The influence of predator type on the effectiveness of nest concealment as an anti-predatory strategy

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Abstract

Nest predation is the main cause of reproductive failure in birds. One strategy birds could adopt to reduce predation risk is to choose a well-concealed nest site. The "nest-concealment hypothesis" states that nests that are better concealed have a lower probability of being predated. However, there is no consistent support for this hypothesis. This might be because different predators use different cues to locate nests, with some predators relying on visual cues, and others use olfactory or auditory cues. Here, I studied whether the effectiveness of nest concealment depends on the predator's method of nest detection. Using an artificial nest experiment in a savannah ecosystem in southern Africa, I isolated the response of visual predators. Predation rates were lower in well-concealed nests than in unconcealed nests. In addition, I identified nest predators using camera traps at natural nests to monitor whether the same patterns were present under natural conditions. In natural nests, only one of three concealment variables, ground vegetation density, was significantly associated with reduced predation, particularly from visual predators. These findings suggest that the effectiveness of concealment depends on the predator community. This might explain why studies grouping all predation events together do not find support for the nest-concealment hypothesis. Moreover, in ecosystems with a high nest predator diversity, such as tropical regions, no single strategy might be effective against all predators. However, it might still be adaptive to select a nest site that limits detectability by one group of predators. For example, in an area with primarily visual predators, having a well-concealed nest might be an effective strategy to reduce predation risk. Overall, this study highlights the importance of identifying predators when studying nest predation patterns.

Keywords
artificial nests, nest concealment, nest predation, savannah, visual detection

Introduction

Predation is an important selective pressure, shaping behaviour and life histories of prey species. For birds, the reproductive phase is especially vulnerable to predation, as they are bound to one location: the nest. Nest predation is the most important cause of nest loss (Martin, 1992; Ricklefs, 1969), with approximately 70% of all nests lost to predation (Colombelli-Négrel & Kleindorfer, 2009). Nest predation is, therefore, an important factor in shaping avian life history traits and nesting behaviour (Lima, 2009; Martin, 1995, 2004; Ricklefs, 1969). The selective pressure on the evolution of strategies that lower the risk of nest predation is expected to be strong (Lima, 2009). One such strategy reproducing birds could adopt is selecting a safe nest site to avoid predation (Filliater *et al.*, 1994; Remeš, 2005).

Choosing a well-concealed nest site is one way in which birds could lower predation pressure (Collias & Collias, 1984; Martin, 1992). According to the "nest-concealment hypothesis", nests that are better concealed have a lower probability of being predated (Filliater *et al.*, 1994; Martin, 1993). This pattern has received much attention, but results are mixed. Some studies, including research on Audubon's hermit thrushes (*Catharus guttatus auduboni*; Martin & Roper, 1988) and Harris' Sparrows (*Zonotrichia querula*; Norment, 1993), report a positive relationship between nest concealment and survival. However, this relationship has not been supported in studies on hooded warblers (*Wilsonia citrina*; Howlett & Stutchbury, 1996), northern cardinals (*Cardinalis cardinalis*; Burhans & Thompson III, 1998, 2001; Filliater *et al.*, 1994), and song thrushes (*Turdus philomelos*; Götmark *et al.*, 1995). A review on the relationship between concealment and survival in open-cup nesting North American songbirds reported that only 26% of 106 studies found support for the nest-concealment hypothesis (Borgmann & Conway, 2015).

This inconsistency in the relationship between concealment and survival has puzzled many researchers, prompting them to explore additional mechanisms. For example, in song thrushes, concealment significantly increased survival in artificial nests, but there was no effect in natural nests (Götmark *et al.*, 1995). The authors argued that birds select for intermediately-concealed nest sites as a trade-off between concealment and visibility of the surroundings to be able to escape and avoid adult predation. Other studies suggest that parents can behaviourally compensate for poor nest concealment, through nest guarding or nest defence (e.g., Cresswell, 1997; Remeš, 2005). More recently, a growing number of studies have highlighted the importance of identifying the predator species, suggesting that the differences between predator species could underlie the mixed support for the nest-concealment hypothesis (e.g., Benson *et al.*, 2009; Ibáñez-Álamo *et al.*, 2015; Thompson III, 2007). Borgmann and Conway (2015) acknowledged that predator search strategy likely affects the importance of nest concealment but noted that most studies in their review did not identify the predators, therefore limiting them to test concealment effects across predator types. More broadly, studies on the relationship between concealment and survival usually group all predation events together, as often the predator species is not known. While this grouping could be appropriate for certain research aims, it could obscure predator-specific patterns, since different predators might use different cues to locate nests, and might therefore not be equally affected by concealment (Benson *et al.*, 2009; Colombelli-Négrel & Kleindorfer, 2009; Weidinger, 2002). For example, some predators rely on visual

search to detect the nest itself, directly, while other predators use auditory (e.g., begging of nestlings), olfactory (e.g., smell of faeces), or indirect visual cues (e.g., parental movement), or a combination of cues (e.g., Naguib *et al.*, 2024). Predators relying on visual search (hereafter: visual predators), such as corvids (Thompson III & Burhans, 2004), may be more affected by nest concealment than non-visual predators, such as snakes, many of which rely on olfactory cues to locate nests (Soanes *et al.*, 2015). Indeed, in a study on superb fairy-wrens (*Malurus cyaneus*), researchers found that visual predators predated only exposed artificial nests, not concealed ones, and that olfactory predators predated nests irrespective of their concealment (Colombelli-Négrel & Kleindorfer, 2009).

Although there is an increased recognition that identifying predators is important, most studies have been conducted in temperate regions, where predator communities are relatively simple, often consisting of only one or a few predator species (e.g., Benson *et al.*, 2009). Tropical regions, characterised by a higher predator diversity, with predators relying on different cues to locate nests (França *et al.*, 2009), remain understudied (Ibáñez-Álamo *et al.*, 2015; Lahti, 2009). Moreover, predator identity is frequently inferred by analysing cues left by predators at artificial nests, such as teeth marks in plasticine eggs (e.g., Colombelli-Négrel & Kleindorfer, 2009). However, the use of artificial nests should be treated with caution, as predator communities have been shown to differ between artificial and natural nests (Thompson III & Burhans, 2004). Nowadays, the use of cameras to capture predation events is more accessible and widespread, enabling a more reliable way of predator identification (Cox *et al.*, 2012).

