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1 **Revisiting an old question: which predators eat eggs of ground-nesting**
2 **birds in farmland landscapes?**

3

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14

15 **Abstract**

16 Nest predation is a major cause of reproductive failure in birds, but predator identity often
17 remains unknown. Additionally, although corvids are considered major nest predators in
18 farmland landscapes, whether breeders or floaters are involved remains contentious. In this
19 study, we aimed to identify nest predators using artificial nests, and test whether territorial
20 or non-breeders carrion crow (*Corvus corone*) and Eurasian magpie (*Pica pica*) were most
21 likely involved. We set up an experiment with artificial ground nests (n=1429) in farmland
22 landscapes of western France, and assessed how different combinations of egg size and egg
23 material (small plasticine egg, large plasticine egg, quail and natural hen eggs) might
24 influence predation rates and predator species involved. Nest predators were identified using
25 remotely triggered cameras and marks left in plasticine eggs. Corvids were by far the
26 predators most involved (almost 80% of all predation events), independent of egg type.
27 Carrion crows alone were involved in 60% of cases. Probability of predation increased with
28 egg size, and predation rate was higher for natural than for artificial eggs, suggesting that, in
29 addition to egg size, predators might perceive plasticine and natural eggs differently.
30 Predation rates of artificial nests by corvids was related significantly to corvid abundance,
31 and far more to breeder than floater abundances, for both carrion crows and magpies. This
32 study emphasizes the importance of identifying predators at species level, and considering
33 their social status when assessing corvid abundance impact on prey population dynamics.
34 Combining camera traps and plasticine eggs can achieve this objective. Given the high
35 predation rate by carrion crows, a better understanding of landscape-mediated changes in
36 predator diet seems mandatory to design mitigation schemes able to confront ecological
37 challenges raised by generalist predators.

38 **Keywords:** carrion crow, magpie, floaters, breeders, camera trap, plasticine eggs

40 **1. Introduction**

41 Predation is a major selective pressure and driving force acting on population dynamics
42 through individual demographic traits, such as survival (DeCesare et al., 2014) and
43 fecundity (Zanette et al., 2011). Predation effects have been demonstrated for a wide range
44 of taxa, especially birds (Caro, 2005). Ground-nesting birds, a group that includes many
45 farmland, steppe and prairie species, are known to be highly impacted by predation through
46 its effects on nesting success (Gibbons et al., 2007). Indeed, tree nesting has long been
47 regarded as an anti-nest predation adaption in birds (Collias, 1997), since ground-based
48 nests, and the offspring therein, are more exposed to predators.

49 Many studies have investigated predation rate on ground-nesting birds using experimental
50 dummy eggs or nests (Major and Kendal, 1996). However, such set-ups have limitation as
51 they may not assess natural predation rates accurately, and predator-specific patterns are
52 difficult to analyse (Moore and Robinson, 2004). For instance, artificial nests might be more
53 attractive to predators than those in natural situations. Moreover, the lack of parental activity
54 at artificial nests could either decrease predation rate by removing cues for predators, or
55 increase it by parent-mediated removing egg concealment (Major and Kendal, 1996; Moore
56 and Robinson, 2004). Despite these limitations, artificial nests have been extensively used to
57 explore patterns of nest predation, mainly because of their non-intrusiveness and the ease
58 with which a large number of replicates can be deployed, allowing investigation of the
59 impacts of various environmental factors on nest predation.

60 Several parameters have been shown to affect observed predation rates. Egg size matters,
61 with large eggs generally preventing predation (Latorre et al., 2013), though not always
62 (Vazquez, Rodríguez-Cabal, Gonzalez, Pacheco, & Amico, 2018). Egg material, in
63 particular whether eggs are natural or not (i. e. plasticine or clay eggs), also affect predation

64 rates (Major and Kendal, 1996). The smell of plasticine eggs may attract mammalian
65 predators, and enhance predation rates compared to natural eggs (Rangen et al., 2000),
66 whereas the eggshell of quail or hen eggs may not be crushed by small mammals (Bayne et
67 al., 1997). Thus, it is crucial to recognize that artificial nest set-ups aim to assess relative
68 rather than actual predation rates (Moore and Robinson, 2004).

69 If predation on ground-nesting birds has long been studied, predator identification remains a
70 major challenge (Benson et al., 2010). Several methods have been used to identify predators,
71 including nest cues, hair catchers, tracking boards and bait marker chemicals (Jones, 2007;
72 Staller et al., 2005). However, all have their pitfalls (Major, 1991; Williams and Wood,
73 2002). Marks left in plasticine eggs is one of the most powerful method to identify predator
74 species (Bayne et al., 1997), though it may obscure the importance of secondary predator
75 species (Hanssen and Erikstad, 2013) and predation attempts (i.e., without effective
76 predation), which contribute to perceived risk of predation. Recently, the use of camera traps
77 has become widespread (Cox et al., 2012), as videos enable indisputable identifications of
78 predators when they visit nests. Furthermore, camera traps allow secondary predators and
79 predation attempts to be identified. However, camera traps may decrease predation rates
80 (Richardson et al., 2009), since many predators, particularly corvids, are neophobic, i.e. they
81 cautiously avoid novel objects (Herranz et al., 2002). Consequently, most studies that have
82 used camera traps have been conducted in wooded habitats, so providing cover for camera
83 concealment (Richardson et al., 2009). In open habitats, such as agricultural landscape,
84 studies with camera traps have reported either increased predation rates (Renfrew and Ribic,
85 2003), no effect (Capstick et al., 2019; Pietz and Granfors, 2000), or did not explicitly test
86 the camera effect (Krüger et al., 2018; Ponce et al., 2018). In grasslands and open habitats,
87 studies have used plasticine eggs in artificial nests as an alternative to camera traps when

88 visibility is high (Arbeiter and Franke, 2018; Dion et al., 2000; Muchai and du Plessis,
89 2005), but none to our knowledge have ever compared the two methods.

90 When predator identity has been confirmed, corvids were often involved and they are
91 regularly claimed to be key drivers of bird abundance (Fuller et al., 1995; Luginbuhl et al.,
92 2001; Stoate and Szczur, 2001), especially in farmland landscapes (Andrén, 1992). While
93 corvid and passerines densities or breeding success have been reported as negatively
94 correlated (Dunn et al., 2010; Gabriel et al., 2010; Paradis et al., 2000), the generality of
95 such patterns has been repeatedly questioned, since corvid populations are not always
96 associated with changes in nest predation (Madden et al., 2015; Newson et al., 2010).

97 Predator breeding status might also influence prey selection (e.g. Sacks, Jaeger, Neale, &
98 McCullough, 1999). Indeed, breeding status in corvids shapes social structure, with
99 monogamous pairs defending breeding territories while non-breeding individuals (floaters)
100 are gregarious (Clayton and Emery, 2007). Despite increased predation risk near corvid
101 nests (Roos and Pärt, 2004), and the known effect of breeding status on predation rate (Bui
102 et al., 2010; Capstick et al., 2019), whether predation by corvids is mainly attributable to
103 breeding individuals remains uncertain.

