



# The new faces of nest predation in agricultural landscapes—a wildlife camera survey with artificial nests

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## Abstract

European populations of many ground-nesting farmland birds have declined in recent decades. Increases in predator populations and nest predation may play an important role in this decline, along with habitat loss. However, the role of various predators has often remained unclear. We conducted a study with artificial nests and wildlife cameras ( $n = 104$ ) in agricultural landscapes during 2015–2016 in South Finland. Our trials formed a 400-m wide gradient from forest to field. The aim of our study was to monitor nest survival and nest predators in a spatial and temporal scale. We tested the effect of distance to the forest and nest visibility to nest predation. During an 8-day period, 39.4% of the artificial nests were predated. Fifty percent of the predators were birds, 40% mammals, and 10% remained unknown. The three dominant predators of our artificial nests were the raccoon dog (*Nyctereutes procyonoides*) with 11 nests and the hooded crow (*Corvus corone cornix*) and the magpie (*Pica pica*) with 10 depredated nests each. Our analysis indicates that avian predators preyed upon nests in open fields further away from the forest edge, whereas mammalian predation concentrated closer to the forest edge. Predation occurred more likely at the beginning of the survey and nest survival increased as days passed. Our study highlights the efficiency of using wildlife camera traps in nest predation studies. We also suggest that the ongoing expansion of alien predators across Europe may have a greater impact on ground-nesting bird populations than previously anticipated.

**Keywords** Nest predation · Edge effect · Farmland birds · *Phasianus colchicus* · *Nyctereutes procyonoides* · Wildlife camera trap

## Introduction

The populations of many farmland birds in Europe have declined during the last 30 years (Tucker and Heath 1994; Chamberlain et al. 2000; Robinson and Sutherland 2002; Gregory et al. 2008), and agricultural intensification is considered the key element behind this phenomenon (see Ponce et al. 2018 and references therein). Loss and degradation of suitable habitats, such as pastured fields and meadows, negatively affect many farmland and shorebird populations (Potts 1986; Chamberlain et al. 2000; Møller 2001; Lehikoinen et al. 2017).

Nest predation is one of the most important factors affecting the reproductive output of birds (Newton 1998).

According to Evans (2004), habitat deterioration can emphasize the effect of nest predation on breeding success in several ways: (1) habitat change may cause an increase in predator numbers; (2) increased nest densities, e.g., owing to a loss of suitable nest-site habitat, can result in higher predation rates; (3) habitat change may force birds to nest in more unsafe habitat types; (4) a reduction in the availability of alternative food sources may cause generalist predators to change their diets; and (5) habitat changes can lead to shortened breeding seasons and thus to less re-nesting opportunities, thereby increasing the sensitivity of breeding success to nest predation rates.

While bird populations have declined, predator populations have developed in the opposite direction: evidence shows that the European populations of many predator species preying upon ground-nesting bird nests have grown considerably during recent decades (Panek and Bresinski 2002; Langgemach and Bellebaum 2005; Smith et al. 2010; Kauhala and Kowalczyk 2011). Current nest predator communities in Europe include a variety of bird and mammal species (Langgemach and Bellebaum 2005). Brzeziński et al. (2010)

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underlined that the importance of nest predation has increased over recent years: they found a 25% increase in the overall predation rate over their 12-year study period in Poland.

In addition to the native species, several invasive alien predators are also present, e.g., the raccoon (*Procyon lotor*) and the raccoon dog (*Nyctereutes procyonoides*). The role of these new species as nest predators along with their interaction with other predators remains largely unclear (Salo et al. 2007). For example, it is not easy to show the relationship between the removal of a certain predatory species and the survival of prey among these very variable predator communities (Bolton et al. 2007, Salo et al. 2010; Ellis-Felege et al. 2012; Carpio et al. 2016). Some alien predators have increased dramatically. For example, Finnish hunting bag statistics show an enormous increase in raccoon dog numbers: during the last 20 years, the raccoon dog hunting bag has increased over threefold (1996: 61,000, 2016: 212,000; LUKE 2018).

Besides recognizing the impact of predators on prey populations, certain studies have attempted to distinguish the influence of landscape structure, especially the edge effect on nest predation, with varying results (Major and Kendal 1996; Andrén and Angelstam 1988; Lahti 2001; Evans 2004; Ellis-Felege et al. 2012; Knight et al. 2014). Andrén (1992) showed that Eurasian jays (*Garrulus glandarius*) and common ravens (*Corvus corax*) preyed within larger forest fragments and avoided smaller patches, whereas magpies (*Pica pica*) and Eurasian jackdaws (*Corvus monedula*) preferred agricultural land for nest predation. The hooded crow (*Corvus corone cornix*) was a habitat generalist preying on nests in both habitat types, causing increased predation pressure close to the forest-farmland edge. Lahti (2001) observed that only a few studies on the edge effect have identified predator species, and that nest predation dynamics may be better explained if species-specific predator behavior is placed into context with habitat and landscape features. Recent wildlife camera studies support the hypothesis that landscape affects predation, e.g., forest cover and distance to habitat edge. Predators show varying relationships to, e.g., cover types and scale (Cox et al. 2012b; Chiavacci et al. 2018).

