Nest predation risk and predatory presence around kingfisher (Alcedo atthis) nests in the Gooi and Vechtstreek

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Abstract

Justification: Nest predation has been identified as one of the main reasons for nest failure in bird species across the globe. However, very little is known about the external mechanisms increasing chances of nest predation, especially in burrow-nesting species. Such external factors include both the type of predator as well as local and multi-scale habitat characteristics driving predator presence and the chance of nest predation. **Aim:** This study aimed to investigate causes and extent of nest predation of a burrow-nesting species, the common kingfisher (*Alcedo atthis*), as well as identify multi-scale factors that affect the vulnerability of its nests for predation events. **Methods**: Data on predatory presence, identification and predation events were gathered using camera traps during the breeding season. The effect of nest characteristics on predatory visits at breeding walls, was investigated using Generalized Linear Modelling. A multiscale habitat selection analysis was performed to assess the effect of habitat characteristics on predator presence in the surroundings at multiple landscape scales. **Principal findings**: Multiple expected predatory species were observed in the study area: Pine martens (*Martes martes*), stone martens (*Martes foina*), least weasels (*Mustela nivalis*), brown rats (*Rattus norvegicus*) and red foxes (*Vulpes vulpes*). Only one predation event, by a brown rat, was documented during the study but compelling evidence was found that intraspecific competition may also be a driver of nest failure in the area. The diameter of the nest opening, the depth of the water column underneath the nest, the width of the breeding wall, and especially the naturalness of the breeding wall all had a significant influence on the chance of predators visiting kingfisher nests. The multiscale habitat selection modelling revealed clear differences between and within predatory species in habitat preference on multiple scales. **Conclusion**: Nest predation rarely occurred while intraspecific competition was found to potentially be a driving force for nest failure in the Gooi and Vechtstreek. Furthermore, this study highlights the importance of taking both local nest site characteristics as well as multiscale habitat suitability into account when investigating predation risk for burrow-nesting species, like the common kingfisher. Nest predation is a complex, ecological process influenced by many dynamic and interlinked processes and is often highly site-specific. Understanding these underlying mechanisms are crucial for species conservation.

Keywords: Alcedo atthis, intraspecific competition, multiscale habitat selection analysis, nest predation, predator-prey interactions

Introduction

Nest predation is known to be one of the main causes of nest failure in many bird species and can have destructive consequences on both the population and community level (Martin, 1992; Newton, 1998; Ricklefs,1969). However, nest predation is very rarely documented, especially when more confined nests are build, like for burrow-nesting birds. Investigating nest predation on burrowing birds is challenging because these locations are often hard to reach, leading to a lack of understanding the causes of failed breeding attempts. Most cases of nest predation on nests of burrowing birds have therefore been determined based on evidence left by the predator, like excavated holes by red foxes, badgers and marten species (Heneberg, 2013; Turčoková, 2016). However, there is a large risk of misidentification of the predator species when the cause of predation is solely based on the remains of a predation event (Angelstam, 1986; Benson, 2010; Larivière,1999; Williams & Wood, 2002). In addition, predation events by multiple species on one individual nest can hinder the understanding of the effect of a single species (Larivière,1999; Reidy & Thompson III, 2012). The use of camera traps can however circumvent these difficulties (Cox et al., 2012a). Camera traps are extremely useful to document potential nest predators as well as effectively document the success of species specific nest predation (Ibáñez-Álamo et al., 2015; Williams & Wood, 2002). Nonetheless, this method has, to my understanding, very rarely been used to capture nest predation on burrowing bird species. Some exceptions are studies on cavity breeding seabirds and a penguin species (*Eudyptula minor*) which found that camera traps can effectively identify nest predator species, the predation techniques used by predators, and to identify additional reasons for nest failure of burrowing bird species (Bird et al., 2022; Ekanayake et al., 2015).

In addition to a solid understanding of the extent of nest predation and the identity of nest predators, it is relevant to understand the drivers of the presence of potential predators as well as the nest characteristics that make particular nests more vulnerable to predation than other nests (Schmidt, 1999). Predators use multiple visual, auditory, and olfactory cues to locate and evaluate potential predation sites (Geller & Parker, 2022; Ibáñez-Álamo et al., 2015). However, complex decision-making trade-offs could drive predators to visit breeding locations but not necessarily predate them (Schmidt, 1999). In addition, selective pressures also drive kingfishers to use multiple anti-predator strategies to determine suitable breeding grounds and to lower predation chances (Fontaine & Martin, 2006; Naher & Sarker, 2016; Lima, 2009; Turčoková, 2016). The type of soil of the breeding wall, and the exact location of the nest opening are factors mentioned as anti-predatory strategies used by the common kingfisher (*Alcedo atthis*) when choosing a suitable breeding ground (Čech, 2007*;* Heneberg, 2013; Turčoková, 2016). Another nest-borrowing species, the Western burrowing owl (*Athene cunicularia*), use alarm calls emitted by California ground squirrels (*Otospermophilus beecheyi*) as anti-predator behaviour and will nest in close proximity to squirrels colonies (Henderson & Trulio, 2019). Nevertheless, these dynamics and decision-making strategies from a predator's point of view are still badly understood, especially regarding burrow-nesting birds.

Moreover, landscape composition and scale-dependency are also important mechanisms causing increased risk of nest predation (Chiavacci et al., 2018). Species are affected by multiple different ecological and biological processes which can have fluctuating effects on a species' behaviour and their movements on multiple scales (Bowyer & Kie, 2006; Suárez-Castro et al., 2018). Subtle differences among habitat scales determines an animal's response and therefore may potentially play a vital role in understanding a predator's decision making relating to nest predation (Chiavacci et al., 2018). Multiscale habitat selection analysis has shown to be a powerful tool to unravel scale-dependent habitat preferences both within and between species (McGarigal et al., 2016; Timm et al., 2016). Especially in a highly urbanised landscape where suitable habitat can be scarce, the impact of scale-dependency on habitat selection may be more important than in less anthropogenic landscapes (Bauder et al., 2018; Klaassen & Broekhuis, 2018; Knopff et al., 2014). However, scale-dependency has hardly been addressed in studies that assess the effect of a predator's habitat selection on the chance of nest predation.

A burrow-nesting species for which little is known regarding 1) potential nest predators, 2) the extent of nest predation, and 3) multi-scale factors that affect the vulnerability of nests to predation events, is the common kingfisher, which breeds in steeps, sandy walls of waterbodies (Heneberg, 2013; Naher & Sarker, 2016). Multiple studies have documented the consequences of nest predation on kingfisher nests, including excavated nests by red foxes (*Vulpes vulpes*), but none have observed nest predation happening in the act (Rubáčová et al., 2020; Turčoková, 2016). Nest predation has only been occasionally mentioned and limited research has been conducted to define which predators are at play and in which way they effect the nests of kingfishers (Heneberg, 2013; Turčoková, 2016). Even though kingfisher populations are currently increasing in numbers, their densities can fluctuate heavily depending on the severity and duration of winter (BirdLife International 2024, Morgen & Glue, 1977). During severe winter conditions, shallow waterbodies freeze over and become inaccessible as hunting grounds, which can lead to a complete collapse of kingfisher populations (Morgen & Glue, 1977; Rubáčová et al., 2021). Climate change increases the frequency of extreme weather events, including the possibility of severe winters, with potential detrimental consequences for common kingfisher populations (Beniston et al., 2007; Michelfelder & Pilotte, 2022). Which implies the necessity for continuous conversational efforts for the species. Knowledge on nest predators identification, the extent of nest predation, as well as factors that lead to increased risk of nest predation is crucial when implementing effective conservation efforts. Here, I monitored 17 active nests of the common kingfisher in an urbanised area in the Netherlands, the Gooi and Vechtstreek with the aim to investigate causes and extent of nest predation as well as multi-scale factors that affect the vulnerability of nests for predation events. The research questions addressed in this study were:

1) **Which species are responsible for nest predation of the common kingfisher, and to what extent does this occur in the Gooi and Vechtstreek?** brown rats (*Rattus norvegicus*), Mustelids (Mustelidae), and red foxes (*Vulpes vulpes*) have been identified as nest predators for common kingfishers in Europe and are therefore also expected to be potential predators on kingfisher nests in the Gooi and Vechtstreek (Turčoková, 2016; Čech, 2007). The Netherlands is part of the distributional ranges of the species mentioned above, increasing the likelihood of identifying one or more of these species as nest predators of the kingfisher in this region (Long, 2003; Mos & Hofmeester, 2016; Niewold, 1980).

