Effect of nest age, time and habitat variables on nest survival in Marsh Harrier *(Circus aeruginosus)*

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ABSTRACT

Background

One important anti-predator strategy adopted by birds involves ~~indirect effects such as~~ nest site selection and timing of breeding. Nest-site selection by marsh-nesting birds often involves nest concealment and water depth as the key features influencing nest survival. Marsh harrier *(Circus aeruginosus)* is an obligate ground nester, which sets it apart from other raptors. The aim of the present study was to identify for the first time possible temporal and habitat factors affecting nest survival in Marsh Harrier. Understanding features which affect nest survival are essential for assessing relevant conservation strategies.

Methods

To understand the relative contributions of different temporal and habitat variables to brood losses, it is useful to determine the daily survival rate (DSR). We examined 82 Marsh Harrier nests located on fishponds in eastern Poland, where predation is~~was~~ the main cause of nest failure. Six habitat variables were measured for each active nest. DSR was calculated using known-fate models with the RMark package.

Results

The best-fitted model predicted that DSR decreased both with advancement of nest age? and day in the season, and was positively affected by the water depth and the diameter of reed stems, but not the height or density of vegetation at the nest site. The distances of nests to the fishpond dyke

and to open water were not important factors either. This result suggests that Marsh Harrier nests are more susceptible to mammalian than avian predation, and that this bird of prey is not well adapted to nesting in wetlands in comparison to other species doing so.

Comentado [.1]: Mucho énfasis en resultados negativos y poca discusión de los positivos, no se entiende cómo llegan a sugerir que son mamíferos

Keywords: Breeding time, Fishpond, Nest site selection, Predation risk, Daily survival rate

INTRODUCTION

Comentado [.2]: Until the presentation of the objectives (several paragraphs), the information is about "birds in general". I think there is too much variety of background in these opening paragraphs. I suggest adjusting this section to raptors (if possible ground nesters) and in this way be clearer.

For most species of birds, nest survival is an important component of fitness, while predation is usually the main ~~a~~ cause of breeding failure (Martin, 1993). Many aspects of the nesting behaviour of birds appear to be adaptations to prevent predators from detecting the nest (citation). Anti-~~-~~predator strategies adopted by birds involve direct effects of parental behaviour (nest defence) as well as indirect ones, such as the decision where (nest site selection) and when (timing) to breed (Lima, 2009).

Comentado [.3]: Hay citas más relevantes y actuales, además de Martin (1993)

Studies of nest success have focused mostly on relationships between nest site characteristics and nest fate (Chalfoun & Schmidt, 2012). Thus, avian reproductive success has been relatively well studied in comparison with nest site characteristics (citations). Nest site selection is important, but especially so in ground-nesting birds. Predation models?~~affects~~ breeding site choice: nests located at sites inaccessible to predators or well-concealed ones have a higher breeding success (Latif, Heath & Rotenberry, 2011).

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Comentado [.5]: missing connection between sentences

In most bird populations, the risk of nest predation varies over time and space (Lima, 2009). Owing to seasonal changes in predator abundance and activity, much of the variation in this risk is associated with the nesting date (Roos, 2002). In addition, nest age (days after clutch initiation) is often mentioned as a key factor determining the risk of nest loss (citations). Besides temporal and habitat variables, inclement weather conditions may adversely affect brood survival in birds (Dawson & Bortolotti, 2000). However, local weather conditions in eastern Poland seem not to affect reproduction in our study population (Kryński, Goławski & Kasprzykowski, 2017).

Comentado [.6]: Martin et al 2000, Segura and Reboreda 2012

To better understand the relative contributions of different temporal aspects of nest survival, it is useful to determine the daily survival rate (DSR), i.e. the probability that a nest survives a single day. The effects of nest age and time on DSR vary between species and are often contradictory. For many altricial birds, DSR decreases with nest age owing to greater parental activity during the chick-rearing phase, which makes the nest more susceptible to detection by visually oriented predators (Martin, Scott & Menge, 2000). With regard to the timing of breeding, some authors have noted that DSR decreases over time during a season (Jobin & Picman, 1997; Grant et al., 2005), while others report the opposite trend (Wilson, Martin & Hannon, 2007; Polak, 2016). If synchronized, however, the effects of nesting season and nest age can be confounded (Smith & Wilson, 2010).

