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Delayed nest predation: a possible tactic toward nests of open-nesting birds

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Abstract. Predators use various tactics to find and depredate bird nests. This study examines a possible tactic of visually orientated predators termed “delayed nest-visit”. This consists in remembering the positions of incubating parents and subsequent easy depredation of eggs when the parents are away from their nests. Conditions for use of this tactic were experimentally simulated by installing artificial nests with quail eggs and plastic dummies of northern lapwings (*Vanellus vanellus*) at 11 actual breeding grounds with various habitat conditions in southern and eastern Bohemia, Czech Republic. Habitat, presence of the dummy, and their interaction significantly affected nest survival. While 17.2 % of the nests baited with the dummy were depredated, this occurred in only 6.9 % of the nests without the dummy. This depredation rate was affected by the visibility of the dummies in particular habitats. The results suggest that predators may remember the nest position to delay their first visit to a previously located bird nest from a remote place and may use this tactic to easily capture the clutches. The use of this tactic showed that at least some predator species are able to apply much more sophisticated approaches in search of birds’ nests than previously assumed.

Key words: artificial nests, ground-nesting birds, egg predation, nest crypsis, search image tactic, *Vanellus vanellus*

Introduction

Predation of bird nests specifically contributes to avian mortality (Ricklefs 1969, Nilsson 1984), and therefore, an understanding of mechanisms responsible for nest predation, including search image tactics, is a key topic of behavioural ecology and evolutionary biology in birds (Martin 1995, Lima 2009). Bird eggs may be a valuable food item the acquisition of which motivates predators to locate nests and deplete entire clutches (Salathé 1987, Careau et al. 2008). Predators’ finding of bird nests has often been considered incidental, such that when predators are searching for food across suitable habitats they occasionally come upon nests (Vickery et al. 1992, Vigallon & Marzluff 2005). Sometimes, however, nests can be depredated after they have been purposely detected and visited. This is especially the case of nests concentrated in large colonies where the predators deliberately return based on their previous experience (Andersson & Waldeck 2006, Varela et al. 2007) and/or return to the nests if all eggs cannot be carried off at once (Salathé 1987, Olsen & Schmidt 2004).

For their part, breeding birds apply various defence tactics against nest predators (Montgomerie & Weatherhead 1988). If parents actively defend the

nests, if they fastidiously incubate the clutches (Montgomerie & Weatherhead 1988, Opermanis 2004), or if finding the nest is difficult or time consuming (e.g. because of vegetation cover or low nest density), predators can address the trade-offs between costs (risk of injury or time expenditure) and benefits (obtaining food) arising from the active search of a nest (Wiklund & Andersson 1994, Thyen & Exo 2005, Cresswell 2011). In such cases, predators may develop more effective nest search tactics to increase their gains relative to costs. One such tactic used by visually orientated bird predators in open habitats may include to overview fields from elevated vantage points such as trees or pylons (Olsen & Schmidt 2004, MacDonald & Bolton 2008, pers. obs.). This tactic could be particularly efficient if the predator is able to find and remember locations of incubating parents and consciously postpone the egg depredation until such time as the parents are away from the nest. To the best of the authors’ knowledge, however, this potential “delayed nest-visit” tactic has never been observed directly or experimentally tested in the field. It has been established that at least corvids (Corvidae) have rapid learning and cognitive abilities (Emery 2006). They are able to develop various foraging tactics (Eggers

et al. 2005), including to form visually based search images from elevated points (Olsen & Schmidt 2004, Fernández-Juricic et al. 2010). In addition, corvids are known to possess a memory for caching locations of long duration (Brodin 2005). It was therefore presumed that remembering nest positions from remote perches followed by a delayed intervention whenever the parents were away from the nest might be one of their regular search image tactics.