2) which nest site characteristics best explain the presence of potential predators at a micro scale, i.e. around breeding walls and the chance of successful nest predation events? It is expected that walls that provide little to now leverage for animals to climb, like artificial walls made from wooden plates or concrete, to be least attractive for predators. Nesting walls that are covered in vegetation of any kind, are on the other hand expected to have a higher chance of predators coming to the breeding wall (Harder, 2012). It is therefore most likely that the material of the outer wall will be most important to explain predatory visits at breeding walls.

3) Which habitat characteristics determine the presence of the potential predatory species at multiple scales in the study area? All three species mentioned above are expected to be documented during this field study. The Gooi and Vechtstreek is a highly urbanised region and the following expectation have been made accordingly (Provincie Noord-Holland, n.d.; Tgooi.info, n.d.). The common brown rat is a synanthropic, water dwelling species which is known to live in close proximity with humans (Bonnefoy et al., 2008; Sacchi et al., 2008). In addition, papers have indicated that brown rats initially prefer more rural regions, including agricultural lands (Bonnefoy et al., 2008; Feng & Himsworth, 2014; Sacchi et al., 2008; Yahmer, 2001). It is therefore expected to find a positive association between brown rat presence and these land-use types, where rural habitat patches are expected to play more prominent role on bigger scales while urban habitats more on the finer scales. Water is expected to be less scale-dependent due to being highly abundant in the study area (Tgooi.info, n.d.). Martens on the other hand are expected to use more nature-based patches in highly fragmented landscape and venture in close proximity to forest patches (Pereboom et al., 2008). Forest patches are scarce in the Netherlands and it is therefore expected that this habitat type will become more important on bigger scales (Schelhaas et al., 2021). Red foxes are known to avoid highly populated areas and a negative relation between red fox presence and the extent of human-influenced habitat types is expected to appear, where a higher density of human-influenced patches are expected to be found on the finer scales (Červinka et al., 2014; Duduś et al., 2014; Harris & Rayner, 1986; Kobryn et al., 2023). On broader scales, it is expected that red foxes will prefer more natural habitat patches which allow them to navigate their landscape more effectively (Kobryn et al., 2023).

Material and methods

Study area

The Gooi and Vechtstreek (Netherlands. 52.253102̊ N; 5.126662̊ E) is a highly urbanised region, especially the Gooi, in the province of Noord-Holland with a surface area of around 27.000 ha (Provincie Noord-Holland, n.d.; Tgooi.info, n.d.). This area has a big variety of different habitat types, including lakes and other watery bodies, heathlands, marshlands, temperate and mixed forests (see Figure 1). Many kingfisher breeding walls have been built by the "IJsvogelwerkgroep Gooi en Vechtstreek, which are intensively maintained and monitored (Vogelwerkgroep Het Gooi en Omstreken, n.d.).

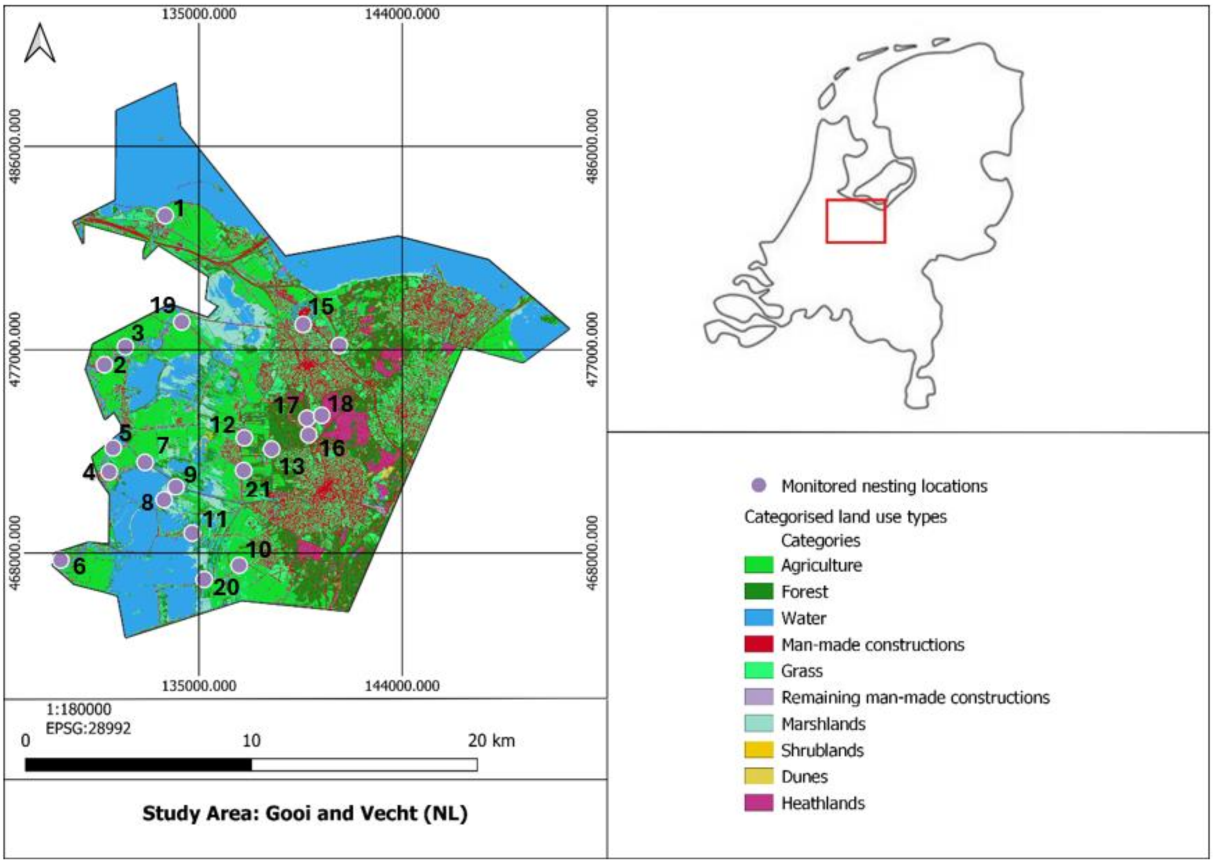

Figure 1: Overview of the study area, Gooi and Vechtstreekin the Netherlands. The study area is located in the province of Noord-Holland and comprises the municipalities Blaricum, Gooise Meren, Hilversum, Huizen, Laren and Wijdemeren (Provincie Noord-Holland, n.d.). The purple dots show all 21 locations where at least one of the camera setups (see methods) has taken place. In addition, see Appendix Table 1 for the specific names given to all study site numbers.