Predator identification has often been based on the use of artificial nests and dummy eggs, and possible predators have been identified by marks left either on the dummy eggs or in the nest surroundings (Andrén 1992; Major and Kendal 1996; Draycott et al. 2008; MacDonald and Bolton 2008). Follow-ups in these studies were performed a few days after each initial experiment, leaving plenty of time for secondary predators to also locate and leave their marks at the nest sites. Even in a best case scenario, where dividing the predators into mammals and birds was possible, a great deal of uncertainty would still exist in the interpretation of which predator was first at the nest. For example, Opermanis et al. (2001) noted that nests were fairly often visited by several predators, and they thus had to classify these nests as having been predated

by unknown predators. Several authors conducting experiments with cameras have concluded that nest cues are unreliable for identifying predators (Larivière 1999; Pietz and Granfors 2000; Thompson and Burhans 2003). The review by Cox et al. (2012a) elucidates how the use of cameras in nest predation studies has increased in recent years.

In our study, we use wildlife cameras with artificial nests to monitor the nest survival rate in agricultural landscapes within a 400-m zone (stretching 150 m into the forest and 250 m into the open field) and to identify nest predators of ground-nesting birds. We first test the effect of two different habitat-related factors on the level of nest predation: (1) distance from the forest and nearest tree (stalking perch for predatory birds) and (2) the effect of visibility of the nest from the air on predation. Based on earlier studies (e.g., Angelstam 1986; Andrén 1992), we hypothesize that avian and mammalian predators predate nests in different parts of our study zone. Moreover, (3) the use of wildlife cameras enables us to identify the primary animals visiting our artificial nests and even the secondary predators, i.e., predators that visit the nest after the actual primary predator. We are also able to (4) record the exact predation date. Artificial nests provide little insight in to predation rates of natural nests. However, they can give insight into potential predator type and allow one to consider spatial temporal trends. This is what our paper focuses on.

## Materials and methods

### Study area

Our study was performed in southern Finland at 12 different locations during 2015–2016. The study areas are quite similar in climate and geomorphology (see Kallioniemi et al. 2015). They are located south of the glacial esker running southwest to northeast through Finland in Länsi-Uusimaa (approximately 60° N, 24° E), with the exception of one area, which is located north of the esker. These areas are lowlands with hills, forest patches, small lakes, and rivers with smaller waterways. Because of the Finnish climate and high yearly precipitation, all fields are drained and larger fields are usually separated by open ditches, creating narrow edge areas along field boundaries. Spring wheat, spring barley, spring oats, and rye are the most common crop types, along with oil-seed crops, beans, and peas. The majority of fields are plowed during October and sown again in May. Grasslands are also common to be used for feed production and grazing as well as set-a-side land.

Several predator species occupy the study areas. Mammalian predators include the red fox (*Vulpes vulpes*), raccoon dog, mink (*Neovison vison*), pine marten (*Martes martes*), stoat (*Mustela ermine*), badger (*Meles meles*), and the domestic cat (*Felis catus*). These species are common throughout Southern-Finland (Lindén et al. 1996). Avian

predators include all common corvids in Southern Finland, such as the hooded crow, raven (*C. corax*), magpie (*P. pica*), and the jackdaw (*C. monedula*) (Valkama et al. 2011). Two species of snakes are also present, the common European viper (*Vipera berus*) and the grass snake (*Natrix natrix*), both of which may be able to eat pheasant eggs. In addition, several deer species inhabit the areas: European roe deer (*Capreolus capreolus*), white-tailed deer (*Odocoileus virginianus*), and fallow deer (*Dama dama*; in five study areas).

All areas consisted of fragmented agricultural landscapes. One main criterion for choosing an area was that it had to have open field patches at least 500 m in width, allowing us to place a camera 250 m from the forest if necessary. On the other hand, the areas also needed forest patches at least 300 m in width, allowing us to place cameras within the forest, 150 m from the forest/field edge (hereafter, forest edge). These measures were quite limiting, and in our study landscapes, using greater distances would have excluded many of the study areas, as we wanted to have a continuous zone from the forest out to the fields.

We defined an open agricultural area as a field and did not sort out vegetation types. This experiment included several fallows and most cameras were placed on the edge of field patches, mostly for practical reasons (farming activities could have destroyed the nests). We did consider that predators are believed to use edge areas on agricultural lands more frequently (Storch et al. 2005; Holmala and Kauhala 2009; Sálek et al. 2009, 2010), but as nesting farmland birds also often prefer the edges of cultivated fields (Robertson et al. 1993), we found this to mimic natural circumstances. The cameras were placed in coniferous and deciduous forests.

During our study years, the weather conditions were varying, as is typical for Finland. Yearly changes between growing seasons are measured as the thermal growing season length. It is defined as the number of days between the first 5-day period with average temperatures above +5 °C to the first 5-day period with temperatures below +5 °C. The effective temperature sum is also calculated during the thermal growing season, to describe the intensity of assimilation. For a particular year, this is calculated as the sum of the positive differences between the diurnal mean temperatures and +5 °C (Solantie 2004). The thermal growing season began on the seventh of April in 2015 and on the fourth of April in 2016. However, a rather large delay was recorded in the effective temperature sum in 2015, as the degree of 300 °C was reached first on the 17th of June, approximately a week later than the 30-year average. Precipitation was 150 mm on the same date in 2015 and 50 mm over the 30-year average. In 2016, the effective temperature sum reached 300 °C already on the 29th of May, nearly 2 weeks earlier than the average. Precipitation was very low during May and the beginning of June in 2016, affecting vegetation growth (Finnish Meteorological Institute 2017).

