Factors influencing nest predation across multiple species in an African savannah ecosystem

Linda Verhoeven (1032340)

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Supervisors: Andries Janse van Vuuren, Sjouke Kingma & Marc Naguib

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Abstract:

Nest predation is the main cause of nest failure in birds and is therefore an important determinant of reproductive success. Birds can respond in several ways to reduce nest predation, and those responses could be related to behaviour, nest-site selection and timing of breeding. However, the factors that influence nest predation may vary across habitats, and not much is known about what affects nest predation in African savannah habitats. This study aimed to identify which factors influence nest predation across multiple species in this understudied region. I analysed both nest-site and temporal factors. Nest-site factors included multiple concealment variables, nest height, and whether an area had been recently burned. Temporal factors included timing of breeding and nest stage. I used data from monitored bird nests and analysed nest survival using daily survival rates. Of all factors considered, only ground vegetation density showed a significant effect on daily survival rate, suggesting that increased ground vegetation density is associated with lower predation risk. This may be explained by reduced detectability and accessibility of nests by predators caused by increased ground vegetation. Different predator types and their behaviour, as well as species-specific anti-predatory strategies used by birds, may explain the lack of significant effects of the other variables on nest survival. Further research focusing on predator types or on specific bird species may be valuable for explaining nest predation patterns. Overall, these findings could have implications for conservation and management strategies used in African savannah habitats, since changes in ground vegetation could influence predator-prey dynamics and consequently affect breeding success of multiple bird species.

Keywords: daily survival rate, nest predation, nest-site variables, savannah ecosystem, temporal variables

Introduction

Nest predation is an important selective pressure that can influence breeding ecology and life history characteristics of birds (Martin, 1995). Nest predation is the primary cause of nest failure in birds, accounting for up to 80% of nest losses (Ricklefs, 1969; Martin, 1993). The nest stage is a critical stage in the life of birds, since eggs and nestlings are bound to a specific location (Ibáñez-Álamo *et al.,* 2015). Being immobile during the egg stage, and as nestlings being limited in the ability to defend themselves or to flee, makes offspring vulnerable to predation. Therefore, several anti-predator strategies have evolved to limit nest predation, and in this way increase reproductive success of birds.

The adaptive responses to predation can vary considerably across species (Lima, 2009). Some species rely on camouflage to reduce the chances that predators find their nest. For example, ground nesting birds such as nightjars lay eggs with cryptic coloration (Kilner, 2006) and make use of camouflaged plumage of the incubating adult to avoid nest predation (Troscianko *et al.*, 2016). Other birds use specific nest defence behaviours to deter or distract predators. Examples are aggressive behaviours, such as mobbing or attacking predators, or deceptive behaviours such as broken-wing displays (Montgomerie & Weatherhead, 1988; Smith & Edwards, 2018). There are also species that use the aggressive or defensive behaviours of other species to their advantage by nesting in association with them (Quinn & Ueta, 2008). For instance, choughs (*Pyrrhocorax pyrrhocorax*) nesting inside lesser kestrel (*Falco naumanni*) colonies, had higher breeding success, in terms of a lower percentage of failed nests, compared to coughs nesting outside of these colonies (Blanco & Tella, 1997). This example touches upon the concept of nest-site selection. Deciding where to place the nest could be one example of a proactive response (Lima, 2009) that birds can use to reduce the risk of nest predation (Mainwaring *et al.*, 2014). In areas with a high abundance of small predators, dusky warblers (*Phylloscopus fuscatus*) chose to place their nests in safer sites, even though there were costs associated with these locations, such as higher wind exposure. Siberian Jays (*Perisoreus infaustus*) showed a similar response when perceived predation risk was experimentally increased (Eggers *et al.*, 2006).

Detectability and accessibility of nests by predators can affect predation risk, and important factors related to this are nest concealment and nest height (Colombelli-Négrel & Kleindorfer, 2009). Concealment of a nest can affect the detectability by predators. Increased vegetation around the nest can reduce the transmission of visual, auditory or chemical cues (total foliage hypothesis, Martin (1993)), that predators might use to find the nest. The nest-concealment hypothesis predicts that more concealed nests should have higher success compared to less concealed nests (Filliater *et al.*, 1994). However, studies testing this hypothesis have found mixed results (Borgmann & Conway, 2015). Some studies found support for this hypothesis (e.g. Martin & Roper, 1988; Weidinger, 2002; Colombelli-Négrel & Kleindorfer, 2009), while others failed to find support (e.g. Götmark *et al.*, 1995; Filliater et al., 1994). One explanation for this is that there can be trade-offs associated with building a nest at a well-concealed site. A well-concealed location can reduce nest predation risk, but might negatively impact nest microclimate (Lima, 2009). It could also increase adult predation risk, since increased vegetation can block the view of the surroundings for adult birds on the nest, which increases the risk of being ambushed by predators (Götmark *et al.*, 1995; Wiebe & Martin, 1998). In addition, the types of predators present an area might also influence the effectiveness of nest concealment. Concealment can be of importance for predators that hunt visually (Weidinger, 2002; Remes, 2005a), but might be less important for predators that use different cues, such as olfactory cues (Remes, 2005a; Colombelli-Négrel & Kleindorfer, 2009). Nest height might affect how accessible nests are to predators. Similarly, predator types present in an area could influence the effectiveness of nest height in reducing predation risk. For example, Oahu Elapaio (*Chasiempis ibidis*) increased the height of their nests in response to introduced mammalian predators, thereby decreasing rates of nest predation (Vanderwerf, 2012). However, an opposite pattern was observed in long-tailed tits (*Aegithalos caudatus*). Here, higher nests had a higher chance of being predated, and avian predators were responsible for the majority of predations (Hatchwell *et al.*, 1999). These examples illustrate that whether and how nest concealment and nest height influence nest predation risk can be highly context-specific.

Similar to factors related to the nest site, temporal factors can also affect predation risk. Nest predation risk can vary throughout the breeding season. Some studies have found higher predation risk early in the season (Borgmann *et al.*, 2013), or lower predation risk early in the season (Grant *et al.*, 2005), while others have found higher predation risk midway through the breeding season (Sperry *et al.*, 2008). These variations in predation risk might be explained by differences in predator activity or abundance over time (Sperry *et al.*, 2008; Grant *et al.*, 2005). For example, an increase in the activity of snakes was negatively correlated with nest survival of black-capped vireos (*Vireo atricapilla*) (Sperry *et al.*, 2008). Grant *et al.*, (2005) suggested that increased predator abundance and movement could explain the decline in nest success later in the breeding season at their study site. Deciding when to breed might thus be important in determining nest success if predation risk varies over time.

