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Source: Folia Zoologica, 67(3-4) : 154-157

Published By: Institute of Vertebrate Biology, Czech Academy of Sciences

URL: https://doi.org/10.25225/fozo.v67.i3-4.a6.2018

Folia Zool. – 67 (3–4): 154–157 (2018) DOI: 10.25225/fozo.v67.i3-4.a6.2018

Switches in covering of eggs in grey partridge *Perdix perdix* clutches during laying and incubation

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Received 11 June 2018; Accepted 24 September 2018

Abstract. Covering of eggs is important antipredator behaviour which is known for several bird species. Generally this behaviour is considered consistent throughout the whole nesting cycle but there can be exceptions in some species. We found two switches in egg covering during nesting in grey partridge: the first between two early laying phases, the second between later laying and incubation. The clutch containing only the first egg remained uncovered, larger clutches were covered with dry vegetation in the laying period, but the eggs remained uncovered during incubation breaks. There was a strong consistency of this behaviour among females. From four tested factors, only nesting period significantly affected egg covering. We assume that the first uncovered egg may serve as a bait for predators to test nest-site safety whereas the motion in the course of egg covering during short incubation breaks may increase predator attraction.

Key words: birds, nesting phase, nest depredation, nest survival, antipredator tactic, testing egg

Introduction

Animal camouflage represents one of the most important ways of preventing or facilitating predation (Stevens & Ruxton 2018). Covering of eggs with down, dry plants or soil by a parent before leaving the nest is generally used for enhancing nesting success in several taxa (e.g. Anatidae, Podicipedidae, Charadriidae; Kreisinger & Albrecht 2008, Prokop & Trnka 2011, Amat et al. 2012). This behaviour is however linked to conspicuous movements of parents at the unconcealed (e.g. open) nests, which may attract predators (Skutch 1949). Therefore, egg covering can be a subject of trade-off.

Generally, among species covering their eggs, this behaviour is considered consistent throughout the nesting cycle from laying to incubation. Exceptionally, there are observations in grebes (*Podiceps cristatus* and *P. nigricollis*) revealing a general tendency to cover the clutch with a specific number of eggs (Broekhuysen & Frost 1968, Goc 1986). Majority of incomplete clutches with 1-2 eggs have been left uncovered in contrast with covering them in later stages. Similarly, just only the first egg left uncovered was episodically documented in the grey partridge (*Perdix perdix*) by Sprake (1930).

The ground nests of the grey partridge are exposed to many potential predators for long-lasting period of egg laying (sometimes > 20 days) as well as incubation period (up to 25 days, Jenkins 1961). Whereas the incubating female is perfectly camouflaged, light greenish eggs are much more visible. The females reduce the conspicuousness of unattended eggs by masking them with dry plants during laying period (Jenkins 1961). However, after the clutch completion, female incubates the eggs very firmly and with one to three short breaks a day (up to five hours long in sum; own observations). Therefore, the female's motion at the nest due to repeated manipulation with nest content increasing nest predation risk (Skutch 1949) versus eggs concealment may become a matter of possible trade-off. Using own long-term data from three different populations we analysed the variation in egg covering

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within and among grey partridge females during their nesting cycle from the early stage of the first egg until late incubation. We tested effects of actual clutch size and nesting phases (two phases of early laying, late laying and incubation period) on female egg-covering behaviour. We hypothesized that females leaving the nests will cover the eggs during most of the laying period but will remain them uncovered in the stage of the first egg (according to Sprake 1930) and during incubation as a result of the trade-off between egg concealment and female detectability. We also asked, whether individuality of females can explain the observed egg-covering pattern.

Material and Methods

The study was carried out in three different populations in following areas of the Czech Republic: Písek (2001-2002, 49°17′ N, 14°09′ E), Prague (2004, 50°02′ N, 14°18′ E), and Milešín (2009-2010, 49°22′ N, 16°12′ E). Písek and Milešín represent an agricultural landscape, whereas Prague consisted of uncultivated and weedy land in suburban part of the capital. Nests were found in 59 radio-tagged females (Písek: 9, Prague: 13, Milešín: 37) equipped with TW-4 necklace radio-transmitter (Biotrack, Wareham, U.K.). To discover nests, we tracked signals of each female from late April daily, once or repeatedly during daylight. If female moved away from the patrolling male and stayed hidden for at least 20 minutes in one place, we triangulated her location from distance > 30 m (depending on habitat complexity) as a possible nest site. We waited until the female leaved > 50 m without her disturbance and returned to carefully check the location and its surroundings in a radius of 5 m. We recorded number of eggs and clutch status (covered – including partially covered clutches – or uncovered). We distinguished four nesting phases: 1) initial first-egg stage, 2) early two- to three-egg stage, 3) later laying period with more than three eggs, 4) incubation period. Unfortunately, high nest predation rate disabled to observe all nesting phases in all nests. Laying initiation was estimated for some nests backwards, providing that one egg is laid daily or using flotation test during incubation (van Paassen et al. 1984).