## Study design

### Artificial nests

We used artificial nests with four common pheasant (*Phasianus colchicus*) eggs in each. The eggs were received from a commercial pheasant-rearing farm. They were unwashed and handled using rubber gloves to minimize contamination by human odors. We received data from a total of 104 nests (eight nests/study site). All nests were placed at sites where a pheasant hen could possibly lay a clutch (based on our own experience from earlier pheasant and duck studies, see Kallioniemi et al. 2015; Väänänen et al. 2016). A round nest bottom was formed on the ground by spinning a wooden stick, making it look like a natural pheasant or duck nest. To try to avoid possible density-dependent nest predation (see Gunnarsson and Elmberg 2008), we placed our artificial nests around a 1-km<sup>2</sup> area. This area consisted of more cultivated fields than forest, as we had to place more artificial nests in the fields (see study procedure below).

We had four sample gradients in each of the areas that we randomly set nests in. To test the forest edge effect, we divided the sample gradients into four zones ranging from forest to open field: (1) (−150 to −50 m), (2) (−50–50 m), (3) (50–150 m), and (4) (150–250 m). The edge between forest and field is marked as 0 m. In the case of shrub lands and pastures, the edge is always the area where the forest begins. The actual place of the nest within a category was determined using a random number generator. We gave a value between 0 and 10 for each starting 10 m, and we were therefore able to place the nests randomly along the 100-m distance in each corresponding area.

All nest sites were described in detail. We measured the distance to the nearest forest edge, and any potential perches for birds of prey to sit on. We also described and measured the height of the surrounding vegetation and marked the visibility of the nest from the air either as covered or open.

Each nest site was equipped with a light-triggered passive wildlife camera (Swann et al. 2011), approximately 1.5 m away from the nest. We used many different types of cameras, but all responded to movement and were adjusted to take pictures at similar intervals: one picture every 20 s. Sensitivity was adjusted to low, because of our previous experience that the cameras are very sensitive to vegetation moving in the wind. The camera types used were (number of cameras in parentheses): Uovision UM565 (9), Niteforce 2G-SMS (10), KeepGuard (2), WildGame IR4 (1), WildGame LO5 (1), Uway U150 (1), ScoutGuard SG550B-11 (1), ScoutGuard 560PV (1), LtlAcorn (1), and TC541 (1).

The experiment was carried out between the beginning of May and the end of July in 2015 and 2016, as this is the time span during which pheasants and many other ground-nesting birds tend to nest. Our nests were held at one place for 8 days.

During this time, the nests were left undisturbed. After this, the cameras were collected and the memory cards checked to identify any animals that visited the nests. A pheasant hen needs approximately 2 weeks to lay and about 25 days to incubate its eggs (Hill and Robertson 1988), so keeping the nests in place for a longer time period would potentially have provided a more realistic picture of the survival possibilities of a nest. Our time span, however, mimics the egg-laying period, where the pheasant hen is not yet incubating and sitting on the eggs. Duck hens also leave their nests open during the egg-laying period until the last days of the period when they begin covering the nest using nest material and down (Väänänen unpubl.). During incubation, the hen visibly covers and warms the eggs and also leaves a great deal more scent on the nest. The incubation time would be much more difficult to mimic with artificial nests. Other studies rarely mention what nesting period the artificial nests represent.

### Predator visits at the nests

All predators visiting the nests were recorded. The first predator at the nest was classified as the primary predator and included in our further analyses if it depredated at least one egg. Other predators were classified as second, third, fourth, and so on. They were counted as predators if they depredated eggs that were left by the first predator or even if they just scavenged or searched for remains of eggs at the nest site. Repeated visits of the same species were counted as new visits with an interval of 24 h.

### Signposts

We used signposts with wildlife cameras to gain some perception of the number of the mammalian predators, as well as the species present in our study areas. A signpost is a method that is used to estimate relative mammalian predator densities (Kauhala 2004; Sálek et al. 2010). After each experiment, we placed four signposts with cameras at each of the same study sites using the same four distance zones in relation to forest edge, i.e., a total of 52 cameras (see “Study design”). The signposts were scented with “gray ambush” gray fox (*Urocyon cinereoargenteus*) gland lure that was placed on a 10-cm long stick and on a flat stone to make sure the scent was not lost if signpost visitors rolled on it. The stick and stone were placed on flattened ground, and a wildlife camera was placed approximately 1.5 m from the post. The signposts were kept in place for 5 days.

## Statistical methods

### The effect of nest site characteristics

The effect of the habitat variables on nest predation was analyzed with generalized linear mixed modeling (GLMM,

Bolker et al. 2009; Zuur et al. 2009) using the lme4 (Bates et al. 2018) and MASS (Ripley et al. 2018) libraries in R 3.4.0 (R Development Core Team 2017). Nest fate (survived or predated) was analyzed as a binary response variable and explained by habitat characters. We used two different approaches to measure our a priori nest predation models. First, we used the whole data ( $N = 104$  nests with known fate, 41 predated, i.e., pooled data), where we pooled successful nests and all predated nests (including all predator species as well as unknown predators) to examine common habitat predictors for nest predation. Secondly, we separated the two major predator groups, mammal and avian, for a more specific investigation of habitat characteristics (i.e., predator groups).