To date, nest survival models have been used mainly for waterfowl, shorebirds, and passerines that nest on or near the ground (Davison & Bollinger, 2000; Grant et al., 2005; Smith & Wilson, 2010); only a few studies of raptors have analysed this pattern (Brown & Collopy, 2008; Brown et al., 2013; Crandall, Bedrosian & Craighead, 2015, Segura & Bó 2018). The aim of the present study was to investigate for the first time key factors affecting nest survival rate in Marsh Harrier (*Circus aeruginosus*) in wetland habitats with varied vegetation structures and hydrological regimes. This bird is an obligate ground nester, which sets it apart from other raptors. As suggested by Simmons & Simmons (2000), all harriers may have nested in trees at one time, but the abundance of prey in open grasslands where trees are not common may have driven them to such habitats.

Numerous studies have shown that, for many typical marsh-nesting birds, water depth and emergent vegetation are key features influencing nest site selection and nest survival (Krasowski & Nudds, 1986; Sutherland & Maher, 1987; Polak, 2016). Well-concealed nests are less at risk to predation (Schranck, 1972; Cempulik, 1994). However, the efficacy of nest concealment varies between species; some studies have shown no positive influence of nest concealment on nest success (Borgo & Conover, 2016) and sometimes nest cover can even increase probability of nest predation (Schüttler et al., 2009).

In the present research, answers were sought to the following questions: (1) Do temporal variables influence Marsh Harrier DSR in a wetland habitat? (2) Does the Marsh Harrier DSR pattern differ from that of birds well adapted to nesting in aquatic environments? (3) Do the vegetation cover and nest location influence Marsh Harrier breeding success? To address these questions, we assessed the relevance of nest age, time and habitat variables as possible predictors of the daily nest survival rate. Thus, we anticipated a higher DSR of better concealed nests over deeper water and situated in dense vegetation. We also hypothesized that Marsh Harrier DSR would decrease with increasing nest age and day in the season. Determining time-specific patterns of nest survival may improve our understanding of predator-prey interactions. It is also

Comentado [.7]: This does not seem relevant for a raptor that aggressively defends the nest.

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Comentado [.9]: The objective is not clear from the background (see comment above).

Comentado [.10]: Harriers are ground nesters, I don't understand the use of this word

Comentado [.11]: irrelevant

Comentado [.12]: After introducing the species under study, it doesn't seem right to talk about "birds in general" again, it's very confusing.

important for understanding raptor population dynamics, as reliable estimates of nest survival are essential for assessing relevant conservation strategies.

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MATERIAL & METHODS

Study area

The study was conducted over five breeding seasons (2008, 2009, 2011, 2018 and 2019) in eastern Poland on four fishpond complexes: Siedlce, Rudka, Szostek, Mościbrody (52°05´–52°11´N, 21°58´–22°18´E); all are mainly used for the commercial breeding of Common Carp *Cyprinus carpio*. Pond areas varied from 47 to 83 ha. Most of the ponds were partially covered by tall marsh vegetation consisting of Bulrush (Common Reedmace) *Typha latifolia*, Common Reed *Phragmites australis* and Sedges *Carex* spp. These plants tend to increase rapidly and can quickly cover the surface of a pond or wetland, creating suitable breeding habitat for Marsh Harrier. The ponds were similar in water depth but water levels in the emergent vegetation varied from 7 to 92 cm in spring, falling as the breeding season progressed. During the fieldwork, the presence of several possible opportunistic predators of aquatic birds' nests were recorded: the invasive American Mink *Neovison vison*, and the native Wild Boar *Sus scrofa*, Red Fox *Vulpes vulpes*, European Otter *Lutra lutra*, European Badger *Meles meles*, Magpie *Pica pica*, Raven *Corvus corax* and White-tailed Eagle *Haliaeetus albicilla*.

Comentado [.14]: I would try to select the ones that are relevant to a harrier (due to their active nest defense)

Field procedures

At the beginning of each breeding season, each study pond was visited at 1-3-day intervals between mid-April and mid-May to locate breeding pairs and nests. The observations were made with 8x42 binoculars from the fishpond dyke. The birds were observed carrying nest material to the emergent vegetation belt and during aerial food-passes near their potential nest site. After selecting a potentially favourable site, the observers inspected the vegetation belt on foot along fixed line transects. When located, the nests were numbered and their positions recorded with a hand-held GPS unit. A total of 82 nests were discovered in the study areas – 27 during the egg-laying phase, 53 during egg incubation and 2 during the early nestling period. To minimize disturbance, each nest was visited at 5-7 day intervals to determine clutch size, hatching date, nest fate and the number of live chicks. The first-egg laying date was calculated on the assumption that eggs are laid at 2-day intervals, and that incubation starts after the laying of the first egg and lasts for an average of 33 days (Witkowski, 1989). A nest was considered to have been depredated when it was found empty before the predicted date of fledging, which is 35 days of age according to Witkowski (1989). Six habitat variables were obtained for each active nest (Table 1). All vegetation measurements (height, diameter, density) were made in 100 x 100 cm quadrats placed around the nest during the first visit. The distances of a nest to the fishpond dyke and to open water was measured using GPS equipment. All operations were conducted under the program " Research of birds in the disclimax ecosystems" approved by the Institute of Biological Sciences, Siedlce University of Natural Sciences and Humanities (number of approval: IB.5030.8.2018). The study fulfilled the current Polish Law and was permitted by Ministry of the Environment (approval number: 425/2019) and Regional Directorate for Environmental Protection in Warsaw allowed for this research project by the letter (number of approval: WSTS.6401.34.2018.MO).