104 In the current study, we experimentally quantify ground nest predation in farmland
105 landscapes, asking whether corvid species, especially the carrion crow (*Corvus corone*) and
106 Eurasian magpie (*Pica pica*), were the main predators involved. Using a large data set of
107 1429 artificial nests associated in part with camera traps, we established predator identities
108 and assessed their relative contribution to observed predation rates. More specifically, we:
109 (1) compared predation rates between artificial nests with plasticine or natural eggs of
110 different sizes, (2) compared predation rates between artificial eggs with, or without, camera
111 traps; (3) assessed the accuracy of predator identification from plasticine eggs *versus* camera

112 traps; and (4) quantified relationships between corvid abundance according to their social
113 status (breeders vs. floaters) and the likelihood of predation.

114 **2. Methods**

115 **2.1. Study area**

116 The study was carried out in 2018 and 2019, in the LTSER “Zone Atelier Plaine & Val de
117 Sèvre” (46°15N, 0°30W), a site which covers 450 km² of intensive agriculture in Western
118 France (Fig. 1a), mostly dedicated to cereal production (see Bretagnolle et al. 2018b for
119 general site description). The study area is mostly open, flat (altitude is 40 to 100 m asl) with
120 a temperate Atlantic oceanic climate, sparsely populated (62 ind/km²) and managed almost
121 exclusively for arable and mixed farming. The most common crops are wheat (33.8%),
122 meadows (13.5%, including both permanent grasslands and temporary hay, such as alfalfa),
123 sunflower (10.4%), corn (9.6%), oilseed rape (8.3%) and peas (2%). Five corvid species
124 breed there: carrion crow, Eurasian magpie, western jackdaw (*Corvus monedula*),
125 rook (*Corvus frugilegus*) and Eurasian jay (*Garrulus glandarius*). The study area is an
126 important breeding site for threatened bird species, including little bustard (*Tetrax tetrax*),
127 three harriers *Circus* spp. (*C. pygargus*, *C. cyaneus* and *C. aeruginosus*) and stone curlews
128 (*Burhinus oedicephalus*), as well as for gamebirds such as common quail (*Coturnix coturnix*),
129 red-legged (*Alectoris rufa*) and grey (*Perdix perdix*) partridges, and ring-necked pheasant
130 (*Phasianus colchicus*). The presence of many species covered by the EU Bird Directive led
131 to the designation of a NATURA 2000 site in 2004 (FR5412007) on half of the LTSER.

132 **2.2. Experimental design**

133 **2.2.1. Artificial nest deployment**

134 We conducted an artificial nest experiment in 2018 (n=529 nests) and 2019 (n=900 nests).
135 Artificial nests were set up on 104 sampling points from 27th April to 22nd June of 2018, and
136 98 sampling points from 2nd April to 12th June of 2019. A sampling point consisted in a

137 given location within a field, at which several nest types were deployed. Two identical eggs
138 were placed in each artificial nest, which were constructed as a shallow depression (made by
139 booted feet to avoid any influence of scent) in the soil. To investigate to what extent the
140 presence of camera traps might bias predation rate, we set up artificial nests with (N=391),
141 or without camera traps (N=1038). We also assessed whether different combinations of egg
142 size and egg material might influence predation rates, though with unbalanced design (see
143 Appendix A Table S1). Nests (one nest per treatment category per sampling point) were
144 grouped per field (Fig. 1b), consisting of four (2018) and seven nests (2019) per group. At
145 each sampling point, artificial nests were placed along a linear transect, with nests spaced at
146 30 m intervals. Nest locations were recorded by GPS position, no markers were used. In
147 2018, the artificial nest experiment consisted in using small plasticine eggs without a camera
148 trap, large plasticine eggs with and without a camera trap, and hen eggs without a camera
149 trap. In 2019, we enlarged the treatment categories, to include: i) small plasticine eggs
150 without a camera trap, ii) large plasticine eggs with and without a camera trap; iii) hen eggs
151 with and without a camera trap; and iv) quail's eggs with and without a camera trap. In 2019,
152 we repeated the experimental scheme twice, at about 4 week intervals per sampling point
153 (first session, 2nd April-6th May; second session, 7th May-12th June). During the second
154 session, nest locations were moved by at least 100 m from that used in the first sampling to
155 avoid any influence of the first session. To select sampling points, we used stratified random
156 sampling design by hedgerow density providing a representative variability of the study
157 area. The mean (\pm SD) distance between sampling points was 9.5 ± 4.8 km (range from 0.35
158 to 26.1 km).

159 Artificial nests were exposed to predators for 7 days (Fig. 1b), no nest visit were carried out.
160 After 7 days, all nests were removed. This time span was a proxy of risk of predation during
161 the egg-laying period of large grassland birds such as partridges, harriers or bustards,

162 especially during the period in which the individuals leave their nests open and are not yet
163 incubating or sitting on the eggs. Red-legged or grey partridges may have longer egg-laying
164 period (up to 20 days, though this is exceptional, Cabezas-Díaz and Virgós, 2007; Černý et
165 al., 2018) than little bustard, great bustards or Montagu's harrier (2-7 days, Arroyo et al.,
166 2004; Lapiedra et al., 2011; Magaña, 2007).

167 **2.2.2. Egg types**

168 We varied egg size independently (four classes) and material (natural *versus* artificial) as
169 both egg size and material may affect predation rates. Plasticine eggs were made using an
170 off-white, nontoxic modeling compound (J. Herbin plasticine, Chelles, France). Plasticine
171 eggs were fixed by a thin wire and a nail in the ground, in order to prevent predators from
172 carrying them away. To standardise egg types, natural color of quail and hen eggs was
173 removed with acetic acid (10%) and cleaned with water, so that all eggs were white. Size
174 however varied: largest eggs were hen eggs (5.5 x 4.2 cm, L x W), then large plasticine eggs
175 (5.0 x 3.0 cm), quail (3.4 x 2.6 cm) and small plasticine eggs (2.5 x 1.5 cm). Therefore, two
176 size categories of plasticine eggs (small and large), and two size categories of natural eggs
177 (quail and hen) were available.

178 **2.2.3. Predator identification**

179 Camera traps used were light-triggered passive wildlife cameras. We used two models,
180 Coolife Wildlife Camera (n=20) and Spypoint Force 11D (n=15). Trigger speed was 0.7 s
181 and a delay of 10 s between triggers. Sensitivity was set to "high". Each camera was placed
182 approximately 1.5 m away from the nest, hidden as much as possible within crop vegetation.
183 Cameras were programmed to record 30 seconds of video per trigger, either during daylight,
184 or with a night-time with infrared illumination for nocturnal predators. Coolife Wildlife
185 model had no-glow IR LEDs (940nm), whereas Spypoint Force 11D model had low-glow
186 IR LEDs (850 nm). Low-glow LEDs are about 30% brighter than no-glow LEDs. We check

187 for possible differences in behaviour of animals between the two types of camera models
188 (see Appendix B). There were no detectable differences. First, nocturnal individuals looked
189 toward the camera in 38.9% (± 46.9) of cases, independently of the camera trap model
190 ($W=1659.5$; $p=0.74$; Fig. S1, Appendix B). Second, the model of camera traps did not affect
191 either the total number of recorded events (Fig. S2A, Appendix B), nor the number of
192 recorded events between nocturnal and diurnal animals (Fig. S2B and C, Appendix B), and
193 the number of videos triggered according to periods of the day (morning, afternoon,
194 evening, night, Fig. S3, Appendix B).

