Detectability and predator strategy affect egg depredation rates: Implications for mitigating nest depredation in farmlands

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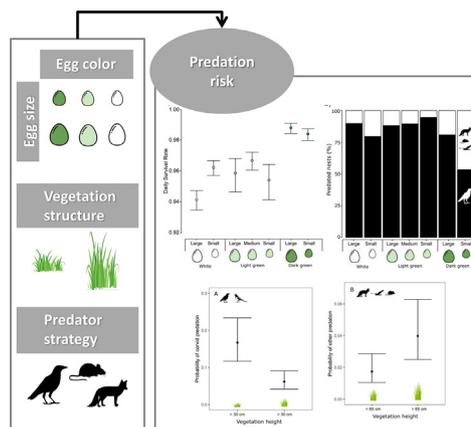[d] Fédération Nationale des Chasseurs, 92136 Issy-les-Moulineaux Cedex, France
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HIGHLIGHTS

- Vegetation higher than 30 cm strongly reduced dummy eggs predation rates by corvids.
- Predator type affects predation rates because of spatial and temporal cues.
- Nest predation by corvids might be the result of an active search strategy.
- Management of vegetation structure may be a key tool to mitigate predation risk.

GRAPHICAL ABSTRACT

ABSTRACT

Predation is a major evolutionary force in animal ecology. Mechanisms by which prey coloration provides camouflage has been widely studied. However, predator response to prey camouflage and concealment has received less attention. Understanding vegetation structure effect on depredation success could help managers design strategies to mitigate the depredation of managed species (e.g., threatened or hunted). We aimed to investigate the relationship between depredation rate, nest camouflage and concealment in ground-nesting birds of farmlands, and their predators. We set up an experiment of 2576 artificial ground nests to assess the role of egg coloration (white, light green, and dark green), egg size (small, medium, and large), and vegetation structure (vegetation height and land use) in nest survival rates. We also explored the role of predator searching strategies by analysing clumped depredation and multiple depredation events. Of the nests, 34.0% were depredated, with corvids as the predators 78.5% of the time. Corvid depredation decreased by 40–60% in grasslands and spring crops above a vegetation height of 30 cm. In contrast, vegetation height and land use may be of far less importance in avoiding depredation by other predators. The probability of depredation was spatially clumped, suggesting that predators increase search effort in areas where a nest was previously encountered. Neighboring depredation and depredation repetition were more frequent in corvids than in other

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Search strategy
Nest predation

predators. Our study indicates that nests in vegetation higher than 30 cm had a drastic reduction in depredation rates by corvids. Management of vegetation structure is a key tool to mitigate depredation risk, and improving the availability of alternative food resources may be a complementary tool.

1. Introduction

Predation is one of the major ecological and evolutionary forces driving and shaping animal population dynamics and community structure (Allesina and Tang, 2012). To reduce predation risk, prey have developed a range of traits, including camouflage, chemical defences, protective armour (Ruxton et al., 2004), and behavioral traits including direct defence (Groenewoud et al., 2019), predator detection (Poulin et al., 2018), and breeding site selection (Indermaur et al., 2010).

Camouflage is one of the main adaptations to reduce visibility against predators using visual cues, making a prey indistinguishable from its background (Stevens and Merilaita, 2009). Furthermore, the vegetation structure of the habitat may conceal prey and thus, reduce its detectability (Camp et al., 2012). However, the effectiveness of camouflage depends on the interplay between prey color, the appearance of the surroundings, and the type of predator involved (e.g. visually oriented predator) (Robledo-Ospina et al., 2017). The mechanism by which prey coloration may provide camouflage in natural environments has been widely studied (Hughes et al., 2019) but that by which predators respond to prey camouflage and concealment has received less attention (Galloway et al., 2020). Understanding how vegetation structure affects predation risk and predator strategy can help managers design strategies to mitigate (de)predation of threatened or hunted species. This is particularly relevant in highly dynamic ecosystems (e.g. farmland landscapes) in which habitat structure including vegetation height changes continuously and can be used to conceal prey.

In ground-nesting birds, two main strategies to reduce depredation risk have been reported. Some species may nest in the open with low vegetation height and rely on early predator detection and nest/egg camouflage (e.g. stone curlews *Burhinus oedicnemus* (Solis and de Lope, 1995)). Others can conceal their eggs in dense and tall vegetation, having either cryptic or conspicuous eggs (e.g. partridges or harriers, Gillis, Gauffre, Huot, & Bretagnolle, 2012). As tall vegetation reduces nest detectability and provides habitat for other potential prey (i. e. alternative food) (Laidlaw et al., 2017), managing vegetation height has been proposed as a strategy to mitigate the impact of depredation (Wilson et al., 2005). For instance, while taller vegetation at field margins increases insect abundance and nesting cover for Grey Partridge (*Perdix perdix*) (Sotherton, 1998), it also increases the abundance of small mammals as an alternative food source and consequently, reduces the need for predators to search for nests in open fields (Laidlaw et al., 2015).

It is assumed that prey camouflage reduces depredation rate (Stevens and Ruxton, 2019) but this phenomenon is still debated for bird eggs. Cryptic eggs usually have reduced depredation, largely going undetected by predators (Troscianko et al., 2016). Large eggs are more visible but preclude smaller predators. Therefore, the effectiveness of egg camouflage or size against depredation depends on predator species and their different search tactics and sensory inputs. While mammalian predators presumably rely on olfactory stimuli, avian predators are thought to be mainly visually oriented, although some of them, like corvids, might also use olfactory cues (Molina-Morales et al., 2020). Therefore, depredation by predators using olfactory cues may not be affected by vegetation height while nest depredation risk would decrease in tall vegetation as avian predators rely on visual cues (Clark et al., 1991). Although the effects of egg size and color, and vegetation cover on depredation rates have been widely studied (Bellamy et al., 2017; Gillis et al., 2012), the relationship between egg visibility and nest detectability has rarely been explored.