Data collection

The fieldwork was conducted from the beginning of March till the beginning of June 2024. Data collection was done in two parts: part one) the documentation of presence of potential predators in areas surrounding kingfisher nests, and part two) the documentation of predatory events at kingfisher nests. During part one, which started in the beginning of March 2024, the area surrounding the breeding walls were monitored for the presence of potential predators. This part was performed at 21 different study sites before the start of the first breeding attempt (see Appendix Table 1). These sites were selected as they were active breeding locations in previous years (J. Harder, expert communication, 2023). At every study site, a standard wildlife camera (either model Reconyx HC600 HyperFire or Reconyx HC500 HyperFire, depending on availability) was placed at locations where the chances of capturing the potential predatory species was highest. Determining these locations was based on environmental cues including natural and man-made trails, natural funnels, small water crossings, an open area in dense forest or potential crossing locations in an open area (Di Cerbo & Biancardi, 2013; Mos & Hofmeester, 2020; Tourani et al., 2020; Kelly & Holub, 2008). Distance from the breeding wall ($50m \pm 300m$) and camera height placement ($30cm \pm 130cm$) were almost near impossible to standardise due to high variability of area coverage. Nonetheless, it is not expected to influence the results significantly, for the only focus of this part was species detection and identification.

In addition to the camera traps, so-called Struikrover® (see Appendix Figure 1) were employed to increase the detection rate of small mammals. Struikrover® devices are a specially developed camera setup to maximise the documentation of smaller mammals, especially mustelid species, by using a scent-marking tool (small container filled with sardines/anchovies) (Smaal & van Manen, 2022). To prevent any bias caused by the scent-marking device, Struikrovers® were only used when at least 250m distance between the breeding wall and the Struikrover® could be guaranteed, which was the case for 17 study sites (different sites as for part two, see Appendix Table 1). The Struikrovers® were moved to a new location after two to three weeks.

From April onwards, study sites were visually inspected to determine if a nest was actively used by a breeding pair (presence of eggs or adult kingfishers in the nest cavity). Breeding walls were checked weekly on breeding activity throughout the month of April and when a breeding attempt was confirmed (at 17 study sites), part two of the research started. This involved the movement of the wildlife cameras to positions where they faced the breeding walls to monitor potential predatory activity. Due to a non-synchronous start of breeding attempts, part two of the research did not start simultaneously at every study site. The cameras were either attached to a nearby tree or a pole stationed in the water at a suitable distance in which both the nest opening and the top of the breeding wall would be in the camera frame. The use of the Struikrovers® remained unchanged. The cameras stayed active till the end of the first breeding attempt (beginning of June 2024). Both the wildlife cameras as the Struikrovers® were active 24 hours a day and were checked every two to three weeks to replace memory cards and batteries when necessary. During checkups, a visual inspection of the nest contents was performed as well to evaluate the progress of the breeding attempt at the study sites. All wildlife camera and Struikrover® footage was stored and processed in the Agouti software (ENETWILD consortium et al., 2022; https://www.agouti.eu).

Habitat and nest site characteristics

Land-use data from 2022 with a resolution of 5m was obtained from The Land-use Database of The Netherlands (Hazeu et al., 2023, https://lgn.nl) and used as a baseline for the multiscale habitat selection modelling. There are 51 different land-use classes in the dataset, which were categorised into ten different land-use categories for simplification purposes: (1) Agriculture, (2) Forests, (3) Water, (4) Man-made constructions, (5) Grass, (6) Remaining man-made constructions, (7) marshlands, (8) Dunes, (9) heathlands, (10) shrub vegetation (see Table 1). Next, ten nest site characteristics (see Table 2) were measured at all 17 actively used breeding walls.

Table 1: The land-use categories based on The Land-use Database of The Netherlands (Hazeu et al., 2023, https://lgn.nl) and the explanation regarding the individual habitat types of which that specific category is comprised of.

Habitat category	**Explanation of category**
Agriculture	All agricultural land-use ranging from several crops, to agricultural grasslands & orchards
Forest	Temperate & pine forests
Water	Fresh- & saltwater
Man-made constructions	All road types and other forms of infrastructure & building formations in both primary and secondary urban areas
Grass	Including all present grass excluding grass present in one of the other habitat categories (e.g. grass formation in heathlands or grass formation in dune habitat)
Remaining man-made constructions	Bare ground, solar parks and remaining land-use in urbanised areas
Marshlands	Reed, salt marshes and remaining marsh vegetation including forests and shrub vegetation in marshland

Dunes	Sand areas in dune regions & other vegetation types in dune regions (including, shrub and grass vegetation)
Heathlands	Heathland, including all vegetation types in heath areas
Shrub vegetation	Shrub vegetation, excluding shrub present in other habitat categories

Table 2: All investigated nest site characteristics used in the study, including explanatory information regarding every individual measurement or categorical division.

Nest site characteristics	**Explanation characteristic**
Total height of breeding wall (cm)	The distance between the upper part of the breeding wall and the lower part where it reached the water column below. When measuring natural walls, the total height was quantified as the distance between the water column and the transition point where the steepness of the wall levels out.
Total width of the breeding wall (cm)	When measuring artificial nesting walls, the total width was quantified as the total width of the construction. For natural walls, the width was quantified as the distance between two clearly distinguishable objects enclosing the nest opening. These objects were often trees, a sudden change of angle of the wall, or a sudden change in overall appearance (vegetation or material) of the wall.
Vertical length above nest opening (cm)	The distance of the top of the nesting wall, measured as explained for the total height of the wall, and the most upper edge of the nest opening.
Vertical length below the nest opening (cm)	The distance between the most lower edge of the nest opening and the water column.
Depth of the water body directly below the entering (cm)	The depth of the water column was measured in close contact to the breeding wall and directly under the nest opening
Diameter of the nest opening (cm)	Measured as the distance between the upper edge and the lower edge of the nest opening.
Vegetation covering the breeding wall (categorical)	The vegetation coverage present on top of the breeding wall. The category was categorised into the following classes: no vegetation (0%), herbaceous cover low (<50%), herbaceous cover high (>50%).
Material of the outside layer of the breeding wall (categorical)	Material of the outer layer of the breeding wall was classified into the following two categories: natural materials (including sand, clay, and peat)

	and man-made constructions (including concrete and wooden construction)
Overall material of the whole breeding wall (categorical)	This variable explains what the overall material of the breeding wall was comprised of, excluding the outer layer of the breeding wall. The following categories were used: Sand, clay and peat.
Type of nesting wall (categorical)	This variable explains if the nest was either an artificial nesting walls or a natural cavity. The natural category also included all breeding walls in which a pre-made starting point in the wall was made by human intervention

Nest site characteristics' influence on predator visits

Depending on whether the data was continuous or categorical (see Table 2), and based on the normality of the data from a Shapiro-Wilk normality test, different statistical tests were applied. Either a t-test, Kruskal-Wallis test, or a Chi-square test with Monte Carlo simulation was used to assess significant differences between nest site characteristics of nests visited by predators and those that were not. Due to the small sample size (see results), no distinction between different predatory species was made.

To further test which variables best predicted the chance of a predatory visit, three linear models were performed using the total count of predatory visits per site as the response variable: two generalized linear mixed model (GLMM) and a final generalized linear model (GLM). Overdispersion ("AER" package: Kleiber & Zeileis, 2008) led to the use of an adjusted family and the "hurdle" package (Zeileis et al., 2008) was used to account for the presence of many zero count values in the dataset. The final set of fixed effects was selected based on the two GLMM models in which the numerical and categorical variables were tested separately and "locationID" was added as a random factor. The continuous and categorical variables were first tested separately to locate significantly important variables before testing all factors simultaneously. This was needed due to the complexity of the model causing convergence and singularity issues. Within these two GLMM models, the fixed effects were tested on multicollinearity and correlation and were handled according to the results of these tests. The selected fixed effects were standardised to further deal with convergence issues and the random effect was removed due to continuous singularity problems, which led to the final model being a GLM. Lastly, to properly interpret the intercept in this modelling setup, the intercept was exponentiated using the following equation (Coxe et al., 2009):

$$\mu = exp^{\beta_0}$$

Where μ is the mean count when all other variables are zero and β_0 is the intercept.