Here, by considering predator identity, I aimed to study whether the effectiveness of nest concealment depends on the predator's mode of nest detection in savannah-living birds, exposed to multiple predator species in eSwatini, southern Africa. This relatively undisturbed area is characterised by very high nest predation rates of around 80-90%, and contains both visual predators (e.g., primates and certain bird species), and non-visual predators (e.g., snakes). I used two complementary approaches. Firstly, I used artificial nests to focus on predators that find the nest visually, as I predicted that only these predators are affected by nest concealment. The use of artificial nests has been criticised, as predation patterns have shown to differ between artificial and natural nests (Remeš, 2005; Thompson III & Burhans, 2004; Zanette, 2002). However, this difference is exactly what makes artificial nests interesting to use in this study. At artificial nests, parental movement, auditory cues, and olfactory cues are absent, meaning that predators relying on these cues to find nests (hereafter: non-visual predators) will likely not be able to find the artificial nests. Therefore, I predicted lower predation rates at well-concealed artificial nests, when focussing exclusively on predators that are able to find nests directly, using visual cues (visual predators).

Secondly, I monitored natural nests and used camera traps to identify the nest predators. This allowed me to test whether the patterns observed at artificial nests were also present under natural conditions. I assessed whether the relationship between concealment and survival differed between visual and non-visual predators. I predicted that concealment would reduce predation risk from visual predators, but that there is no relationship between concealment and survival for non-visual predators.

Methods

Study area

This study was conducted in the Mbuluzi Game Reserve in northeast eSwatini (26°09'S, 31°59'E), from mid-August to mid-December 2024 as part of a long-term monitoring project. We initially did fieldwork in an area of approximately 5 km^2 in the northern part of the reserve. Later in the fieldwork season, when we monitored many active nests, we primarily focussed on a core area of approximately 3 km^2, within the initial area. The climate of eSwatini is subtropical, with most of the rain falling in the summer (October to March) (Matondo *et al.*, 2005). Mbuluzi Game Reserve is characterised by savannah and woodland vegetation and hosts a wide variety of bird species.

Nest searching and monitoring

A team of students and fieldwork assistants searched for nests of various bird species (Table A1, Appendix). The breeding season runs from September to January. We performed systematic transect surveys to find nests, with walked transects approximately 30 metres apart. Upon finding a nest, we marked the nest location with a GPS device (Garmin eTrex 32x) and recorded the species and nest-site characteristics: nest contents, nest height (estimated), nesting tree height (estimated), nesting tree species, and a short description of the nest.

We observed nests approximately every four days to monitor the contents, until the nests fledged or failed. A nest was considered predated when (1) the nest was empty at a nest check, and the nestlings were too young to have fledged; (2) we recorded the predation event on camera; or (3) there were signs of predation, such as the nest being destroyed. A nest was considered successful when at least one nestling fledged. We assumed a nest to have fledged when nestlings were close to fledging age and when they were not observed at a subsequent nest observation, or when we recorded the fledging event on camera. A nest was considered abandoned when eggs were cold at multiple consecutive nest checks and did not hatch, or when nestlings were dead without signs of predation. When walking transects, we noted down predator sightings and vocalisations, as an estimate for predator density in the different areas of the reserve. However, considering these data was beyond the scope of this research project.

Predator identification

To identify predators and to record nesting behaviour at natural nests, we placed motion-triggered cameras (Wilsus Tradenda 4G Wireless) at active nests once they contained eggs or nestlings, until nests fledged or failed. We placed cameras at a distance of approximately 0.5 to 1.5 metres away from the nest, either attached to a nearby tree with a strap or a Gorillapod (a small tripod with bendable legs), or placed on a tripod on the ground. Cameras were powered by batteries and a solar panel, and when triggered they took a photo and recorded a 25 s video. At each nest check we checked the battery level of the camera and SD storage space.

We used 26 cameras, relocating each to another active nest when the previous nest fledged or failed. Initially, we put cameras at all active nests containing eggs or nestlings, but when there were more active nests than cameras, we prioritised nests in the core area and those where we could measure concealment (see below). At dark-capped bulbul (*Pycnonotus tricolor*) nests we never placed motion-triggered cameras,

as in previous years this was suspected to lead to nest abandonment. Four predation events were recorded with other cameras used for other projects. We analysed the camera footage from each day to record nest fate and, when the nest was predated, predator identity. In all but one recorded predation events, the predator was identified. In that single case, it was not possible to distinguish between a female boomslang (*Dispholidus typus*) and a black mamba (*Dendroaspis polylepis*).

To test whether the effectiveness of nest concealment depends on the predator's mode of detection, I categorised predators recorded in 2024 into the predator type 'visual' or 'non-visual'. This distinction is, however, a simplification. Ideally, the influence of concealment and other factors would be analysed separately for each predator species, to account for their specific ecology, as demonstrated in previous studies (Benson *et al.*, 2009; Phringphroh *et al.*, 2024). However, in a study area with a wide variety of predators, such as this one, such an approach is not feasible due to sample size limitations. Therefore, I categorised predators based on their primary sensory searching strategy, as a broad indication of their ecology. If a predator could find artificial nests (see below), it was placed into the 'visual' category (thus 'visual predators'). This means that the predator could find the nest directly, by searching for the nest itself, without needing other cues, such as parental movement, or auditory or olfactory cues. Predator species that did not find artificial nests were categorised as 'non-visual' (thus 'non-visual predators'), except for the red-backed shrike (*Lanius collurio*), because this predator finds nests visually (Birds of the World, 2020).

