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Temporal and spatial variation in the distribution of predators of the Black-tailed Godwit in Southwest Friesland

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Abstract

Vast changes related to increasing anthropisation are occurring in ecosystems across the planet. Nowadays, agriculture, urban areas and infrastructure cover more than 40% of the land surface of the Earth. These areas pose new challenges and sometimes also opportunities for species. In Europe, including the Netherlands, populations of many farmland bird species declined dramatically in the last decades. Besides intensification of agriculture, another factor often mentioned as cause of the decline of meadow breeding bird populations, is increased nest and chick predation. The European Black-tailed Godwit (*Limosa limosa limosa*) is one of those meadow bird species, suffering from population decline. To halt further population declines of Black-tailed Godwits (hereafter called 'godwits') and other Dutch meadow birds, several measures are already being taken, such as the establishment of meadow bird reserves, the implementation of agri-environmental schemes and predator control. However, despite all these measures, the populations of meadow birds continue to decline, and although potential causes are known, it is unknown what exactly makes that in some areas godwits can still sustain themselves, while in others they dwindle. Since 2004, the University of Groningen is conducting research on the demography of the godwit in Southwest Friesland, which has expanded over the years and grew out to be the "Godwit Landscape Project" in which factors within the food web of the godwit are studied in parallel. Key to the project is that the godwit is viewed as a sentinel of sustainable agriculture. Within this "Godwit Landscape Project", I focussed on better understanding top-down processes in the food-web of the godwit. In particular, I aimed to determine temporal and spatial variation in the distribution of both avian and mammalian predators of godwits, their nests, and their chicks. While doing so, I also considered the influence of biological factors such as the presence of prey and different land-use regimes, which could play a role in the distribution of predators. Therefore, we monitored known nest predators (avian and mammalian), and their prey (voles and godwits), throughout different seasons. By relating the presence of godwit families to the distribution of avian predators, we investigated the consequences for godwit pairs that successfully produced offspring. Mammalian predators were monitored by placing camera traps in parcels varying in land-use intensity. By using generalised linear mixed models, we found a significant negative relationship between the abundance of prey (voles and godwits) and land-use intensity. Predator occurrence varied in both time and space. The number of avian predators was greater in winter than in spring and during the chick-phase of godwits. Both avian and mammalian predators had species-specific relationships with land-use intensity, and avian predators had a species-specific relationship with the presence of godwit families. These findings underscore the dynamic nature of predator presence and the intricate relationship between agricultural practices and the composition of the local predator community. The latter suggests that in the protection of meadow birds, one should not focus on predator control exclusively, but rather focus on better understanding the influence of the agricultural landscape in determining predator presence and how land-use can be changed to the meadow-birds' advantage.

Table of contents

Introduction.....	4
Materials and methods.....	5
Study area	5
Research sites selection	5
Monitoring avian predators	6
Monitoring mammalian predators.....	7
Land-use intensity	8
Prey presence.....	9
Voles	9
Godwit breeding pairs	9
Godwit families	9
Analysis.....	9
The relationship between avian predators and LUI and season.....	10
The relationship between mammalian predators, LUI, and season	11
The relationship between LUI and prey presence (voles, godwit breeding pairs, and godwit families)	12
The relationship between avian predators and godwit families	13
Results	13
The relationship between avian predators, season and LUI	13
The relationship between avian predators and season.....	14
The relationship between avian predators and LUI.....	14
The relationship between mammalian predators, season and LUI	15
The relationship between LUI and prey presence	17
The relationship between LUI and voles.....	17
The relationship between LUI and godwit breeding pairs.....	18
The relationship between LUI and godwit families	19
The relationship between avian predators and the presence of godwit families.....	20
Discussion	22
The presence of prey in relation to LUI.....	22
Temporal and spatial variation in the distribution of predators.....	22
Temporal variation.....	22
Spatial variation	23
Relating avian predator presence to godwit breeding success.....	24
Conclusion and future directions.....	25
Policy implications	26
References	26

Introduction

Vast changes related to increasing anthropisation are occurring in ecosystems across the planet (Steffen et al., 2011). Nowadays, agriculture, urban areas and infrastructure cover more than 40% of the land surface of the Earth (Ellis, 2023). These areas pose new challenges and sometimes also opportunities for species (Hunter, 2007). Meadow-breeding birds, traditionally breeding in wet, herb-rich grasslands, at first seemed to profit from changes in agricultural methods (Groen & Hemerik, 2002; Kentie et al., 2013). However in the last decades across Europe populations of many farmland bird species declined dramatically, including the Netherlands (Donald et al., 2001; Roodbergen & Teunissen, 2019; Voříšek et al., 2010). The declines are thought to be mainly caused by the intensification of agriculture (Chamberlain et al., 2000; Donald et al., 2001; Kentie et al., 2013). Agricultural land comprises 65% of the land surface of the Netherlands, of which 54% is grassland (Berkhout et al., 2015; Roodbergen & Teunissen, 2019). Common ground-nesting farmland birds in the Netherlands, such as Northern Lapwing (*Vanellus vanellus*), Eurasian Oystercatcher (*Haematopus ostralegus*), European Black-tailed Godwit (*Limosa limosa limosa*), and Common Redshank (*Tringa totanus*), are mainly dependent on agricultural grassland for breeding habitat (Kentie et al., 2015; Roodbergen & Teunissen, 2019). The intensification of grassland use involves the rapid growth of monotonous, dense vegetation; lower groundwater tables; early and more frequent mowing; the use of pesticides; and an increased use of fertilisers (Groen & Hemerik, 2002; Kentie et al., 2013; Roodbergen & Teunissen, 2019). All these factors can have a negative effect on both nest and chick survival (Van der Wal & Teunissen, 2018). The use of fertilisers leads to dense vegetation which is harder for chicks to move around in, making foraging more difficult (Kentie et al., 2013). Lower groundwater tables and the use of pesticides have been shown to lead to a decrease in the number of insects and early mowing decreases insect availability as food for precocial chicks even further (Kentie et al., 2013; Roodbergen & Teunissen, 2019). Additionally, early mowing during the breeding season can result in nest and chick losses (Kentie et al., 2013).