Overall, many factors could affect nest predation, and which factors are of importance might depend on the habitat or region (Thompson, 2007). Habitats can differ from each other in aspects such as diversity of bird species, range of predator types present, availability of food and nest sites and overall structure of the vegetation. For this reason, it is difficult to determine what factors influence nest predation in a particular study species or specific study system, based on results of studies conducted in different environments, with differences in the previously mentioned aspects. Currently, the majority of nest predation research has focused on forested temperate areas (Vetter *et al.*, 2013), creating a geographic bias (Ibáñez-Álamo *et al.*, 2015). Other regions, such as tropical regions, are less well studied. These areas differ from temperate areas, as they host a higher diversity of bird and predator species (Vetter *et al.*, 2013; Söderström, 1999). Afrotropical regions, including savannah habitats, are especially understudied (Lathi, 2009), and not much is known about the factors influencing nest predation in these regions. Savannahs are characterised by grasses and woody vegetation, and fire plays an important role in maintaining vegetation structure here. Prescribed burning is an important management practice that is often applied in reserves, and is used, for example, to prevent woody encroachment (Nieman *et al.*, 2021). Prescribed burning can interfere with natural fire regimes in an area, which can have multiple effects, including changes in vegetation structure and species interactions (Doherty *et al.,* 2022). This may affect predator-prey dynamics and nest success of birds, and is therefore an important factor to investigate in savannah ecosystems.

Here, I investigated multiple factors to get an overview of what may affect nest predation across species nesting in same African savannah habitat. I focused on factors related to nest site, including concealment, nest height and whether an area was burned or not. I expected that more concealed nests, in the form of higher nest concealment, higher ground vegetation density and increased canopy cover, would show higher survival. I also expected higher nests to have higher survival, since these might be less accessible to predators moving from ground level. Furthermore, I expected higher survival in burned areas, because of reduced vegetation cover for ground predators such as snakes, which could increase their own risk of predation (Wilgers &

Horne, 2007). Additionally, I investigated temporal variables, focusing on the timing of breeding and nest stage. I expected that nests initiated later in the breeding season would have lower survival, because activity or abundance of predator species may increase later in the breeding season. Regarding nest stage, I expected a higher predation risk and lower survival during the nestling stage, similar to findings by Burhans *et al.*, (2002), due to a possible increase in cues available to predators, such as increased parental movements and begging calls of nestlings (Skutch, 1949). Identifying factors that affect nest predation risk can improve understanding of predator-prey dynamics and can inform conservation and management strategies in African savannah habitats.

Methods

Study area and species

This study was conducted in Mbuluzi game reserve (26°08'18.5"S 31°59'59.9"E), a private game reserve in the north-eastern part of eSwatini. It is located in the lowveld region and characterised by a savannah habitat. The climate is subtropical, with a wet season from October to March and a dry season from April to September (Matondo *et al.*, 2004). At the start of the breeding season we searched the entire area, however later in the season the focus was shifted towards only the core area (**Fig S1**). On the 27th of August a part of the study site was burned (**Fig S1**).

The reserve hosts a wide range of bird species and also a wide range of nest predators. We focused on finding and monitoring nests of all bird species that we could find (except for weaver species). We found the most nests of dark-capped bulbuls (*Pycnonotus tricolor* (n=39)), white-bellied sunbirds (*Cinnyris talatala* (n=27)), black-crowned tchagras (*Tchagra senegalus* (n=18)), arrow-marked babblers (*Turdoides jardineii* (n=17)), speckled mousebird (*Colius striatus* (n=15)) and brown-crowned tchagras (*Tchagra australis* (n=15)). Nests in the reserve were predated by mammals, reptiles and birds. The main predators of each group were vervet monkeys *(Chlorocebus pygerythrus),* boomslang *(Dispholidus typus)* and Burchell's coucals *(Centropus burchellii)*, respectively.

Nest searching and monitoring

The fieldwork season lasted from mid-August until mid-December in 2024. To ensure that all areas were regularly searched for nests, search effort was kept consistent throughout the breeding season. We searched for nests by walking transects in the study area. We aimed to maintain a distance of approximately 30 meters between two adjacent transects, so that on each side of the transect we could scan 15 meters of the surrounding vegetation for nests. When a nest was found, we saved the coordinates on a GPS device (Garmin eTrex 32x). For each nest we recorded the date it was found, the bird species, nest content (whether it was empty or contained either eggs or nestlings) and nest height. When nests contained nestlings we estimated their age.

Active nests were checked every four days or earlier, whenever possible. During each check we recorded the content of the nest. We stopped monitoring when the nest became inactive (either fledged or failed). We assumed fledging when a nest that contained nestlings near fledging age was found empty during the next check, without any signs of predation, or when we observed fledglings around the nest. We assumed the nest was predated when it was empty before the estimated date of fledging, and/or when we observed clear signs of predation (e.g. broken eggs, feathers, blood or a damaged/destroyed nest). Nests were considered abandoned when they contained dead nestlings, or when they contained cold eggs for multiple nest checks.

Concealment measurements

After nests became inactive, we visited them again to measure concealment. We used three measures of concealment, to account for the different predator types occurring in the study area, and how they move and might find nests (**Fig S2a**):

*Canopy cover (**Fig S2b**):* This was used to indicate the visibility of the nest from above. A higher percentage of canopy cover would mean that a nest is more concealed from above. We estimated the percentage of canopy cover using a spherical densiometer (model C) (Lemmon, 1956). We measured canopy cover while standing with our backs towards the nest. We did this for all four cardinal directions, and then took the average of all measurements.

*Nest concealment (**Fig S2c**):* This was used to indicate how visible the nest itself is. We scored this by placing a ball (15cm in diameter) in the nest, and then we estimated what percentage of the ball was visible from eye-level, from a distance of 0.5 and 1.5m from the nest. We did this for all four cardinal directions, and took the average of all eight measurements. Finally, we subtracted the obtained value from 100, to get the percentage of the ball covered by vegetation.