### Pooled data

To determine the most important factors affecting the total nest predation in the area, we generated different sets of a priori models. We began with three habitat variables: distance to forest edge (FOREST), distance to nearest tree (TREE), and nest coverage (COVER). The first two are continuous variables, while coverage is a factor (0 = open, 1 = cover). We made a natural logarithmic transformation for the distance variables FOREST and TREE. To allow the change, we first transformed our forest transect line to begin in the deep forest, continuing 400 m towards the open field. In the second approach, we studied the actual edge effect and transformed the distances to be positive, starting from the forest edge and continuing towards both forest and field. We used a piecewise two-level factor to describe the habitat type. Here we first compared random intercept model with random intercept and random slope model, and based on the AIC values ( $\Delta AIC > 2$ ), decided to use the previous one. We began our data analysis with all variables and followed protocol recommendations in Zuur et al. (2010). Data exploration included searching for outliers using Cleveland dot plots, but no outliers were found. We tested pairwise collinearity with Pearson correlations and found strong relationships ( $r = 0.60$ ) between factors TREE and FOREST. This is a natural result in an agricultural landscape, where the nearest trees to the nest tend to be near/at the forest edge. We decided to leave out factor TREE.

The data have a nested structure, and data exploration (Zuur et al. 2009) exposed a strong areal effect, but a fairly weak year effect. Therefore, a random part including a categorical random factor for the area effect was included in all the model candidates to account for any areal effect. With the two explanatory variables, we formed all the possible model combinations in addition to the intercept-only model and ranked the candidate models using Akaike information criterion corrected for small sample size ( $AIC_c$ ). We used binary distribution and a logit link function for the model to constrain the nest fate between 0 and 1.

The model we used for the effect of habitat factors on nest fate was:

$$\text{Nest fate}_i = \alpha + \beta X_i + a_i + \varepsilon_i \quad (1)$$

where Nest fate<sub>*i*</sub> is the nest fate (survived, predated) of nest *i*, where *i* = 1, ... 104,  $\alpha$  is the intercept, and  $\beta$  the coefficient of the habitat variable(s) *X*. Term  $a_i$  is the random effect, and term  $\varepsilon_i$  represents unexplained variation.

### Predator groups

To determine the importance of the monitored variables for nest predation concerning different predator groups, we conducted a second nest survival analysis. We divided predators into two groups: mammalian predators (raccoon dog *n* = 11 and badger *n* = 1) and avian predators (European magpie *n* = 10, hooded crow *n* = 10, and Eurasian jackdaw *n* = 1). The European roe deer differs from the other mammalian predators, and because there were only four observations of deer destroying nests, we left the deer observations out. We therefore had two groups: one composed of successful (*n* = 63) and mammalian-predated nests (*n* = 12) and another of successful (*n* = 63) and avian-predated nests (*n* = 21). The successful nests were included in the analysis to incorporate background information of the successful nests when examining the factors affecting group-specific predation. We used the same two explanatory variables as above to explain nest fate. Data exploration revealed that the year effect was again weak for both groups, and we thus only used area as a random effect in each model. With the two explanatory variables, we formed all possible model combinations in addition to the intercept-only model and ranked the candidate models using AIC<sub>c</sub>. The model used was similar to model (1) with predator group-specified data. To test whether the two predator groups differ in their predation occurrence in relation to time, we used the Mann-Whitney *U* test on the independent samples.

### Daily survival analysis

We analyzed the daily nest survival probability with a logistic exposure method (Shaffer 2004) using the entire data set for 8 days. A day was classified to begin at 12 am and continue for 24 h. The logistic exposure method is a modification of logistic regression and maximizes the use of nest survival data by treating each measurement day as a discrete trial. Thus, the nest counts for each trial from day 1 (the starting point) to day 8 are 96, 89, 85, 77, 72, 70, 68, and 65. We used data from the 96 nests for which the exact predation date was revealed (33) or nests that were known to have survived the entire period (63). We used the GLMM framework to calculate daily nest predation, because that allowed us to account for possible

areal effects. The nest fate of each day (DAY) was analyzed as a binary response variable (1 = survived, 0 = predated).

The model used differs from the logistic regression model described above (1) in the form of the link function and the explanatory factors:

$$\text{Nest fate}_{iD} = \alpha + \beta D_i + a_i + \varepsilon_{iD} \quad (2)$$

where Nest fate<sub>*i*</sub> is the fate of nest *i*, where *i* = 1, ... 96 on day *D*, where *D* = 1, ... 8.  $\alpha$  is the intercept and  $\beta$  the coefficient of the day variable *D*. Term  $a_i$  is the random effect, and term  $\varepsilon_{iD}$  represents unexplained variation.

## Results

Of the 104 artificial nests, 39.4% (*n* = 41) were depredated or destroyed during the 8-day period. Of the 41 cameras, four failed to capture a single predator, while we were able to record the predator species from another four cameras, but the exact date or time is missing from these, thus leaving us with 33 predation acts with exact predation date and time.