Besides intensification of agriculture, another factor often mentioned as cause of the decline of meadow breeding bird populations, is increased nest and chick predation. In the last decades, predation on ground-nesting birds by both mammalian and avian predators has increased in the Netherlands (Van der Wal & Teunissen, 2018). Mammals are primarily responsible for egg predation (Teunissen et al., 2008) while chicks are more often taken by avian predators (Schekkerman et al., 2009; Teunissen et al., 2008). In the Netherlands, the most common mammals identified as nest predators are nocturnal and include polecat (*Mustela putorius*), red fox (*Vulpes vulpes*), beech marten (*Martes Foina*) and badger (*Meles meles*). Diurnal avian predators responsible for nest predation include herons, corvids, gulls, and raptors such as western marsh harrier (*Circus aeruginosus*) and common buzzard (*Buteo buteo*) (Hooijmeijer et al., 2024; Teunissen et al., 2008).

While these increased predation rates may partly be explained by an increase and recovery of predator species such as the red fox, badger, beech marten and many birds of prey in the last decades (Thissen & van Norren, 2020), they may also have been enhanced in interplay with the intensification of agriculture (Roodbergen & Teunissen, 2019; Schekkerman et al., 2009). For example, agricultural intensification might have made grasslands more accessible for predators (Kentie et al., 2015). Increased and earlier mowing in monocultures decreases vegetation cover and therefore reduces the availability of safe nesting and foraging sites, and thereby may increase predation rates (Gibbons et al., 2007; Roodbergen & Teunissen, 2019). Furthermore, the lower food availability leads to riskier behaviour of the chicks and longer foraging times, putting them potentially at greater risk of predation (Kentie et al., 2013). Ultimately, through such processes, predation may be a limiting factor in the recovery of the already diminished meadow bird populations or can even cause further declines (Bolton et al., 2007; Malpas et al., 2013; Mason et al., 2018; Schekkerman et al., 2009).

The European Black-tailed Godwit (hereafter “godwit”) is one of those meadow bird species, suffering from a population decline. In the last decades their nest success was too low to maintain a stable number of breeding pairs (Roodbergen & Teunissen, 2019). More than 50 decades ago, the number of breeding pairs in the Netherlands was estimated to be around 100,000 – 120,000 (Groen & Hemerik, 2002). By 2022, those numbers have dwindled to an estimated 27,600 (Schekkerman et al., 2022). The godwit is an iconic wader bird of the Dutch meadows (Roodbergen et al., 2008). The European subspecies is primarily dependent on the Netherlands (Lourenço & Piersma, 2008; Senner et al., 2019), since 85% of this population breeds in the Dutch

agricultural grasslands (Kentie et al., 2015). Since the godwit has similar needs as other meadow birds, it is a good indicator for all meadow bird communities (Waterman et al., 2022).

To halt further population declines of godwits and other Dutch meadow birds, several measures are already being taken, such as the establishment of meadow bird reserves, and the barring and hunting of predators. Since a few decades, the most common conservation measure is the use of agri-environmental schemes (AES). These schemes are implemented to encourage sustainable farming practices for which farmers are financially compensated (Kentie 2013, Roodbergen 2008). Such measures include postponed mowing, creating wet areas, and nest protection. However, AES for the conservation of meadow birds, often showed ineffective in the Netherlands (Kleijn et al., 2006; Roodbergen & Teunissen, 2019), and despite all these measures, the populations of meadow birds continue to decline. Although potential underlying causes of the population declines of meadow birds are known, the precise effects on meadow birds, and how these aspects relate to each other, remain unclear (Kentie et al., 2013; Roodbergen et al., 2008).

In order to take effective measures to conserve the Dutch meadow birds, knowledge is needed about the driving factors of their declines (Kentie et al., 2015). Since 2004, the University of Groningen is conducting research on the demography of the godwit. This was expanded over the years and in 2021 grew out to be the “Godwit Landscape Project” in which all factors within the food web of the godwit are studied in Southwest Friesland, such as insect populations, soil fauna, and predator and prey distribution. Their aim is to link godwit population data to all these factors within its food web. Furthermore, by using the godwit as indicator species, the effects of landscape changes implemented towards developing a more sustainable agriculture can be studied.

Within this “Godwit Landscape Project”, I focussed on better understanding top-down processes in the food-web of the godwit in Southwest Friesland. Specifically, my first aim was to answer the question whether mammalian and avian predator abundance differ spatially within the study area and over the annual seasons. Secondly, I investigated whether the observed spatial variation in predator abundance could be related to variation in land-use intensity and the abundance of prey. Thirdly, I investigated the consequences for godwit families by relating the observed avian predator abundance to the number of godwit pairs that managed to successfully produce offspring. In this way, information is acquired about the relation between predation and the breeding success of godwits, in varying locations and seasons, which in turn could have important implications for the conservation of this iconic Dutch meadow bird.

Materials and methods

Study area

The study was conducted in 2023 in Southwest Friesland, the Netherlands, and consisted of 3244 parcels, divided over sixty-two polders (fig. 1). It spans an area of 11460 hectares and mainly consists of grassland. The management of the parcels ranged from intensive farmland practices to extensively managed farmland such as meadow bird reserves.