The northern lapwing (*Vanellus vanellus*) is a useful prey model for testing whether at least some predators use the delayed nest-visit tactic. This ground-nesting shorebird breeds in open landscapes across the Palearctic (Cramp & Simmons 1990). Non-hidden parents incubate their clutches in sparse vegetation (Cramp & Simmons 1990), which enables early detection of approaching predators (Götmark et al. 1995). Moreover, the cryptic colouration of their eggs might play a role in camouflaging the nests (Lloyd et al. 2000). Consistent with an assertion that motion at the nest may serve as an impulse for nest detection by a predator (Skutch 1949), it is easier to search out lapwing nests by means of the incubating parents and from a distance than by immediate scanning (walking through or flying over) large field areas in search of cryptic clutches. However, lapwing parents actively defend their nesting territories against avian predators (Elliot 1985, Kis et al. 2000, Seymour et al. 2003), similar to some other shorebirds (Larsen et al. 1996, Hegyi & Sasvári 1997), so it is easier for the predators to visit the nests during the absence of parents in the territories. In addition, northern lapwings usually leave the nest immediately at the approach of a predator penetrating into the territory (Šálek & Cepáková 2006), probably behaving so in order to prevent disclosing the nest's position (Walters 1982, Koivula & Rönkä 1998). A predator's success in searching out a nest once it has walked into the proximity of the nest is therefore limited by nest crypsis. If, however, the predator knows the exact nest position from previous perching, it can easily find and depredate the eggs. Indeed, crows (*Corvus corone*), which often use perching at field edges, are considered to be common predators of northern lapwing eggs along with foxes (*Vulpes vulpes*) in many areas (e.g. Kis et al. 2000, Seymour et al. 2003, Olsen & Schmidt 2004, MacDonald & Bolton 2008, pers. obs.), even though direct observations of depredation events are scarce (Olsen & Schmidt 2004) and the dominant predators of lapwing nests remain unknown.

This study experimentally tested the use of this possible predatory tactic by examining nest predation

risk on artificial nests with quail eggs and plastic adult northern lapwing dummies installed in crow nesting territories at northern lapwing breeding grounds. The idea is based on that if predations will occur with a delay after removing the dummy, there must be that at least some predators are able to remember the remote position of previously occurring subject in the field and potentially use this tactic in nest searching. Its existence would prove that predators are able to apply much more sophisticated approaches when searching out bird nests than was previously assumed.

Material and Methods

The study was conducted in southern and eastern Bohemia, Czech Republic, in areas with breeding northern lapwings and crows (Šťastný et al. 2006, Kubelka et al. 2012). The experiment was conducted from April to May 2012 using artificial nests simulating small, open-nesting shorebird nests. Nests were formed as shallow open pits lined with a small amount of dry plant material from the surrounding area, then baited with four quail eggs with their tip ends facing to the centre of the nest. The nests were installed in the early morning (05.00-08.00 h) as nest pairs (trials), where the two nests (30 m apart) within each trial did not differ in any measured parameter (installation time, habitat, vegetation height, and distance to a perch for avian predators and to the field edge). A commercially produced plastic dummy of the northern lapwing in real size and colour was attached to one randomly selected nest within each trial to imitate incubating bird. After ca. 12 h of exposure, the dummy was removed and two eggs were exchanged between the nests within each pair in order to provide the same handling time and olfactory characteristics. If any nest was found to be destroyed during this inspection, the trial was excluded from further analysis. Successfully surviving nest pairs were subsequently exposed for 48 h. The fates of nests (predation or survival) were determined and surrounding vegetation height was estimated. Nest pairs destroyed by machinery were excluded from the analysis. We avoided using cameras and other tools allowing detection of individual predators as any other objects at the nests except the dummy may strongly influence the results and their interpretation. This experiment was designed to maximize the probability of locating nests from perches by visual bird predators, particularly crows. The trials were therefore situated in areas of nesting crows and close to northern lapwing nesting territories where predators may have experience with their nests. The trials were

not, however, within the protective zone which may be created by northern lapwings and were at least 200 m from the nearest active lapwing nest (Elliot 1985). The nests were located up to 100 m from elevated points (perches), as a previous study in that area had confirmed a higher predation risk to northern lapwing nests from this distance (Štorek 2011). A perch was defined as any fixed object (e.g. a tree or pylon) in the field or at its edge enabling a predator's lookout from a height of at least 5 m. The choice of habitats for nest placement was limited to those habitats usually occupied by nesting lapwings in the study areas (Kubelka et al. 2012), including (a) crop fields with denser and/or taller dark growth where dummies are hidden from visual predators; (b) ploughed fields and maize with mosaic of bare ground and sparse vegetation cover, where dummies can easily blend in with the substrate; and (c) managed meadows with uniform short-grass cover where dummies are easily found. Trials were deployed in sets of 8-9 nest pairs around a given breeding area with a distance of at least 300 m between two neighbouring trials.

Specifically of interest was whether predation would occur more often at nests after removal of the dummy than at control nests (not previously provided with the dummies). Software R 2.12.0 (R Development Core Team 2010) was used for computations of a generalized linear mixed-effect model (GLMM, 'lmer' in R package 'lme4') with log link function and binomial error distribution to test the effects of dummy's presence, habitat, vegetation height, distance to a perch, and the first-order interaction of the dummy's presence with perch distance, vegetation height and habitat on predation risk (depredated or not). The GLMM framework was applied to account for the proximity of nests within trials and breeding grounds by including the trial identity and breeding

ground as random effects. The null hypothesis was rejected at $P < 0.05$.