Concealment of nests

When possible, we measured three additional nest site vegetation characteristics indicating how well the nest is concealed: (1) eye level nest concealment (measure for concealment of the nest itself); (2) ground vegetation density (measure for concealment from the ground); (2) canopy cover (measure for overhead nest concealment). We measured eye level nest concealment by placing a red ball with a 15 cm diameter in the nest and scoring what percentage of the ball was visible, to the nearest 5%, at the four cardinal directions (N, E, S, W). We scored this by observing from eye level at 0.5 m and 1.5 m from the nesting tree. We measured ground vegetation density by placing the ball on the ground at 3 m from the nesting tree and scoring what percentage of the ball was visible, to the nearest 5%, at the four cardinal directions, with our backs facing the nesting tree. We used a spherical densiometer with a concave mirror (Model-C) to estimate the percentage of canopy cover. We measured this from the nesting tree at the four cardinal directions, with our backs facing the nesting tree. For all three concealment variables, we calculated an average score by averaging the values from the four cardinal directions. For eye level nest concealment, we additionally averaged the 0.5 m and 1.5 m measurements. The eye level nest concealment and ground vegetation density variables were transformed by calculating 100 minus the original value, so that for all three concealment variables a higher value meant that the nest was better concealed.

Two observers with a height difference of 3 cm, and thus similar eye level, measured the concealment variables. At 12 nests, both observers measured all concealment variables to test for inter-observer repeatability. The intraclass correlation coefficient was 0.977, meaning that there was no significant difference between measurements of the observers ($P < 0.001$; Wolak *et al.*, 2011). We aimed for measuring concealment within a week after nests fledged or failed, to score the concealment before

the vegetation around the nest changed substantially (Burhans & Thompson III, 1998; Vega Rivera *et al.*, 2009). In December, we measured concealment at active nests, after carefully removing the eggs or chicks from the nest.

Due to height limitations, we were not able to measure concealment at all nests. By using a small step ladder, we could reach nests up to approximately 2.3 m. At speckled mousebird (*Colius striatus*) and dark-capped bulbul nests we occasionally used a larger ladder to reach nests up to 4.0 m. Additionally, we did not measure concealment for cavity or ground nesting species. We measured concealment for species with open-cup nests, platform nests, pouches, pendulous nests and domes. At open-cup and platform nests, we placed the ball on top of the nest. For other nest types, we hung the ball as close to the nest as possible and scored the parts of the nest that covered the red ball as if they were part of the ball (i.e., a higher percentage of the ball being visible). Ultimately, we measured concealment at 65% of the active nests (173 of 266 nests).

Artificial nests

To exclude predators that use cues such as parental movement, or auditory or olfactory cues to find nests, we performed an artificial nest experiment. We made artificial nests using dead grass collected in the reserve, producing nests with a diameter of approximately 10 cm. To reduce human scent, we placed the nests into the field at least 24 hours before we placed eggs in them. We placed nests in trees or shrubs at a height between 1.05 m and 2.10 m (median = 1.48 m), which is slightly lower than the nest height of most natural nests (median = 2.00 m). This was done to ensure easy accessibility for placement and monitoring. In each nest, we placed one common quail (*Coturnix coturnix*) egg, commonly used in artificial nest studies (Major & Kendall, 1996). Prior to handling eggs, we rubbed our hands in leaf litter to reduce human scent. We placed 20 artificial nests at a time, with a distance of at least 30 metres between them.

In total, there were three rounds, each round in a different area in the reserve, leading to a total of 60 artificial nests. Each round, ten nests were placed in 'concealed' locations, and ten in 'unconcealed' locations. We measured concealment of artificial nests the same way as for natural nests. Concealed nests had high concealment values for all three concealment variables (eye level nest concealment, ground vegetation density, and canopy cover), unconcealed nests had low values. Consequently, for artificial nests, the three concealment variables were correlated ($r > 0.5$). Because of the study design, the nests could be split in two groups: concealed nests and unconcealed nests. This split was made based on eye level nest concealment, with nests with an eye level nest concealment value above or equal to 45% receiving the concealment label 'concealed' and nests having an eye level nest concealment value below 45% receiving the concealment label 'unconcealed'. This led to 29 'concealed' (48.1–98.1% eye level nest concealment) and 31 'unconcealed' (6.3–30.6% eye level nest concealment) nests.

At each nest, we placed Moultrie M-40 trail motion-triggered cameras (model MCG-13181), taking a photo and a 10 s video when triggered. We checked for nest fate, camera battery level and SD storage space approximately once every four days (ranging from two to seven days between nest checks), until the egg disappeared, or until two weeks passed. When the egg and/or nest disappeared due to a storm, we replaced it with a new egg and/or nest.

I analysed camera footage from each day, using the same approach as for recordings of the natural nests. I considered a nest to be predated when the egg was

damaged or missing at the next nest check, without video footage showing the egg or nest blowing away due to the wind, or when a predator was recorded on the video footage. When a predator species was recorded, the nest was considered predated when the predator was eating the egg, but also when the predator attacked the egg but was unsuccessful in breaking the shell, and when the predator was closely inspecting the egg. Black-backed puffbacks (*Dryoscopus cubla*) and southern boubous (*Laniarius ferrugineus*) often inspected the egg, but because they also attacked eggs on camera, and because the camera recordings sometimes missed predation events, all the times I spotted a black-backed puffback or southern boubou near the nest on camera I labelled it as a predation event.

Statistical analyses

All statistical analyses were performed in R 4.4.3 (R Core Team, 2025). Since I focus on differences in survival due to differences in predation risk, I excluded abandoned nests (n = 4) and nests for which we could not determine the fate (n = 3) in the analyses.

To determine how different explanatory variables influence nest survival, I estimated daily survival rate (DSR). DSR is the probability of a nest surviving to the next day. DSR is recognised as a better estimate of nest survival than apparent nest success, i.e., the percentage of successful nests, because apparent nest success does not account for exposure time. Successful nests are observed for longer, leading to an overestimation of nest survival with apparent nest success (Brown *et al.*, 2013; Mayfield, 1961; Shaffer, 2004).