*Ground vegetation density (**Fig S2d**):* This was used to indicate how much vegetation there is on the ground surrounding the nest. We scored this by placing a ball (15 cm in diameter) on the ground, 3 meters away from the nest. We then estimated what percentage of the ball was visible, while standing with our backs towards the nest. We did this for all four cardinal directions, and took the average of all measurements. Finally, we subtracted the obtained value from 100, to get the percentage of the ball covered by vegetation.

We only collected these concealment measurements for nests that we could reach ourselves, or could reach by using a small step, since we had to place a ball in the nest to measure nest concealment. All speckled-mousebird nests and some dark-capped bulbul nests were an exception to this, for these nests a large stepladder was used to reach the nest. We did not measure concealment for ground-nesting or cavity-nesting birds. Concealment was measured by two observers. To assess inter-observer repeatability, a subset of 10 nests was independently scored by both observers, and the results were visually compared to analyse consistency in scoring (**Fig S3**).

Camera monitoring and video analysis

Wildlife cameras (Wilsus Tradena 4G WIRELESS) were placed at active nests, whenever a camera was available. We placed cameras close to the nest, at a distance of approximately 0.5 to 1.5m, using tripods, gorilla pods or by using straps to bind them to nearby trees. Solar panels were attached to cameras to recharge the batteries. No cameras were placed at dark-capped bulbul nests, since they were likely to abandon their nests when a camera was placed nearby. During each nest check, we checked the battery levels and SD cards of the cameras. We removed the cameras after nests became inactive.

The purpose of the cameras was to record nest fate (fledged/predated/abandoned) and to identify the predator species and timing of predation for predated nests. For each day with camera footage available, we recorded nest stage (egg or nestling), whether there was a predation event (including predator species and timing), and whether there was a parasitism event (including species and timing).

Statistical analysis

For my analysis, I only used nests where all concealment measurements were collected. Since I was interested in the factors affecting nest predation, I excluded abandoned nests and nests with an uncertain fate. So my dataset only consisted out of predated and fledged nests. The variables I was interested in could be divided into nest-site and temporal variables. Regarding nest-site variables, I looked at concealment (ground vegetation density, nest concealment and canopy cover), height of the nest (in meters), and burn status. For burn status I used the classification “burned” for nests built in areas that were burned early in the breeding season, and “unburned” for nests built in unburned areas. Regarding temporal variables, I looked at the timing of breeding and nest stage. For timing of breeding I used the date the nest was found. For each nest check interval, I included the stage the nest was in during the interval, which was either empty, egg or nestling.

I used daily survival rate (DSR) as a measure of nest success, instead of apparent nest success, to determine the effects of the above-mentioned variables on nest survival. Apparent nest success uses the number of fledged and failed nests to calculate the proportion of successful nests. Apparent nest success can be biased, as recognised by Mayfield (1961). One reason for this is that nests predated very early in the nest cycle are more likely to go undetected by nest searchers, and can therefore be underrepresented in the total sample of nests. In addition, older nests, which are closer to hatching or fledging, are more likely to survive, leading to an overestimation of nest success (Mayfield, 1961; Mayfield, 1975).

All analyses were performed in R 4.5.0 (R Core Team, 2025). I used a logistic exposure model to estimate daily survival rate. This model uses the time between nest observations (exposure days) to estimate nest survival probability (Shaffer, 2004). This particular model can be used for datasets with varying exposure days, and allows the use of categorical, continuous and time-specific variables (Shaffer, 2004). I applied a generalised linear mixed model (GLMM), using the *lme4* package in R (Bates *et al.*, 2015), and included a logistic-exposure link function (De Labra-Hernandez & Renton, 2025; Shaffer, 2004). The response variable was the outcome of the nest during the exposure interval, with nest surviving the interval = 1, nest predated during the interval = 0. Nest ID was used as a random effect, to account for the fact that nests occurred multiple times in the dataset. I used the five nest-site variables and two temporal variables as fixed factors. I checked whether the continuous nest-site variables were strongly correlated ($r > 0.5$), using a correlation matrix (**Fig 1**).

I first created a full model including all explanatory variables. For model selection, I used the *dredge* function from the *MuMIn* package (Bartoń, 2025). This generated models with all possible combinations of the variables included in the full model. I selected the best models based on Akaike Information Criterion corrected for small sample sizes (AICc), with the criterium of ΔAICc < 2 for selecting supported models (Burnham & Anderson, 2002). I then performed conditional model averaging across all the supported models to determine which of the included factors significantly affected nest survival. I used the top model to create figures explaining the relationship between significant predictors and daily survival rate (similar to Hart *et al.*, (2021)).

Figure 1: Correlation matrix of the continuous nest-site variables: ground vegetation density, nest concealment, canopy cover, nest height (m). All variables were included in the full model, since there was no strong correlation between variables.

Results

We found 288 nests in total, and measured concealment at 173 of them. Of these nests, 30 fledged (17.3%), 136 were predated (78.6%), 4 were abandoned (2.3%), and 3 had an uncertain fate (1.7%). After removing the abandoned nests and nests with uncertain fate, 166 nests remained, which contained nests of 25 species. Out of all predated nests, 99 were predated during the egg stage (72.8%) and 37 during the nestling stage (27.2%).

Daily survival rate analysis

Model selection resulted in 8 supported models (with ΔAICc < 2) (**Table 1**). These models included different combinations of nest-site variables and temporal variables. Burn status was not included in any of these models. Conditional model averaging across all supported models showed that only ground vegetation density had a significant positive effect on daily survival rate (**Table 2, Fig 2**). All other variables showed no significant effect on daily survival rate (**Table 2**).

Nest-site and temporal factors

Additional figures showing the distribution of nest-site variables related to concealment and nest height are presented in the supplementary material (**Fig S4** and **Fig S5**).

The number of active nests increased over the course of the breeding season (**Fig 3**). Timing of breeding (which was based on date found) did not significantly affect daily survival rate (**Table 2**), and daily survival rate did not change over time (**Fig 4**).

Table 1: Model selection output of the supported models (selected based on the criterium of ΔAICc < 2). In all models nest ID was used as a random effect.

Model	k	AICc	ΔAICc	weight
Nest concealment + ground vegetation	3	692.93	0.00	0.22
Ground vegetation	2	693.06	0.13	0.21
Ground vegetation + nest stage	3	694.29	1.36	0.11
Date found + nest concealment + ground vegetation	4	694.34	1.41	0.11
Nest concealment + ground vegetation + nest stage	4	694.36	1.43	0.11
Canopy cover + ground vegetation	3	694.80	1.87	0.09
Date found + ground vegetation	3	694.89	1.96	0.08
Nest concealment + ground vegetation + nest height	4	694.89	1.96	0.08

Table 2: Parameter estimates obtained using conditional model averaging across all supported models (Tabel 1). Significant variables are shown in bold.