Results

A total of 96 nest pairs were installed at 6 breeding areas in southern Bohemia and 5 breeding areas in eastern Bohemia. With the exception of 3 areas in southern Bohemia provided with 8 trials each, 9 trials were installed at each of the remaining 8 areas. Seven nests in 7 pairs were depredated before removal of the dummy and 2 other pairs were destroyed by machinery. Therefore, 9 nest pairs distorting the original experimental design were excluded and 87 pairs were included into the analysis. In this final sample, crop fields constituted the most represented habitat (52 trials), followed by meadows (20). Samples from ploughed fields (6) and maize (9) were pooled for further analysis, as the dummies in these habitats were regarded as similarly camouflaged.

The GLMM analysis revealed that habitat, presence of the dummy, and their interaction significantly influenced nest predation risk (Table 1). Whereas in meadows only those nests provided with the dummy were depredated (23.8 % of all such trials), 40 % of such nests, compared with only 20 % of control nests, were lost due to predation in ploughed fields and maize. Low predation risk (6.8 % of all nests) was recorded in crop fields regardless of dummy presence (Fig. 1).

In sum, 15 nests previously exposed with the dummy were depredated (17.2 %) compared to six control nests (6.9 %). At seven (the majority) of 11 breeding areas, the nests previously exposed with the dummy were more depredated than control nests (consistent with the prediction), at two breeding areas these predation rates were identical, at one breeding area the result was opposed to the prediction and at one

Table 1. Results of the mixed-effect model explaining the effects of factors on predation risk to experimental nests. The order of levels included into the model among the categorical variables was as follows: "habitat" – crop fields (reference value), ploughed fields and maize, meadows; and "dummy" absent (reference value) or present.

Predictor	Estimate	Std. error	χ^2	df	P
habitat	-0.213	0.1269	9.67	2, 7	0.008
	0.058	0.0835			
habitat × dummy	-0.237	0.1481	6.58	2, 11	0.037
	-0.218	0.0961			
dummy	0.169	0.1776	6.41	1, 8	0.011
height	-0.032	0.0452	1.53	1, 8	0.216
perch × dummy	-0.031	0.0284	1.23	1, 12	0.266
height × dummy	-0.036	0.0526	0.49	1, 12	0.486
perch	0.022	0.0240	0.13	1, 8	0.715

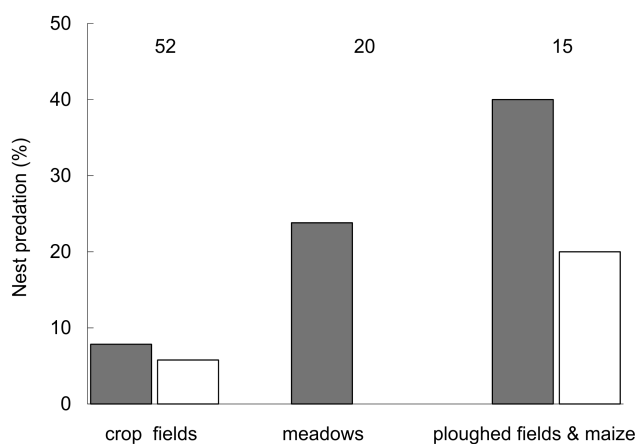


Fig. 1. Proportions of nest predation on dummy (grey bars) and control (white bars) nests in 87 experimental pairs. The numbers indicate sample sizes.

area the depredation did not occur at all. Vegetation height, distance to perch, and their interactions with a dummy's presence did not contribute significantly to the predation rate in this model.

Discussion

Significantly ($2.5\times$) higher depredation rate of nests previously provided with dummies compared with control nests confirms that, in at least on some places (7 of 11 breeding grounds, i.e. 63.6 % of the sites included in this study), the predators registered the dummies as subjects of increased interest and subsequently inspected the corresponding positions preferably. Although the absolute differences between predation rates on dummy-provided nests and the control nests did not seem very great, it must be taken into account that nest exposure lasted only a few hours, which was certainly not enough time for relevant inspection of complete home feeding ranges by many predators present at the study sites. In addition, some of the nests of both types were apparently depredated incidentally (Vickery et al. 1992). On the other hand, a scent at the nests that might influence nest attractiveness for predators using olfactory cues (Rangen et al. 2000) did not contribute to this difference because manipulation and time spent by an observer at all nests were the same. In addition, the dummies were exposed on the nests only during daylight, so their presence was convenient for predators with daily activity, i.e. primarily birds.