I used Shaffer's (2004) logistic-exposure models to estimate DSRs, which allow for the modelling of the influence of both continuous and categorical variables on survival, the former not being possible using Mayfield's (1961) method. I used the *glmer* function from the *lme4* package (Bates *et al.*, 2015) to run Generalised Linear Mixed Models with a binomial response distribution and a logit link function modified according to Shaffer (2004), to account for differences in exposure days and the stages at which nests are found. The response variable was survival of the nest at each nest check, with 1 = nest survived and 0 = nest failed. Explanatory variables were concealment variables, continuous for natural nests, categorical ('concealed' or 'unconcealed') for artificial nests. I included nest ID as random effect, to account for the multiple nest checks per nest.

Following Shaffer's (2004) methods to estimate DSRs, I used the coefficients from the best model, i.e., the model with the lowest Akaike Information Criterion corrected for small sample sizes (AICc; Burnham & Anderson, 2002), in the formula:

$$\mathrm{DSR} = \frac{e^{\beta_0 + \sum_{i=1}^{n} \beta_i x_i}}{1 + e^{\beta_0 + \sum_{i=1}^{n} \beta_i x_i}}$$

With DSR = daily survival rate, β_0 = intercept, β_i = slope variable of each explanatory variable, x_i = each value of the i-th explanatory variable, n = number of explanatory variables. To assess how DSR varied with specific explanatory variables, predicted DSR values were generated across a continuous range of values for the variable of interest, while keeping all other variables fixed at their mean values. I calculated the probability of a nest surviving the whole nesting period by raising DSR to the power of the duration of the whole nesting period (Mayfield, 1961).

For artificial nests, I compared the null model, which predicts the daily survival rate to be constant across all nests, with the model with concealment label ('concealed' or 'unconcealed') as explanatory variable.

For natural nests, there was no correlation between the three concealment variables. I used automated model selection with the *dredge* function from the *MuMIn* package (Bartoń, 2025). The model with a combination of fixed effects that has the lowest AICc is regarded as the best model (Burham & Anderson, 2002). In total there were eight models for estimating the effect of concealment on survival – the null model, the full model, with the three concealment variables as fixed effects, and six models with different combinations of one or two of the concealment variables as fixed effects. I first tested whether there is a general relationship between concealment and survival in natural nests, by taking all successful and predated nests. To determine whether concealment was related to survival differently for different predators, I made two subsets of the data, one including nests predated by visual predators and fledged nests, and one including nests predated by non-visual predators and fledged nests. Additionally, I tested for an interaction effect between ground vegetation density and predator type (visual or non-visual predator). Here, I excluded four avian predators that are likely not influenced by ground vegetation density (African goshawk, red-backed shrike, southern boubou, and Wahlberg's eagle).

Results

Artificial nests

Of 60 artificial nests, 35 nests (58%) were predated, with a total of 51 predation events (16 at concealed nests, 35 at unconcealed nests). For 32 predation events the predator was identified on video, of which 12 at concealed nests and 20 at unconcealed nests (Table A2, Appendix).

The logistic-exposure model with concealment label ('concealed' or 'unconcealed') as explanatory variable was better than the null model (ΔAICc = 4.8). Unconcealed nests had a lower DSR than concealed nests ($\beta = -1.02$, SE = 0.39, $z = -2.60$, $P = 0.009$, Fig. 1). The predicted DSR for concealed nests was 0.959 ± 0.010 (95% CI: 0.940–0.978), giving a probability of 0.55 (55%) that nests survive for 14 days, which is approximately the incubation period of the bird species we monitored in the Mbuluzi Game Reserve. The predicted DSR for unconcealed nests was 0.894 ± 0.026 (95% CI: 0.843–0.945), giving a probability of 0.21 (21%) that nests survive for 14 days.

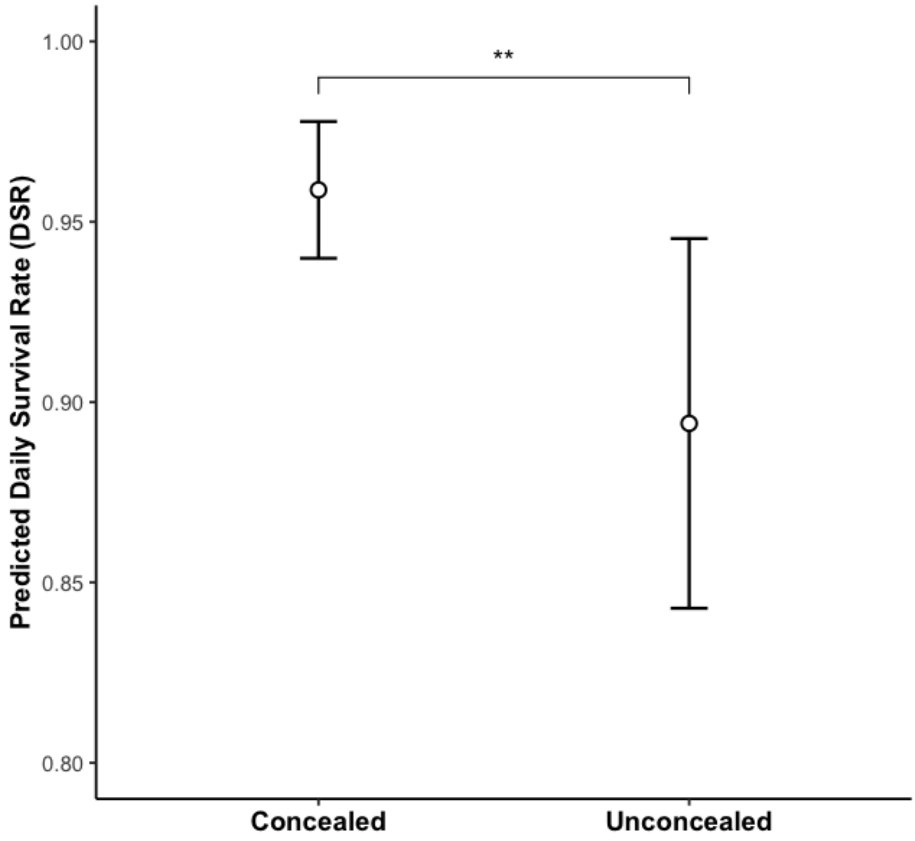

Fig. 1. Daily Survival Rate (DSR) (predicted values with 95% CI) of concealed ($n = 29$) and unconcealed ($n = 31$) artificial nests. ** indicates $P < 0.001$.