Variable	β	Adjusted SE	Z	P
Intercept	2.085	0.769	2.71	0.007
Nest concealment	0.007	0.005	1.48	0.139
Ground vegetation	**0.009**	**0.004**	**2.16**	**0.031**
Nest stage (nestling)	0.165	0.200	0.83	0.409
Date found	-0.003	0.005	0.61	0.543
Canopy cover	-0.003	0.005	0.53	0.598
Nest height	-0.033	0.126	0.26	0.796

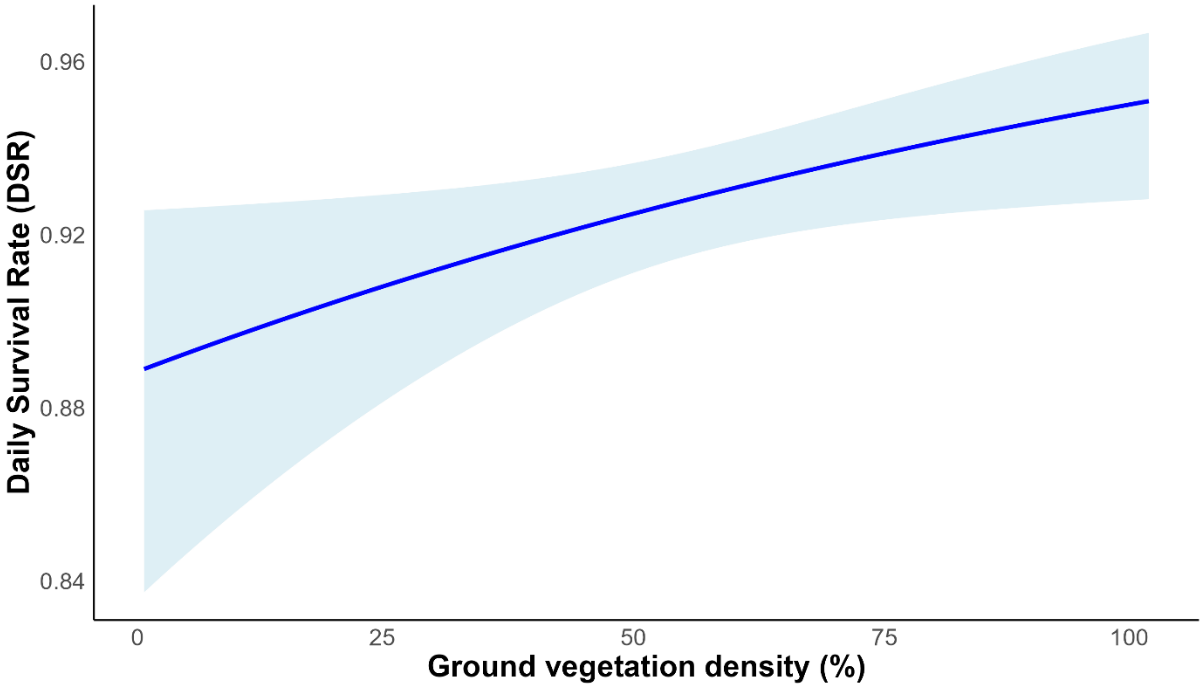

Figure 2: Daily survival rate estimates (including 95% confidence intervals) as a function of ground vegetation density. These estimates were obtained using the top model (Table 1), which included ground vegetation density and nest concealment as predictors. Here nest concealment was kept constant at its mean value. Predictions were made using the data of 166 nests.

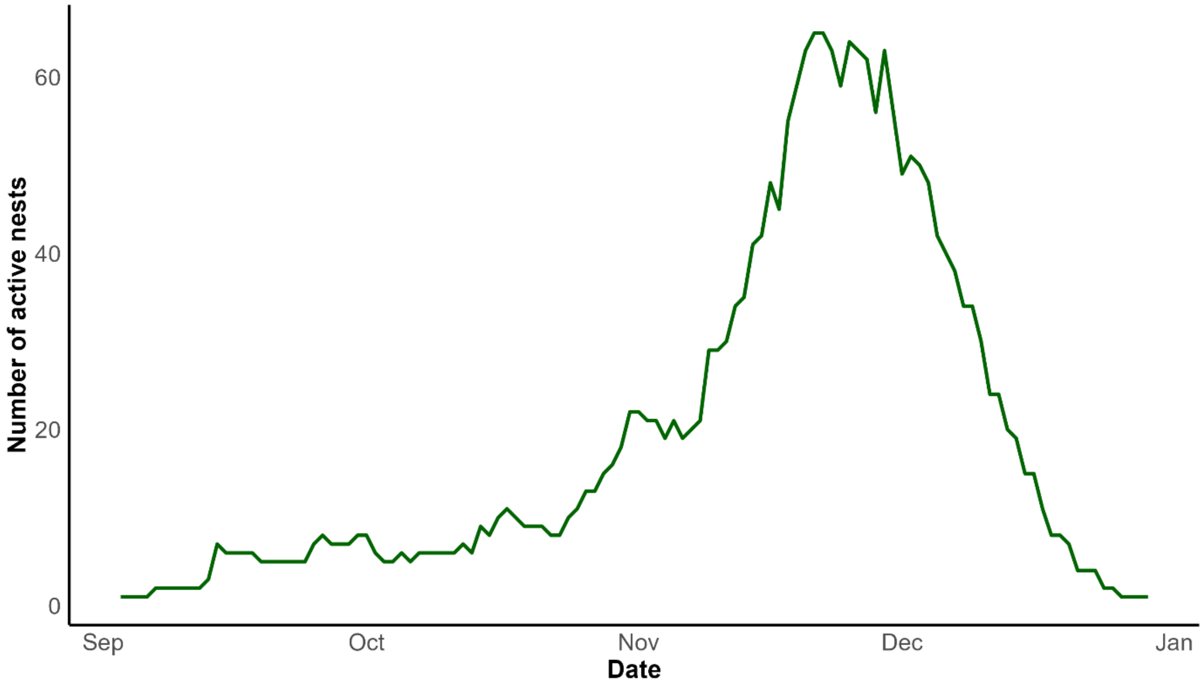

Figure 3: Number of nests that were active throughout breeding season. This figure includes only the 166 nests for which concealment was measured. Search effort was consistent during this period.