Depredation rate also depends on predator search strategy. Active search depredation exhibits two key characteristics (Vickery et al., 1992). First, the depredation rate at a focal nest depends on spatial cues (e.g.

local nest density) as predators are foragers that show area-restricted search behavior. Second, temporal cues may also be important (e.g. previous depredation events close by or nest discovery can change the foraging behavior of predators). It has been reported that corvids can be major predators of nests in farmland landscapes (Bravo et al., 2020) and may exhibit active search behavior (Marzluff and Balda, 1992). However, their diet comprises only occasional egg items (Díaz-Ruiz et al., 2015) and very little is known about how they locate nests and whether they change their foraging tactics with changes in nest detectability (vegetation structure) and egg visibility (camouflage).

In this study, we aimed to quantify the effect of egg visibility and nest detectability on depredation rates by predators exhibiting different search strategies. We set up experiments to assess the role of egg coloration, egg size, and vegetation structure around the nest on nest depredation by corvids and other predator species. As corvids are considered to be visually oriented predators, we hypothesised that they would be hampered by the microhabitat surrounding nests, particularly by vegetation height. We hypothesised that (1) visible eggs (large white eggs) would experience higher depredation rates and (2) vegetation height would decrease depredation risk; (3) depredation rate by Corvids on cryptic eggs (dark green) would be low, particularly in tall vegetation. Furthermore, we assessed the effect of spatial and temporal cues of predators by accounting for neighboring depredation and multiple depredation events. Under an area-restricted searching behavior, we expected (4) a higher depredation rate when neighboring nests were depredated or when multiple depredation events occurred.

2. Methods

2.1. Study area

The study was carried out in the spring of 2017–2019 in the LTSER "Zone Atelier Plaine & Val de Sèvre" (46°15′ N, 0°30′ W), which covers 450 km² of intensive agriculture mostly dedicated to cereal production in Western France with the most common land use being wheat (33.8%), corn (9.6%), sunflower (10.4%), oilseed rape (8.3%), pea (2%), and meadows (13.5%) including permanent grasslands and temporary hay (such as alfalfa, see Bretagnolle et al. (2018) for general site description). The area is also an important breeding site for threatened species including little bustard (*Tetrax tetrax*), harriers (*Circus* spp.), and stone curlew and gamebirds including two partridges (*Perdix perdix* and *Alectoris rufa*), quail (*Coturnix coturnix*), and pheasant (*Phasianus colchicus*). Local corvids include carrion crow (*Corvus corone*), Eurasian magpie (*Pica pica*), western jackdaw (*Corvus monedula*), rook (*Corvus frugilegus*), and Eurasian jay (*Garrulus glandarius*). The area also includes other potential nest predators such as red fox (*Vulpes vulpes*), stone marten (*Martes foina*), and weasel (*Mustela nivalis*) (see Bravo et al., (2020)).

2.2. Artificial nests

We conducted an experiment by monitoring a total of 2576 artificial nests set up at 112 sampling sites (see details in Table S1). A sampling site had four or five nests placed at 30 m intervals along transects. To select sampling sites, we used stratified random sampling design, according to hedgerow density. Transects were oriented parallel to field margins at distance 43.5 ± 22.4 m from field margins (range 9.3–99.5 m). Field size in the study area is on average 2.83 ± 8.13 ha (0.097–35.18 ha). In 2017 and 2018, two transects per sampling site were set in two adjacent fields whereas, in 2019, one transect per sampling site was set. The average distance (±SD) between transects was 129.4 ± 52.9 m (range 52.2–355.7 m).

Although the number of transects per sampling site differed among years, we did not detect any spatial autocorrelation in the model residuals using semi-variograms, Moran's index or plotting spatial distribution of residuals (see Fig. S1). Thus we assumed that there was a negligible effect of spatial autocorrelation of depredation events between transects.

Each nest was formed as a shallow depression in the soil and contained two plasticine eggs of the same type (see below) that were fixed by a thin wire and a peg in the ground to prevent predators from taking it away. The location of each nest was recorded using GPS and no markers were placed. To control the seasonal variation during the breeding period, nests were set up from 26th March to 19th June each year. The nest location was moved by at least 100 m from the location used the previous year. In 2017, a pilot nest experiment was conducted with an exposure time of 7 days. In 2018 and 2019, nests were exposed to predators for 15 days during the egg-laying period (when individuals leave their nests open and are not incubating the eggs), which varies from 2 to 7 days for little bustard or Montagu's harrier and is up to 15 days for partridges. The nests were monitored on days 1, 3, and 7 in 2017 and days 1, 3, 9, and 15 in 2018 and 2019.

2.3. Types of eggs

Plasticine eggs were made with an off-white nontoxic modelling compound (J. Herbin plastiline, Chelles, France), allowing the identification of nest predators. Egg camouflage and conspicuousness were described by two proxies, egg size and egg color, which were used as explanatory variables to explain the probability of depredation. We used three sizes, that is, large (5 × 3 cm), medium (3.5 × 2.5 cm), and small (2.5 × 1.5 cm) and three colors of eggs, that is, white, light green, and dark green. We painted the eggs to mimic the eggs of different species. The white eggs (hex color: #f7ecd5; LRV (Light Reflectance Value): 84.8%; HSL (Hue, Saturation, Lightness): 41°, 68%, 90%) were the most conspicuous and possibly the least costly coloration for females (Gillis et al., 2012), similar to the eggs of Montagu's harrier. The light green eggs (#c5bfa9; LRV: 52.5%, HSL: 48°, 18%, 72%) were relatively conspicuous and mimicked eggs of the pheasant and grey partridge. The dark green eggs (#978953; LRV: 25%, HSL: 48°, 29%, 46%) were cryptic and similar to the eggs of the little bustard and skylarks. In 2017, the following four types of nests were deployed per transect: large white, small white, large light green, and small light green. In 2018 and 2019, the following five types of nests were deployed per transect: large white, small white, large dark green, small dark green, and medium light green (details in Table S1).