Natural nests

Of the 173 nests where we measured concealment, 30 nests (17%) fledged at least one young, 136 nests (78%) were predated, 4 nests (2%) were abandoned, and for 3 (2%) nests the nest fate was unknown.

The highest-ranked logistic-exposure model for the 166 nests that were either successful or failed due to predation included both eye level nest concealment and ground vegetation density as explanatory variables (Table 1). Only ground vegetation density had a significant effect: an increase in ground vegetation density was associated with a higher DSR ($\beta = 0.010$, SE = 0.004, $z = 2.45$, $P = 0.015$, Fig. 2). Eye level nest concealment was not significantly associated with survival ($\beta = 0.007$, SE = 0.005, $z = 1.50$, $P = 0.134$).

Table 1. Model selection of logistic-exposure models predicting daily survival rate (on 166 natural nests in 2024). Fixed effects: three uncorrelated concealment measurements (ground: ground vegetation density, eye nest concealment: eye level concealment of the nest, canopy: canopy cover). Random effect: nest ID.

Model	***K***	***AICc***	***ΔAICc***	w_i
ground + eye level nest concealment	3	699.7	0.00	0.324
ground	2	699.9	0.20	0.292
ground + canopy	3	701.6	1.87	0.127
full model (ground + eye level nest concealment + canopy)	4	701.7	1.99	0.119
null model	1	703.3	3.58	0.054
eye level nest concealment	2	703.7	3.96	0.045
canopy	2	705.1	5.34	0.022
eye level nest concealment + canopy	3	705.7	5.94	0.017

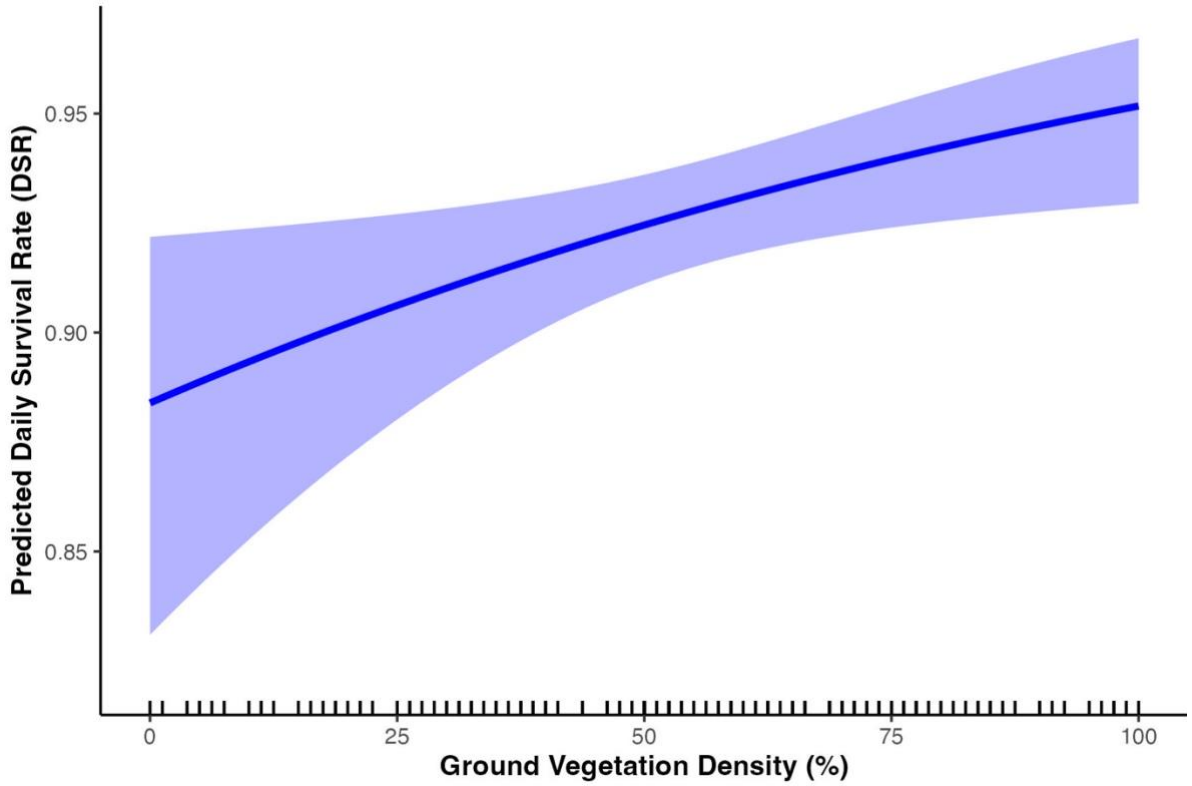

Fig. 2. Daily Survival Rate (DSR) (with 95% CI) related to ground vegetation density, predicted by the best logistic-exposure model (with ground vegetation density and eye level nest concealment), setting eye level nest concealment to its mean. Lines along the x-axis represent the distribution of observed ground vegetation density values.

Predator species were identified for 33 predation events (Table A3, Appendix), with 14 predation events by visual predators and 19 predation events by non-visual predators. In a logistic-exposure model with 44 nests that were successful or were predated by visual predators, the highest-ranked model contained the explanatory variables ground vegetation density and eye level nest concealment (Table 2). Ground vegetation density was positively associated with survival ($\beta = 0.047$, SE = 0.018, $z = 2.59$, $P = 0.010$, Fig. 3). Eye level nest concealment was not associated with survival ($\beta = 0.031$, SE = 0.020, $z = 1.57$, $P = 0.117$).

Model selection on GLMMs with successful nests and nests predated by non-visual predators led to a highest-ranked model with only ground vegetation density as explanatory variable (Table 3). Ground vegetation density was positively associated with survival ($\beta = 0.021$, SE = 0.011, $z = 2.00$, $P = 0.046$), meaning that the probability of a nest surviving increased with higher ground vegetation density (Fig. 3).