To evaluate the performance of the model, the pseudo Nagelkerke R^2 and the Likelihood Ratio Test Statistic were calculated as well (Hagquist & Stenbeck, 1998; Nagelkerke, 1991).

Habitat preferences of potential predators

Multiscale habitat selection analysis was used to investigate whether there were differences in habitat preferences of the potential predators at different landscape scales. Multiple steps in both QGIS version 3.28.8 and Rstudio version 4.2.1 (QGIS.org, 2024, http://www.qgis.org; RStudio Team, 2020, http://www.rstudio.com/) were conducted to investigate the potential predatory species' habitat selection around kingfisher nests. First, multiple pre-processing steps were conducted in QGIS.

All study sites contained either two or three individual camera setups (depending on the activity of breeding wall and if a Struikrover® was present): one wildlife camera to monitor potential predator presence in the area during part one, one Struikrover®, and one wildlife camera to monitor predation event at the nest site during part two of the research. These camera locations were combined into one centre point to create one point per study site. Next, 800 pseudo-absences were generated to investigate the difference in habitat occupied and habitat available in the study area. Available habitat included all habitat types excluding infrastructure, buildings and waterbodies and pseudo absences generated within these habitat types were manually removed from the data, leading to the use of 621 pseudo absences. After manually checking the generated pseudo absences, the ratio presence: absence was set at 1:2 (presence ($N = 300$): pseudo-absences ($N = 621$)). A small ratio was chosen to increase the statistical power of the model and to cover the whole study area. A larger amount of pseudo absences would have created a bias in the model as the whole study area would in that case have been covered in both presence and absence points (Hengl et al., 2009; Iturbide et al., 2015; Wisz & Guisan, 2009). To investigate the impact of different scale effects on habitat use, three different buffer zones of 200m, 500m, and 1000m were created around both the pseudo absence points as well as the centre points (Boulet et al., 2000; Chiavacci et al., 2018).

Next, multiple univariate generalized linear models (GLM) were performed in Rstudio for every land-use type per scale separately to identify any significantly important land-use types. Within these models, the binomial presence/pseudo-absence data was used as the response variable and the proportions for every land-use type at a specific scale were used as the predictor variables. All land-use types were checked for high levels of correlation ($corr < 0.7$) and multicollinearity ($VIF < 5$) based on the Variance Inflation Factor (VIF) (using the "car" package: Fox & Weisberg, 2019). Next, GLM's per buffer scale were performed which include all land-use types that were identified to have significant importance in explaining presence-absence of the potential predators and that were not affected by high levels of correlation or multicollinearity. Furthermore, the "cloglog" binomial link function was used as it is most suitable for skewed presence/absence data (Prasetyo et al., 2019). High levels of separation amongst variables could lead to removal of variables when standardisation efforts could not resolve the issue. The model with the lowest Akaike Criterion value (AIC) value was then extended to a GLMM, where the "locationID" variable was added as a random factor in the model. Afterwards all selected variables per scale were combined into a multiscale GLMM analysis. First, all selected variables were checked for high correlation and multicollinearity again and the variables were handled according to the results of the tests. The remaining variables were standardized and analysed using a GLMM with a "bobyca" optimizer to deal with convergence issues. To interpret the intercept coefficient results correctly, the following transformation had to be performed because of the use of the "cloglog" function (Prasetyo et al., 2019):

$$\pi_i = 1 - \exp\left(-\exp\left(x_i^T * \beta\right)\right)$$

Where π_i is the probability of success for the response variable and $x_i^T * \beta$ is the linear predictor for the regression model, in other words, the intercept value.

Lastly the marginal R^2 and conditional R^2 were calculated to evaluate the performance of the GLMM models. Where the marginal R^2 explains the performance of the model when only the land-use types are taken into account, while the conditional R^2 takes both the land-use types as well as the random effect into account (Nakagawa & Schielzeth, 2013).

If due to singularity issues, the extension to a GLMM was not possible, a multiscale GLM was performed instead. For the multiscale GLM, the pseudo Nagelkerke R^2 and the Likelihood Ratio Test Statistic were calculated to evaluate the performance of the model (Hagquist & Stenbeck, 1998; Nagelkerke, 1991).

Results

During three months of field work, 17 breeding attempts were monitored, of which the gathered camera data confirmed six failed breeding attempts. However, only one attempt can be marked as "failed due to predation". Two other cases of failed breeding attempts worth mentioning relate to intraspecific competition. Unfortunately, camera malfunctions made it impossible to further determine the reason of failure for the three remaining cases.

Only one clear predation event was observed. At study site six (Fort Nieuwersluis), a brown rat was frequently observed entering the nesting cavity on multiple different days. During its first visit (28th of April 2024), the rat was photographed carrying prey away from the nest, confirming the event of predation (see Figure 2). Based on the expertise of an expert, it was determined that the prey was likely a chick between one to three days old (J. Harder, expert communication, September 2024). Apart from nest predation, two instances of intraspecific competition were also observed. At study site two (Eilandse weg) a photograph of an adult kingfisher holding an flawless egg was taken (see Figure 3). The camera footage and field observations showed that the intraspecific competition was performed at the second breeding attempt and led to nest failure of the whole brood (the last inspection on the 4th of June showed no eggs at the nest site). Aggressive behaviour between multiple adult kingfishers was recorded on camera 30 days before the predation event (see Appendix Figure 2), leading to two documented counts of disturbance at this breeding location relating to intraspecific competition. At study site 15 (Vesting Naarden; Abri) a heavily depredated nest with multiple dead chicks and a dying chick was found during visual inspection of the nest (see Figure 4). Furthermore, aggressive behaviour was visually observed from multiple adult kingfishers around the time of the event (visual observation). In addition, the wall at his location had two nest cavities and at the time of the discovery of the depredated nest, a new nesting attempt was already happening in the other cavity.

Figure 2: Photograph showing the predation event study site six (Fort Nieuwersluis) by a brown rat. The rat (red circle) is clearly carrying a juvenile kingfisher away from the nest opening. Photograph was taken at the 28th of April 2024.

Figure 3: Photograph showing an adult kingfisher carrying an egg at study site two (Eilandse weg). Photo taken on the 30th of May, around 30 days after the documentation of the defensive behaviour portrayal.

Figure 4: A dead chick found in the nest tunnel of study site 15 (Vesting Naarden: Abri). This location showed many compelling sings of intraspecific competition without camera footage. Apart from this individual, two other dead individuals were found in the nest cavity, along with a dying chick. In the other nest opening in this wall, a new breeding attempt was already happening, indicating that this nest was abandoned and most probably due to acquisition of a new adult individual.

Nest site characteristics and potential predator visits

Of the 17 active study sites, nine breeding walls were visited by at least one predator during the study period (see Table 3), of which the brown rat was observed most frequent. All observed predatory visits happened over land and none through the water column (see Table 3). None of the nest characteristics differed significantly between locations that were visited by predators and locations that were not (see Figure 5). The final GLM model did reveal multiple significantly important variables. The nest site characteristics "diameter of nest opening" ($\beta = 3.023, p = 0.033$), "depth of water column" ($\beta = 5.975, p = 0.0357$) and "natural nesting walls" ($\beta = 8.989\ p = 0.0196$) had a significant, positive association with the chance of a predator visiting a breeding wall. On the contrary, "width of breeding wall" ($\beta = -3.520, p = 0.0331$) significantly decreased the chance of a predator visit. Next, the characteristic "height of upper wall section" ($\beta = 2.511, p = 0.0720$) was also identified as moderately important, showing a positive, yet insignificant effect on the chance of a predatory visit at a breeding wall. The final model explained around 69.7% of all variance in the counts of predatory visits

($Nagelkerke\ R^2 = 0.697$), indicating that the selected variables are a strong fit for the model. The Likelihood Ratio Test Statistic of $G^2 = 19.85$ ($p = 0.006$) confirms as well that the fitted model performs significantly better than expected from the base model on explaining predator visits.