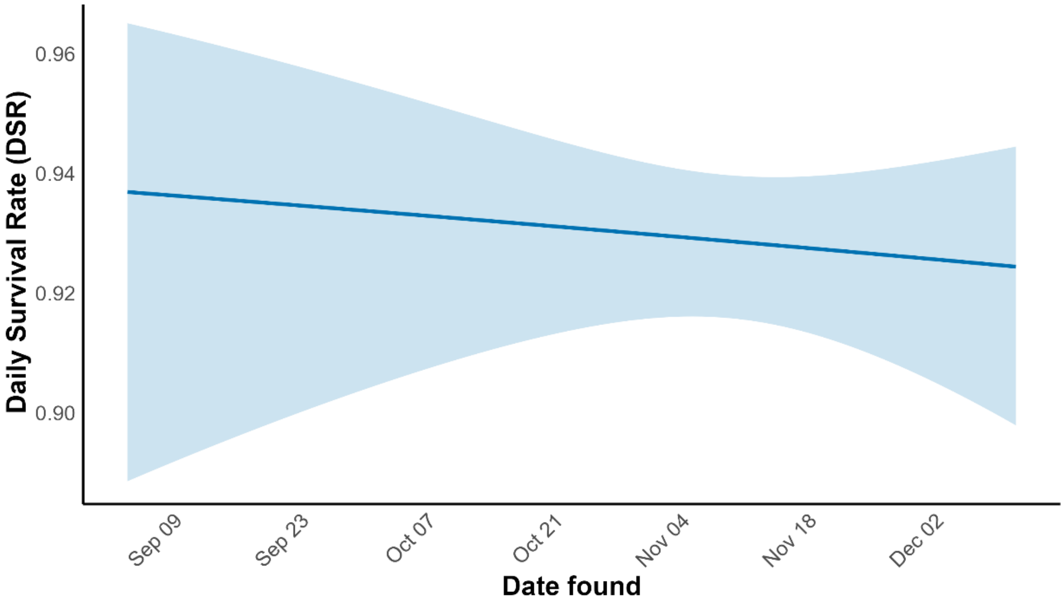

Figure 4: Daily survival rate estimates (including 95% confidence intervals) as a function of date found, which is defined as the date on which the nest was found during nest searching. These estimates were obtained using the model that included the variables date found, nest concealment and ground vegetation density (Table 1). Here nest concealment and ground vegetation density were kept constant at their mean values. Predictions were made using the data of 166 nests.

Discussion

In this study, I investigated nest predation in relation to various nest-site and temporal variables, to assess which factors might influence nest predation across multiple bird species nesting in an African savannah habitat. Multiple models that each included different combinations of variables had similar fits to the data. However, subsequent conditional model averaging across all these models showed that only ground vegetation density had a significant positive effect on daily survival rate. This suggests that predation risk is lower for nests built at sites with higher ground vegetation density. The other variables included in the models showed no significant effect on nest survival.

Nest-site variables

Concealment variables:

Of the three concealment variables measured, only ground vegetation density significantly affected nest survival. This suggests that vegetation at ground level may play an important role in determining nest predation risk in a savannah habitat, whereas nest concealment and canopy cover appear to have less influence.

This finding is in line with several other studies that also found support for an effect of ground vegetation on nest survival and predation risk. For example, successful nests of sage grouse (*Centrocercus urophasianus*) were more covered by tall grasses and shrubs (Gregg *et al.*, 1994), and for grassland birds in South Africa nest success increased when vegetation density increased over the course of the breeding season (Little *et al.*, 2015). Both studies hypothesised that this increased vegetation improved concealment of nests, leading to reduced nest predation. Studies using artificial nests found similar results. Daily predation rates of artificial ground nests decreased when the density of near-ground vegetation increased (Seibold *et al.*, 2013). A similar effect was observed for artificial tree nests: a study comparing nest predation between olive groves with and without ground cover found lower predation rates for artificial tree nests in areas with ground cover (Castro-Caro *et al.,* 2014).

The importance of ground vegetation in determining nest predation risk may be explained by the effect that it may have on detectability and accessibility of nests by predators (Klug *et al.*, 2010). In a savannah habitat, ground vegetation could be of greater importance due to the relative openness of the landscape, where grasses may play a larger role in providing cover. Rather than being concealed by vegetation directly surrounding the nest, nests might be concealed by vegetation on the ground below them. Similar to vegetation around the nest, vegetation on the ground could also block visual and olfactory cues, making it more difficult for predators to detect nests (Gregg *et al.*, 1994; Seibold *et al.*, 2013). Additionally, high and dense ground vegetation might serve as a physical barrier, that could limit predator mobility and could interfere with search strategies of predators (Martin, 1993; Seibold *et al.*, 2013). This may reduce the accessibility of nests to predators moving at ground level. Ground vegetation could therefore be an important determinant of nest predation in areas where the majority of predators approach nests from ground level, which is likely the case in this study system.

Nest concealment, determined by vegetation directly surrounding the nest, did not have a significant effect on nest survival. One explanation could be that birds avoid nesting at very well-concealed spots, because of trade-offs associated with these locations. One trade-off that may be important in this study area could be increased predation risk for adult birds. A wide range of predator species is present in the area that may also prey upon adults. Dense vegetation around the nest could hinder the visibility of the surroundings for adults on the nest, making it more difficult to detect predators. Having a clear view of the surrounding area may help adults to spot predators sooner, reducing their own predation risk. This could be a reason why birds would select spots with intermediate concealment, instead of the most well-concealed spots (Götmark *et al.,* 1995). Moreover, some bird species may employ alternative strategies, such as active nest defence, to reduce nest predation rather than relying only on nest concealment (Weidinger, 2002; Borgmann & Conway, 2015). Birds using this strategy may prefer open nest sites, which allow them to detect threats earlier and to respond appropriately. Another strategy that could be important for some birds in the study area is nest camouflage. For example, sunbirds build well-camouflaged pendulous nests, and the structure of the nest itself may reduce detectability by predators, decreasing the need to conceal the nest by surrounding vegetation. Alternatively, it is possible that well-concealed nest sites are less available in some parts of the study area, but that some birds are able to behaviourally compensate for reduced concealment. For example, birds could increase nest defence or decrease nest visitation rates in order to reduce predation risk (Lima, 2009; Remes, 2005b). These compensatory behaviours could lead to similar predation risks across nests with different degrees of concealment, which may explain the lack of an effect of nest concealment on survival. Overall, these explanations highlight the complexity of nest concealment, and it is possible that multiple of these mechanisms operate simultaneously.