Statistical analyses

Daily survival rate (DSR), the probability that a nest will survive a single day, was calculated using known-fate models with the RMark package (Laake, 2019). RMark is an R package (R Core Development Team, 2020) that provides a formula-based interface for the MARK program (White & Burnham, 1999). The analysis included only nests which succeeded or were depredated (*N*=82). Nest failures were due to flooding (*N*=1), desertion (*N*=2) and other, unknown reasons (*N*=2). The dates were scaled such that day 1 was the day when the first nest was found and day 84 was the day the last nest was checked. Thus, the 84-day nesting season was defined as beginning on 30th April and ending on 22nd July. The season thus consisted of 83 intervals, which represent an 83-day nesting cycle with each interval equivalent to one day. We therefore modelled DSR as a function of temporal (day of the season and nest age) and habitat variables (water depth under the nest, density of reed stems, height and diameter of vegetation, distance to open water and distance to the dyke). We constructed models of nest survival that incorporated combinations of individual covariates, and compared them to the null model of constant survival rate, S(.). The set of competing models was based on a combination of factors assumed *a priori* to affect DSR. The better concealed nests were expected to have a greater chance of survival. We used an information-theoretic approach (AIC) to compare the competing models (Burnham & Anderson, 2002) and analysed model support using the AICc value, which

Comentado [.15]: previous sentence is clear, so this sentence is irrelevant corrects for small sample sizes and evaluates the strength of evidence for each model using normalized weights (w_i). The models selected with the smallest AICc as being the best of all the models compared, where the models were within a Δi AIC of 2.00, were considered to be equally supported (Burnham & Anderson, 2002).

RESULTS

We monitored a total of 82 Marsh Harrier nests: 52 were successful and~~but~~ 30 were depredated. The mean breeding success (at least one fledgling produced) over all the study years was 63%; success was the highest (84%) in 2011 and the lowest (9%) in 2018, when only one pair successfully raised young. Eight (27%) of the depredated nests were destroyed during the egg-laying stage, 16 (53%) during incubation and 6 (20%) during the nestling period. The average height of the reed stems in the nesting squares was 1.9 m (SD = 39.2; *N* =82; range 106-300) and the average diameter of the shoots was 7.3 mm (SD = 1.8; *N*=82; range 3.3-12.1). The density of stems varied between 31 and 191 (mean = 86.9; SD = 31.1; *N*=82). The level of water at the nest at the beginning of the nesting season varied between 21 and 92 cm (mean = 50.4; SD=15.6 cm; *N* = 82). The average distance of a nest to the fishpond dyke was 69.8 m (SD= 49.1; *N*=82; range 15-233) and the average distance of a nest to open water was 51.0 m (SD=50.2; *N*=82; range 1-278).

Comentado [.16]: apparent nest success?

Comentado [.17]: Destroyed? 27% were predated during egg-laying.....

In the constant model, DSR calculated for all nests was 0.992±0.001 SE (95% CI [0.989–0.994]). The analysis revealed that both temporal and habitat variables affected Marsh Harrier DSR (Table 2). Two of the 15 *a priori* models with the highest ranking (Δi AICc<2) included combinations of both temporal variables (nest age and time) and habitat variables (diameter of reed stems and water depth).

Comentado [.18]: Null model?

The model with the best fit was the one with the lowest AICc value, but models within a delta AIC of 2.00 were considered equally supported (Burnham & Anderson 2002). In the candidate model set, the two top models with Δi AICc<2 overall received 90.4% support (sum of w_i, Table 2). The best-fitted model with the lowest AICc predicted that Marsh Harrier DSR gradually decreased with nest age (Fig. 1). The second-best model included time as a temporal variable and was less well supported with 1.50 AICc points and predicted that DSR of Marsh Harrier broods decreased with day of the season (Fig. 2). The habitat factors with the greatest influence on the likelihood of nest depredation were the diameter of reed stems around the nest and water depth: in both cases, DSR gradually increased with these parameters (Figs. 3 & 4). The quadratic effect of time was less well supported than the linear effect. The analysis also showed that factors such as density of vegetation, distance to open water and distance to the fishpond dyke had no effect on the survival of Marsh Harrier broods. There was greater support for the null model of constant survival rate S (.).