The effect of ground vegetation density on DSR was stronger on nests predated by visual predators than on nests predated by non-visual predators. The difference in DSR between the minimum (1.25%) and maximum (98.8%) ground vegetation density was 0.12 and 0.06, respectively (Fig. 3). This interaction between ground vegetation density and predator type (visual and non-visual) was marginally significant ($\beta = 0.043$, SE = 0.023, $z = 1.90$, $P = 0.058$), when analysing DSR of only nests with identified predator.

Table 2: Model selection of logistic-exposure models predicting daily survival rate for nests predated by visual predators ($n = 14$) and fledged nests ($n = 30$). Fixed effects: three uncorrelated concealment measurements (ground: ground vegetation density, eye level nest concealment: eye level concealment of the nest, canopy: canopy cover). Random effect: nest ID.

Model	***K***	***AICc***	***ΔAICc***	***weight***
ground + eye level nest concealment	3	115.5	0.00	0.349
ground	2	116.0	0.51	0.270
ground + canopy	3	116.5	1.01	0.210
full model (ground + eye level nest concealment + canopy)	4	117.4	1.88	0.137
canopy	2	122.4	6.87	0.011
eye level nest concealment	2	122.9	7.44	0.008
null model	1	122.9	7.45	0.008
eye level nest concealment + canopy	3	124.0	8.47	0.005

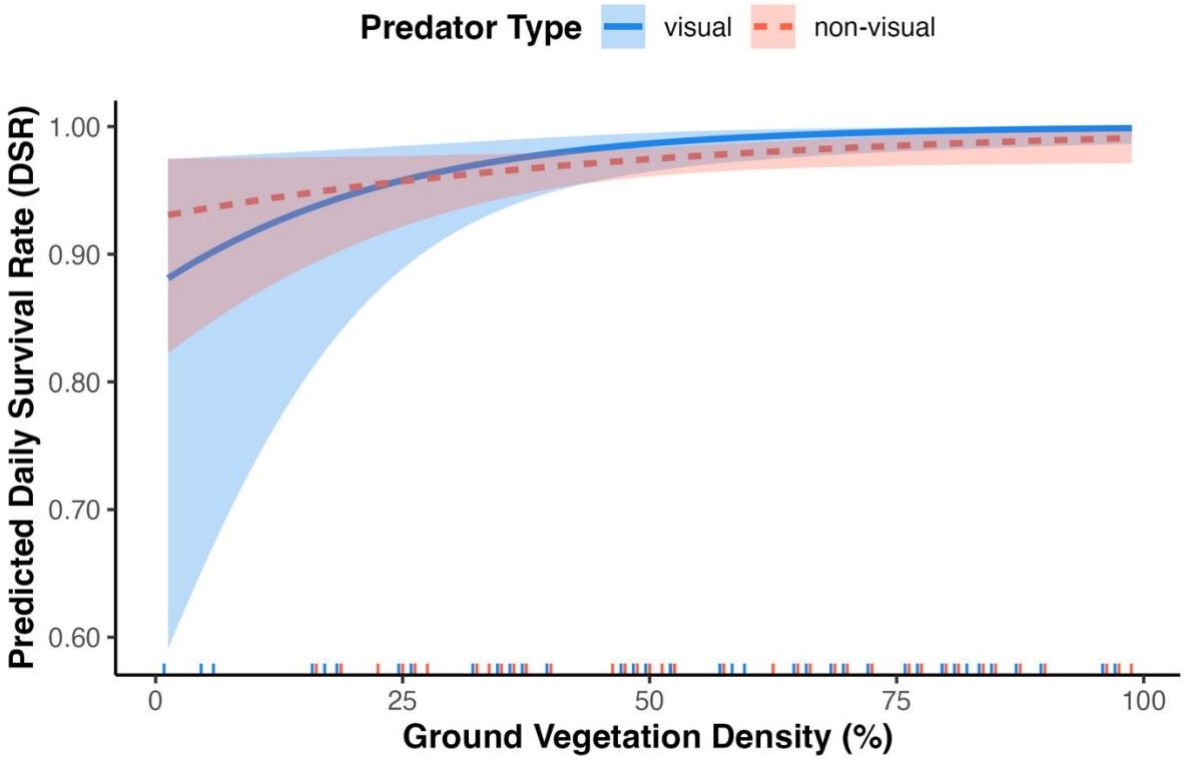

Fig. 3. Daily Survival Rate (DSR) (with 95% CI) related to ground vegetation density, predicted by the best logistic-exposure model. For 'visual' (blue, solid) this is with ground vegetation density and eye level nest concealment, setting eye level nest concealment to its mean. For 'non-visual' (red, dashed) this is with only ground vegetation density. Lines along the x-axis represent the distribution of observed ground vegetation density values.

Table 3: Model selection of logistic-exposure models predicting daily survival rate for nests predated by non-visual predators (*n* = 19) and fledged nests (*n* = 30). Fixed effects: three uncorrelated concealment measurements (ground: ground vegetation density, eye level nest concealment: eye level concealment of the nest, canopy: canopy cover). Random effect: nest ID.

Model	***K***	***AICc***	***ΔAICc***	***weight***
ground	2	168.4	0.00	0.364
ground + canopy	3	169.7	1.21	0.199
ground + eye level nest concealment	3	170.5	2.02	0.132
null model	1	170.6	2.18	0.122
full model (ground + eye level nest concealment + canopy)	4	171.7	3.27	0.071
canopy	2	172.5	4.04	0.048
eye level nest concealment	2	172.6	4.20	0.045
eye level nest concealment + canopy	3	174.5	6.02	0.018

Discussion

In this study, I investigated whether the effectiveness of nest concealment as an anti-predatory strategy depends on the predator's mode of nest detection. The results demonstrate that in artificial nests, aimed to exclude non-visual predators and thus filtering for the response of visual predators, there was a significant relationship between nest concealment and predation. This suggests that concealment reduces the predation risk from visual predators. However, this pattern was less clear in natural nests, where a broader range of predators was present. Out of three uncorrelated concealment variables – eye level nest concealment, canopy cover, and ground vegetation density – only ground vegetation density was significantly positively associated with survival. This relationship was significant when grouping all predators together, and when separately analysing the two predator types. These findings suggest that ground vegetation density might reduce predation risk across a variety of predators, though the effect is potentially stronger for visual predators.