195 A nest was considered predated when at least one of the eggs had been damaged. Predator
196 species were identified by tooth and bill imprints in plasticine eggs, and by camera traps
197 when available. At camera-monitored nests, predator visits were also counted when
198 predators were observed at short distance from the nest or/and looking at the eggs but
199 without predating. We considered these latter cases to be predation attempts. Thus, for
200 camera-monitored nests, we considered two categories: i) *predated*, when at least one of the
201 eggs was damaged; and ii) *predated and/or attempt to predate*, when eggs were damaged
202 and/or predator visits to the nest had occurred, but without predation.

203 **2.3. Estimating corvids abundance**

204 Corvid abundance (i.e. carrion crow and magpie, by far the most numerous) was estimated
205 during spring 2018 and 2019 ($n=104$ and $n=98$, respectively). In each sampling point,
206 corvids were counted using 10 minutes duration point counts. Each sampling point was
207 visited four times per year, at about 2-week intervals. Sampling points were surveyed from
208 13th April to 21st June of 2018, and from 29th March to 19th June of 2019.

209 During each visit, all auditory and visual contacts, their precise location, and the behaviour
210 of every single corvid individual were recorded within a 300-m radius around the observer.
211 Surveys were carried out within 4 h after sunrise, while avoiding rainy or strong wind

212 (Bretagnolle et al., 2018b; Luginbuhl et al., 2001). Before starting corvid abundance
213 sampling, all observers spent one day of training so as to standardize count protocol and
214 reduce observer bias. We carried out repeated counts was to discriminate territorial breeders
215 from non-breeders (floaters) at a given sampling point. Presence of territorial breeders was
216 determined using a combination of proxies. First, nests (whether active or inactive) were
217 located in early spring (before bud burst, typically early March). Second, corvid behaviour
218 was used as a proxy indicating breeding and territorial behaviour, such as bringing nest
219 material, feeding and territorial defence against other corvids, alarm calls and attacking
220 raptors (Röell and Bossema, 1982). And third, by analysing the four samples per point: if a
221 pair was observed at least in 2 out of 4 counts, it was assumed to be a territorial pair.
222 Absence of territorial pair/breeder was determined by using inverse evidence, i.e. if no nest
223 had been observed, no breeding or territorial behaviour had been observed in any of the four
224 samples, and no pair seen twice. Then, the total number of pairs (per species) per sampling
225 point was obtained, as well as the abundance of non-breeders determined as the maximum
226 number of corvids (per species) recorded at a given point minus the number of breeders.

227 **2.4. Statistical analyses**

228 **2.4.1. Factors affecting predation rate**

229 We tested whether the egg size (large/small) and material (plasticine/natural) affected the
230 probability of predation using generalized linear models (GLM, binomial error, link = logit)
231 with Egg size and Egg material as factors, including their interaction, as fixed factors. Since
232 no nests with small plasticine eggs were set with a camera trap, and to remove the effect of
233 camera trap on other nests, we used only nests without camera traps for this particular
234 analysis.

235 We then tested whether the presence of camera traps affected the probability of predation or
236 predation attempts using GLM (binomial error, link = logit). We ran separate models for

237 predation, and predation plus predation attempts. Camera trap presence (with *vs.* without),
238 egg type (small plasticine, large plasticine, quail *vs.* hen), and the two-way interactions were
239 included as fixed effects. We used post-hoc Tukey's test to identify significant differences
240 between egg type with camera trap presence/absence. Temporal and spatial variables (i.e.
241 year, session and sampling point) were not included in the models because pre-tests had
242 shown they were not significant (see Appendix C).

243 **2.4.2. Predator identification**

244 Differences in the frequency of predation events between predator classes (corvids, other
245 birds, mammals), or between nests with camera trap and plasticine eggs without camera
246 traps, were tested using Pearson's Chi-square tests. For the few nests (n=7, see Appendix A
247 Table S1) that were preyed upon by two different species, we considered only the first
248 predator for statistical analyses.

249 **2.4.3. Timing of predation**

250 We used Cox proportional hazards models to evaluate time to predation as a function of
251 predator identity and egg type. Survival time for each nest was estimated using the number
252 of days elapsed between nest deployment and predation or predation attempt at nests with
253 camera traps. Some nests were predated more than once by the same species (n=49). For
254 these we then considered first predation event or first predation attempt when calculating
255 survival time. We included predator species (corvids *vs.* other species) and egg type (large
256 plasticine *vs.* quail) as fixed effects. We used only large plasticine and quail eggs because
257 sample size of hen eggs with camera traps was too small to allow comparisons (n=19, see
258 Appendix A Table S1). We checked that the Schöenfeld residuals of the model were time
259 independent (proportional hazard assumption) to validate the use of Cox model ($\chi^2=4.43$,
260 $p=0.43$, (Therneau and Grambsch, 2000). Temporal and spatial variables (i. e. year, session

261 and sampling point) were not included in the Cox model because pre-tests had shown they
262 were not significant (see Appendix D).

263 **2.4.4. Predation rate in relation to corvid breeding status and abundance**

264 To establish whether predation rate was linked to corvid abundance, we also used GLM
265 (binomial, link = logit). Three models were built. The first for explaining Corvid predation
266 using Corvid breeder and Corvid floater numbers. The second for explaining Carrion crow
267 predation using Carrion crow breeders, Carrion crow floaters, Magpie breeders and Magpie
268 floaters, while the third for explaining Magpie predation using Carrion crow breeders,
269 Carrion crow floaters, Magpie breeders and Magpie floaters.

270 In the first model, corvid predation was defined as the response variable (N=1048), and
271 included nests predated by any corvid species identified with camera traps or by in-
272 plasticine marks. For this model, corvid abundances (breeders and floaters) were defined as
273 fixed factors. In the second and third models, the response variable (predated/not predated)
274 included predated nest by a camera trap-identified carrion crow or by magpie (N=654 and
275 N=589, respectively). Abundance of carrion crow breeders, magpie breeders, carrion crow
276 floaters and of magpie floaters, were included as fixed factors. To avoid multi-collinearity
277 (i.e. Variance Inflation Factor < 2), two-way interactions between these variables were
278 excluded. Breeder abundance (number of pairs per sampling point) was defined as the
279 categorical variable, while number of floaters was defined as the continuous variable.
280 Temporal and spatial variables (i. e. year, session and sampling point) were not included in
281 the models because pre-tests had shown they were not significant (see Appendix E).