2.4. Habitat around nests

The effects of habitat around the nest on depredation rate were investigated using vegetation height and land use as predictors. Vegetation height (cm) was measured as the average height around each nest (within a 2 m radius) on the day of nest deployment. Land use was classified according to vegetation type and structure as follows: *cereals* (mainly wheat and barley), *grasslands* (meadows and alfalfa), tall *spring crops* (sown in late February and after, including mainly sunflower and corn), and *other crops* (oilseed rape, ryegrass, wax, peas, and lens). Controlling for the effect of date, vegetation height differed significantly between land uses ($\chi^2 = 3976.9$, $p < 0.01$, $n = 563$, Fig. S2). On average, *cereals* were the tallest (67.6 ± 24.8 cm) followed by *other crops* (39.0 ± 26.1 cm), *grasslands* (31.3 ± 20.1 cm), and *spring crops* (21.9 ± 21.4 cm) during the experiment.

2.5. Depredation records

A nest was assumed to be depredated when at least one egg was damaged. Predator species were identified by tooth and bill imprints in the plasticine eggs. Nests destroyed by farming practices (less than 5%) were removed from the analyses. Nests were removed once they were depredated, except in 2018. In 2018, to quantify the repeatability of depredation, new eggs were placed in the depredated nests, allowing multiple depredation

events per nest to be recorded (including by different predator species). The maximum number of depredation events per nest was four (survey days were 1, 3, 9, and 15 allowing to replace eggs up to 4 times). We considered only the first depredation event by any (total depredation) or particular (species-specific depredation) predator species when tabulating depredation rates; consequently, depredation rates were comparable to those measured in 2017 and 2019 (without egg replacement).

2.6. Statistical analyses

2.6.1. Egg camouflage and conspicuousness: size and color

We calculated the daily survival rate of nests (DSR), that is, the probability of survival of a nest for one day within a specific time interval and used "Nest Survival" function in MARK program using the RMark package (Laake, 2013; White and Burnham, 1999), a procedure that allowed considering that DSR is not constant with time and variation in the length of observation intervals. The following parameters were included: i) the first day when a nest was encountered, ii) the last day when the nest was checked undepredated, iii) the last day when the nest was checked, and iv) the fate of the nest (depredated/not depredated). The first day was always the first experimental day for each sequence because we used artificial nests. The exposure time of eggs to depredation was 7 or 15, depending on the year. To test for egg size and color effects on DSR, we ran a model including egg color with three levels (white, light, and dark green) and egg size with three levels (small, medium, and large). The interaction between egg size and color could not be included in this model as all the size-color combinations had not been sampled. Thus, we ran another model replacing the two variables, egg size and egg color, by a variable called egg type with seven levels: large white, small white, large light green, medium light green, small light green, large dark green, and small dark green egg. To control for temporal variation, we included: i) day of monitoring and its quadratic term to account for the temporal variation within monitoring; ii) julian day and its quadratic term to account for seasonal variation within year and iii) year to account for variation between years. As the probability for a focal nest of being depredated might be higher if any nest within transect had been depredated (hereafter, neighboring depredated nest), we included in the model a binomial variable contrasting whether (yes vs. no) this was the case. Candidate models describing different types of egg camouflage and temporal structure of the dataset were compared using AICc-based criterion (Akaike Information Criteria corrected for small sample size), including AICc weights (ω), to evaluate the relative support of each model. The best model was the one with the lowest AICc value and highest ω, assuming all models with ΔAIC<2 from the best model had similar statistical supports. From this best model, we used 95% CI to assess the consistency of size of effects. Finally, the effect of predator type contrasting corvids vs. other predators within the seven levels of egg type on the proportion of depredated nests during 3-day period (see explanation below) was tested using Pearson's Chi-square test.

2.6.2. Nest detectability: vegetation height and land use

We used the depredation rate at day 3, first because it was available all three years, second, as a standardized measure of depredation rate, and third, because DSR followed a quadratic pattern (see Table 1) and thus DSR was not constant along the monitoring. To model the relationship between vegetation height and depredation rate by corvids, vegetation height was considered as a binomial variable, which allowed searching for a threshold value of vegetation height below which the depredation rate was significantly different. We then contrasted the depredation rate at day 3 testing several threshold values between 5 and 65 cm every 5 cm (i.e. <5 vs. >5 cm, <10 vs. >10 cm, etc.). We used generalized linear models (GLM, binomial, link = logit) with depredation as the dependent variable (depredated/not depredated) and vegetation height as binomial explanatory variable. Again, a model including neighboring depredated nest (yes vs. no) was ran to control for potential statistical effect of depredated nests within the transect. Year and julian day were also included in the model. Models with varying threshold values were compared using AIC,

Table 1

Effect of egg type along survey (day) and breeding season (julian day) on the daily survival rate of artificial nests (see Table S2 for AIC-based model selection). The reference level for egg type is *large white*, *2017* for year and *No* for neighboring depredated nest (i. e. depredation within transect).