Canopy cover, the last concealment variable considered in this study, also did not significantly affect nest survival. One possible explanation is that canopy cover may be less important in savannah habitats. In the study area, average canopy cover at nest sites was low. Canopy cover may mainly influence nest predation by raptors, as was shown in a study by Benson et al. (2010), which analysed the factors predicting nest predation by different predator types. However, in this study area, raptors may be less important in determining overall predation patterns, since they are generalist predators and nest contents are likely not the main components of their diets. Although they do predate nests, it is plausible that other predator species, that are less affected by canopy cover, play a more important role in driving nest predation patterns.

Nest height:

Nest height did not have a significant effect on nest survival. It is possible that I missed a potential effect of nest height on survival by only considering nests up until a certain height. A comparative study by Matysioková & Remês (2024) showed that nest predation rates decreased significantly for nests built above 5 meters, while no change in nest predation rates was found for nests built below this height. One suggested explanation for this finding is that very high nests may be difficult or even impossible to access for certain predator guilds, which results in lower overall predation risk since only a smaller group of predators is able to reach these nest (Matysioková & Remês, 2024). If a similar pattern applies to the study area, I could have missed it because nests higher than 4 meters were not included in the analyses. Alternatively, it could also be possible that there is no safe nesting height with reduced predation risk because different predator types may target nests at different heights, resulting in a similar predation risk across all heights. For example, this has been observed in Medium Tree-Finches (*Camarhynchus pauper*), where rats were responsible for predating lower nests, while avian predators were responsible for predating higher nests (Kleindorfer *et al.,* 2021).

Burned and unburned areas:

Whether a nest was built in a recently burned or unburned area did not affect nest survival. One explanation for the lack of a difference in nest survival could be that burning only has a temporary effect on predation risk. An artificial nest study showed that nests placed in areas burned less than two months ago had a higher chance of being predated, compared to nests placed in areas burned more that two months ago (Morris & Conner, 2016). In this study area, birds only started nesting again in burned areas a few weeks after the burn. By that time, sufficient vegetation cover may have regrown, increasing the similarity in vegetation structure between burned and unburned areas, which could explain the similar predation rates. Another possibility is that predation rates were similar between burned and unburned areas, but that the dominant predator types differed. For example, Jones *et al.* (2002) found that avian predation was dominant in burned areas, while small mammal predation was dominant in unburned areas. A similar pattern could be present in this study area, but this was not tested. Overall, the actual effect of burning on predation risk remains unclear and is likely more complex than initially assumed. It could be that my approach of classifying areas as either burned or unburned was too simplistic, because there may have been differences in the degree of burning within burned areas. Further research specifically focused on the effects of fire would be needed to reveal potential effects on nest predation in savannah habitats.

Temporal variables

Timing of breeding:

Timing of breeding did not have a significant effect on nest survival, and daily survival rates did not change over the course of the breeding season, contrary to my predictions. Timing of breeding may reflect variation in factors such as the number of nests available, behaviour or population levels of predator species, or the availability of alternative prey (Thompson, 2007). In the study area, the number of active nests increased over time. It is possible that predator abundance or activity followed a similar pattern, resulting in a relatively constant predation pressure over time, and this could explain why daily survival rates did not change. However, this suggestion remains speculative, since I only collected data on nests and did not measure predator abundance or activity over time. In addition, it could be that the measure I used to indicate timing of breeding did not accurately reflect the actual time birds decided to build their nests. I used the date the nest was found as a proxy for timing of breeding, but there was variation in when nests were found. For example, some nests were found while still empty, whereas others were found during the egg or even nestling stage. This variability may have obscured a potential effect of timing of breeding on nest predation.

Nest stage:

The majority of nests were predated during the egg stage, yet daily survival rates did not differ significantly between the egg and nestling stages. This apparent discrepancy between absolute predation numbers and daily survival rate estimates may be explained by differences in which nests are included in the analysis of each stage. For the egg stage analysis all the nests in the dataset are considered. In contrast, for the nestling stage analysis only successful nests and nests predated during the nestling stage are considered, and nests predated during the egg stage are excluded since they never reached the nestling stage. This difference in which nests were included in the analyses could result in similar predicted daily survival rates across stages, even if the total number of predation events during the egg stage was higher. The lack of a difference in daily survival rates between the two stage could be explained by predator preferences for specific stages. For example, Benson *et al.* (2010) found that snakes and raptors mainly predated on nestlings, while another avian predator mainly focused on eggs. If nest predators in the study area show a similar stage-specific preference, their effects may balance out, which could result in a similar predation risk across both stages. However, the effect of nest stage on predation risk remains complex, and it possible that my approach of comparing only the egg and nestling stages was too simplistic. Predation risk may vary even within these stages (Grant *et al.,* 2005), which I did not account for, but which could be important for understanding how and why predation risk may change during the nest cycle.

Different perspectives for future research

While this study may provide insights into the factors affecting nest predation across multiple species, further research may benefit from more specific approaches that consider different perspectives. Many of the provided explanations for the lack of significant effects of other factors on nest survival could be related to predator type and differences in their behaviour. However, in this study I did not focus specifically on predator types and therefore these explanations remain speculative. Further research, taking predator identity into account may reveal species-specific patterns of nest predation. Studies by Benson *et al.* (2010) and Phringphroh *et al.* (2024) showed that different factors are important in predicting predation by different predators, and could serve as examples for predator-specific approaches for future studies. Additionally, further research could focus on specific bird species, since different species may use other strategies to reduce nest predation and may be influenced by different factors. These species-specific patterns may be obscured when all species are analysed together. For example, studies by Pierce *et al.* (2020) and Phringphroh *et al.* (2024) analysed factors affecting nest success across multiple bird species, but also performed species-specific analyses, and found differences among species in which factors influenced nest success. Further research in this study area could adopt a similar approach by shifting focus towards specific species to reveal potential species-specific patterns and determinants of nest predation.