282 Likelihood ratio tests (chi-squared test) were used to assess the significance effect of each
283 predictor in all models by using package ‘car’ (Fox and Weisberg, 2019). Estimates of the
284 models were calculated only for models that contained significant terms. We used the

285 packages 'lme4' to run GLMM (Bates et al., 2015) and 'survival' to run the Cox model
286 (Therneau, 2012). All models were tested using R version 3.5.0 (R Core Team, 2018).

287 **3. Results**

288 **3.1. *Factors affecting predation rate***

289 Overall, 40.1 % of nests (n=1429) were predated, with an additional 10.1% of nests with
290 cameras that were visited but not predated. The probability that a nest would be preyed upon
291 was affected by egg size and egg material (Table 1A): large size and natural eggs were more
292 likely to be predated than small sized and/or artificial eggs (i.e. plasticine). Highest
293 predation rate was recorded for hen eggs (67.6%, N=193), followed by quail eggs (47.2%,
294 N=288), large plasticine eggs (36.4%, N=618) and small plasticine eggs (24.5%, N=330;
295 Fig. 2). There was a significant effect of camera traps on nest predation (Table 1B): nests
296 with camera trap were less likely to be predated (by about 17%: Fig. 2). However,
297 considering predation attempts (i.e., predation plus visits without predation) instead of
298 predation *sensu stricto*, sharply reduced the statistical effect of camera traps (Table 1C),
299 with large plasticine and quail eggs no longer being significant (post-hoc test: $p>0.05$,
300 Appendix F). Cameras decreased the act of predation, likely as a result of predator
301 neophobia as shown in video images (see Appendix G).

302 **3.2. *Predator identification***

303 Predators were identified to species level at 98% of nests with camera traps, whereas for
304 plasticine eggs without camera traps, predators were grouped into corvids, undetermined
305 birds (potentially including corvids), large mammals, small mammals and undetermined
306 (3.4% of all cases for the latter category). Predator identification of quail and hen eggs in
307 nests without camera traps was not possible in most cases because eggs were entirely
308 removed from the nests, and pieces of shell were found in or near the nests in less than 3%
309 of cases. In total, we recorded 11 species visiting, removing or preying eggs at 158 nests

310 with cameras (Appendix A Table S2). Proportions of predator classes differed significantly
311 between egg type ($\chi^2=68.14$, $df=4$, $p<0.01$, Fig. 3), but this effect was only due to small
312 plasticine eggs (all without camera traps; Fig. 3D) as shown by post-hoc Tukey tests (small
313 plasticine - large plasticine: $\chi^2=37.00$, $p<0.01$; small plasticine - quail: $\chi^2=17.71$, $p<0.01$;
314 small plasticine - hen: $\chi^2=7.48$, $p<0.01$; all other paired tests being non-significant, $p>0.01$).
315 In particular, there was no statistical difference between observed predators with camera
316 traps and predators inferred from marks on plasticine eggs ($\chi^2=8.42$, $df=4$, $p=0.36$). Corvids,
317 particularly carrion crows and magpies, were the main predators for all egg types,
318 accounting for 79.3% (60.3% for carrion crows alone) of predation events overall (Fig. 3).
319 In seven nests with camera (4.4% of predated nests), eggs were preyed upon by two
320 different species (we then only considered the first predator in statistical analyses): Carrion
321 crow-Magpie ($n=3$), Carrion crow-Rook (1), Magpie-Jay (1), Magpie-Montagu's harrier (1)
322 and Montagu's harrier-Red fox (1). Of 391 nests with camera traps, 27.9% were predated
323 and 10% were visited, but without predation. Most visits without predation were carried out
324 by carrion crows (71.8%, $N=28$).

325 **3.3. Timing of predation**

326 Nest survival probability did not differ statistically between large plasticine and quail eggs
327 (Table 2), but it did according to predator species (Table 2, Appendix D Fig. S2). Nests were
328 preyed upon significantly sooner by corvids than by other species (Table 2), with carrion
329 crows and magpies predating, respectively, a mean of 2.00 (± 1.51) days and 1.96 (± 1.34)
330 days after nest deployment, compared to 3.15 (± 1.92) for other species. Carrion crows and
331 magpies visited nests 2.2 ± 1.4 days before predating the eggs in 35.1% ($n=33$) and 16.0%
332 ($n=4$) of the nests. For nests predated by carrion crows, 38% were preyed more than once
333 (2.1 ± 2.0 times, range 1-12 in plasticine eggs; 1.3 ± 0.73 times, range 1-2 in natural eggs,
334 $n=36$), while magpies did this for 61.9% of nests they predated (2.5 ± 2.0 times, range 1-15 in

335 plasticine eggs; 1.5 ± 0.57 times, range 1-2 in natural eggs, $n=13$). All avian predation of
336 nests with cameras occurred during daylight ($n=135$), whereas mammalian predation all
337 occurred at night ($n=8$).

338 **3.4. *Predation rate in relation to corvid breeding status and abundance***

339 Corvid presence was recorded at least once during point counts in 94.5% of sampling points
340 (2018 and 2019 combined), indicating that they were near-ubiquitous at the study site, with
341 1.2 ± 2.1 carrion crow (range 0-72) and 0.8 ± 1.0 magpies (range 0-17) per sampling point
342 ($n=104$ and $n=98$ in 2018 and 2019, respectively). Territorial pairs were observed in 64.2%
343 of the sampling points (0.64 ± 0.48 pairs, range 0-3), 55.2% for carrion crow (0.40 ± 0.49
344 pairs, range 0-2) and 26.7% for magpie (0.27 ± 0.46 pairs, range 0-2). Floaters were
345 observed at 70.3% of the sampling points for carrion crow (2.3 ± 6.1 individuals, range 0-
346 72), and at 35.2% of sampling points for magpie (0.6 ± 1.1 individuals, range 0-15).
347 Probability of predation by corvids increased significantly with corvid breeder abundance
348 but not with floater abundance (Fig. 4A, Table 3). Probability of predation increased by 0.2
349 (20%) per additional breeding pair. Analysed by species, we found the same results:
350 predation by carrion crow increased with carrion crow breeders' abundance (Fig. 4B, Table
351 3), but not with floater carrion crow abundance, and it was unrelated to either floater or
352 breeder magpie abundances (Table 3). The same result was obtained for magpies (Table 3,
353 Fig. 4C).