Table 3: Overview of all active breeding locations, indicating which animals were observed at the breeding walls and the frequency count per observed species. Furthermore information about the breeding success, if nest predation or intraspecific competition happened and a small overview of some of the nest characteristics is provided as well. If the predator visited the breeding wall over land or through the water is also mentioned within the nest site characteristics column.

ID	**Name of location**	**Observed predators and frequency (count) at nest**	**Breeding attempt successful**	**Predation/ intraspecific competition/ unidentified**	**Nest site characteristics**
1	Muiderslot	Brown rat (6) & Mustelidae (1)	✓	X	Natural wall (riverbank); Low vegetation cover; Total height breeding wall=75cm; Width of wall= 60cm; Depth water= 9cm; Predator visits over land
2	Eilandseweg	0	X	Intraspecific competition	Natural wall (compost heap); High vegetation cover; Total height breeding wall=90cm; Width of wall= 280cm; Depth water= 80cm; No predator visits
5	Van Belle	Brown rat (9)	✓	X	Natural wall; High vegetation cover; Total height breeding wall=130cm; Width of wall= 100cm; Depth water= 5cm; Predator visits over land
6	Fort Nieuwersluis	Brown rat (11)	X	Nest predation by brown rat	Natural wall; No vegetation cover; Total height breeding wall=95cm; Width of wall= 70cm; Depth water= 4cm; Predator visits over land
7	Fort Kijkuit	Brown rat (7)	✓	X	Artificial wall; No vegetation cover; Total height breeding wall=97cm; Width of wall= 130cm; Depth water= 22cm
8	Wijde Blik, Moleneind	0	✓	X	Artificial wall; No vegetation cover; Total height breeding wall=112cm; Width of wall= 100cm; Depth water= 16cm; No predator visits
9	Jachthaven Kortenhoef	Red fox (1)	✓	X	Natural wall; Low vegetation cover; Total height breeding wall=110cm; Width of wall= 280cm; Depth water= 17cm; Predator visits over land
10	Kasteel Sypesteijn	0	X	Unidentified	Natural wall (fallen tree trunk); No vegetation cover; Total height breeding wall=130cm; Width of wall= 200cm; Depth water= 5cm; No predator visits
11	Oud Loosdrechtsedijk	0	✓	X	Artificial wall; No vegetation cover; Total height breeding wall=103cm; Width of wall= 81cm; Depth water= 11cm; No predator visits
12	Landgoed Spanderswoud	Mustelidae (9) (Martes sp., Pine	✓	X	Natural wall; No vegetation cover; Total height breeding wall=85cm; Width of wall=

		marten) & Red fox (1)			130cm; Depth water= 6cm; Predator visits over land
13	Beeldentuin De Zanderij	0	X	Unidentified	Artificial wall; Low vegetation cover; Total height breeding wall=175cm; Width of wall= 140cm; Depth water= 20cm; No predator visits
14	Landgoed De Beek	0	✓	X	Natural wall; No vegetation cover; Total height breeding wall=77cm; Width of wall= 175cm; Depth water= 22cm; No predator visits
15	Vasting Naarden: Abri	Brown rat (13)	X	Intraspecific competition	Natural wall; No vegetation cover; Total height breeding wall=85cm; Width of wall= 220cm; Depth water= 22cm; Predator visits over land
17	Zanderij Crailo, Infoschuur	Mustelidae (1)	✓	X	Artificial wall; No vegetation cover; Total height breeding wall=200cm; Width of wall= 300cm; Depth water= 0cm; Predator visits over land
19	Fort Uitermeer	0	X	Unidentified	Artificial wall; No vegetation cover; Total height breeding wall=78cm; Width of wall= 240cm; Depth water= 12cm; No predator visits
20	Van de Wetering	0	✓	X	Natural wall; High vegetation cover; Total height breeding wall=80cm; Width of wall= 40cm; Depth water= 3cm; No predator visits
21	Landgoed Trompenburgh	0	✓	X	Natural wall; No vegetation cover; Total height breeding wall=80cm; Width of wall= 150cm; Depth water= 6cm; No predator visits

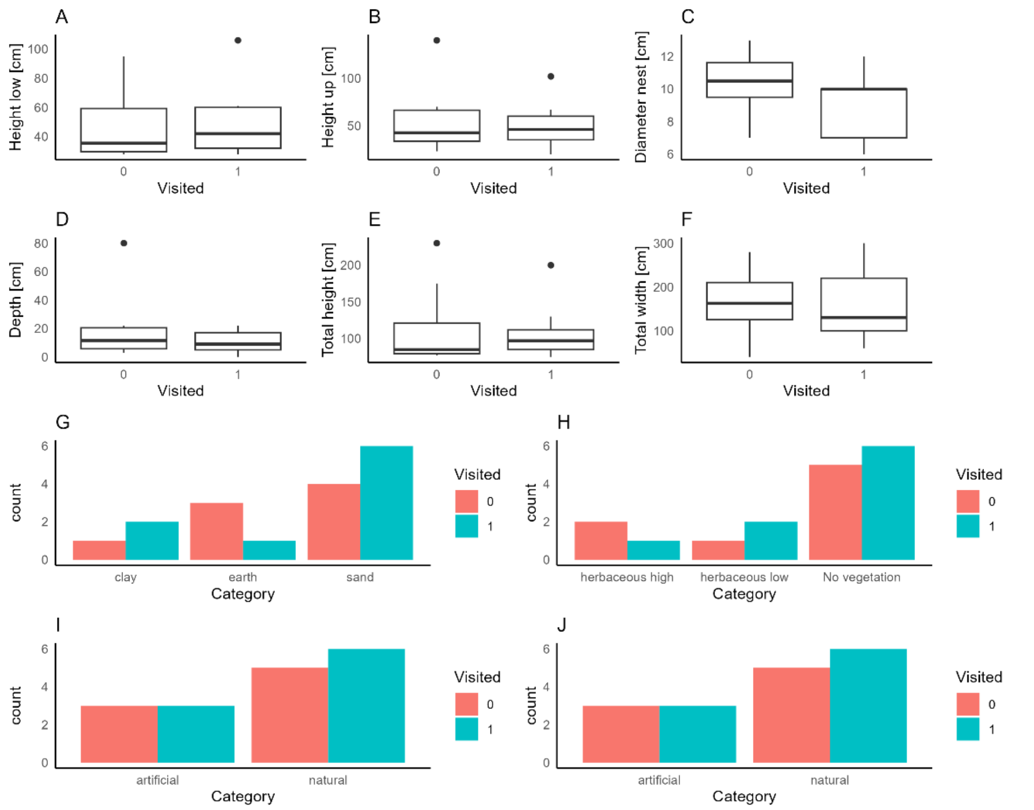

Figure 5: Nest site characteristics at breeding walls that were visited by potential predators, indicated by count, versus breeding walls that were not visited. A) Height of lower part wall, B) Height upper part wall, C) Diameter of nest opening, D) Depth of water column, E) Total height of breeding wall, F) Width of breeding wall, G) Material of inside wall, H) Vegetation cover, I) Material of outside wall" and J) Type of nesting wall. Where "visited" is either 0 (no visits) or 1 (visited).

Multiscale habitat selection

Out of all the 8145 species observations obtained during this study, only 3.5% ($N = 292$) showed potential predator species. The most commonly observed species were mice (Rodentia) (38.8%). In total 72.3% ($N = 211$) of the potential predator observations were of the common brown rat, 26.8% ($N = 49$) were of the red fox, and 10.9% ($N = 32$) of mustelid species. Within the Mustelidae family, the pine marten (*Martes martes*) was documented most frequently ($N = 19$). Other mustelids recorded include the stone marten (*Martes foina*) ($N = 1$) and the least weasel (*Mustela nivalis*) ($N = 4$). Ten observations of Mustelidae could not be identified to the species level. All mustelid species were grouped together for further analyses.