We used R 3.0.3 (R Core Team 2014) and glmer function from the “lme4” package for generalized mixed-effects modeling (Bates et al. 2015) to test the effect of population, nesting phase, clutch size and number of days from clutch initiation on female decision to cover (1) or not cover (0) the eggs (binary response). The effect of female individual repeatability on this decision (given nest-to-nest different number of observations; see Table S1, S2) was tested using R package “rptR” and mixed-effect modeling (Nakagawa & Schielzeth 2010, Dingemanse & Dochtermann 2013). We used the permutation test for obtaining the significance of repeatability (n = 1000). The models include females affiliation with the nests as random effect.

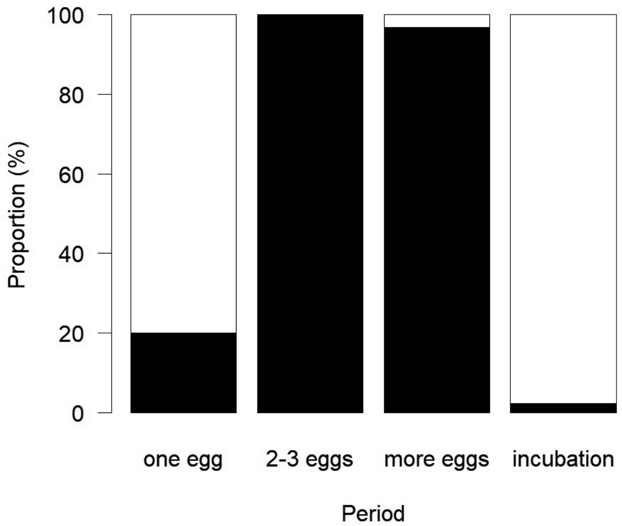

Fig. 1. Proportion of observations in grey partridge nests with covered (black) or uncovered (white) clutches during laying and incubation periods: (1) one egg stage (10 observations), (2) 2-3 eggs stage (10 observations), (3) laying period with more than three eggs in the nest (63 observations), (4) incubation period (87 observations). All observations including repeated visits of the same nests included. The total number of clutches was 59.

Table 1. Results of the generalized linear mixed-effects model with logit link function analysing the effect of population (Písek, Prague and Milešín), nesting phase (first-egg stage, two- to three-egg stage, later laying stage, and incubation), clutch size and number of days from clutch initiation on clutch covering in the grey partridge. In population and nesting phase, the treatment contrasts between Písek (reference level) and other population, and between one egg (reference) and other nesting stages, are shown.

Factor	Estimate	SE	df	χ^2	*P*
Intercept	0.199	0.0715			
Population					
Prague	0.032	0.0711	2	0.24	0.886
Milešín	–0.004	0.0543			
Nesting phase					
2-3 eggs	0.789	0.0079			
Later laying	0.788	0.0703	3	212.49	< 0.0001
Incubation	–0.065	0.0930			
Actual clutch size	0.001	0.0060	1	< 0.01	0.979
Laying date	–0.004	0.0028	1	2.40	0.122

Results

Clutches in the initial nesting phase (the first egg in the nest) were found for 10 females and in eight cases (80 %) these eggs had remained uncovered (Fig. 1). Incomplete clutches during later laying stages were observed for 9 (2-3 eggs) and 30 (> 3 eggs) females and these clutches were in almost all cases with two exceptions (96.8 % of cases) covered with dry plant material. In contrast, among 35 nests repeatedly checked during incubation breaks, only two clutches (2.3 %) were covered (with one event in each of them). The nesting phase was the only significant predictor of nest covering (Table 1). A similar result (the effect of nesting phase: $\chi^2_3 = 89.26$, $P < 0.0001$, all other predictors: $P > 0.26$) was obtained by analysing the subset of 18 nests in which continuous data for two or more subsequent periods of the same females were collected. The effect of female identity on nest covering was not significant ($R \pm SE = 0 \pm 0.060$, $P > 0.9$), i.e. females changed the behaviour consistently according to the nesting phase.