354 **4. Discussion**

355 **4.1. *Predator identity***

356 Corvids were the main predator group in our study (almost 80% of predation events). They
357 preyed eggs earlier and faster than other predators, whatever the egg type. Corvids are
358 well-known nest predators in agricultural landscapes (Andr n, 1992; Capstick et al., 2019;
359 Kr ger et al., 2018), but the proportion of corvid predation in this study is one of the highest

360 reported: in farmland habitats, previously-reported corvid predation rates have ranged from
361 4% to 50% (Arbeiter and Franke, 2018; Capstick et al., 2019; Ponce et al., 2018) and crows
362 tend to have greater effect on prey population than magpies (Madden et al., 2015). In our
363 study, carrion crows were involved in 60% of recorded predation events, whereas magpies
364 were involved in 19%. Nest predation by raptors was infrequently observed in our study area
365 (4%), as was predation by mammals (7.1%). Lower mammal predation in our study
366 contrasts with other studies where mammal predation ranged 39-84% (Arbeiter and Franke,
367 2018; Krüger et al., 2018; Purger et al., 2012). We possibly altered odour cues when
368 removing natural egg colour with acetic acid, suggesting that mammal predation studies
369 using real eggs may underline odour cues used by mammals. It should be noted also that
370 since natural eggs usually disappeared, we could not identify predators involved, though we
371 suspect that they were mostly corvids predation, since corvids always remove eggs
372 according to our video records.

373 4.2. *Factors affecting predation rate*

374 Observed predation rates differed significantly between egg types, supporting previous
375 observations (Lindell, 2000; Major and Kendal, 1996). However in many preceding studies,
376 the different egg types have been placed together in the same nest (Bayne and Hobson,
377 1999; Purger et al., 2008), which might affect both predator perception and detectability of
378 each egg type. We found that larger eggs had higher predation rates than small ones.
379 Although large eggs are likely to be more conspicuous to corvids, large plasticine and quail
380 eggs were predated at comparable rates despite their differences in size. Hence, in addition
381 to size, corvids might detect, but then reject, plasticine eggs and prefer natural ones, a
382 reflection of their high cognitive abilities (Grodzinski and Clayton, 2010). Higher predation
383 levels by small mammals of small plasticine eggs compared to large plasticine eggs
384 confirmed previous results with small mammals that showed that predation rates decrease

385 with increasing egg size, as larger units are more difficult to bite, manipulate and break
386 (Bayne et al., 1997). Therefore, since egg size influences propensity to predate at the
387 predator species level, using eggs of different sizes appears to be a way to avoid biases in
388 the identification of predators across a broad-based predator assemblage.

389 Camera traps are powerful tools for identifying predator species and behaviour (Cox et al.,
390 2012). In open habitats, such as agricultural landscape, a situated camera remains quite
391 conspicuous to predators and this can significantly decreases predation rate (Richardson et
392 al., 2009), but not visit rate (the current study). Predator visits may be considered as attempts
393 at predation: corvids are suspicious, and detecting the camera may alter their behaviour such
394 that they withdraw from the area (see Appendix G). Therefore, using camera traps might
395 underestimate predation rate, but this effect can be controlled by adding predator visits to
396 predation events. However, camera presence did not alter predation rate differentially for
397 either predator species, since recorded predator assemblage composition was the same
398 whether cameras were present or not. Identifying predators based on plasticine eggs may
399 thus be valid, though it does not always allow species identification (e.g. it cannot
400 differentiate between magpie and carrion crow) and detection of some secondary predation
401 events. Although camera traps provide more detailed information, the number of cameras
402 that can be managed is cost-limited. In contrast, plasticine eggs are a simple and cheap
403 method that allows large numbers of replicates to be deployed. Therefore, to identify the
404 predator assemblage and test drivers of predation rate variation in farmland landscapes, we
405 recommend the use of both camera traps (for a small number of nests with detailed
406 information) and plasticine eggs (for a far larger sample).

407 An interesting extension of using camera trap technology may be to combine it with
408 individual identification of corvids. Corvids are long-lived birds with known cognitive
409 abilities, such as long-term memory and learning mechanisms (Taylor, 2014). Marking birds

410 individually would allow investigating the effect of social status and particularly whether
411 (and if so, for how long) corvids predate the same nests.

412 4.3. *Breeding status of corvid predators and implications for management*

413 We found correlational evidence that predation rate was related to corvid abundance and that
414 breeding pairs were more likely to be responsible for most predation events. Such evidence
415 held for both carrion crow and magpie. Despite methodological constraints listed and
416 discussed above, and although we could not estimate corvid age or breeding status, we
417 believe our design and methodology have sufficient power to account reliably for predation
418 patterns and measure corvid abundance because (i) predation patterns did not vary with
419 years or session, (ii) there was no spatial autocorrelation between sampling points
420 guarantying statistical independence, iii) in all three tested cases, relationships between
421 breeders abundance and predation rate was strong, while was absent for floater abundance,
422 and iv) predation rate attributed (by camera traps) to carrion crow did not correlate with
423 magpie abundance and vice versa. Although breeding pairs may predate more effectively
424 than floaters (Erikstad et al., 1982), it is also likely that breeding pairs defend their territories
425 against floaters (Bui et al., 2010), and that breeders have higher food demand than floaters
426 due to the presence of offspring. We have, however, some indirect evidence of potential
427 floater predation: even when we detected no corvids at all, predation rate by corvids was c.
428 0.2 (Fig. 4 A), suggesting that a truly predator-free space does not exist in our study
429 (Schmidt et al., 2001). In addition, detection probability was not perfect (i.e. <1), even for
430 breeders and perhaps especially so for floaters. Finally, corvids are mobile birds and some
431 individuals from outside the area of detection could enter the area. Floaters being especially
432 mobile, they can remain undetected by our sampling procedure, but still be responsible for
433 incidental predation.

434 Generalist predators (including corvids) have increased in recent decades, e.g. in UK
435 (Gregory and Marchant, 1996) and USA (Peery and Henry, 2010), and this may have
436 increased predation pressure (see Terraube and Bretagnolle (2018)). However, in France,
437 although magpies have increased (+13.91% in 18 years), the carrion crow population
438 appears stable, and may even have declined in the last few years (Vigie-Nature, 2020). Both
439 species are managed by hunting associations, notably to improve gamebird breeding
440 success. However, controlling corvid populations is time-consuming, costly and
441 controversial (Bolton et al., 2007). Culling corvids increase dispersal (Marzluff and
442 Heinrich, 1991) and replacement rate (Bodey et al., 2009). Removing of territorial pairs may
443 result in a compensatory influx of non-breeding birds (Bolton et al., 2007), that can become
444 nest predators. Reduced availability of alternative food as a consequence of agricultural
445 intensification may also have forced corvids to shift their diets towards nest content
446 (Newton, 2004; Schmidt, 1999; Whittingham and Evans, 2004). Consequently, if high
447 corvid predation rate is a consequence of low food availability due to agricultural
448 intensification, new management options should be possible. A detailed understanding of
449 predation patterns is the cornerstone of accurate management and, therefore, feeding
450 behaviour of corvids and nest predation should be compared between areas rich and poor in
451 corvid food (i. e. insects and worms). Mitigation schemes of corvid predation of nests should
452 be experimentally tested, and could include offering alternative (and possibly more
453 palatable) prey to carrion crows. Many experimental studies have reduced corvid density
454 (e.g. Dinkins, Conover, Kirol, Beck, & Frey, 2016; Fletcher, Aebischer, Baines, Foster, &
455 Hoodless, 2010), but to our knowledge there is no experimental studies that managed food
456 availability for corvids (but see Kubasiewicz et al. (2016), for other species). Other studies
457 have suggested that negative impacts of corvids could be mitigated by improving habitat

458 quality (Dunn et al., 2016; Evans, 2004). The limitation of negative impacts of corvids on
459 bird abundance remain a prevalent ecological and management challenge.

