in a well-designed experimental study: there was no evidence that predators, among which the polecat and the red fox, learned to associate camera traps with food (Salewski and Schmidt 2022).

The decrease in nest predation by beech martens over the study years was also observed in other areas of nest monitoring in the province of Friesland. This work was undertaken to monitor the effects of a large beech marten culling "meadow bird conservation pilot" on nest success which took place in 19 meadow bird areas in the province (Dekker and Jonge Poerink 2022). In total in the 19 areas' 463 beech martens were culled in the period from 2018 until 2022. Two of these areas (Idzega and Workumerwaard) were located in our study area and here 30 beech martens were culled (Dekker and Jonge Poerink 2022). After this conservation pilot ended, a permit was provided to cull 200 beech martens per year from 2023 onwards in the 19 areas (Jonge-Poerink 2024). Dekker and Jonge Poerink (2022) showed that in area-year combinations where predator management was deemed optimal, i.e. all known active beech martens *and* red foxes culled, beech martens were responsible for on average 3.5% of the nest losses, against on average 17.7% in the single 'control' year before culling. It was suggested that every year a new influx of beech martens made it to the areas, which is in line with our study where we recorded an overall consistent, yet spatially variable, presence of beech martens across the study years. Since the desired positive effect of the culling measure on overall nest success was only apparent in area-year combinations with 'optimal management' of both beech marten and fox, this suggests that red foxes may predate nests which are left when egg-eating beech martens have been removed. In line with this, in our study a decrease in the relative nest predation by beech martens was associated with an increase in the rates with which, red foxes predated godwit nests (accounting for presence). Such forms of compensatory nest predation complicate predator management which targets particular species (Beggs et al. 2019; Ellis et al. 2020).

Cats are known for their large impact on local prey species (Roos et al. 2018; Trouwborst and Somsen 2021; Badenes-Pérez 2023), yet domestic cats together with brown rats were rarely detected as predators of eggs, despite their high presence in our study area. These findings concur with earlier work indicating that brown rats and domestic cats did not often predate meadow bird nests, but were found to feed on meadow bird chicks after they left the nest (Teunissen et al. 2008). However, the apparent abundance of both domestic cats and brown rats in our study area could have exerted indirect effects, by affecting the perceived predation risk (Lima 2009; Mathot et al. 2024). For example, in an experiment where domestic cat models where briefly presented to breeding blackbirds (*Turdus merula*), the birds reduced provisioning rates to their nestlings, which in turn led to higher nest predation rates by corvids (Bonnington et al. 2013).

Challenges in measuring predator-meadow bird dynamics using camera traps

The presented inference on predator-prey relationships in an agricultural landscape will obviously be skewed by the observation methods used. For example, a methodological study on camera grid setups revealed that even when only 20 m apart, different camera traps can already paint a different picture on predator capture and detection rates (Kolowski et al. 2021). This study was in a forest, however, where the possibilities for animals to bypass camera traps are likely to be much greater than in our study where camera traps were placed at field entrances, preferred by humans and other animals alike to the crossing of canals. Note also that, within a forest the influence of local microvariation at camera sites is larger than the relatively similar configuration of meadows and the field entrances to access them.

Another challenge with our camera trapping setup is that it cannot easily be determined how many individuals of a certain predator species were exactly present in the area and how many of these were responsible for the observed nest predation. However, we can make some inferences based on where the nest predation was recorded by the focal species (Figs. S4-S6) in relation to the spatial range where the species were detected using the camera network (Figs. 2 and 3). Nest predation mostly occurred at places where the species were also detected during more of the camera trapping days in the area. For species responsible for a higher proportion of the recorded nest predation from 2021 to 2023, namely

the red fox, badger and beech marten, the observed patterns are likely due to the activity of several individuals rather than single individual predators. This because the nest predation by the species was recorded at locations relatively far apart and isolated from one another across the study area (Figs. S4-S6). Follow-up research to investigate this in detail would require the GPS tagging of individuals and monitoring their area use in combination with monitoring their nest predation (e.g. Peterson et al. 2022; Black et al. 2023; Porteus et al. 2024), and/or individual identification of predators using facial and coat markings, e.g. with special camera setups to do so (e.g. Hofmeester et al. 2024).

Conclusions

This study demonstrated how camera trapping can be used to quantify the connections between a meadow bird and their often-elusive nocturnal nest predators. We showed that a high presence of a potential meadow bird predator does not imply it will necessarily appear as an important nest predator of godwit nests. We also established that, when the effect of one predator species diminishes, the influence of others may increase. This underscores the importance of (1) measuring effects of predators on meadow birds over multiple study years as local conditions may determine which predators proportionally are more important in nest predation rates, and (2) always considering predators within the context of the entire predator community of which they are part. While meadow birds are often the primary focus in policy and for the general public, for predators, meadow bird eggs, chicks and adults just constitute a part of a broader and seasonably variable diet. Research on the complex interplay of attributes of the agricultural landscape, such as foraging and shelter opportunities, with the annual ecology of predators and subsequent observed predation rates on meadow birds, would provide an important next step forward.

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Author contributions RWF: Conceptualization, Methodology, Data Curation, Validation, Formal analysis, Visualization, Writing- Original draft preparation. DB & EV: Conceptualization, Methodology, Data Curation, Validation, Writing- Reviewing and Editing. MS, MEJ & OB: Data Curation, Validation, Writing- Reviewing and Editing. JCEWH: Funding acquisition, Project administration, Data Curation, Writing- Reviewing and Editing. TP: Funding acquisition, Supervision, Writing- Reviewing and Editing.

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Data availability The datasets gathered and studied for this manuscript are not publicly available yet, pending other publications, but are available from the corresponding author upon reasonable request.

Declarations

Ethical approval The work conducted on the black-tailed godwits was carried out under an IVD-protocol light issued by the IVD-FSE of the University of Groningen. Furthermore, yearly authorization to find and follow godwit nests was obtained from the province of Friesland (document nr. 2020-090726, case nr. K13079).

Competing interests The authors declare no competing interests.

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