Discussion

This study documents unusual two switches in egg-covering behaviour of grey partridge females from the first-egg phase (no covering) across later laying phase (covering with dry plants) to incubation period (no covering). This custom seems to be valid for the studied species because we found strong consistency in this behaviour among different females and populations.

Although our sample of nests in the first-egg phase was limited, it seems that keeping the first egg uncovered until the second egg is laid, i.e. for 24-48 hours of known laying interval 1-2 days, is a rule in this species. The first uncovered egg, brightly contrasting with the darker nest background, may serve as bait for potential predators, which is by Goc (1986) interpreted as a tactic to test for nest-site safety. This site-testing strategy could be vitally important for the grey partridge, whose nesting period is long, females invest to large clutches and whose nests and nesting females suffer from a high predation (Rymešová et al. 2013). Thus, if the first uncovered egg is depredated on site with a high predation risk, the female may immediately choose another nest location nearby and start a new clutch without significant loss of time and energy. The site-testing strategy existence is also supported by the fact that the grey partridge females are extremely sensitive during early laying and an unwanted disclosure of the nest by an observer in the presence of female may lead to nest abandonment and re-nesting elsewhere (Jenkins 1961).

In general, birds' ability to predict nest site quality has been considered important because the nest site strongly influences nest predation risk (Ricklefs 1969). Grey partridges are short-living, probably unable to gain enough experience about choosing the safest nest sites during their life. The use of the first "testing" egg could be therefore a good alternative how to test the actual nest site quality. However, there is still a simple explanation that there is not enough material around the nest to cover the first egg, and this material is collected by the female gradually after the production of the second egg. If this possible explanation was right, we should find an effect of clutch initiation date on egg-covering behaviour, as more material is accessible later in the nesting season. Nevertheless, this effect was not found.

Covering eggs with dry plant material was characteristic during laying period from the second-egg stage. This behaviour is well known in ground nesting birds (waterfowl, plovers; Kreisinger & Albrecht 2008, Amat et al. 2012) which are exposed to high nest predation risk too (Ricklefs 1969). Beyond this anti-predation function, however, egg covering can serve for regulation of temperature or humidity (Prokop & Trnka 2011, Amat et al. 2012, Stevens & Ruxton 2018). Both these reasons might be also important for the grey partridge.

Grey partridge females did not cover the eggs during their short incubation breaks. This fact is in line with the suggestion about the risk associated with predator attraction during egg covering (Skutch 1949). However, the incubation of the clutches takes place mostly in June or later, when the vegetation has been already relatively tall, which may form a partial or substantial nest shelter. Egg covering thus does not have to be necessary at that time for many nests. On the other hand, this behaviour was consistent in all females regardless of habitat.

To conclude, we assume that the two switches (uncover – cover – uncover) in the grey partridge represent an unusual behaviour among birds. Leaving incomplete clutches uncovered specifically in the first-egg stage is a unique feature known only in grebes up to date. Its finding in the grey partridge populations thus indicates a possible convergent behavioural trait. However, this phenomenon is poorly explored and future studies should focus on more species and should employ continuous video-monitoring which may help to understand this phenomenon much better.

Acknowledgements

The study was supported by the Czech Science Foundation (GA206/08/1281) and appears through financial support provided to the Moravian Museum by Ministry of Culture of the Czech Republic as part of its long-term conceptual development programme for research institutions (ref. MK000094862). We thank all our collaborators and the anonymous referees for their valuable comments.

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Supplementary online material

Table S1. Results of nest checks in three grey partridge populations (coding of covering: 0 = uncovered eggs, 1 = covered eggs; coding of period: 1 = one egg stage, 2 = 2-3 eggs, 3 = more than three eggs in the nests, 4 = incubation period; ClutchSize = number of eggs, Days = number of days from clutch initiation).

Table S2. Nest survival and final fate of grey partridge nests (Visits = number of nest checks; coding of period: 1 = one egg stage, 2 = 2-3 eggs, 3 = more than three eggs in the nests, 4 = incubation period; coding of covering: U = uncovered eggs, C = covered eggs) (http://www.ivb.cz/folia_zoologica/supplemetarymaterials/cerny_et_al_table_s1_s2.docx).