Explanatory variable	Estimate ± SE	95% CI	
		Lower	Upper
Egg type	(Intercept: 0.47 ± 1.44)	−2.36	3.30
	Large light green: 0.57 ± 0.17	0.23	0.91
	Large dark green: 1.48 ± 0.16	1.17	1.79
	Medium light green: 0.40 ± 0.12	0.16	0.63
	Small white: 0.51 ± 0.10	0.31	0.72
	Small light green: 0.46 ± 0.17	0.13	0.79
	Small dark green: 1.18 ± 0.14	0.90	1.46
Day	0.27 ± 0.03	0.21	0.34
Day^2	−0.01 ± 0.003	−0.02	−0.01
Julian day	0.03 ± 0.02	−0.01	0.07
Julian day^2	−0.0001 ± 0.0001	−0.0002	0.0001
Year	2018: 0.28 ± 0.12	0.05	0.52
	2019: 0.17 ± 0.13	−0.08	0.42
Neighboring depredated nest	Yes: −1.59 ± 0.10	−1.78	−1.39

and the model with the lowest AIC indicated the vegetation height at which the probability of depredation changed the most. As egg type (seven levels) may also affect the relationship between vegetation height and depredation rate, we included the two-way interaction between vegetation height and egg type (seven levels) in the best model obtained from model comparison. The same procedure was repeated for nests depredated by other predators.

As vegetation height may affect the relationship between land use and depredation rate, we added land use as an explanatory variable to the aforementioned models, that is, with the vegetation height threshold determined with the previous statistical procedure. Therefore, we included land use with four levels (cereal, grassland, spring crop, and others), the two-way interaction between land use and vegetation height (obtained from previous statistical procedures), and julian day and year to control for temporal variation, in the GLM model, separately for corvid and other predators as vegetation height threshold differed between predator types. Neighboring depredated nest (yes vs. no) was included in the model to control for the effect of depredated nests within the transect. Additionally, as egg type (seven levels) may also affect the relationship between land use and depredation rate, egg type (seven levels) was also included as a two-way interaction between land use and egg type. However, the latter interaction could only be analysed for corvid depredation considering the low number of depredations by other predators.

2.6.3. Accounting for spatial and temporal cues

In order to infer predator behavior from depredation rate patterns, we included spatial and temporal variables in our modelling procedure. Firstly, we investigated whether depredation events were spatially clumped, i.e. whether a depredation within a transect would increase the likelihood of a nest being depredated. We evaluated the *between* (random variance) and *within* (residual variance) variance of transects on model using a GLMM (binomial, link = logit) with depredation rate by corvids at day 3 as a response variable and transect identity as a random factor. We calculated the intraclass correlation coefficient (ICC) which is a measure of correlation between observations from the same transect and is expressed as ICC = $d^2/d^2 + \sigma^2$, where d^2 is the variance of the random effect. ICC ranges from 0 to 1, with values close to 1 indicating high similarity of values within transects, hence suggesting a clustered depredation. Additionally, we calculated the conditional-R^2, which indicates the amount of variation explained by the random effect (i. e. *between* transect variation) (Nakagawa et al., 2017; Nakagawa and Schielzeth, 2013). The same procedure was repeated for nests depredated by other predators.

Secondly, we investigated whether depredation events were temporally related as nests could be depredated several times during the exposure period. For this, we used data collected in 2018 (i.e. with replacement of depredated eggs, $n = 1130$). To analyse the variation in proportion of depredated and not

depredated nests in relation to the number of depredation event per nest (i. e. 1, 2, 3, 4) we performed a chi-squared analysis on a contingency table. For this, we counted the number nests with a first depredation and not depredated. Among nests depredated once, we counted the number of nest with a second depredation and not depredated and so on. Similarly, as visibility and detectability of nests might influence the proportion of nest depredated once or depredated multiple times, we also explored possible differences by egg type (five levels), land use (four levels), and vegetation height (30 cm for corvids and 65 cm for other predators) using chi-squared analyses. These analyses were carried out separately for corvid and other predators.

We used 95% CI to investigate the significance of factors on the DSR and probabilities for nest of being depredated. Indeed, we considered that there was not a consistent effect when 95% CI overlapped the zero value. We checked that residuals fulfilled statistical requirements including the distribution of residuals against fitted values and the lack of spatial autocorrelation using semi-variograms, Moran's index and plotting spatial distribution of model residuals. None was significant (Fig. S1). All analyses were performed using R 3.6.2 (R Core Team, 2019). Results are shown as mean ± SD.

3. Results

3.1. Effect of egg camouflage and conspicuousness on depredation rates

Of the 2576 artificial nests, 34.0% were depredated ($n = 875$) and 3.8% were destroyed by farming practices ($n = 99$). The average DSR was 0.966 ± 0.034. DSR was affected by egg type, survey day, year and neighboring depredated nest (Table 1). Of all the predictors of egg visibility that were tested (i.e. egg type, egg color, or egg size), models including egg type (seven levels) showed higher statistical support (AICc = 4611.00; Table S2A) than models including egg color and egg size separately (AICc = 4625.94; Table S2B). Large white eggs had the lowest DSR whereas, large dark green eggs had the highest, and other types of eggs exhibited intermediate values (Table 1, Fig. 1A). A temporal quadratic variation in DSR was apparent (Table S2). DSR increased significantly by 2–9% on the survey day (Table 1, Fig. S3).

In total, 78.5% of depredated nests were depredated by corvids and the remaining nests by small mammals (11.7%), other mammals (5.1%), raptors (0.1%), and unidentified predators (4.6%). All predators except corvids were subsequently grouped in a category called "other predators". Egg type significantly influenced predator type ($\chi^2 = 30.87$, df = 6, $p < 0.01$, Fig. 1B); small and dark green eggs were more frequently depredated by predators other than corvids.

3.2. Nest detectability: vegetation height and land use

The depredation rate by corvids varied with vegetation height with a threshold vegetation height of 30 cm (Table S3A), whereas 60 and 65 cm were the thresholds for other predators (Table S3B, Fig. S4). Below 30 cm height, the corvid depredation rate doubled (Fig. 2A). For other predators, the threshold value (65 cm) only increased the depredation rate by 10% (Fig. 2B). The interaction between vegetation height and egg type nearly significantly affected the depredation rate by corvids and other predators. In small dark and light green eggs, probability of depredation tended to be similar above or below 30 cm or 65 cm height for corvid depredation and for other depredation, respectively.