460

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466 **6. Author contributions**

467 Conceived and designed the experiments: CB VB OP MS. Performed the experiments: CB.
468 Analyzed the data: CB OPV. Wrote the paper: CB OPV MS VB.

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471 **7. Bibliography**

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Fig. 1. Map of the study area showing: A) the location of the Long-Term Social- Ecological Research (LTSER) site ‘*Zone Atelier Plaine & Val de Sèvre*’ within France, the Chizé forest reserve (in grey) and the sampling points. B) Image of a sampling point showing the location of the artificial nests (n=1429) and the location of the point count for estimating corvid abundance.

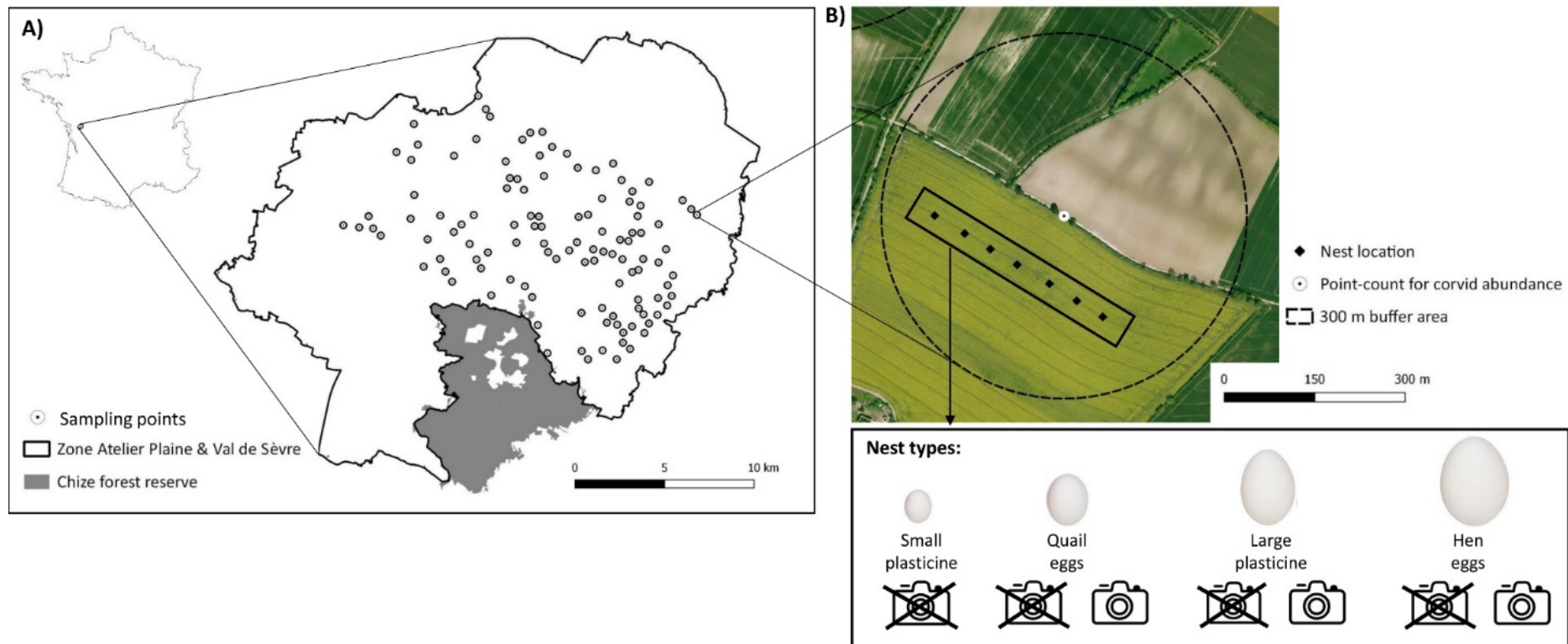


Fig. 2. Probability ($\pm 95\%CI$) of predation (black) and predation attempts (white) in relation to type of artificial nest, both years combined. Predation attempts denote cases where a predator visited the nest but did not predate eggs. Note that eggs were ordered by size, the smallest to largest, from left to right.