Comentado [.19]: Irrelevant, just mentioning that "the rest of the models had less support than the null model"

Comentado [.20]: Fugures: since the best models have additive variables (ie, diameter + water depth + nest age, or diameter + water depth + time, Table 2), authors should not make individual graphs with each variable, but one or two that represent these associations.

DISCUSSION

Comentado [.21]: Since in Introduction it is mentioned that there is no data on TSD in this harrier, it would be interesting a first paragraph that discusses the importance of these first studies.

Nest age

Comentado [.22]: I suggest to discuss the results only among raptors and, if possible, ground nesters.

Recent studies have yielded mixed results for the influence of nest age on DSR in both altricial and precocial birds. Some species exhibited an increase in DSR with nest age (Polak, 2016; Specht et al., 2020), while others displayed the opposite trend (Zhao et al., 2020). Our results showed that Marsh Harrier DSR was not constant from the egg phase to fledging, decreasing gradually with nest advancement. One potential explanation of this pattern is that after hatching, parents and young provide more behavioural cues at the nest, which increase the possibility of its being detected by predators (Martin, Scott & Menge, 2000). As nest age increases, adults invest more in the nest and typically intensify defensive behaviour (Smith & Wilson, 2010). Despite the fact that Marsh Harriers actively defend their nests, this does not compensate for increased predation. One possible explanation is that with nest advancement, parents need to make more frequent foraging flights to provide for their offspring. The times when the parents are absent are when the nest is more vulnerable to predation.

Comentado [.23]: this makes sense only to some nest predators (see comments above)

Decreasing DSR may also reflect a cumulative risk: the longer a nest is active, the more likely it will lose eggs to predation. In Marsh Harriers, the period from the start of incubation to the fledging of the young birds is relatively long in comparison to other species nesting in the same fishpond habitat. For example, chicks of Eurasian Bittern (*Botaurus stellaris*) leave the nest at the age of just two weeks post hatching, i.e. before reaching full independence (Kasprzykowski & Polak, 2012). The female continues to care for the young, which hide in vegetation near the nest until fully fledged. This could be an adaptive strategy diluting the risk of detection by predators and preventing DSR from decreasing with nest age in this species. In contrast, Marsh Harrier chicks cannot leave the nest until they are capable of flight: this species is therefore especially vulnerable to detection by predators with increasing nest advancement.

Comentado [.24]: Adjust discussion to raptors (see other comments above)

Time

The daily survival rate of Marsh Harrier recorded in our study varied over time, decreasing as the nesting season progressed. Early breeders achieved a significantly higher reproductive success than birds breeding later. These results are consistent with previous studies, which associated higher nest survival with early breeding in Marsh Harrier (Buczek & Keller, 1994; Němečková, Mrlík & Drozd, 2008) and other species of Harriers (Barnard et al., 1987, Corbacho et al., 1997; Millon et al., 2002; Segura & Bó, 2017). The reason for this pattern could be that the earliest breeding birds are often older and more experienced than late nesters. This was confirmed by studies of Marsh Harrier demonstrating that older pairs arrive earlier in the breeding area, start breeding earlier, have larger clutches and raise more young (Altenburg, 1987). The same pattern was observed in Montagu's Harrier *Circus pygargus* (Arroyo, Bretagnolle & Leroux, 2007).

Comentado [.25]: this seems like a result

The seasonal decline in DSR could also be attributed to food availability (Newton & Marquiss, 1984; Daan et al., 1989). At the beginning of the nesting season, more prey may be available, especially inexperienced juvenile prey, which may account for the higher productivity of earlier breeding birds. Later in the season, prey availability decreases, which could also contribute to a decrease in DSR. In addition, a lower DSR is often associated with a greater local abundance of predators (Borgmann, Conway & Morrison, 2013). This might further explain the significantly lower breeding success later in the season, as the increase in predator abundance raises the risk of nest detection.

Nest concealment

Comentado [.26]: It is not clear the 'point' that the authors want to discuss (both paragraphs). It is important to discuss the variables that were relevant and not so much those that were not.