Mammals depredated 39% of the predated nests (*n* = 16). Mammalian predators were raccoon dogs (*n* = 11, 27% of total predation and 69% of mammalian predation), roe deer (*n* = 4, 10 and 25%, respectively) and a badger (*n* = 1, 2, and 6%, respectively). Avian predators depredated 51% of the nests (*n* = 21). Avian predators were magpies (*n* = 10, 24% of the total predation and 47.5% of the avian predation), hooded crows (*n* = 10, 24 and 47.5%, respectively) and jackdaws (*n* = 1, 2 and 5% respectively). Four nest depredations were unidentified due to camera failure (*n* = 4, 10% of total predation).

### Spatial distribution and the cover effect on predation rate

For the pooled data, two models were equally good at explaining the nest predation rate according to AIC<sub>c</sub> values ( $\Delta\text{AIC}_c < 2$ , hereafter “the best models”), with the global model being one of the two. We present the global model parameters with all the variables (Table 1). The model has no significant variables, although the variable FOREST is quite nearly significant with a rather high coefficient. Nests inside the forest might have higher survival. When studying the effect of the forest edge, it shows some tendency to have a lowering effect on nest predation, while habitat type did not affect the predation rate (Table 2, Fig. 1).

Concerning the forest edge, a great deal of variation appears to occur between the groups (Fig. 2). Mammals predate around the forest edge, while avian predators are active out on the field. The non-predated nests are distributed very close to the forest edge, on both the

**Table 1** Parameters of the global model explaining overall nest predation. COVER is a piecewise two-level factor, representing open (intercept) and covered nest sites. Variance for the random effect representing the between-area variation is 0.65

Global model	Value	SE	95% conf. int.	<i>P</i>
Intercept	-3.21	1.51	-6.606, -0.588	0.033*
FOREST	0.50	0.28	0.017, 1.128	0.072
COVER	0.27	0.50	-0.725, 1.245	0.590

forest and field sides (Figs. 2 and 3), whereas the few observations of roe deer predation and unidentified predators are quite scattered over the gradient. Due to the varying preferences of the different predator groups, it is reasonable to separately analyze the main groups.

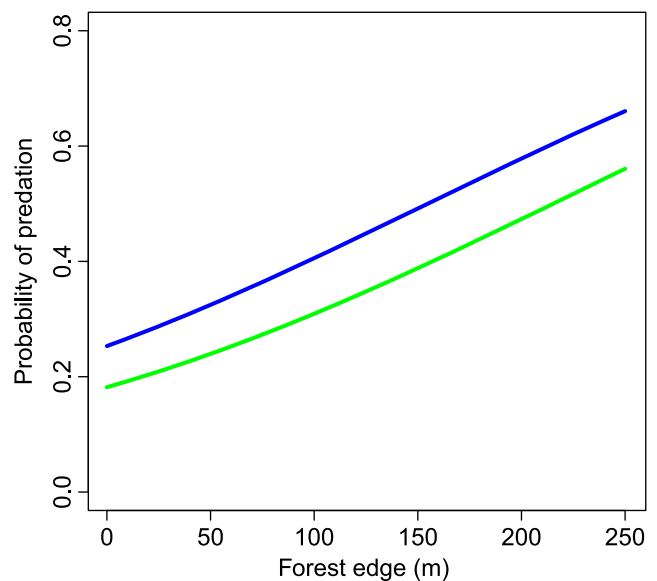
The independent samples *t* test between mammals (raccoon dogs and a badger) and avian predators shows a significant difference between predation distance from the forest edge ( $t = -3.24$ ,  $df = 31$ ,  $P = 0.003$ ). The mean distance from the forest edge was 18.75 m for mammalian predation ( $n = 12$ ) and 128.21 m for birds ( $n = 21$ ).

## Predator groups

In mammalian predators, the intercept-only model had the best fit according to the  $AIC_c$  values ( $\Delta AIC_c > 2$ ), and thus, we cannot explain the distribution of mammalian predation and do not present any models here. The two best models for avian predators, according to the  $AIC_c$  values, were the ones with FOREST and COVER and FOREST only. We present the global model with both variables in Table 3. Avian predation appears to occur more likely in the field far from the deep forest. Hooded crows and magpies were able to locate some of the concealed nests: hooded crows preyed mainly on open nests (predation rate = 0.9), whereas 40% of the nests depredated by magpies were covered. We found no difference in predation in relation to distance to the forest edge between these two species according to the independent samples *t* test ( $t = -0.099$ ,  $df = 18$ ,  $P = 0.922$ ).

**Table 2** Parameters of the model explaining overall nest predation at the forest edge. Habitat type is a piecewise two-level factor, representing forest (Intercept) and field. Variance for the random effect representing the between-area variation is 0.764

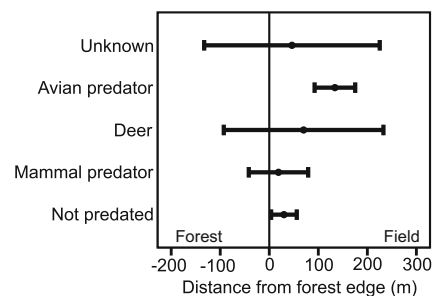
	Estimate	Std. Error	95% Conf. int.	<i>P</i>
(Intercept)	-2.95	1.17	-5.581, -0.875	0.012
Forest edge	0.49	0.25	0.039, 1.051	0.055
Habitat type	0.52	0.50	-0.455, 1.530	0.301