Research sites selection

Within the study area fifty-nine camera traps were placed to monitor mammalian predators of which I selected twenty as location for my research (fig. 2). The selection of these locations was mainly based on obtaining a wide variety of land-use intensities between the fields, to be able to relate the abundance of predators to land-use intensity. In addition, I ideally wanted an even distribution across the larger study area and ensure that there was as little overlap of fields as possible. Practical reasons also played a role, such as exclusion of camera locations that were surrounded by water or where other obstacles, such as dikes and forest patches, made avian predator observation difficult. I gathered data around these 20 camera traps in circles of two different spatial scales: 500m and 1000m (for further details on data collection see sections below). To keep the size of the areas equal, the positions of some circles were shifted slightly so that as much land area as possible

belonging to the study area was kept in the circle, instead of, for example, water, buildings, and roads. In addition, for some circles this was also done due to practical considerations, such as the presence of a railway or dike that made counting of avian predators and godwits difficult. In those cases, the camera was no longer the exact centre of the circle.

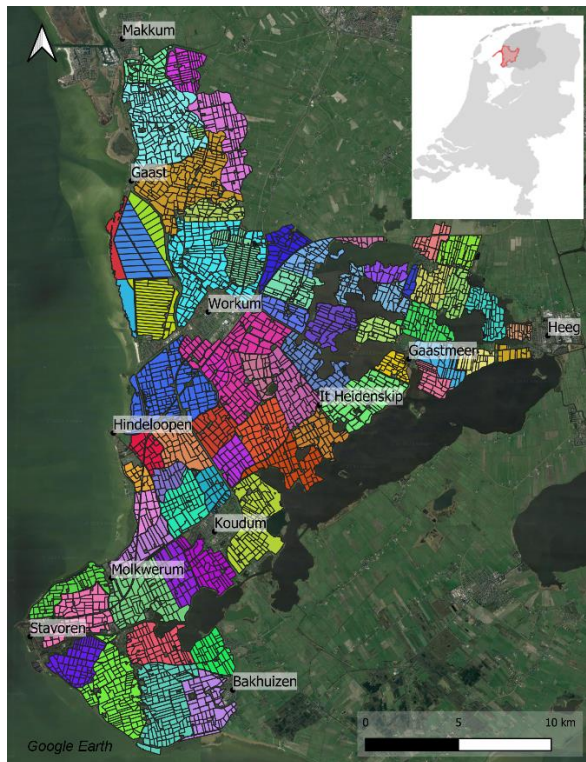


Figure 1. Location of the study area in Southwest Friesland, the Netherlands. The colours depict the sixty-two different polders.

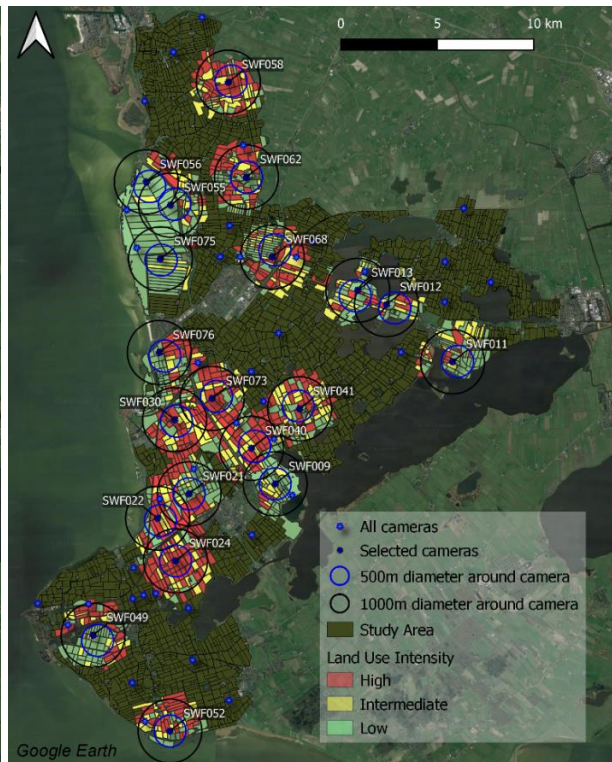


Figure 2. Selected camera trap locations at which the presence of mammalian predators was monitored, within the broader study area. The black-lined circles depict areas with a diameter of 1000m around each selected camera trap, in which I used the data of the numbers of godwit breeding pairs and godwit families, as well as data on the presence of voles. Parcels within these areas were categorised into three levels of land-use intensity, ranging from high to low. In the blue-lined circles, with a diameter of 500m, I collected data on the numbers of avian predators.

Monitoring avian predators

To determine spatial variation in the distribution of avian predators of godwits, I monitored these predators on all parcels within a circular area with a diameter of 500m around each of the twenty selected cameras. Since while being in the field I could not actually envision where this “circle” would be located, I decided to include all parcels of which at least 50% of their area was within the circle, so I could use whole parcels instead as “borders” for the research areas. Within these areas, I counted the number of potential predators of adult godwits, godwit nests, and/or godwit chicks on the included parcels. The decision for predatory species to be included was determined by known potential diurnal avian predators of godwits in the Netherlands (Teunissen et al., 2008); and sightings, nest-camera images and nest predation traces at godwit nests in the study area (Hooijmeijer et al., 2024). See table 1 for a list of these species along with a description of their time of presence in the study area. To determine temporal variation in the distribution of these predators, especially variation between the seasons, I monitored these species in three different periods in 2023, namely in the winter, spring, and during the chick-phase of the godwits. I conducted weekly counts in each area, over the course of three weeks per period: in winter from the 4th to the 26th of February, in spring from the 5th to the 19th of April, and in the chick-phase from the 22nd of May to the 10th of June. The birds were counted by scanning the field with binoculars and/or a bird-watching telescope, where I aimed to look at all the fields

within the circle from one location. However, often I had to relocate to get a better view of certain fields. I usually started by scanning the area for birds (with binoculars) and then used the telescope to zoom in to identify them if necessary. The numbers of large groups of the same species were estimated. In addition to the field in which the bird was located, I also noted the start and end time of each observation session for each monitoring area. When a target bird was only flying by it was not recorded, unless it was scanning for prey, then it was linked to the meadow it was first seen scanning.