In the artificial nest experiment, designed to investigate the response of visual predators, I found a clear association between concealment and predation. Concealed nests had a higher DSR than unconcealed nests. This finding supports my hypothesis that visual predators are restricted in their ability to find well-concealed nests. This is in line with findings by Colombelli-Négrel and Kleindorfer (2009), who detected visual predators (avian predators, such as currawongs) only at exposed and not at concealed artificial nests. My results provide support for the nest-concealment hypothesis, which predicts that nests that are better concealed have a lower probability of being predated (Filliater *et al.*, 1994; Martin, 1993). Support for this hypothesis has been limited (Borgmann & Conway, 2015). However, by using artificial nests, confounding factors such as parental behaviour could be excluded. The artificial nest experiment, therefore, appears as a suitable method to test whether concealment limits the transmission of visual cues, thereby decreasing the probability of detection by visual predators. Similarly to Thompson III & Burhans (2004), I showed here that the main predator species differed between natural and artificial nests (Table A4, Appendix, showing an overview of predator species identified over three breeding seasons), indicating that results from the artificial nest experiment should be interpreted with caution when extrapolating them to natural conditions. Yet, the results from the artificial nest experiment suggest that concealment matters for visual predators: nests that are more concealed appear to have a lower probability of being predated by visual predators.

In addition to the artificial nest experiment, I examined natural nests to discover if the same pattern holds in more complex conditions. I expected to only find support for the nest-concealment hypothesis when excluding non-visual predators from the analysis. In contrast to my predictions, in a pooled analysis with all predators, ground vegetation density emerged as a significant predictor of survival. Previous studies have suggested that the lack of a clear relationship between concealment and nest survival might result from grouping all predator species together (e.g., Benson *et al.*, 2009; Colombelli-Négrel & Kleindorfer, 2009; Weidinger, 2002). I anticipated a similar outcome, expecting that the inclusion of non-visual predators would obscure any effect of concealment. My findings can be interpreted in multiple ways. One possibility is that dense ground vegetation limits the detection of nests by both visual and non-visual predators, for example by physically reducing their mobility and, therefore, accessibility

to nests (Colombelli-Négrel & Kleindorfer, 2009; Martin, 1993; Seibold *et al.*, 2013), or by reducing the transmission of all cues predators can use to locate nests, as suggested by Martin (1993). Alternatively, if visual predators are responsible for most predation events, they could disproportionally drive the overall pattern. Benson *et al.* (2009) reported that the significant relationship between concealment and survival they found in natural nests could be explained by them having primarily visual predators in their study system. Having only identified the predator species at 33 predation events in this study, out of 136 predated nests, it is hard to tell whether visual predators predominated. However, out of the 33 identified predators, 14 were visual, 19 were non-visual. Assuming an equal chance of recording both predator types, this suggests that visual predators did not predominate.

Instead, in contrast to my predictions, results from separate analyses on visual and non-visual predators indicate that ground vegetation density affects both predator types. These findings support the former explanation that both visual and non-visual predators are limited in their ability to detect nests with denser ground vegetation. However, although the interaction between predator type and ground vegetation density was marginally non-significant, it nevertheless suggests a potential trend indicating that visual predators might be more sensitive to changes in ground vegetation density than non-visual predators. This would align with my original hypothesis that concealment, here in the form of ground vegetation density, limits visual predators in their ability to find nests. Further research with larger samples sizes could continue investigating this pattern.

Surprisingly, only ground vegetation density was significantly associated with survival. Canopy cover is low in savannah ecosystems, such as our study area, offering little variation upon which selection can act. Moreover, canopy cover will likely only affect predators that view the nest from above, such as raptors. Benson *et al.* (2009) showed decreasing nest predation by raptors with increasing canopy cover. Given the limited role of raptors in our study area, responsible for approximately 6% of the nest predations (Table A4, Appendix), the absence of a relationship between canopy cover and survival is to be expected. When studying the relationship between concealment and survival, concealment is often measured from the eye level of the observer. While practical, it also brings its limitations, as no predator has the same eye level as the observer. As a result, measuring concealment from the observer's eye level might not accurately reflect how predators perceive nests (Hancock *et al.*, 2023). Nevertheless, measuring from eye level provides a consistent method, reproducible across nests, sites, and studies. However, in open or semi-open habitats, such as savannah ecosystems, visual detection of the nest might not be blocked by vegetation directly surrounding the nest, as captured by eye level nest concealment, but rather by ground vegetation. This, combined with the fact that most predators in our study system approach from the ground, could explain why only ground vegetation density was significantly associated with survival in this study. In different regions with different predator assemblages, other nest-site characteristics might be more important in limiting detectability and accessibility of nests to predators (Phringphroh *et al.*, 2024). For example, in Hawaiian Oʻahu ʻelepaio (*Chasiempis ibidis*), higher nests reduce predation by invasive rats (Vanderwerf, 2012). However, another study reported that in their study area, no nest height was safe, as each height was accessible to different predator species (Kleindorfer *et al.*, 2021). It would be interesting to investigate whether birds are able to assess, in ecological time, which predators are

present, and select nest sites to reduce predation risk from the dominant predator type in the area.