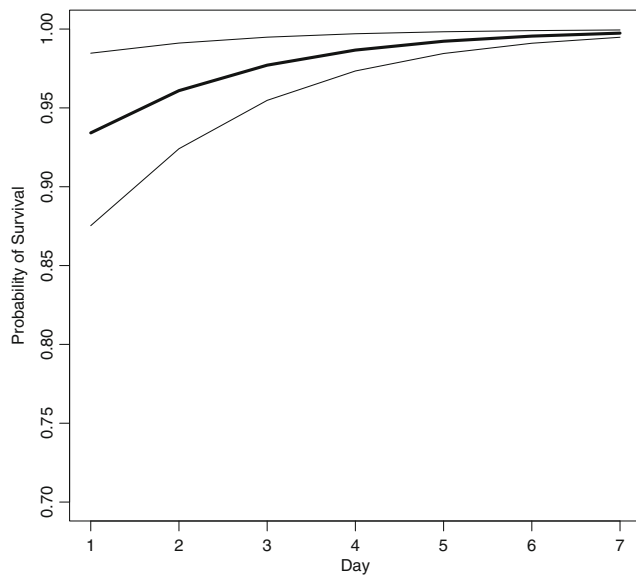
**Fig. 1** Probability of predation in relation to the forest edge. Blue = field, green = forest

## Temporal occurrence

When comparing the predation day of the two predator groups (mammalian vs. avian), we found that it took an average 3.2 (median 3) days for mammals to locate the nests and an average 3.5 (median 3) days for the avian predators. This difference is not significant according to the Mann-Whitney *U* test ( $n = 28$ ;  $U = 99$ ;  $SE = 20.46$ ;  $P = 0.660$ ). The data is not sufficient for testing between avian and mammal predation events and the time of the day. In Finland, the concept of nocturnal is vague during June and July. Day length during our study period fourth of May and ninth of July was 16.5–19 h, with a twilight time of 1–2 h (you can see clearly even though the sun is not visible).



**Fig. 2** Mean distance from the forest edge for both predated and unpredated nests. Negative values indicate nests within the forest, while positive values are from the field. Edge is presented as a zero line. Groups include observations as follows: unpredated  $n = 63$ , mammalian predators  $n = 12$  roe deer  $n = 4$ , avian predators  $n = 21$  unidentified  $n = 4$ . The circles represent the mean and the whiskers the 95% confidence intervals



**Fig. 3** Daily nest survival rate in relation to monitoring days. The thick solid line represents the logistic-exposure model involving a linear effect of experimental days. Thin lines represent 95% confidence limits for the random intercept showing the variation between the predicted values per region

**Daily survival**

We found evidence that the probability of daily survival increases with time (Fig. 3, Table 4). The logistic-exposure model (linear in the logistic scale) implies a slightly curvilinear relationship between survival and time.

**Predator visits at the nests**

Half of the predated nests were visited more than once. Of the 37 predated nests (35.6% of all nests) that we had pictures of, 19 (51.4%) were visited again by a possible secondary predator (Fig. 4). The raccoon dog was the most common primary predator at the nests (with 11 predated nests), and it was also the most common predator observed later on at the nests. We observed 31 individual raccoon dog sightings on the study nests, i.e., 37% of all observations ( $n = 84$ ). Birds appeared on the nest as second or third predators mainly if the same

**Table 3** Parameters of the global model explaining nest predation by avian predators. COVER is a piecewise two-level factor, representing open (Intercept) and covered nest sites. Variance for the random effect representing the between-area variation is 0.13

Model	Value	SE	95% conf. int.	P
Intercept	- 12.52	4.32	- 22.552, - 5.558	0.004*
FOREST	2.02	0.77	0.764, 3.779	0.009*
COVER	0.93	0.64	- 0.264, 2.361	0.148

**Table 4** Model estimate for the daily survival rate of artificial nests

Model	Value	SE	95% conf. int.	P
Intercept	2.67	0.45	1.273, 3.066	< 0.001
Survival	0.39	0.09	4.408, 0.772	< 0.001

species had robbed the nest in the first place. The four cameras that we were only able to identify the primary predator from lacked also all information regarding the secondary predators.

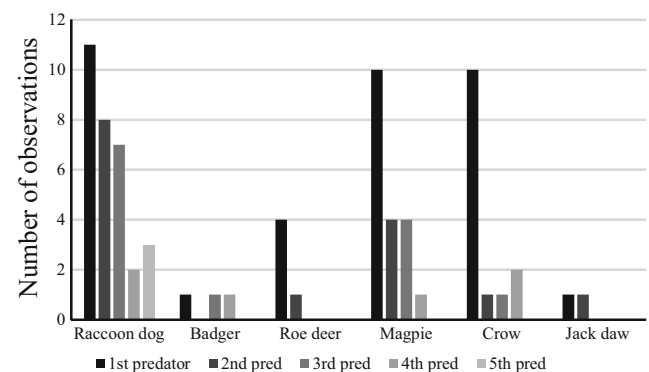
**Signposts**

Of the 52 signposts, seven cameras failed to produce data, mainly because of human error. Of the 45 cameras that we obtained data from, 30 (67%) were visited by mammalian predators over the 5-day period. The signposts interested several animals; we recorded 25 raccoon dogs, 23 deer (roe, fallow, or white-tailed deer), four red foxes, four badgers, and a dog.