Regarding the brown rat; the final GLMM model explained 68.7% of the variance in its presence ($R_c^2 = 0.687$). The land-use types alone explained a similar variance levels of 67.8% ($R_m^2 = 0.678$) in brown rat presence. Yet, none of the land-use types significantly explained brown rat occurrence. The baseline chance of encountering a brown rat was found to be 3.01% ($\beta = -3.490, p < 0.001$). The multivariate, single scale models did, however, reveal some (moderately) significantly important land-use types. At a 200m scale, the availability of water ($\beta = 9.685,\ p = 0.065$) was positively related to the presence of brown rats. At the 500m scale, the presence of remaining man-made constructions ($\beta = 61.058,\ p = 0.039$) and water ($\beta = 4.035, p = 0.064$) were positively related to the presence of brown rats. And at a 1000m scale, the presence of agricultural lands ($\beta = 3.471,\ p = 0.097$) was positively related to the presence of brown rats.

The final GLMM model of the Mustelidae explained 71.1% of variance in its occurrence ($R_c^2 = 0.711$). No significantly important land-use types were identified that explained the mustelids presence, apart from one marginally important link to the availability of water on the 200m scale ($\beta = 0.789, p =$

0.066). Nonetheless, the land-use types alone still explained a moderate level of the variance in Mustelidae presence, 58.8% ($R_m^2 = 0.587$). The baseline chance of encountering a mustelid was found to be 3.22% ($\beta = -3.490, p < 0.001$). The single-scale multivariate models only revealed one significant land-use type. At the 200m scale, the availability of water ($\beta = 8.302, p = 0.0374$) was found to be positively related to presence of mustelids in the study area.

Regarding the red fox; the final GLM model explained 44.9% of the variance in red fox presence ($Nagelkerke\ R^2 = 0.449$). Two land-use types were found that significantly explained the red fox presence in the study area. On the 500m scale, the occurrence of remaining man-made constructions ($\beta = 0.606, p = 0.0478$) positively affected the presence of red foxes. On the 1000m scale, the availability of shrub vegetation ($\beta = 0.768, p = 0.00522$) was positively related to the chance of encountering red foxes. Next, the model including the land-use types significantly performed better ($likelihood\ Ratio\ test\ Statistic, G^2 = 25.55$ ($p < 0.001$) in explaining the red fox presence in comparison to the baseline model. Moreover, the multivariate, single-scale models revealed three significantly (moderately) important habitat types that increased the chance of red fox occurrence. On the 500m scale, the availability of remaining man-made constructions ($\beta = 2.458, p < 0.001$) positively increased the chance of encountering a red fox. On the 100m scale, the presence of remaining man-made constructions ($\beta = 0.659, p < 0.01$), shrub vegetation ($\beta = 983, p < 0.001$) and marshlands ($\beta = 0.4125, p = 0.0717$) positively affected the presence of red foxes in the study area.

Discussion

Nest predation events and predator identification

Although nest predation is a common cause for nest failure in birds (Martin, 1992; Newton, 1998; Ricklefs,1969), still little is known about the causes and extent of nest predation as well as which factors affect the vulnerability of birds' nests for predation events. Especially little is known about burrow-nesting species. This study aimed to investigate 1) potential nest predators, 2) the extent of nest predation, and 3) multi-scale factors that affect the vulnerability of nests for predation events of a burrow-nesting species, the common kingfisher (*Alcedo atthis*), in an urbanised area in the Netherlands, the Gooi and Vechtstreek. There were several potential predators observed during the study period: the common brown rat, multiple mustelid species (pine marten, stone marten and least weasel) and the red fox. However, only one predation event was documented where the predatory species, a brown rat, was identified without a doubt. Rodents, including the common brown rat are known to be an important nest predator globally for many bird species and in many ecosystems (Angelici et al., 2012; Bradley & Marzluff, 2003; Brown, 1997). *Rattus* spp.'s high impact on nest failure is often linked to their generalist behaviour and their good climbing abilities (Harper & Bunbury, 2015; Smith et al., 2016). These climbing abilities enable them to reach borrow-nests like that of the common kingfisher. In addition, rodents are known to predate on all nest contents, including juvenile birds, supporting the findings in this study (Bradley & Marzlff, 2003; Sarmento et al., 2014).

The timeline following the predation event by the brown rat shows strong evidence to believe that the impact of predation was destructive for this specific breeding attempt. Although a brown rat was photographed carrying only one chick away from the nest cavity at the end of April, other chicks may have been predated as well. If not, the other chicks should have fledged at the end of May. Yet multiple chicks of around six days old were observed in the second nest cavity at this study site at the start of June, indicating that these chicks resulted from a second brood. Indeed, any form of disruption around birds' nests frequently causes the breeding pair to abort the attempt and leave the location altogether (Baudains & Lloyd, 2007; Borges & Marini, 2010; Strasser & Heath, 2013). This information adds to the still limited amount of knowledge on the impact of nest predation on the breeding success of kingfishers. Studies in eastern Europe have shown that predation is one of the main reasons for failed breeding attempts in the species but contributed only to 6% of the nests to fail (Turčoková et al., 2016). In the Gooi and Vechtstreek, kingfishers have had more breeding attempts with bigger clutches over the last few years, which is often linked to lower predation pressures (J. Harder, expert communication, May 2024; Turčoková et al., 2016; Martin 2004). This, together with the findings of this study, suggests that nest predation is detrimental for the nests targeted, but it does not have severe consequences on the larger population as it does not occur frequently.

Intraspecific competition may however play a larger role in nest failure than predation. Two confirmed cases of intraspecific competition led to nest failure during my study period. Very little information is available about the occurrence of intraspecific, territorial competition among common kingfishers. Aggressive behaviour against territorial intruders is a common trait among birds, and often encompasses both physical and vocal behaviour to defend nesting grounds, including kingfishers (Amrhein & Lerch, 2010; Gese, 2001; Legge et al., 2004). Within kingfisher research, only an experimental study on intraspecific competition during the non-breeding season was conducted, showing playback responses and physical attacks on artificial intruder-models in the buff-breasted paradise kingfisher (*Tanysiptera syliva sylvia*) (Legge et al., 2004). Nonetheless, no information about the frequency of intraspecific competition in kingfishers species is, to my understanding, available in current literature.

However, intraspecific competition may play a relatively large role in nest failure in the Gooi and Vechtstreek due to the high breeding pressure present here. The population trends of the last two decades have shown a steady increase (apart from years with detrimentally, strong winters) in breeding pairs in the area, making suitable breeding grounds a limiting factor (IJsvogelwerkgroep Gooi en Vechtstreek, 2009, 2021, 2022). Resource competition, including competition for suitable breeding grounds, are known to be dependent on population density and increases with higher population pressures (Legge et al., 2004; Newton, 1992). Common kingfisher prefer to breed in areas where human activity is limited (Naher et al., 2021). Habitat fragmentation in a highly urbanised region like the Gooi and Vechtstreek can limit the availability of suitable breeding grounds and could therefore increase the occurrence of intraspecific competition (Bayne & Hobson, 2001; Hagan et al., 1996).

The aggressive behaviour 30 days prior to the event of nest failure caused by intraspecific competition was marked as an independent event also relating to high levels of disturbance at the site by intruder kingfisher adults. This behaviour is known to be common defensive behaviour among kingfishers and similar behaviour was documented at the same time as the observed nest failure at a different location as well. Although the camera footage did not show any signs of predation at the other location, a heavily depredated nest with multiple dead chicks and one dying chick in the nest cavity were found upon inspection. This was likely caused by kingfishers as the people monitoring in that location mentioned high levels of kingfisher activity around the time of the event, where multiple adult kingfisher were observed chasing one another. Furthermore, the fact that a new nesting attempt was already underway in the other cavity of the same breeding wall suggests the mortality of one or both parents and the start of a new breeding attempt by new adults, leading to abandonment of the depredated nest (J. Harder, expert communication, October 2024). The combined evidence from these two independent incidences do provide strong evidence that intraspecific competition is common in the common kingfisher. Nonetheless, more extensive research focusing on properly documenting this type of behaviour is vital to fully understand population-level consequences.