Table 1. List of potential diurnal avian predators of godwits, their nests and/or their chicks. Sighting and breeding information based on the information on the websites of Sovon and Vogelbescherming, and in "Vogelgids van Europa" (Sovon Vogelonderzoek Nederland, 2014; Svensson, 2012; Vogelbescherming Nederland, 2009).

Species	Species group	Time period in study area	Breeding season	Greatest encounter chance	Predates godwit eggs / chicks / adults
Carrion Crow (<i>Corvus corone</i>)	Crow	resident	March - June	Year-round	eggs / chicks
Lesser Black-backed Gull (<i>Larus fuscus</i>)	Gull	April - Sept	April - July	April - Sept	eggs / chicks
Grey Heron (<i>Ardea cinerea</i>)	Heron	Jan - June / resident	Feb - May	Year-round	chicks
Great Egret (<i>Ardea alba</i>)		Oct - March, wintering	Does not breed in study area	Oct - March	unknown
Common Buzzard (<i>Buteo buteo</i>)	Raptor	resident	April - May	Year-round	eggs / chicks
Common Kestrel (<i>Falco tinnunculus</i>)		mainly resident	April - July	Year-round	chicks
Western Marsh Harrier (<i>Circus aeruginosus</i>)		March - August	April - June	April - May & Aug - Sept	eggs / chicks
Hen Harrier (<i>Circus cyaneus</i>)		Oct - April	Does not breed in study area	Oct - April	unknown
Northern Goshawk (<i>Accipiter gentilis</i>)		resident	March - May	Year-round	eggs / adults
Peregrine Falcon (<i>Falco peregrinus</i>)		resident	Feb - April	Aug - April	adults

Monitoring mammalian predators

Since 2021, fifty-nine camera traps have been employed each year throughout the study area to monitor mammalian predators, especially in and around the time of the breeding season of the godwits. The locations of the cameras were decided in 2021 by a randomised grid to ensure sampling points were not dependent on variations in the landscape. Each individual camera position (preferably) does not change over the years, making it possible to track changes within the years over time and between the years. The camera traps were placed on access dams to fields, to increase the chance of capturing predators. The camera traps (Browning 2018 Dark Ops Pro XD) were attached to a green dyed metal pole which could be pushed into the ground. The cameras were placed facing northwest-northeast direction to avoid the glare of direct sunlight. The cameras were attached to the pole at a fixed distance of 50cm above the ground (measured to the base of the camera) and slightly tilted downwards, which allowed for a broad range view of the camera trap, as well as accounted for vegetation growth in spring/summer. The camera traps were fitted with protruding metal pins at the top to prevent birds from landing on them. The cameras were set up to take eight sequential pictures when the motion sensor was triggered, after which it had a cooldown time of one second in which it did not respond. The data on the SD cards was uploaded to Agouti, a software package developed by Wageningen University & Research (WUR), and Research Institute Nature and Forest (INBO), which uses artificial intelligence to identify species in photographs. The photos from each SD card were grouped into sequences of two minutes. Since Agouti was not able to correctly identify the species in all cases (accuracy of 87-98% for the most common mammalian predators (Bos et al., 2022)), we manually checked all sequences that Agouti classified to contain predators. The corrections entered in Agouti also ensure that more training data is fed to Agouti, which over time increases its performance. All sequences Agouti could not classify were also manually checked within a

timeframe in which the predators were thought to be predominantly active (19:00 – 04:00 GMT+1). Target mammalian predator species were based on nest-camera images and predator signs at nests in previous years (Hooijmeijer et al., 2024). See table 2 for a list of these species along with a description of their breeding period, home range and ecology. Although domestic dogs (*Canis lupus familiaris*), otter (*Lutra lutra*), and golden jackal (*Canis aureus*) were captured on camera, I did not include these species in the analysis, since nest predation had not been proved (in previous years), and dogs were accompanied by a human and therefore did not have full freedom of movement. In 2021 and 2022, cameras were employed from the end of winter to spring/summer, until the vegetation became too high for the cameras to effectively detect predators. For my study in 2023, to better capture seasonal variation, 59 camera traps were placed from the first week of January 2023, to the second week of June 2023. We analysed the data of twenty of these cameras which I selected as research locations with a diameter of 1km around each camera. We assumed the occurrence of mammalian predators captured on a particular camera, was representative for at least an area with a diameter of 1km around that camera, since the home ranges of these species typically span multiple kilometres (table 2). We replaced the SD card (usually 32GB) and the six AA batteries of each camera every three to four weeks. From May onwards we removed tall vegetation in front of the camera to avoid the sensor being triggered by moving vegetation, but despite this effort moving vegetation still caused SD cards to become full already before the time of pickup in this final measurement month.

Table 2. Potential mammalian predators of godwits, their nests and/or their chicks. Information based on zoogdierverseniging.nl (Zoogdierverseniging, 2024), and (Hooijmeijer et al., 2024). (Specific references added in the table).