The depredation rate by corvids was significantly affected by land use (Table 2A); it was lower in *cereals* than in other land uses (Fig. 3A, post-hoc in Table S4). The interaction between land use and vegetation height affected the corvid depredation rate with the highest contrast at 30 cm in *grasslands* and the lowest in *cereals* (Fig. 3A, Table S5). For other predators, vegetation height but not land use affected depredation rates (Table 2B). There was also a significant interaction between land use and egg type in corvid depredation rates; large white eggs were depredated significantly more in *grasslands* and *spring crops* than in *cereals*, whereas for small white eggs, this difference existed only between *cereals* and *spring crops* (Fig. S5, Table S6).
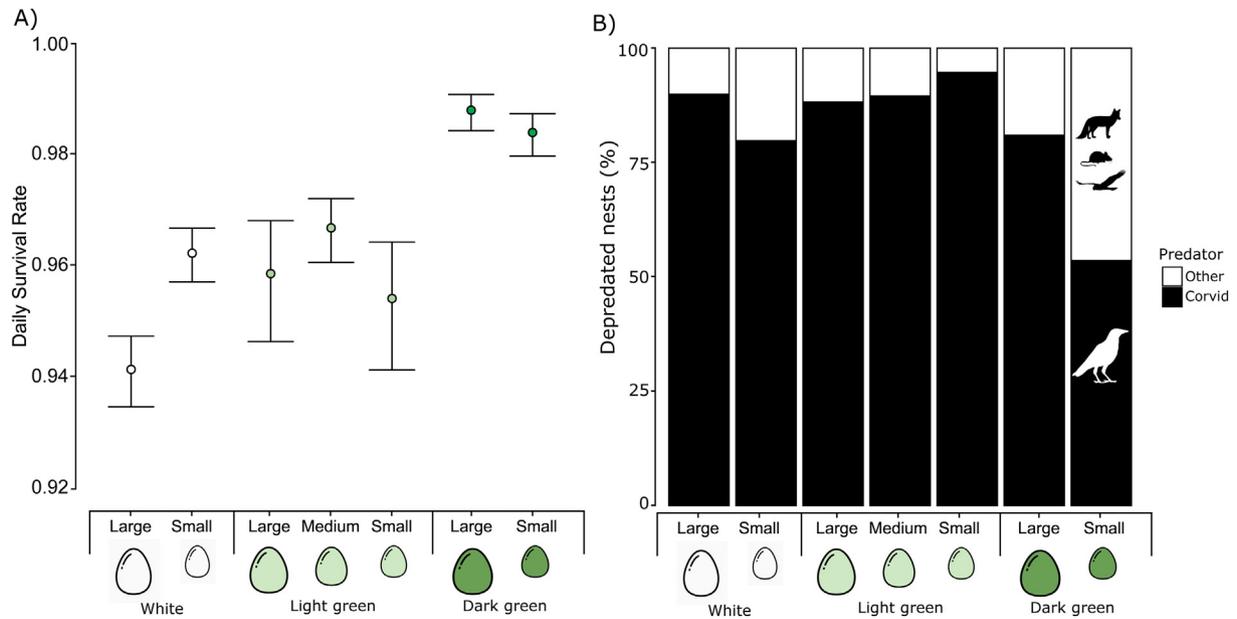
Fig. 1. A) Daily survival rate (± 95%CI) of artificial nests in relation to egg type. Details of model selection and estimates are presented in Tables S2 and 1, respectively. B) Variation of depredated nests (%) during 3-day period by corvids (black) and by other predators (white) with egg type.

3.3. Effect of neighboring nest depredation and repeated depredation events

Of the 878 depredated and 1698 non-depredated nests, 85.0% and 47.4%, respectively had at least one neighboring nest that had been depredated (Fig. S6). Corvids and other predators depredated an average of 1.5 ± 1.0 and 1.0 ± 0.6 neighboring nests, respectively. Predators were the same in 68.8% of focal nests and neighboring depredated nests with 59.2% and 31.4% being depredated by corvids and other predators, respectively. For corvid depredation model, the intraclass correlation coefficient (ICC) was 0.71 (*between* transect variance = 8.22 and *within* transect variance = 3.29), suggesting corvid depredations were clustered in transects. The conditional-R^2 of null model (i. e. *between* transect variation) was

0.56. For other predators, the ICC was 0.91 (*between* transect variance = 34.35 and *within* transect variance = 3.29) and conditional R^2 was 0.04, suggesting also a spatial clustering pattern of depredation.