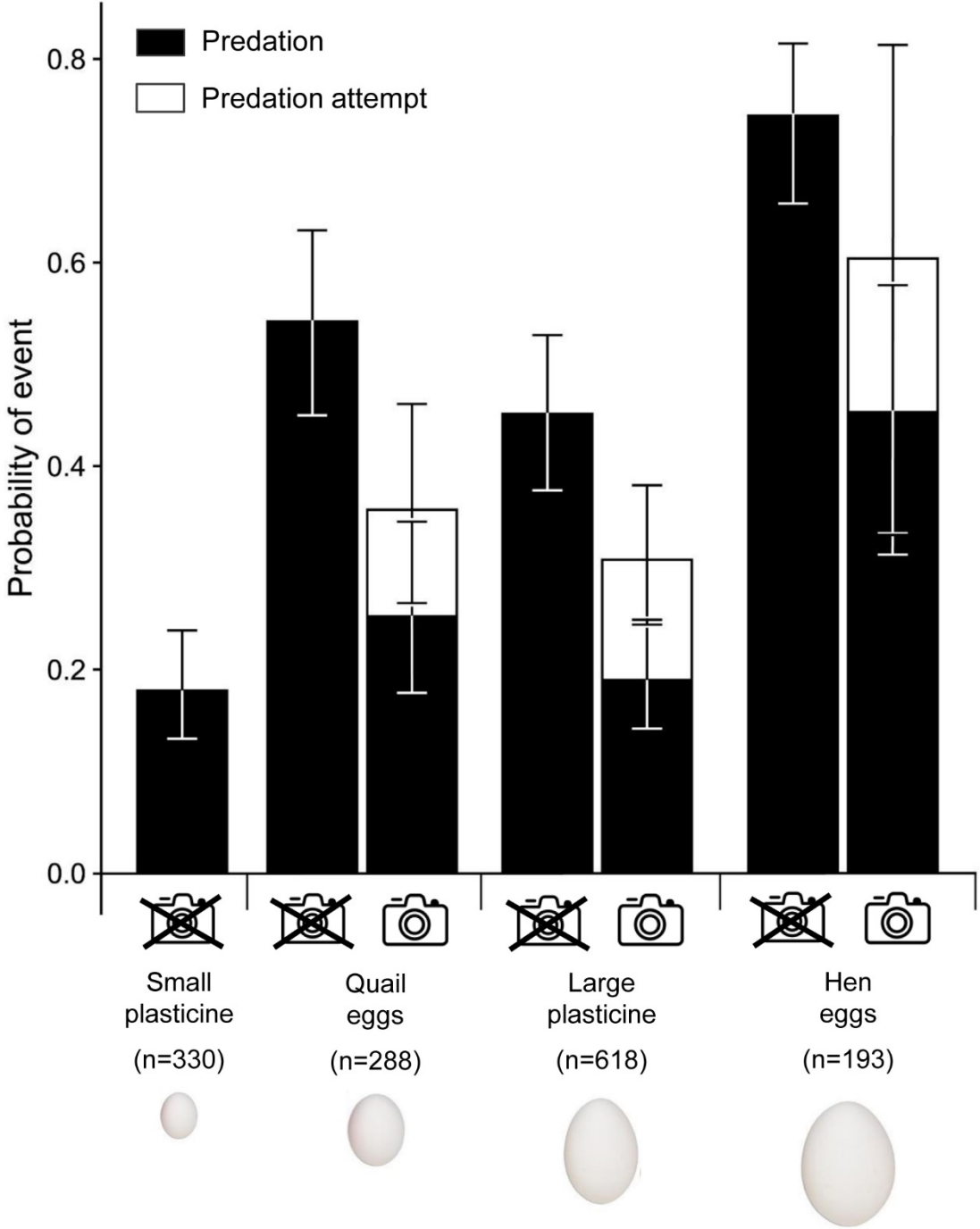


Fig. 3. Identification of predators per nest type in the study area during spring 2018 and 2019 (both years combined). A) Quail eggs with camera (n=73), B) Large plasticine eggs with camera (n=299), C) Hen eggs with camera (n=19), D) Small plasticine eggs without camera (n=330), and E) Large plasticine eggs without camera (n=319). In nests with camera traps, corvids were divided into carrion crow, magpie and other corvids (such as rook, European jay, jackdaw).

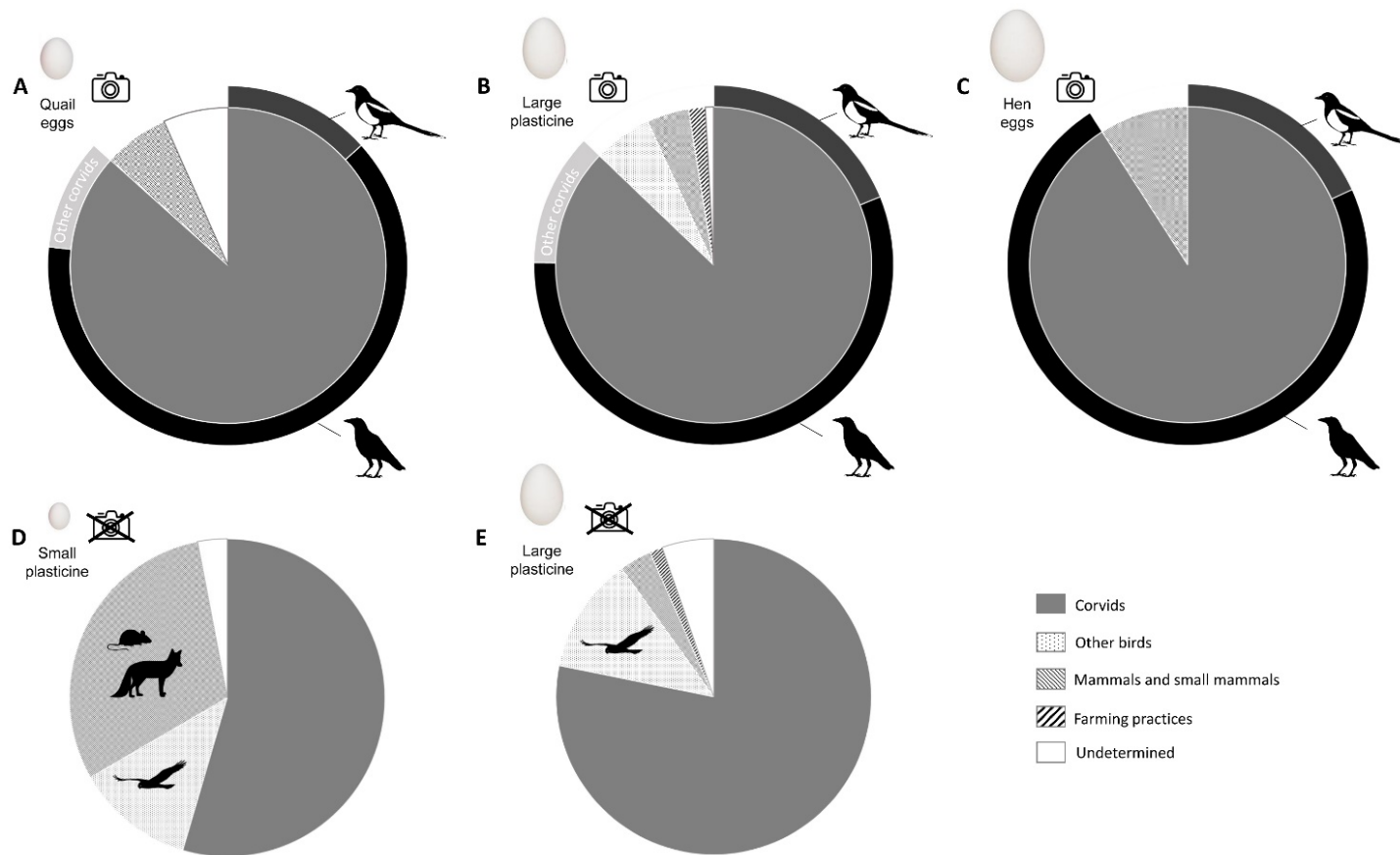


Fig. 4. Predicted probability ($\pm 95\%$ CI) of predation by corvid species (A, $n=1048$ nests), carrion crow (B, $n=654$ nests) and magpie (C, $n=589$ nests) in relation to the abundance of breeders (number of pairs, blue) and floaters (n, dashed grey line) of each species. Probability of predation is predicted from GLM (Table 3).