Species		Breeding season	Activity	Predates godwit eggs / chicks / adults	Main prey	Home range (Hectares)	Ecology
Domestic Cat (<i>Felis catus</i>)		Feb – Sept (Valentini et al., 2022)	Day and night	eggs / chicks	small mammals (Castañeda et al., 2023)	0.9 – 6.6 (Hanmer et al., 2017)	Carnivore; near (farm) buildings
Beech Marten (<i>Martes foina</i>)		June – Aug	Nocturnal	eggs	small mammals + birds (Czernik et al., 2016)	70 – 80	Omnivore; prefers small-scale agriculture, proximity to farm buildings and landscape elements
Badger (<i>Meles meles</i>)		Early spring - summer	Nocturnal	eggs	earthworms	30 – 150	Omnivore; less active during cold periods in winter; habitat: burrow, proximity to grass and arable land, prefers short grass
Polecat (<i>Mustela putorius</i>)		March – May	Nocturnal (also diurnal when they have young, June – Sept)	eggs	small mammals, eggs, birds, amphibians, reptiles, fruit	8 – 1000	Omnivore, prefers small-scale agriculture, proximity to farm buildings and landscape elements, less active on cold days in winter
Species group: Mustela E/N	Stoat (<i>Mustela erminea</i>)	April	Day and night	eggs	Small mammals: voles, rats, rabbits	4 – 50	Carnivore, habitat diverse, needs enough cover
	Least Weasel (<i>Mustela nivalis</i>)	Feb – April	Diurnal	eggs	voles + birds (Tapper, 1979)	1 – 25	Carnivore, prefers open, dry nature / culture landscapes
Brown Rat (<i>Rattus norvegicus</i>)		March, Sept - Oct	Nocturnal, day active when nights are cold	eggs / chicks	Grains, seeds, snails, larvae, frogs, mammal young, eggs etc	No territory, 100 m on average	Omnivore, in proximity to buildings
Red Fox (<i>Vulpes vulpes</i>)		Dec – Feb	Nocturnal / crepuscular	eggs / chicks	Voiles and hares	0 – 7300 (Trehwella et al., 1988)	Omnivore, opportunist -> habitat diverse

Land-use intensity

In 2016, Howison et al (2018) developed a new remote sensing technique to quantify agricultural land-use intensity (LUI). This radar-based method C-SAR (C-band synthetic aperture radar) captures the quantity and frequency of biomass removal due to mowing. C-SAR values indicate surface roughness and range from 0 to 1, where 0 corresponds to low LUI (high roughness) and 1 to high LUI (low roughness). With this they established an index for the total variation in land-use change per field and associated habitats, classifying the fields into three categories: high, intermediate, or low LUI. My study area was the same as where Howison et al (2018) conducted their research. They obtained index values for each field in 2016. I used those values as those were

ground-truthed using direct observations and measurements, unlike later years. In the study area, this index ranged from 0.044 (associated with nature areas and herb-rich parcels) to 0.72 (associated with monocultures and herb-poor parcels). Within my twenty selected study locations, with each a diameter of 1km, I calculated the weighted average LUI of each location by taking the hectares per field as weight. In my study locations the per location averaged LUI ranged from 0.16 – 0.21 (low), to 0.22 – 0.29 (intermediate), to 0.30 – 0.34 (high).

Prey presence

Voles

Each year, the number of voles was estimated by researchers and field assistants by counting the number of vole holes along three 100m transects per meadow, in 81 fixed, but randomly chosen, meadows along a land-use intensity gradient. The number of voles varies from year to year as they have a cycle of three to four years (Lambin et al., 2006; Smink et al., 2018). In the Netherlands there was an outbreak of voles in 2019-2020, with the core area in Friesland (Wymenga et al., 2021). After the peak year in 2019, numbers were notably low in the years 2021 and 2022 (Hooijmeijer et al., 2023). The breeding season of voles typically runs from about May, and they can give birth to multiple litters, the number of young culminating around September. Therefore, since the observations on voles were carried out in March, the estimates of the vole holes actually say something about the number of voles in the previous year. However, previous years have shown the holes disappear yearly due to (mechanical) disturbances of the fields, making it a suitable method to compare vole holes between years (Hooijmeijer et al., 2024). To determine if there was a relationship between the abundance of voles and the numbers of both avian and terrestrial predators, I used the collected vole data from meadows which were within an area with a diameter of 1km around the twenty selected cameras, as those were the areas in which I monitored avian predators. Since there was only a small number, or only one field per camera location in which the number of voles was counted, I used the average number of vole holes per camera location as a measure for the number of voles.

Godwit breeding pairs

From the 3rd to the 24th of April, researchers and field assistants scanned every parcel in the study area for territorial and non-territorial godwits. These counts were conducted weekly, before 12:00, because after noon godwits are likely to return to their daytime roosts. The number of territorial godwits is a measure of godwit breeding pairs and is used to estimate the size of the breeding population. All godwits are considered to be territorial unless they exhibit clear non-territorial behaviour, such as exclusively foraging in a group or when on a roost. To determine if spatial variation in the distribution of predators was related to the presence of godwit breeding pairs, I used the data on godwit breeding pairs which were collected within an area with a diameter of 1km around the twenty selected cameras. Since every meadow within the study area was scanned for godwit breeding pairs, I used the total count of godwit breeding pairs (averaged over the three weeks in which they were counted) for every camera location for the analysis.

Godwit families

In the first week of June (from the 1st to the 6th) field researchers counted the number of alarming godwit pairs in every meadow. The number of alarming pairs is used as a measure of the number of godwit pairs with offspring (i.e. godwit families), as only godwits with chicks will make these typical alarm sounds. To determine if the spatial distribution of predators was related to the presence of godwits families, I used the data on alarming godwit numbers which were collected within an area with a diameter of 1km around the twenty selected cameras. Since every meadow within the study area was scanned for alarming godwit pairs, I used the total count of alarming godwit pairs for every camera location for the analysis.

Analysis

The data was analysed and mapped using QGIS 3.10.0 software (QGIS Development Team, 2019). I also used this software to outline circles with a diameter of both 500m and 1km diameter around each camera location. A Google Earth satellite image (© 2023) was used as background to create maps of the study area. All statistical analyses were performed using R Statistical Software (version 4.3.1; R Core Team, 2021).