Conclusion

In this study, I examined the factors influencing nest predation across multiple bird species in the African savannah, a relatively understudied ecosystem. I showed that ground vegetation density is one factor that could influence nest survival. Specifically, higher ground vegetation density was associated with higher daily survival rates, suggesting that predation risk is lower at nest sites with increased ground cover. Ground vegetation may reduce nest predation through its possible effects on detectability and accessibility of nests. All other nest-site and temporal factors considered in this study showed no significant effect on nest survival. However, this does not necessarily mean that these factors have no influence on nest predation. It is possible that existing relationships were obscured by contrasting predation patterns of different predator species or by species-specific responses of birds to reduce predation risk. Further research may therefore benefit from focusing more specifically on predator species and their behaviour, or by focusing on specific bird species. Overall, these findings could have important implications for management and conservation efforts in savannah habitats, because changes in ground vegetation could influence breeding success of multiple birds species simultaneously.

Acknowledgements & Artificial Intelligence statement

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Artificial Intelligence statement

I only used artificial intelligence to solve coding errors in R, but never to generate text for this report.

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Supplementary material

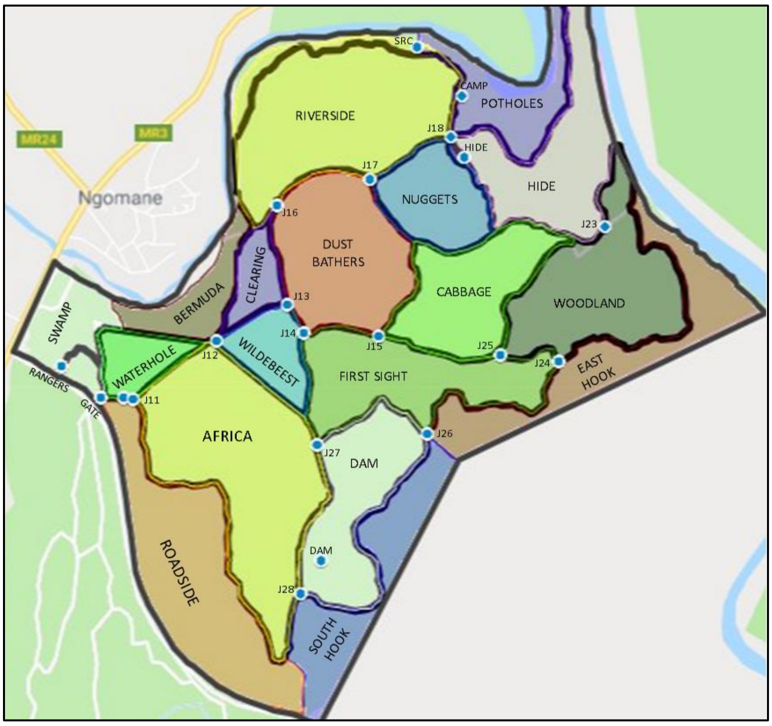

Figure S1: Schematic map of the study area. **Core area:** Dustbathers, Clearing, Hide, Nuggets, Potholes, Riverside and Wildebeest. **Burned areas:** Hide, Nuggets, Potholes and Riverside.

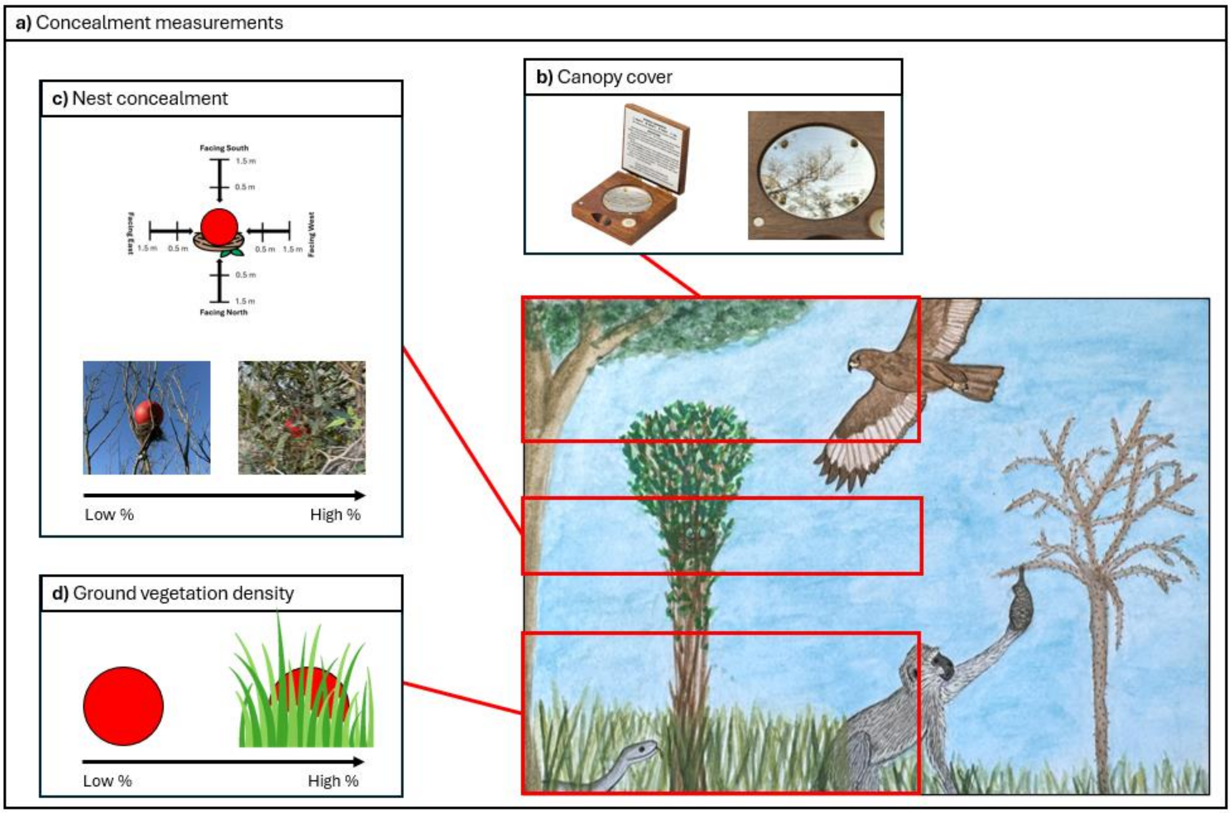

Figure S2: a) Simplified schematic overview of the three concealment measurements that were used. b) Canopy cover was measured using a spherical densiometer. c) Nest concealment was scored by placing a ball in the nest. d) Ground vegetation density was scored by placing a ball on the ground 3m away from the nest.