Predation on lapwing nests strongly varies among habitats (Berg et al. 1992, Sheldon et al. 2007) including the study area (Šálek & Šmilauer 2002) and, according to the results of this study, one reason for this variation may be different visibility of incubating

parents. Good visibility of the dummies in meadows can lead to stronger predation on the dummy-provided nests in contrast with the control nests, all of which survived. Higher nest predation in ploughed fields and maize compared with other habitats may demonstrate this habitat's increased attractiveness for predators searching for food while walking (i.e. incidentally), despite the fact that dummy-provided nests were also disadvantaged more than control nests in this habitat. The suitability of ploughed fields and maize for predators might be based on the fact that these fields abound in bare ground and thus supply various forms of surface-dwelling invertebrates (e.g. carabid beetles) attractive for generalist predators that can then focus on visual searches of such easy prey while walking (Bradbury & Kirby 2006). In contrast, a low predation rate in crop fields regardless of the presence of a dummy could be due to good concealment of both dummies and nests in dense vegetation, which is rather avoided by predators due to the lower general availability of prey there (Tagmann-Ioset et al. 2012). That effects of perch distance and vegetation height on nest predation risk were non-significant in this study may not be surprising, because all nests were purposely located within a distance of 100 m from elevated points. There are two main reasons for this. First, the predation risk in the study area is known to be significantly higher within this range compared to greater distances (Štorek 2011). Second, up to this distance, nests are viewed from above at a relatively sharp angle such that the height of vegetation may play a minor role compared to habitat substrate.

Incubating parents use a variety of tactics to protect their nests from predators (Conway & Martin 2000, Coates & Delehanty 2008), one of which is to passively remain on the nest, as this may immediately discourage approaching avian predators, and defend the nest against direct attack (Montgomerie & Weatherhead 1988, Opermanis 2004). This is known in species such as ducks, which have cryptic plumage but uniformly coloured eggs that are much more easily found from above (Albrecht & Klvaňa 2004, Andersson & Waldeck 2006). This tactic is obviously not the case for the northern lapwing, however, even though its incubation effort represents in average more than 80 % of the daytime and the nests remain unattended for only a very short time during the day (Grønstøl 2003, pers. obs.). Because lapwings leave the nests at the time of a predator's approach (Šálek & Cepáková 2006), a predator such as crow that has surpassed the protective umbrella formed by aggressive lapwing adults attacking intruders in

nesting territories and has reached the proximity of the nest by walking, is therefore no longer hindered by incubating parents (pers. obs.). The success of its search is therefore limited in particular by crypsis of the nest. However, if the predator knows the nest's exact position as a result of previous perching, it can easily and quickly find and depredate these cryptic eggs, doing so in a manner which would not be detected by a casual observer. The common use of this tactic could then easily explain why successful depredation of clutches at the time of fighting between incubating parents and predators is rarely observed (if at all), even though predation rates on northern lapwings nests are generally high (MacDonald & Bolton 2008), including in the study area (Šálek & Šmilauer 2002).

Only seven experimental nests in this study (3.7 % of nests) were depredated before removal of the dummy, which suggests that a few predators ignored its presence in the nest. Unfortunately, there are no other data useful for clarification of these incidents as no cameras were added to the nests. It may at least be excluded that these depredations were due to nocturnal mammalian predators such as foxes or hedgehogs (*Erinaceus* spp.); because the dummies were exposed exclusively during daylight, avian predators were probably responsible for these attacks. The generalization of real proportions of depredation events must be treated with a caution. First, to increase chance that the object will be found from distance, we designed the experiment using proximity of elevated points. Second, large areas were included to detect whether general pattern exists throughout sites, habitats and regions regardless other non-controlled variables potentially influencing predation patterns. Third, the plastic dummies may attract more or less the predators than living lapwings (e.g.

because of difference in plumage reflectance). In spite of these uncertainties, however, this should not call into question the principle of the specific predation tactic's consisting of delayed reaction to a remote stimulus that disappeared after a certain time. After all, predators preferentially visited those places with a previous subject of interest over the neighbouring, control, places where this subject had never been present. We therefore conclude that, while depending upon habitat, at least some predators can remember the nest positions during perching from observing incubating parents and delay the first visit there until after the parents leave the nest. The tactic proves that predators are able to apply a much more sophisticated approach in searching out birds' nests than was previously assumed. For example, it would explain how the predators avoid conflicts with the incubating lapwings at the nests and why these events are not commonly observed in spite of a generally high loss of northern lapwing nests due to predation. Although the predators in this study were not specifically determined, the study was designed in order to maximize the effect of visually orientated bird predators, particularly crows. However, much remains to confirm that corvids or even other predators are responsible for this predation tactics on birds' nests and whether they respond similarly to dummies as real parents. Also, there is a need for more detailed studies to assess the rate of actual application of this tactic in various prey species.

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