Mammals were very attracted to the signposts in all study areas. We were able to catch foxes and raccoon dogs rolling on the signposts and marking them with their own scent. It is to be noted that red foxes were present at four different study sites despite not predated any nests.

**Discussion**

Artificial nest studies we found usually mimic the egg-laying period (nest uncovered), but data of real nests usually only covered the incubation period. This makes a comparison between real and artificial nests very challenging. Other sources of bias are also present in the comparison. For example, Willebrand and Marcström (1988) state that artificial nests lack the scent of the incubating hen and are therefore more difficult for mammalian predators to locate, which may then exaggerate the role of avian predators. Jahren (2017) showed that black grouse (*Lyrurus tetrix*) and capercaillie (*Tetrao*



**Fig. 4** Order of predator visits and total numbers of visits at experimental nests ( $n = 37$ )

*urogallus*) defend their nests against corvids, and therefore, avian predation was much lower in his study than earlier suggested in studies with artificial nests.

Nest predation studies with artificial nests show both less and more predation occurring on artificial than natural nests (Major and Kendal 1996; Thompson and Burhans 2003). Major and Kendal (1996) calculated an average nest success of 41% for artificial nests and 51% for natural nests. Predation rate was higher at artificial nests in 14 out of 20 studies. The authors also state that different artificial nest set-ups can attract differing predator populations and care should therefore be taken when interpreting the results. Artificial nests therefore cannot be used to estimate predation rates of natural nests. But they can provide data on nest predator species and a look at spatial and temporal trends in predation of artificial nests that may have some meaning for natural nests.

The link between agricultural land, human density, and forest fragmentation on increased corvid density and thereby increased predation pressure has been shown earlier by Andrén et al. (1985). Gunnarsson and Elmberg (2008) also found higher predation rates in agricultural compared to forested landscapes. They suspected it to result from a combination of predator abundance and nest conspicuousness, both of which are reduced in forested landscapes.

In our study, we found that predation of mammals and birds as a combined group was not explained by a forest-field gradient, i.e., overall the predation was fairly equally distributed over the gradient. However, there are some signs that predation might increase with the distance from the forest edge. When testing these two groups separately, we found that birds preyed on field nests further away from the forest. Mammalian predation was not explained by the forest-field gradient, while on average their predation appeared to be more active closer to the edge, both in the field and forest. However, we did observe that nests closest to the forest edge had the highest survival rate. Previous nest predation studies have not always detected this phenomenon (Lahti 2001 and references therein). Earlier Benson et al. (2010), using confirmed camera identification on natural passerine nests, observed that various predator groups preyed on different parts of the nesting habitats, some preferring to prey closer to edges and some further away. The same was also shown by Ponce et al. (2018) using artificial nests. Benson et al. (2010) remark that the randomness in predation found in earlier studies may be caused by “conflicting patterns of multiple predator species, each of which respond to habitat and landscape features in a different way.” It is difficult to disagree with their statement: it is impossible to understand the relationships between nest success and habitat and landscape factors, if the dominant predators are not identified.

In our study, nest survival was lower further away from the forest edge. The avian group was the largest predator group, where two species dominated the predation; the hooded crow

and the magpie were together responsible for 49% of the total predation. This is in concert with earlier studies showing that corvids are effective nest predators (Andrén 1992).

Certain studies suggest that magpies prefer to prey further away from the edges, whereas hooded crows prey equally on all areas (Angelstam 1986; Andrén 1992). We found no difference between these species. Earlier studies have found varied results concerning this issue (Pietz and Granfors 2000; MacDonald and Bolton 2008).

Nests closer to the forest edge had a higher survival potential. However, nests placed over 20 m from the edge suffered from fairly high predation, mainly caused by the raccoon dog, which has previously been considered rather harmless. A Latvian study observed raccoon dogs to only predate 0.6% of duck nests (Opermanis et al. 2001), but the study used marks left on the nests to identify predators. Kauhala and Auniola (2001) and Kauhala (2004) suggest, based on predator removal studies and wildlife monitoring counts, that the raccoon dog’s impact on game birds and ducks is smaller than expected. However, it is noteworthy that their predator removal experiments fail to show a decline in raccoon dog populations. In a 3-year study, Väänänen et al. (2007) removed, at most, over 20 individuals per km<sup>2</sup> in a wetland area, and their results indicated an improvement in the breeding success of certain bird species.

Our study implies that the raccoon dog may be a common predator of ground-nesting bird nests in agricultural landscapes in Finland. Wang et al. (2016) obtained surprisingly similar results from their study with artificial nests in China: corvids and raccoon dogs were the most important predators in their 30-day long study, predated 60 and 47% of the nests, in two individual areas, respectively. This part of China belongs to the natural range of the raccoon dog. In Finland, the raccoon dog population expanded in the 1980s to its current distribution range (Kauhala and Kowalczyk 2011), but the hunting bag has steadily increased since then. The raccoon dog is a potentially harmful predator not only in agricultural landscapes. It has been shown to have effect on waterbird populations in eutrophic wetlands and in archipelagos in Northern Europe as well (Väänänen et al. 2007; Dahl and Åhlén 2018). Dahl and Åhlén (2018) established a nest predation experiment in the outer archipelago of the northernmost part of the Baltic Sea. They found that the raccoon dogs effectively located both artificial and natural nests and preyed upon the eggs.