On average, each nest was depredated 1.7 ± 0.9 times; 50.8% of nests were depredated more than once (25.5% twice, 15.1% three times, and 10.2% four times). Of the nests with multiple depredation events, 64.9% were repeatedly depredated only by corvids, 7.3% only by other predators, and the remaining 27.8% had different predator type involved. On average corvids and other predators depredated the same nest 2.1 ± 1.0 and 1.2 ± 0 4 times, respectively. A nest depredated once had a 52.2% chance of being depredated again while a nest depredated twice and thrice had a 69.9% and 70.4% chance of being depredated for a third and fourth time,
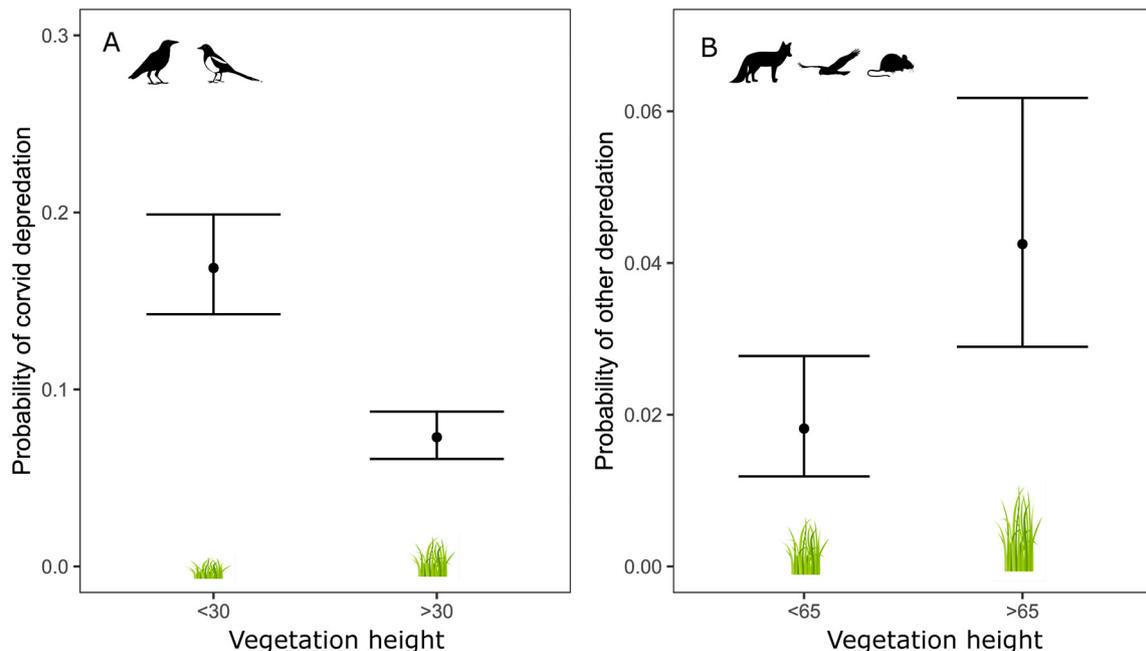

Fig. 2. Effect of vegetation height (<30 vs. >30 cm for corvid depredation and < 65 vs. >65 cm for other predators) on the probability of a nest being depredated (mean ± CI 95%) by corvids (A) and other predators (B) during 3-day period.

Table 2

Effects of land use and vegetation height on the probability of a nest being depredated by a corvid (A) or other predators (B). The reference level for land use is *cereals,* for vegetation height is *>30 cm* (in A) and *> 65 cm* (in B), and neighboring depredated nest (i. e. depredation within transect) is *No*. See Table S4 and S5 for other pairwise comparisons.

Response variable	Explanatory variable	Estimate ± SE	95% CI	
			Lower	Upper
A. Corvid depredation		(Intercept: −2.15 ± 0.58)	−3.33	−1.05
	Land use	Grasslands: 1.07 ± 0.45	0.24	2.02
		Other crops: 0.89 ± 0.45	0.06	1.85
		Spring crops: 1.66 ± 0.46	0.82	2.63
	Vegetation height (<30 vs. >30 cm)	>30 cm: −0.34 ± 0.45	−1.17	0.61
	Land use × Vegetation height (<30 vs. >30 cm)	Grasslands × Vegetation height: −0.10 ± 0.51	−1.15	0.02
		Other crops × Vegetation height: −0.12 ± 0.51	−1.17	0.84
		Spring crops × Vegetation height: −0.23 ± 0.52	−1.32	0.75
	Neighboring depredated nest	Yes: 1.79 ± 0.14	1.52	2.08
	Julian day	−0.01 ± 0.00	−0.01	0.00
	Year	2018: −0.71 ± 0.15	−1.01	−0.41
		2019: −0.70 ± 0.19	−1.08	−0.32
B. Other depredation		(Intercept: −5.02 ± 1.00)	−7.04	−3.10
	Land use	Grasslands: 0.54 ± 0.60	−0.62	1.78
		Other crops: 0.57 ± 0.63	−0.67	1.86
		Spring crops: 0.56 ± 0.70	−0.82	1.97
	Vegetation height (<65 vs. >65 cm)	>65 cm: 1.33 ± 0.56	0.30	2.58
	Land use × Vegetation height (<65 vs. >65 cm)	Grasslands × Vegetation height: 0.37 ± 0.89	−1.51	2.04
		Other crops × Vegetation height: −1.15 ± 0.91	−3.06	0.56
		Spring crops × Vegetation height: 0.22 ± 1.26	−2.92	2.43
	Neighboring depredated nest	Yes: 1.39 ± 0.27	0.87	1.93
	Julian day	−0.01 ± 0.01	−0.02	0.01
	Year	2018: 0.64 ± 0.37	−0.06	1.40
		2019: 1.06 ± 0.39	0.32	1.86

respectively ($\chi^2 = 79.14$, df $= 1, p < 0.01$). A nest depredated once with a vegetation height lower than 30 cm had a 60.6% chance of being depredated by corvids again ($\chi^2 = 15.87$, df $= 1$, p < 0.01). In cereals, a nest depredated once had only a 15.6% chance of being depredated by corvids again ($\chi^2 = 12.95$, df $= 3$, p < 0.01). Large white eggs had a 66.2% chance of being depredated by corvids again ($\chi^2 = 10.95$, df $= 4$, p < 0.01). For other predators, proportion of nests depredated multiple times did not change significantly in relation to vegetation height (65 cm: $\chi^2 = 0.73$,

df $= 1$, p $= 0.79$), land use ($\chi^2 = 4.59$, df $= 3$, p $= 0.20$) or egg type ($\chi^2 = 2.01$, df $= 4$, p $= 0.73$).