Nest site characteristics and predator visits

Nest predation only occurred once. It was therefore not possible to identify nest site characteristics that lead to higher predation instances. However, I did find that nests occurring in natural breeding walls rather than artificially build walls were significantly more likely to be visited by potential predators. Artificial breeding walls are designed to withstand both biotic and abiotic influences, to prevent depredation of the breeding wall and to increase the breeding success of birds (Ekner-Grzyb et al., 2014; Griffith et al., 2008). Especially vegetation growth around the nest opening is known to negatively impact the breeding success of kingfishers (Cornwell, 1963; Harder, 2012). Though the amount of vegetation cover surrounding the nests was not found to significantly influence the chance of visits in this study, an association may still be present within the type of breeding wall. Natural walls are continuously affected by vegetation growing and root formation, which can provide the needed leverage for a predator to reach the nest opening. Indeed, the only nest that was predated upon provided leverage in the form of roots for the predator (a brown rat) to go to the nest. The study site where the predation event with the brown rat took place, is noticeably more covered in tree roots than, for instance, another study site that was frequently visited by all potential predators but no real attempt was ever made to reach the nest (see Appendix Figure 3). This suggests that wall coverage occurring more at natural than at artificial nests, can play an important role in the chance of predation events to occur.

A larger nest opening was also found to increase the chance of predators visiting. An increasing size of the nest opening can enhance the detectability of the nest, which could potentially lead to more predator visits. It is known that predators use visual cues to detect prey and breeding locations (Mouton, 2019; Mullin & Cooper, 1998). A significant association between a larger nest opening and the chance of a visit suggests that this could also positively impact the chance that a visit would lead to actual predation. However, strong correlations between visual cues and an increased chance in predation rates have not been reported (Colombelli-Négrel & Kleindorfer, 2009; dos Santos et al., 2021). The findings in this study thus add to the evidence that an increased diameter of the nest opening helps predators to detect nests but it seems unlikely it would increase the chance of actual predation. Nonetheless, research on visual nest site characteristics and actual predation events specifically is needed to justify the assumptions made here.

The length of breeding walls also played a role in the frequency of visits by potential predators. The longer the breeding walls, the lower the chance of visits to occur. A longer wall may mask the nest opening itself, making it more difficult for a predator to locate its exact location. In addition, site specifics that made the majority of the breeding walls long in this study, such as nests being located in big, fallen tree trunks; breeding walls used by sand martins (*Riperia riperia*); and compost heaps, may make it difficult for predators to reach nests. The link between longer breeding walls and a lower chance of nest visits could therefore relate to the use of such locations as breeding locations by kingfishers in this study.

Lastly, an increase in the depth of the water column below the nest opening was also found to increase the chance of visits by predators. However, camera footage has shown that predators in the study area visited breeding walls from land and hardly ever through the water column, almost contradicting the test results (see Table 3 & Appendix Figure 3). Literature also shows that water depth is decreasing the chance of predation events significantly (Cain III et al., 2003; Hoover, 2006). Therefore, further research may be needed to clarify the relationship between depth of the water column and both predator visits and predation chance.

Multiscale habitat selection analysis

The habitat surrounding breeding walls may also play a role in the chance of predation events as it will have impact on the suitability of predators to occur. To investigate which predatory species were present around kingfisher nests and what drove their presence on multiple landscape scales, a multiscale habitat selection was performed. The results present variability among the investigated scales and among the different target species. None of the land-use types significantly affected the presence of the common brown rat, which is likely because the brown rat is highly adaptable and a generalist (Feng & Himsworth, 2014). Brown rat presence is mostly driven by food availability and breeding/resting grounds, which are predominantly created by human presence (van Adrichem et al., 2013; Langton et al. 2001; Masi et al., 2010). The brown rat occurrence is therefore not necessarily driven by specific land-use types but by human civilisation (Hulme-Beaman et al., 2016; van Adrichem et al., 2013). A significant effect of remaining man-made constructions, was however found on the 500m scale. This land-use type entails low-density and badly maintained locations in human settlements which often provide many hiding sites and breeding grounds for small mammals, including the brown rat (van Adrichem et al., 2013; Kobryn et al., 2023). This, together with the generalist nature of brown rats can explain this finding in the univariate modelling analysis.

Next, a moderately important and positive association with agriculture and water were found, which are in line with the expectations, even though not significant. The brown rat is most and foremost a water-dwelling species, explaining its association with water on both the 200m and the 500m scale (Sacchi et al., 2008; Traweger & Slotta-Bachmayr, 2005). This link may however have been caused by a bias surrounding the kingfisher's breeding ecology. The finest scale represents predominantly the breeding locations of the kingfishers which are exclusively present around fresh water (Naher et al., 2021). For this study, all camera traps were therefore stationed in very close proximity of water, undeniably creating a bias for water at the 200m scale (Stephens et al., 2004). Next, brown rats habituate rural areas frequently due to the lower levels of intensive pest control rates in comparison to urban areas and the high availability of food and shelter resources (Villafañe & Busch, 2007), explaining the positive effect of agriculture on a 1000m scale. Even though not significant, this study does seem to be in line with the current literature about brown rats association with agricultural lands as suitable land-use type outside urban areas.

Apart from a (moderately) significant association with water on the 200m scale, which again may have been linked to the research set-up (Stephens et al., 2004), no significant relations were found for the Mustelids. The lack of significant land-use types found in this study is most likely related to mustelids being rarely observed. Nuanced, but existing differences between marten species' ecology do exist and could therefore lead to the model being unable to identify land-use types that significantly affected the presence of mustelids in general. For instance, the pine marten is known to prefer forest patches over open habitat types, while the least weasel prefers the contrary (Pereboom et al., 2008; Zub et al. 2008). Marten species often fulfil similar ecological niches as mesocarnivores, which should lead to slight differences in at least one ecological force, for instance, habitat preferences (Monterroso et al., 2016; Szabó & Meszéna, 2006; Wereszczuk & Zalewski, 2015). Modelling all mustelid species together likely masked these small, but important differences (Chiavacci et al., 2018; Stephens et al., 2004).

Red fox presence was found to be positively associated with remaining man-made constructions on the 500m scale and shrub vegetation on the 1000m scale. These findings suggest that red foxes, even though often linked to urbanisation, still rely on low human-density patches and high coverage patches to thrive. Studies have shown that these are vital to 1) safely navigate urban landscapes and to 2) provide low-disturbance resting places (Bateman & Fleming, 2012; Harris & Rayner, 1986; Kobryn et al., 2023). The fact that low-disturbance and high coverage patches have been identified as significantly important for the red fox on a 500m scale may relate to their big home range and daily activity patterns. Red foxes' home range can become extensively large and an adult can cover over eight km per day (Main et al., 2020; Kobryn et al., 2023; Tsukada, 1997; Walton et al., 2017). Making both their daily activity pattern and their home range substantially bigger than the scales investigated in this study. The presence of potential resting sites and save crossings will evidently increase on a broader scale, while still enclosing their territory, and can therefore explain the patterns found here and seem to agree with the expectations made in this study.