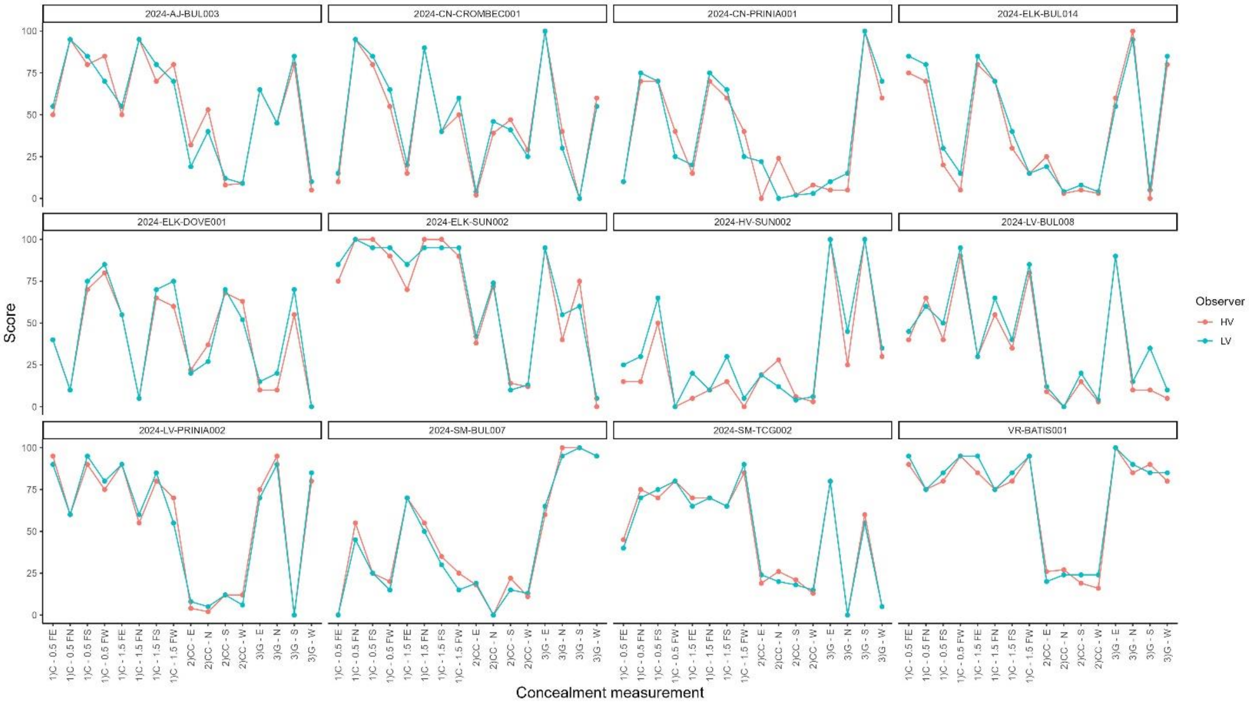

Figure S3: Concealment measurements collected for a subset of 10 nests. Concealment was measured by both observers, to visually check inter-observer repeatability. Numbers on the x-axis represent the following concealment measurements: 1) nest concealment, 2) canopy cover, 3) ground vegetation density.

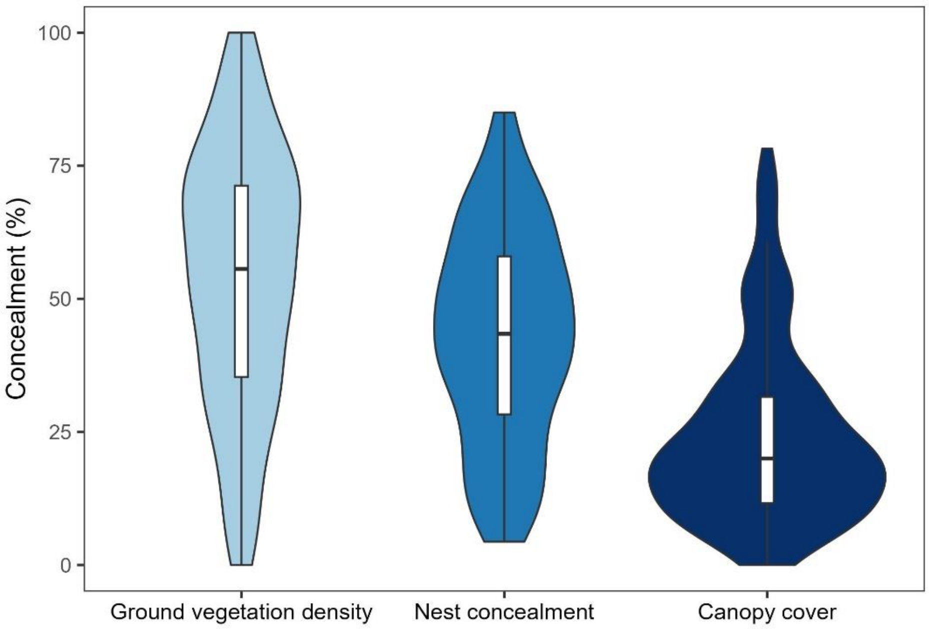

Figure S4: Visualisations of the distribution of the three concealment measurements: ground vegetation density, nest concealment and canopy cover. Data shown here represent measurements from 166 nests.

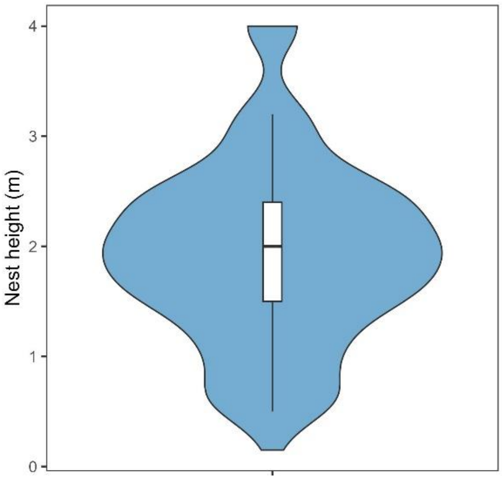

Figure S5: Visualisation of the distribution of nest height (in meters). Data shown here represent measurements from 166 nests.