The relationship between avian predators and LUI and season

I used a generalised linear mixed model from the lme4 package (Bates et al., 2015) to describe the relationship between avian predator counts and LUI, season, and the number of voles and godwit breeding pairs (see table 3 for an overview of these variables). The model was generalised since the response variable, the number of avian predators, was count data and not normally distributed. A mixed model was used to be able to include camera location as a random effect, thereby controlling for non-independent sampling as counts were repeated at the 20 fixed camera locations. I used the logarithm of the number of hectares as offset to correct for variation in area size between camera locations. The model was tested for overdispersion with the gof() function of the aods3 package (Lesnoff & Lancelot, 2022), which is a goodness-of-fit test for models with count data. The model was checked for zero inflation with the function testZeroInflation() from the DHARMA package (Hartig, 2022), which compares the observed number of zeros with the expected number of zeros from simulation. To counter overdispersion, I tried to implement an observation level random effect. However, this made the model too complex. Therefore, I instead used a negative binomial model to counter overdispersion. To deal with convergence issues, I used the optimiser “glmerControl(calc.derivs=F)”, thereby reducing the number of additional evaluations. To determine variation between the avian predator species, I divided them into functional groups (see table 3 for the specific species within each group), because individual species made the models too complex. The interactions were tested between each avian predator species group and season, LUI, the number of voles, and the number of godwit breeding pairs. To test the significance of fixed effects and interactions, models were compared by backwards elimination with the anova() function from base R. I used post hoc tests from the emmeans package (Lenth, 2023) for pairwise comparisons between categorical variables. Since I suspected I spent more time counting per location in the beginning of the fieldwork because I still had to get to know the area, I fitted another model in which the counts were corrected by the amount of time spent counting. Since this model and the pairwise comparisons had the same results, I kept the simpler model. To visualise the variation in the distribution of the avian predators, additionally in relation to LUI, I created a histogram of their distribution in QGIS (fig. 3).

Table 3. Overview of variables used in the generalised linear mixed models

Variable	Range / Levels		Details
Response variable:			
Avian pred counts	range:	0 – 9	Number of avian predators counted
Mammalian pred counts	range:	0 – 0.66	Nr of mammalian predators counted, expressed as the fraction of the nr of days a predator was captured on a specific camera in relation to the number of days that camera was deployed
Offset:			
logHA	range (log): hectare range:	5.3 – 6.1 204 – 428	Log of total Hectare of parcels within an area of 1km diameter around each Camera
Predictor variables:			
Random effect:			
Camera location		SWF009 SWF011 SWF012 etc.	ID of each camera location (20 cameras in total)
Fixed effects:			
Avian Species_group		Crow	Carrion Crow
		Gull	Lesser Black-backed Gull
		Herons	Grey Heron & Great Egret
		Raptors	Common Buzzard, Common Kestrel, Western Marsh Harrier, Hen Harrier, Peregrine Falcon, and Northern Goshawk
Mammalian Species_group		Felis catus	Domestic Cat
		Martes foina	Beech Marten
		Meles meles	Badger
		Mustela Putorius	Polecat
		Mustela_E/N	Stoat & Least Weasel
		Rattus norvegicus	Brown Rat
Season			Avian predator dataset:
		winter	4 – 26 Feb
		spring	5 – 19 April
		chick phase of godwits	22 May – 10 June
			Mammalian dataset:
			3 Jan – 20 March
			21 March – 30 April
LUI_continuous	range:	0.158 – 0.339	Mean LUI within an area of 1km in diameter around each camera, expressed in an index ranging from 0 (low LUI) to 1 (high LUI)

LUI_categorical		low	range: 0.16 – 0.21 (LUI continuous)
		intermediate	range: 0.22 – 0.29 (LUI continuous)
		high	range: 0.30 – 0.34 (LUI continuous)
TerrLog	range (log): count range:	2.5 – 5.3 10 – 194	Log of total count of godwit breeding pairs (territorial godwits) on parcels within an area of 1km in diameter around each camera
VoleCount	range:	3 – 103	Mean count of vole holes on parcels within an area of 1km in diameter around each camera
AlarmCount	Range:	1 – 68	Total count of godwit families (alarming godwit pairs) on parcels within an area of 1km in diameter around each camera

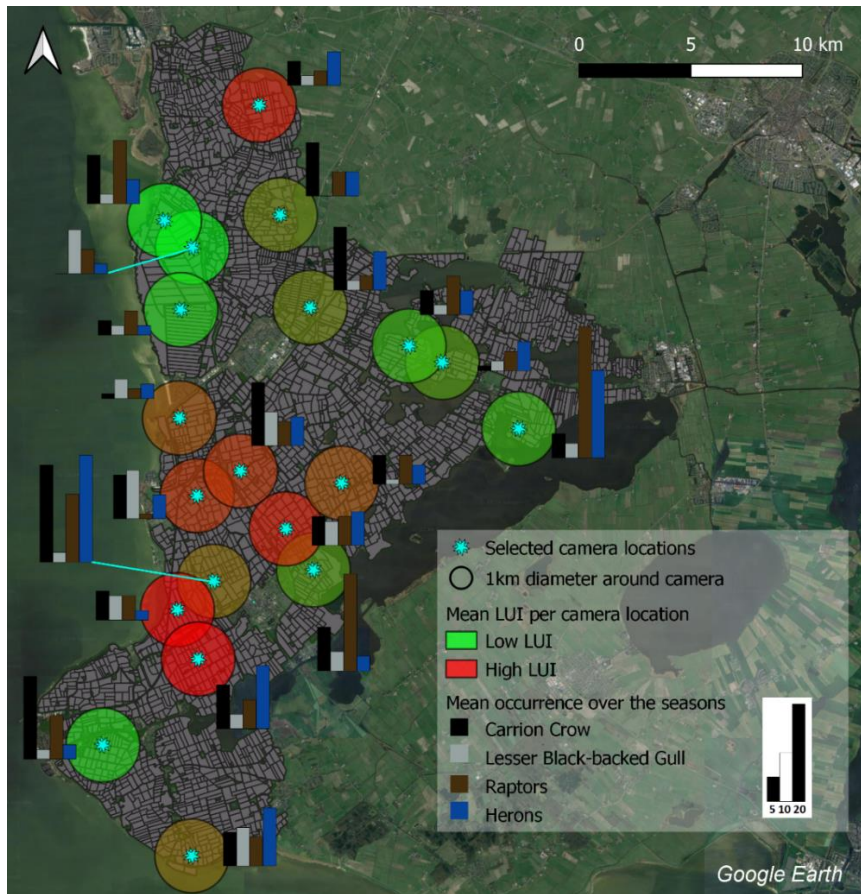


Figure 3. Distribution of avian predator species groups counted at the selected camera locations within the study area. The camera locations are colour scaled by the mean LUI of all parcels within the 1km diameter around each camera, ranging from, CSAR 0.14 (which is in the low LUI category (bright green)) to 0.41 (which is in the high LUI category (bright red)). The histograms give the total number of avian predators counted per camera location, averaged over the seasons.