Conclusion and recommendations

This research study investigated nest predation risk at kingfisher nests in the Gooi and Vechtstreek. Only one predation event was documented during the study but compelling evidence was found that intraspecific competition may be a more important driver in this specific area. However, more extensive research is needed to fully understand the mechanisms and impact of intraspecific competition on the breeding success of kingfishers. Future research on the topic should ideally be conducted using video footage and equipment with higher sensibility power to detect any movement made by the kingfishers (Peterson et al., 2004; Pierce & Pobprasert, 2013; Schaefer, 2004). The nest predation event itself implies that breeding walls that provide enough leverage for predators are more likely to be visited by potential predators. A link between natural walls and higher levels of climbing leverage is likely related to the fact that natural walls are more prone to erosion, creating inconsistencies in the wall and leverage for predators to reach the nest and increase the chance of nest visits (Cadiou et al., 2010; Ekner-Grzyb et al., 2014; Griffith et al., 2008). This highlights that it is important to maintain natural breeding walls by limiting the effects of erosion and with that the chance of nest predation.

Predatory presence and predator-prey dynamics are very fluctuant mechanisms and should be researched over longer periods of time to fully understand the system and to make well-measured recommendations and conclusions (Schmidt, 1999; Stephens et al., 2004). Stephens et al. (2004), indicated that a duration of at least four years is preferred for research studies investigating complex species community dynamics, like nest predation. A multi-year research study can limited the effect of seasonal variance of biological processes over years and can therefore isolate yearly fluctuations from actual ecological effects (Stephens et al., 2004). Similar recommendations are proposed for the effect of nest site characteristics and habitat selection analyses. Still, this study was able to reveal the importance of both local nest site characteristics and multiscale habitat suitability when investigating predation risk for breeding kingfishers. The three potential predators present in the area, the brown rat, the mustelid species, and the red fox showed noticeable differences in habitat preferences on multiple scales. Species-specific preferences are vital to fully understand the effect of the landscape on the risk of nest predation and is therefore also highly recommended for future research on the effect of local characteristics of breeding locations and predation chance (Menezes & Marini, 2017; Reidy & Thompson III, 2012). Nest predation has been mentioned to be less detrimental and destructive for burrowing bird species in comparison to, for instance, open-nesting birds species (Fulton, 2019; Wilcove, 1985). Nonetheless, both the findings of this study and previous research have indicated that nest predation still negatively affects the breeding success of burrowing birds species and further research on the topic is crucial to fully understand the extent and the working mechanisms of nest predation on burrow-nesting species (Ekanayake et al., 2015; Fulton, 2019; Turčoková, 2016; Wilcove, 1985). Nest predation is a complex, ecological process and many intertwined mechanisms are at play, which are often case-specific (Benson et al., 2010; Cox et al., 2012b; Reidy & Thompson III, 2012). It is therefore of high importance to investigate and handle nest predation accordingly to achieve the best possible conservational efforts for endangered burrowing bird species.

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Appendix

Appendix Table 1: List of all monitored study sites. Per study site is mentioned if the site was taken into account for part 2 of the research and if a Struikrover® was present. Furthermore, days when visual inspection of the nests were performed per month are depicted as well.

Number in Study Map	***Name of location***	***Present in part two of the research***	***Starting date of part two of the research***	***Struikrover present***	***Visual inspection days April***	***Visual inspection days May***	***Visual inspection days June***
1	Muiderslot	✓	12th of April	✓	9th, 12th	2nd, 23rd	7th
2	Eilandseweg	✓	21st of April	X	12th, 21st, 29th	23rd	4th
3	Landgoed Zwaanwyck	X	NA	✓	9th, 12th , 29th	NA	NA
4	De Plantage	X	NA	✓	9th, 29th	NA	NA
5	Van Belle	✓	11th of April	X	11th	2nd, 23rd	4th
6	Fort Nieuwersluis	✓	11th of April	✓	11th	2nd, 21st	4th
7	Fort Kijkuit	✓	11th of April	X	11th, 12th, 29th	21st	4th
8	Wijde Blik, Moleneind	✓	11th of April	✓	11th, 29th	21st	4th
9	Jachthaven Kortenhoef	✓	11th of April	✓	11th, 29th	21st	4th
10	Kasteel Sypesteijn	✓	12th of April	✓	12th, 29th	21st	4th
11	Oud Loosdrechtsedijk	✓	11th of April	✓	11th, 29th	21st	4th
12	Landgoed Spanderswoud	✓	16th of April	✓	16th, 29th	21st	4th

13	Beeldentuin De Zanderij	✓	16th of April	✓	9th, 16th	2nd, 23rd	4th
14	Landgoed de Beek	✓	9th of April	✓	9th, 24th, 29th	23rd	7th
15	Vesting Naarden: Abri	✓	16th of April	X	16th	2nd, 23rd	7th
16	Zanderij Crailo GNR Kantoor	X	NA	✓	NA	NA	NA
17	Zanderij Crailo, Infoschuur	✓	9th of April	✓	9th, 29th	21st	7th
18	Golfbaan Spanderswoud	X	NA	X	12th, 29th	NA	NA
19	Fort Uitermeer	✓	11th of April	✓	9th, 11th, 29th	23rd	4th
20	Van de Wetering	✓	21st of April	✓	12th, 21st, 29th	23rd	4th
21	Landgoed Trompenburgh	✓	2nd of May	✓	NA	2nd, 21st	4th

Appendix Figure 1: A photograph of one of the used Struikrovers®, including the bait used as a scent-marking device.

Appendix Table 2: Table showing all final models, together with the corresponding AIC-values and R^2-values. The R^2-value shown for the GLM models is the Nagelkerke R^2 and for the GLMM models is depicted as the conditional R^2-value. Additional information about of the type of model is also given in the table (GLM or GLMM).

Final models used in multiscale habitat selection	**Model choice**	**AIC-value**	R^2
$Brown\ rat\ presence = \mathbf{-3.490} + (0.672 * water_{200m}) + (-1.403 * RemMMC_{200m}) + (0.459 * water_{500m}) + (-0.394 * forest_{500m}) + (0.669 * RemMMC_{500m}) + (0.475 * agriculture_{500m}) + (0.115 * agriculture_{1000m}) + (-0.786 * MMC_{1000m})$	GLMM	58.2	0.687
$Mustelidae\ presence = \mathbf{-3.421} + (0.789 * water_{200m}) + (-0.00463 * RemMMC_{200m}) + (0.0570 * mmc_{500m}) + (0.626 * agriculture_{500m}) + (-0.717 * mmc_{1000m}) + (0.0453 * agriculture_{1000m}) + (-0.234 * RemMMC_{1000m}) + (-1.107 * dunes_{1000m})$	GLMM	71.0	0.711
$Red\ fox\ presence = \mathbf{-2.948} + (0.562 * water_{200m}) + (-0.047 * RemMMC_{200m}) + (0.267 * water_{500m}) + (\mathbf{0.606} * ReMMC_{500m}) + (0.040 * mmc_{1000m}) + (\mathbf{0.768} * shrub_{1000m}) + (0.440 * marsh_{1000m})$	GLM	60.0	0.449
Final model used in nest site characteristics			
$Predator\ visits = \mathbf{-2.960} + (2.511 * Height_{lowerPart}) + (0.117 * Height_{upperPart}) + (\mathbf{3.023} * Diameter_{nest}) + (\mathbf{-3.520} * Width_{wall}) + (\mathbf{5.975} * Depth_{water}) + (\mathbf{8.989} * Type_{nest})$	GLM	85.0	0.697

Appendix Figure 2: Series of photographs showing the defensive behaviour of one adult kingfisher towards another individual at study site two (Eilandseweg). Photo taken on the 1st of May, around 30 days before the intraspecific competition event.

Appendix Figure 3: Two examples where both breeding walls clearly lack the presence of dense tree roots formations. Both sites were frequently visited by the targeted species as well, but no predation events were observed here. The left picture shows the study site nine (Jachthaven Kortenhoef) with a red fox and the right picture shows study site 12 (Landgoed Spanderswoud) with a pine marten.