The absence of a relationship between eye level nest concealment and survival could also reflect the complexity of natural nests. In the artificial nest experiment, it was possible to isolate the relationship between concealment and survival, whereas in natural nests, other processes could play a role. For example, instead of selecting well-concealed nest sites, birds might build camouflaged nests to reduce detectability (Mulder *et al.*, 2021), or compensate behaviourally for poor concealment (Lima, 2009), through nest defence and nest guarding (Cresswell, 1997; Remeš, 2005). Moreover, nest-site selection is not solely influenced by predation, but influenced by many other factors, such as microclimate (Marzluff, 1988; Wiebe & Martin, 1998) or food availability (Ucero *et al.*, 2024). Furthermore, well-concealed nest-sites might be scarce, as we experienced ourselves when searching for concealed sites to place artificial nests. Additionally, concealment is only one aspect of nest-site selection that might reduce nest predation (Vazquez *et al.*, 2021). To minimise the availability of cues that predators might use to locate nests, both parents and offspring might adopt behavioural adaptations, such as altered begging calls in high predation risk areas (Briskie *et al.*, 1999) or reduced parental nest visits (Ghalambor & Martin, 2002). However, compensatory behaviours can be energetically costly (Remeš, 2005) or expose birds to other risks. In areas with a diverse predator community, no single strategy decreases vulnerability to all predator species (Colombelli-Négrel & Kleindorfer, 2009). In natural nests, I found that ground vegetation density was associated with reduced predation risk, particularly from visual predators. These results should, however, be treated with caution when making implications for management. In different ecosystems, different processes could play a role in predator-prey dynamics, and what might prove effective in one system might not be reflected in another. Savannah ecosystems are understudied (Ibáñez-Álamo *et al.*, 2015), and with their rich guild of nest predators it is difficult to draw broad conclusions. In environments with many different predators, protection against one predator may not lead to better survival, as any nest not predated by one predator will remain for other predators and thus may have increased probability of being predated by others. Further research, especially within ecosystems with multiple predators, is needed to untangle the complex interplay of factors influencing nest predation.

Conclusion

Here, I showed that concealment reduces predation, but that its effectiveness depends on who is hunting. Results from the artificial nest experiment show that visual predators are clearly affected by concealment. In natural nests, ground vegetation density seems to protect nests against predation by all predators, but particularly by visual predators. Therefore, I propose a redefinition of the traditional nest-concealment hypothesis: nests that are better concealed have a lower probability of being predated, by visual predators. This more nuanced view acknowledges that concealment is not universally protective, but that reducing the availability of cues used by one group of predators can still lower the overall predation risk. Ultimately, this study highlights the importance of taking predator identity and ecology into account when analysing nest predation patterns. Future studies could investigate whether birds adjust their nest-site selection in response to seasonal variation in predator communities, as they might select for nest sites that minimise detection by the most prevalent predator type at that time.

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Artificial Intelligence statement

Artificial Intelligence was used to help with R coding errors. No generative AI was used to generate text.

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Appendix

Monitored bird species

Table A1. Number of nests per bird species that fledged or failed and for which nest concealment was measured.

Species	***number of nests***
African paradise flycatcher	2
Arrow-marked babbler	17
Black-crowned tchagra	18
Brimstone canary	3
Brown-crowned tchagra	15
Chinspot batis	1
Collared dove	1
Dark-capped bulbul	39
Dove *sp*.	1
Emerald spotted wood dove	2
Golden-breasted bunting	4
Gorgeous bushshrike	1
Long-billed crombec	5
Pale flycatcher	1
Purple banded sunbird	2
Red-faced mousebird	1
Sombre greenbul	2
Southern boubou	1
Speckled mousebird	15
Tawny flanked prinia	4
White-bellied sunbird	27
White-browed scrub-robin	1
White-crested helmetshrike	1
Yellow-breasted apalis	1
Yellow-fronted canary	1

Predator species at artificial nests

Table A2. Number of predation events per predator species at concealed and unconcealed artificial nests.

	Nest concealment	
Predator	***concealed***	***unconcealed***
Southern boubou	6	1
Grey-headed bushshrike	3	5
Black-backed puffback	2	9
Unidentified mouse	1	0
Common slender mongoose	0	1
Pin-tailed whydah	0	1
Vervet monkey	0	3
Total	12	20

Predator species at natural nests in 2024

Table A3. Number of predation events per predator species at natural nests in 2024.

Predator species	**n**
Vervet monkey	7
Burchell's coucal	6
Boomslang	3
African goshawk	2
Black mamba	2
Common egg eater	2
Genet	2
Mongoose	2
Southern boubou	2
Wahlberg's eagle	1
Baboon	1
Black mamba / Boomslang	1
Grey-headed bushshrike	1
Red-backed shrike	1

Predator species at natural nests in 2022-2024

Over three breeding seasons (2022-2024), we identified 26 predator species at 155 predation events at natural nests. Vervet monkeys (*Chlorocebus pygerythrus*) were responsible for the most predation events ($n = 30$), followed by Burchell's coucals (*Centropus burchellii*, $n = 28$), boomslangs (*Dispholidus typus*, $n = 18$), grey-headed bushshrikes (*Malaconotus blanchoti*, $n = 14$), and rusty-spotted genets (*Genetta maculata*, $n = 9$). All other predator species were responsible for less predation events (Table A4).

Table A4. Number of predation events per predator species at natural nests (2022-2024) in nestling stage and egg stage, and at artificial nests (2024).

		natural		***artificial***
Predator	***egg***	***nestling***	***total***	
African goshawk	1	3	4	0
African harrier-hawk	0	2	2	0
Black mamba	0	6	6	0
Black-backed puffback	0	0	0	11
Boomslang	7	11	18	0
Burchell's coucal	24	4	28	0
Chacma baboon	1	0	1	0
Common egg-eater	8	0	8	0
Common slender mongoose	2	1	3	1
Crowned hornbill	0	1	1	0
Grey-headed bushshrike	11	3	14	8
Klaas's cuckoo	0	1	1	0
Mozambique spitting cobra	3	5	8	0
Pin-tailed whydah	1	0	1	1
Red-backed shrike	0	1	1	0
Red-chested cuckoo	1	0	1	0
Rusty-spotted genet	6	3	9	0
Side-striped jackal	1	1	2	0
Snouted cobra	1	0	1	0
Southern boubou	3	0	3	7
Thick-tailed bushbaby	1	0	1	0
Tiger snake	3	0	3	0
Unidentified mouse	0	0	0	1
Unidentified snake	3	1	4	0
Vervet monkey	21	9	30	3
Vine snake	1	0	1	0
Wahlberg's eagle	0	3	3	0
Yellow-billed kite	0	1	1	0
Total	99	56	155	32