The relationship between mammalian predators, LUI, and season

I used a binomial generalised linear mixed model to describe the relationship between the number of mammalian predators and LUI, and season. For these variables I used the same data as described in table 3. I only used the data of the seasons winter (January 3rd to March 20th) and spring (March 21th to April 30th), since the tall vegetation during the chick phase caused SD cards to become full, making the data unusable. Camera location was again included as random effect, as well as the logarithm of the number of hectares as offset. The presence of mammalian predators captured by a camera trap, was expressed as the fraction of the number of days a predator species was captured on a specific camera relative to the number of days that camera trap was deployed. Therefore, I used the count of days of the predators, divided by the number of days a camera was deployed, as response variable. Since the response was now a fraction, I used the number of days a camera was deployed in the “weights” argument, which accounts for the number of trials used to generate each fraction. Because the model was too complex and failed to converge with each mammalian species separate, I decided to remove the species with very little data (raccoon dog (*Nyctereutes procyonoides*) and hedgehog (*Erinaceus europaeus*)) and grouped the species least weasel and stoat together (table 2 & 3). To deal with convergence issues, I used the optimiser “glmerControl(calc.derivs=F)”. I checked the model for overdispersion

and zero inflation. To counter overdispersion, I implemented an observation level random effect. The interactions were tested between each mammalian species group and LUI and season. To test the significance of fixed effects and interactions, models were compared by backwards elimination. I used post hoc tests for pairwise comparisons between categorical variables. To visualise the variation in the distribution of the mammalian predators, additionally in relation to LUI, I created a histogram of their distribution in QGIS (fig. 4).

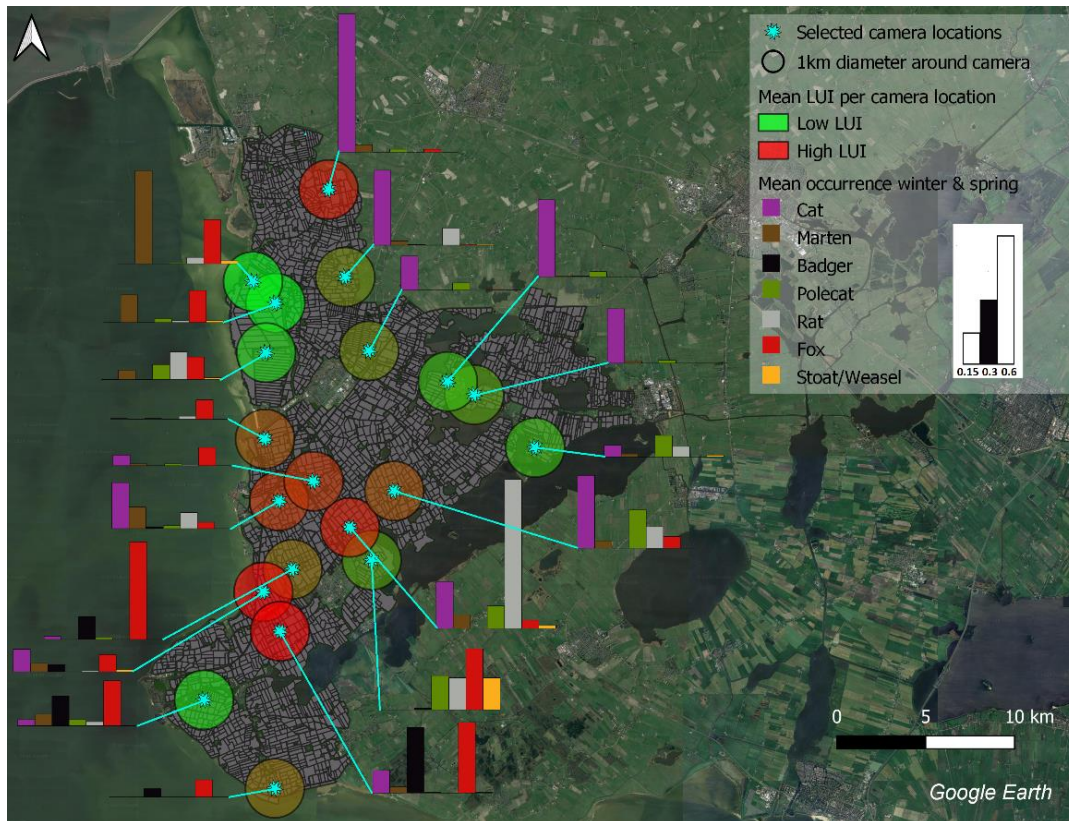


Figure 4. Distribution of mammalian predator species groups counted at the selected camera locations within the study area. The camera locations are colour scaled by the mean LUI of all parcels within the 1km diameter around each camera, ranging from CSAR 0.14 (which is in the low LUI category) to 0.41 (which is in the high LUI category). The histograms give the total number of mammalian predators counted per camera location, averaged over the seasons winter and spring.