Contrary to many other studies, we did not observe predation by red foxes and only one case of predation by badgers, despite these two species often being regarded as the main nest predators (Newton 1998; Draycott et al. 2008; Carpio et al. 2016). The signpost trapping verified the presence of foxes in four of our study areas. In Norway, Jahren (2017) used camera traps on natural nests to show a very high predation rate on black grouse and capercaillie (*T. urogallus*) nests (66 and



79%, respectively), with the red fox and pine marten being the main predators. The use of artificial nests and camera traps might be a too suspicious set up for the wary foxes and a study period of 8 days a too short time for the foxes to become adjusted to. A Finnish study on eutrophic wetlands compared the catch rates of small carnivorous mammals with a cage trap and found that raccoon dogs were caught at 57% rates, while only 12% of the foxes were caught, suggesting that the two species indeed differ in their wariness (Kylmä 2018).

Our study shows some nest predation or trampling caused by roe deer. However, neither fallow deer nor white-tailed deer were observed eating eggs from the nests, even though they were caught on the camera traps. North American studies have noted white-tailed deer to predate the nests of ground-nesting birds (Pietz and Granfors 2000; Ellis-Felege et al. 2008). Ellis-Felege et al. (2008) state that the deer may opportunistically use high-protein and high-energy foods, such as eggs, particularly during antler development and fawning.

Angelstam (1986) suggests that the contribution of eggs to a predator's diet is so insignificant compared to their food requirements that becoming a nest-robbing specialist does not pay off. This could mean that nest robbing is just a random event that reflects the predator community present in an area. Vickery et al. (1992) support this theory of incidental nest predation. Even so, the interactions between species can be complex and affect nest predation rates surprisingly strongly. For example, Carpio et al. (2016) showed that despite wild boars (*Sus scrofa*) predated wader nests in Sweden, the total nest predation was lower in areas with wild boars. The study provides evidence of a negative relationship between the abundance of wild boar and other carnivores (foxes and badgers).

The wildlife camera set-up allowed us to determine the exact date and time of predation, and we found that mammals and birds did not differ significantly in the time needed to locate a nest. Overall, we found evidence that the probability of daily survival increases with time, and a response to this phenomenon has previously been shown experimentally by Gunnarsson and Elmgren (2008). Many authors have speculated on the reason for the increase in nest survival with age. Davis (2005) suggests that increased concealment due to vegetation growth may be a positive factor for certain species. Martin et al. (2000) show that nest sites affect predation rates; nests with a high predation risk on 1 year were more likely to also be depredated during the subsequent year, presumably because the nest site itself was poor. In our study, this could be a combination of both. During our 8-day experiment, we observed dandelions (*Taraxacum officinale*) beginning to grow and flower, along with many monocots stretching over the nests. This increasing cover can effectively hinder predators that visually search for prey. On the other hand, predators, such as the raccoon dog, may not be actively searching for nests, but just looking for anything to eat. This means that places offering raccoon dogs other forms of nutrition, such

as earthworms and insects, are poor places for ground-nesting birds to nest, as the probability of the nest being found increases with predator activity.

The artificial nests were often visited by several predatory animals. First by the primary predator and afterwards by other predators, we check the nest for eggshells or other remnants. On many occasions, the predators were of the same species, in certain cases possibly even the same individuals returning to check the nest again. This could be interpreted as the primary predator returning to the nest to see whether the female had laid new eggs. This could also imply that once a nest is predated (even only one egg), the probability of it being found by other predators increases and the total nest predation rate increases. The abundance of nest visitors elucidates the fact that when planning predator removals, it is important to take into account that nest predation may be compensatory in complex ecosystems, and the removal of one predator species may have no or even a negative effect on total annual nest survival (Bolton et al. 2007; Ellis-Felege et al. 2012).

## Conclusions

Our study indicates that artificial nests are depredated by many different predators that differ in their relation to the nearby forest. Even though these results cannot be directly interpreted on predation of natural pheasant and duck nests, they reflect at least some part of the predation that nests on the ground might be susceptible to. Wildlife camera traps are an essential method for assessing the variety of the predator community.

Predator communities change with time, and all across Europe both alien and invading species may take their share of the prey community. Our results from the nest predation trials indicate that apart for the previously known mammalian nest predators red fox and badger, a new species is successfully inhabiting agricultural habitats: the raccoon dog. The raccoon dog is an alien species invading Europe; it is very opportunistic in its diet and difficult to eradicate (Genovesi et al. 2009, Kauhala and Kowalczyk 2011, DAISIE 2018). In 2017, the European Commission added the raccoon dog to the list of invasive alien species of Union concern (EU IAS 2017).

Understanding how nest predation is related to habitat characteristics within a managed landscape, especially those characteristics that may affect predator abundance and behavior, provides useful information for determining how future management practices will affect the breeding success and survival of ground-nesting birds in agricultural landscapes. All this information is crucial in the objective of halting biodiversity loss by 2020, a target set by the EU (EU Biodiversity Strategy 2011).

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