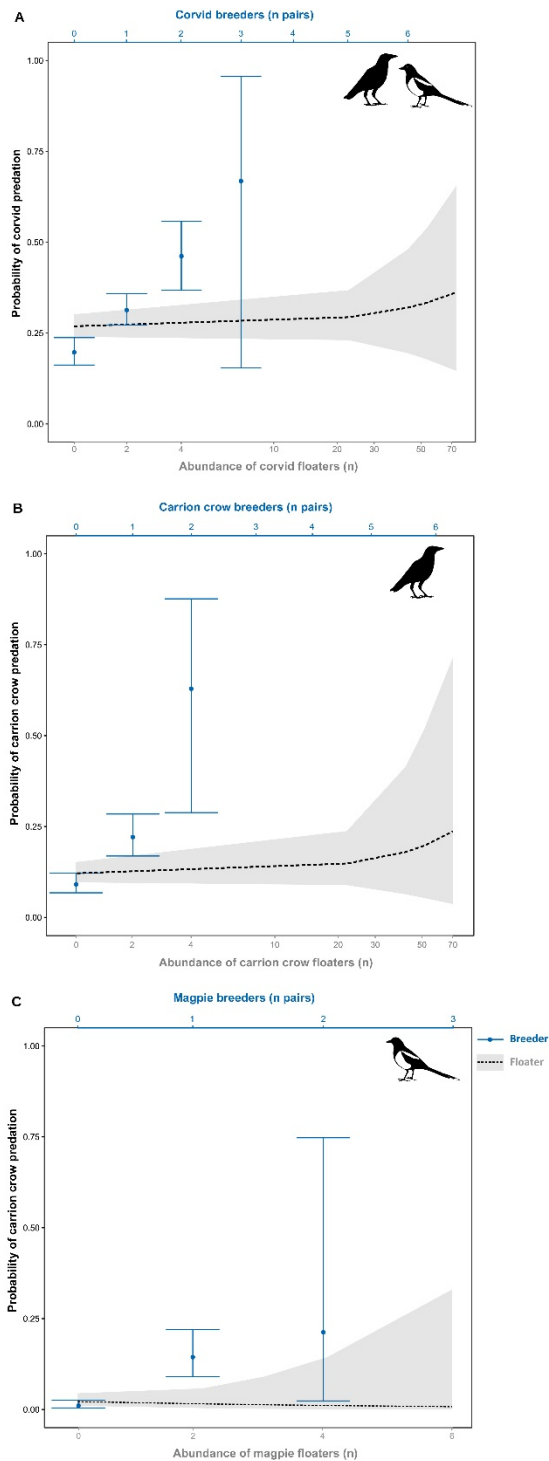


Table1. Likelihood ratio tests (LRT) of the GLM (binomial, link = logit) for the analysis of the effects of egg size (large vs. small), egg material (plasticine vs. natural) and the two-way interaction on predation in A) , egg type (small plasticine, large plasticine, quail vs. hen), the presence (with vs. without) of camera trap on predation and the two-way interaction on predation in B) and predation plus predation attempts in C). Estimate \pm SE were extracted from minimal models including only significant factors. Estimates of the LRT in B) and C) are represented in figure 2. Levels used as references in the models are large size and natural egg in A), and hen egg and without camera in B) and C).

Response variable	Fixed factor	χ^2	df	p	Estimate \pm SE
A. Predation* ¹					(Intercept: 0.93 \pm 0.13)
	Egg size	45.29	1	<0.01	Small: 0.88 \pm 0.13
	Egg material	70.56	1	<0.01	Plasticine: -1.13 \pm 0.14
	Egg size x Egg material	0.62	1	0.43	
B. Predation					(Intercept: 0.82 \pm 0.16)
	Camera presence	42.27	1	<0.01	With camera: -0.91 \pm 0.14
	Egg type	111.46	3	<0.01	Large plasticine: -0.97 \pm 0.18 Small plasticine: -1.95 \pm 0.20 Quail: -0.71 \pm 0.20
	Egg type x Camera presence	0.32	2	0.85	
C. Predation plus predation attempts					(Intercept: 0.84 \pm 0.16)
	Camera presence	11.55	1	<0.01	With camera: -0.46 \pm 0.14
	Egg type	111.37	3	<0.01	Large plasticine: -0.96 \pm 0.18 Small plasticine: -1.97 \pm 0.20 Quail: -0.80 \pm 0.20
	Egg type x Camera presence	1.03	2	0.6	

*¹ Probability of predation estimated only for nests without camera traps (see methods).

Table 2. Effect of predator species (corvids vs other) and egg type (large plasticine vs quail) on time to predation estimated from Cox proportional hazards model. Proportional hazards model coefficients (β) and time ratios ($\exp(\beta)$) for predator species are shown. Note that the reference level for Predator species was *corvids*. Negative coefficients for an effect implies that survival was higher (i.e., hazard was lower). Survival probability of the model is given in Appendix D (Fig. S2).

Fixed effect	χ^2	df	P	$\beta \pm \text{SE}$	Time ratio ($\exp(\beta)$)
Predator species	6.31	1	0.01	Other: -0.56 ± 0.23	0.57
Egg type	0.77	1	0.38		
Predator species \times Egg type	0.56	1	0.46		

Table 3. Likelihood ratio tests (LRT) of the GLM (binomial, link = logit) for the analysis of the effects of the abundance of breeder (n pairs) and floater corvids (n) on probability of predation by corvids in A), the abundance of carrion crow and magpie breeders (n pairs) and carrion crow and magpie floater (n) on probability of predation by carrion crow in B) and by predation of magpie in C). Estimate \pm SE were extracted from a minimal model including only significant factors. The table shows parameter estimates using treatment contrasts. Note that the reference level for Breeders was 0 pairs.

Response variable	Fixed effect	χ^2	df	p	Estimate ± SE
<hr/>					
Corvid predation					(Intercept: -1.36 ± 0.12)
	Corvid breeders	44.274	3	<0.01	1 pair corvid breeder: 0.86 ± 0.17 2 pairs corvid breeder: 1.47 ± 0.27 3 pairs corvid breeder: 14.92 ± 35.41
	Corvid floaters	0.17	1	0.68	
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Carrion crow predation					(Intercept: -2.30 ± 0.16)
	Carrion crow breeders	29.19	2	<0.01	1 pair carrion crow breeder: 1.03 ± 0.24 2 pairs carrion crow breeder: 2.81 ± 0.75
	Carrion crow floaters	0.01	1	0.97	
	Magpie breeders	1.53	2	0.47	
	Magpie floaters	2.63	1	0.11	
<hr/>					
Magpie predation					(Intercept: -4.51 ± 0.45)
	Magpie breeders	41.76	2	<0.01	1 pair magpie breeder: 2.77 ± 0.51 2 pairs magpie breeder: 2.90 ± 1.18
	Magpie floaters	0.02	1	0.88	
	Carrion crow breeders	2.35	2	0.31	
	Carrion crow floaters	5.53	1	0.11	
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Predation of ground-nests in farmland landscapes

Artificial nests

- Egg material

Natural eggs vs Plasticine eggs



>



- Egg size



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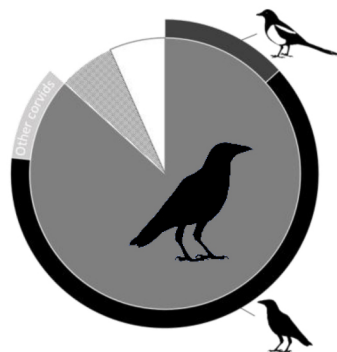


Identification of predator species

Camera trap



Plasticine egg

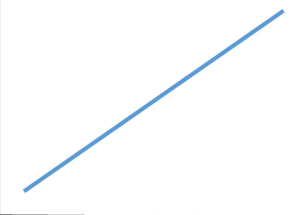


Social status of corvids

Breeders



Predation probability



Corvid breeders

Floater



Predation probability



Corvid floaters