4. Discussion

This study is unique in that it analyses the depredation rate in farmland landscapes by considering the interplay between nest camouflage, nest concealment, and predator types involved. We show that egg camouflage and
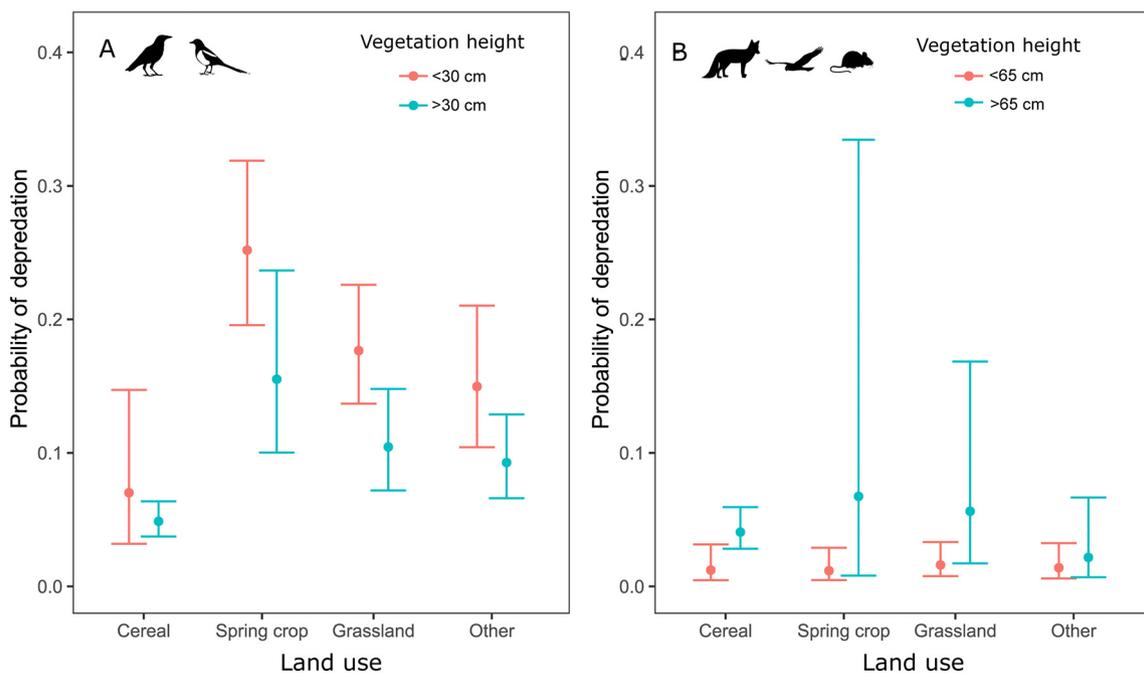

Fig. 3. Effect of land use (cereal, spring crop, grassland, and other crop) on the probability of a nest being depredated (mean ± CI 95%) by corvids (A) and other predators (B) controlling for the effect of vegetation height (<30 vs. >30 cm for corvid depredation and < 65 vs. >65 cm for other predators) during 3-day period. Parameter estimates in Table 2.

nest concealment are the major drivers of depredation rates but predator type also affects depredation rates because of spatial and temporal cues (neighboring depredated nests or previous depredation events). Using artificial nests have strong limitations (e.g., review in Major and Kendal (1996) and Moore and Robinson (2004)), due to lack of parental activity or artificial appearance of nests. For instance, we used painted model eggs which might differ from real eggs or vegetative characteristics of artificial nests might not reflect those of real ones. Although our experimental design attempts to minimize bias associated with this method, we acknowledge that depredation rates likely differ between artificial and real nests. However, in our study, we were interested in comparative patterns of depredation rates, not depredation rates per se, hence assessing relative rather than actual estimates of depredation. Artificial nest/egg methodology is a powerful and non-intrusive tool and further allows large number of replicates to analyse the effect of different environmental factors on nest depredation.

4.1. Egg camouflage and conspicuousness

The higher DSR of inconspicuous eggs (dark green) supported the hypothesis that cryptic eggs reduce depredation risk in ground-nesting birds (Troscianko et al., 2016), although artificial colors might affect the observed patterns (Weidinger, 2001). Our results are consistent with those of previous studies that demonstrated lower depredation rates in greenish eggs than in other color eggs (Blanco and Bertellotti, 2002). Corvids were the main suspected predators in our study and were able to peak all egg types, which is also consistent with a visually oriented predator on eggs regardless of size. Our study suggests that egg color might be a more important visual cue than egg size as DSR significantly differed between colors but not between differently sized eggs of the same color. Daily survival rate by predator type also differed between differently colored eggs, and dark green eggs were depredated significantly more by predators other than corvids. This might be consequence of different UV reflectance between egg types and different UV perception by predators, as green eggs reflect UV lights less than white eggs (Gillis et al., 2012) and mammals in contrast with corvids lack UV sensitivity (Håstad et al., 2005). Further research on the visual perception of predators and egg color should address this finding.

Egg size also influenced the predator type involved; the smallest eggs were mainly depredated by predators other than corvids. This suggests that large eggs may be too large for small predators (see also Bravo et al., 2020). To date, most studies addressing the effect of egg color on depredation rate have been carried out in shrub and tree nesters and have no clear conclusions (Weidinger, 2001). We showed clear effects of egg color and size on depredation rates in ground-nesting birds and further demonstrated the interactive effects between egg type and vegetation structure. This probably results from the perception of color patterns in habitat-specific light environments (Endler, 1993). Specifically, large white eggs (similar to harrier eggs) were depredated less by corvids in *cereals* as cereals were the only crop tall enough to protect such conspicuous eggs (Gillis et al., 2012). Indeed, Montagu's harrier has strong nesting preference for tall cereal crops (Limiñana et al., 2006; Millon et al., 2002), suggesting that they are likely to use cereal crops to avoid avian predators such as corvid.