According to the nest concealment hypothesis, better concealment of nests among vegetation should minimize the risk of their being detected (Martin & Roper, 1988). Vegetation cover is expected to reduce the transmission of auditory, visual and olfactory cues from the nest to potential predators (Martin, 1993). In our study, the diameter of reed stems but not the density or height of vegetation influenced Marsh Harrier DSR. Nests built over deeper water, where reed stems were thicker, were less vulnerable to predation. The height of the vegetation was not a variable significantly improving brood success in Marsh Harrier; this factor has been proven significant, though mostly for populations of birds depredated by avian predators (Jedlikowski, Brzeziński & Chibowski, 2015; Polak 2016).

Comentado [.27]: this seems like a background to Introduction

The distances from nests to open water or the fishpond dyke were not significant. This finding is consistent with previous studies on this species (Stanevičius, 2004). It is well-known that ground-nesting birds, including Marsh Harrier, are particularly vulnerable to predation. Thus, obligate ground-nesters have evolved a method of placing their nests in well-concealed, evenly-spaced sites to reduce the likelihood of detection (Redmond, Keppie & Herzog, 1985). In addition, parental behaviour (nest defence) may compensate for any effects of insufficient nest cover (Lima & Dill 1990). Marsh Harriers are considered top avian predators of wetland habitats, actively defending their nests with alarm calls and physical attacks (Witkowski, 1989). Another possible explanation of our results is that concealment is more important for populations of birds depredated by avian predators than mammalian predators (Clark & Nudds, 1991). This may be because avian predators appear to see nests, whereas mammals depend mostly on olfactory cues (Guyn & Clark, 1997).

Water depth

A strong positive relationship between water depth and DSR has been observed in marsh-nesting birds, e.g. in American coots *Fulica americana* (Austin & Buhl, 2011), Eurasian Bittern (Polak, 2016) and Common Pochards *Aythya ferina* (Albrecht et al., 2006). In the present study, Marsh Harrier nests located at sites with deeper water exhibited the same trait. Such nests were particularly successful, because water presents a barrier to many mammalian predators (Koons & Rolleta, 2003). It is worth noting that the water level throughout the breeding season is not constant. Previous studies have shown that for wetland nesters, predation rates decreased with increasing water depth (Purger & Mészáros, 2006). On the other hand, water depth was not important for the DSR of either Little Crake *Porzana parva* or Water Rail *Rallus aquaticus*, as their main predators are mostly avian (Jedlikowski, Brzeziński & Chibowski, 2015). This pattern suggests that Marsh Harriers build their nests over deeper water because they are more susceptible to predation by mammals than by raptors. The relationship between low water level and mammalian predation was demonstrated in The Netherlands, where Red Fox was a frequent predator of Marsh Harrier nests in dry reedbeds (Dijkstra & Zijlstra, 1997).

During studies in eastern Poland thirty years ago, Buczek & Keller (1994) highlighted corvids and mustelids as being the main predators of Marsh Harrier nests on retention reservoirs (resembling mostly of neglected fishponds) and bogs, respectively. This was further explained by the low water level in bogs, decreasing in the course of the season, thus allowing reedbeds to be penetrated by mammalian predators. Since that study, predator and prey interactions could well have changed significantly, following the spread of non-native invasive predators such as American Mink. This has been confirmed by recent research, which links the declines of several waterbirds and semi-aquatic mammals with the colonization of Poland by Mink (Brzeziński et al., 2019). The occurrence of this invasive species may also be having an impact on Marsh Harrier, making it more vulnerable to mammalian predation. But to explain this possible shift, further studies will be needed to evaluate the causes of nest loss in Marsh Harrier in greater detail.

Comentado [.28]: Is water depth really a barrier for these predators? I find this point somewhat confusing.

CONCLUSIONS

Our study has shown that the daily survival rate of Marsh Harriers is influenced by both temporal and selected habitat variables. DSR is the highest at the beginning of the nesting season and decreases gradually with time (days in season) and nest age. A suggested reason for this temporal decrease in DSR could be that Marsh Harrier is not so well adapted to nesting in wetland environments as other species doing so, e.g. waterbirds. Water depth and the mean diameter of vegetation at the nest site were the habitat variables influencing Marsh Harrier DSR. This pattern might indicate that Marsh Harrier nests are more susceptible to mammalian than avian predators. Further studies are needed in order to better understand the accessibility of wetland birds' nests to terrestrial predators in the context of biological invasions.

Comentado [.29]: This should be discussed above.

Comentado [.30]: I can't find clarity at this point

ACKNOWLEDGEMENTS

We are grateful to Karol Bosek, Rafał Kuropieska, Daniel Paczóski, Marta Szaniawska, Kamil Kryński, Tomasz Pietrzak, Paweł Radzikowski, Monika Budzyńska and Cezary Sadowy for their help in carrying out the fieldwork. We would like to also thank Jay Rotella for helping with the statistical analyses.

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