4.2. Nest detectability

The nest-concealment hypothesis assumes that a lower depredation probability for nests with taller vegetation may depend on the predator species involved (Dion et al., 2000). For instance, the nesting success of grouses increased with dense cover when major predators were birds but not when they were mammals (Schieck and Hannon, 1993). In our study, a vegetation canopy of 30 cm height became an obstacle for corvids, whereas depredation probability by other predators was higher in vegetation above 65 cm. The different height threshold of depredation rate between corvids and other predators might be consequence of different habitat selection. Other predators, mostly mammals and small mammals, might use taller vegetation as a way to be concealed. Vegetation height is a metric commonly used as a proxy for nest concealment, which may provide more

lateral effective cover against depredation from the ground than from the air (Wiebe and Martin, 1998). This suggests that in our study, most depredation might have been done from ground-searching. It is likely that corvids found nests while walking on the ground as 30 cm vegetation height is in their line of sight, whereas other predators, such as mammals, would find nests at their eye level while walking hidden in the vegetation. Our results also show that land use plays a key role in nest concealment. For instance, *cereals* are effective in concealing nests regardless of their height. Corvid depredation decreased by 40–60% in *grasslands* and *spring crops* when the height was above 30 cm. *Spring crops* and *grasslands*, where depredation rates are high, are attractive crops for foraging corvids (Perkins et al., 2000) as they provide easy access and unhindered ground locomotion, facilitating the detection of prey such as insects (Barnett et al., 2004) and seeds on the ground (Moller, 1983).

4.3. Predator searching strategy

Area-restricted searches have been observed in a wide variety of organisms, including mammals (Pelech et al., 2010), insects (Hassel and Southwood, 1978), and birds (Bennison et al., 2019). Our results suggest that (1) corvids show an area-restricted search behavior as a nest was more likely to be depredated when a neighboring nest was depredated, and (2) corvids have short-term memory as most of the depredated nests were depredated more than once. Area restricted search and depredation repetition are both consistent with the hypothesis that nest depredation by corvids might be the result of an active search strategy (Vickery et al., 1992), which is consistent with previous studies (Thorington and Bowman, 2003). In addition to short-term memory, some corvid species like European jays have been shown to use spatial memory for foraging, such as food storing (Bennett, 1993; Smulders et al., 2010). Contrary to experiments using real eggs, predators were not rewarded by food in our study when a nest was located because we used plasticine eggs that lead to a lack of reinforcement mechanism for depredation repetition. Further research is needed to understand how corvids use spatial memory ability to revisit depredated nests.

Active and incidental depredation has been widely studied, particularly in mammals (Pelech et al., 2010). However, no study has addressed the interaction of this behavior with land use, vegetation height, and egg type. We found that depredation repetition might be influenced by land use or vegetation height, suggesting that once a corvid has found a nest vegetation structure may limit corvid depredation. We also found that corvids did not select or avoid habitats, which may suggest the importance of the distribution and abundance of alternative foods to reduce depredation (Schmidt and Whelan, 1999). Furthermore, not only conspicuous eggs (which might be subjected more frequently to random depredation) suffered depredation repetitions. Given that Montagu's harrier breed semi-colonially (either solitarily or in loose assemblages of up to 30 pairs (Arroyo et al., 2002)), area-restricted behavior showed by corvids suggest that harrier's nests might be more vulnerable of being depredated by corvids.

We used the depredation rate at day 3 as it allowed considering the 3 years of our experiments in the same analysis. Moreover, as DSR followed a quadratic pattern with time, using day 3 only allowed in our analyses to avoid complex statistical designs to control for time effect. However, we acknowledge some drawbacks in regard to nest detectability (i. e. land use and vegetation height) and neighboring depredation effect, since it may not correspond to biologically meaningful length of nesting stage. However, given that our aim was not to assess real depredation rates but rather to examine factors that spatially affect depredation rates and DSR, we believe our results are straightforward and do not expect other time frames to change our conclusions.

4.4. Implications for reducing nest depredation of ground-nesting birds

Strategies to mitigate the impact of predators on bird populations are highly debated (Jiguet, 2020) in farmland landscapes with generalist predator populations that determine the abundance of prey (McMahon et al., 2020). In most cases, consensual management strategies suitable for all

local stakeholders, including farmers, hunters, local authorities, scientists, and citizens, are difficult to identify.

Corvids are often considered pests and are subject to lethal population control across Europe (Madden et al., 2015). Although lethal control is commonly proposed by local actors such as hunters to reduce the abundance of predators, it has often been reported that this strategy can be inefficient, time-consuming, costly, and unethical (Roos et al., 2018). The short-term memory behavior shown by corvids suggests the strategies to be applied should operate from the beginning of the breeding season of prey. Our results also have particular implications for reducing depredation risk from visually oriented predators as a vegetation height of 30 cm appeared to be a critical value for corvids to find nests but may be less crucial to other predator-prey systems in which predators use olfactory cues. Thus, a good knowledge of the foraging ecology of predators may be a critical first step before elaborating any management options for reducing depredation pressure through habitat manipulation.

Management of vegetation structure might appear useful in reducing the impact of depredation of ground-nesting birds where corvids are the main predators. Improving the habitat quality of farmland landscapes, such as increasing the presence of natural grasslands and hedges, which improves the availability of alternative food resources (i.e. worms, insects, small mammals, seeds, or fruits) (Wilson et al., 2005) should also be implemented as a complementary tool. To conclude, we encourage the integration of the following strategies during the breeding season: 1) incorporating crops that conceal nests, and 2) improving the habitat quality to allow predators to switch to alternative food sources.

CRediT authorship contribution statement

Conceived and designed the experiments: CB VB OP MS. Performed the experiments: CB. Analysed the data: CB OP. Wrote the paper: CB OP MS VB.

Declaration of competing interest

The authors declare that they have no known competing financial interests or personal relationships that could have appeared to influence the work reported in this paper.

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Appendix A. Supplementary data

Supplementary data to this article can be found online at https://doi.org/10.1016/j.scitotenv.2022.154558.

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