The relationship between LUI and prey presence (voles, godwit breeding pairs, and godwit families)

In the model describing the relationship between the number of avian predators and LUI, season, the number of voles, and the number of godwit breeding pairs; voles and godwit breeding pairs were both included as fixed effects, as well as in interaction with species group. In this model, I could link the abundance of avian predators only to other variables that were also collected in the study sites in which I counted avian predators. Therefore, I only used the data on vole counts, godwit breeding pairs, and godwit families that were collected on the parcels within the 1000m diameter circles of my selected research sites. However, I was also interested in general, whether the number of voles and the number of godwit breeding pairs were related to LUI. Since predators were not a variable in this analysis, I was not limited to the data in the twenty selected study sites. Instead, I used the data on voles, godwit breeding pairs, and godwit families from the entire study area. For every prey type (voles, godwit breeding pairs, and godwit families), I created two separate models in which the prey type was the response variable, and either continuous LUI or categorical LUI was the predictor variable. I used generalised linear models since the vole and godwit data were all count data. The models were tested for overdispersion with the “pchisq” function, by comparing the residual deviance with the residual degrees of freedom. In case of overdispersion, a quassipoisson model was used instead of a poisson model. To test the significance of the relationships, the models were tested with the Anova function from the car package (Fox & Weisberg, 2019) with an F-test. The significance of the difference between LUI categories were then evaluated with a post hoc test.

The relationship between avian predators and godwit families

For the analyses of the relationship between avian predators and the number of godwit families, I used the avian predator counts as response variable, and the number of godwit families and avian predator species groups as predictor variables (see table 3 for the details of these variables). I again used a generalised linear mixed model with the logarithm of hectares as offset, and camera location as random effect. The same avian predator dataset was used as mentioned in the previous section. However, I only used the avian predator data collected in the season “chick”, since this was the period in which there were godwit families. I used the optimizer “glmerControl(calc.derivs=F)” to deal with convergence issues. The model was tested for overdispersion and zero inflation as described in the previous section. The significance of the fixed effect of godwit families, and the interaction of godwit families with avian predator counts, was tested by backwards elimination with the anova function. A post hoc test was performed to determine differences in the effect of the presence of godwit families between the species groups.

Results

The relationship between avian predators, season and LUI

A generalised linear mixed model was used to describe the relationship between the number of predators and LUI, season, the number of voles, and the number of godwit breeding pairs. While comparing models to test the significance of fixed effects, it became clear the original full model suffered multicollinearity. The fixed effects LUI and the number of voles were colinear, as were the number of godwit breeding pairs and LUI (fig. 5). Therefore, the independent contribution of the effects of voles and godwit breeding pairs could not be identified for certain; i.e. the effect of both voles and godwit breeding pairs could have been captured by the effect of LUI. Dealing with the multicollinearity, I decided to drop the variables voles and godwit breeding pairs and include only LUI. LUI I then included as a measure which encompassed variation in voles and godwit breeding pairs. The final selected model included a main effect of season, and an effect of the interaction between the predator species group and LUI on the observed predator numbers (table 4). In the next sections I will go more into detail on each of these effects. The variance of the model was partly explained by the random effect of camera location (table 4).

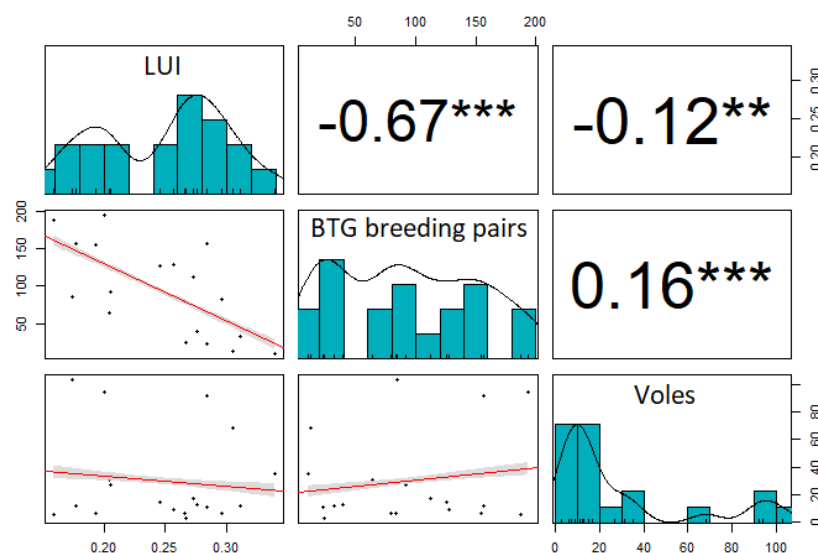


Figure 5. Scatter plots, histograms, and Pearson correlations of the numerical fixed effects (LUI, the number of godwit breeding pairs, and number of voles) of the full model. All pairs were collinear.

Table 4. Random and fixed effects of the final selected model

Random effect:	Name	Variance	Std. Dev.			
Camera location	(intercept)	0.1374	0.3707			
Fixed effects:	Estimate	Std. Error	Chisq	DF	Pr(>Chisq)	Signif. codes
(Intercept)	-7.7689	0.7680				
Season			39.031	2	3.347E-09	***
Seasonspring	0.2270	0.1713				
Seasonwinter	0.9322	0.1594				
Species_groupsHérons	0.2419	0.9171				
Species_groupsLB_Gull	0.4486	0.9855				
Species_groupsRaptors	3.1202	0.8715				
LUI_continuous	5.3962	2.9108				
Species_groups:LUI_continuous			16.111	3	0.001076	**
Species_groupsHérons: LUI_continuous	-1.6226	3.4966				
Species_groupsLB_Gull: LUI_continuous	-4.6617	3.7886				
Species_groupsRaptors: LUI_continuous	-12.6869	3.4098				

Rejected terms: VoleCount, Terr_log, Species_groups:Season

Signif. codes: '***' 0.001, '**' 0.01, '*' 0.05, '.' 0.1

The relationship between avian predators and season

The comparison between a model including "season" as interaction with "species group" and a model without this interaction, showed the model with this interaction was not significantly better ($\chi^2 = 6.40$, $df=6$, $p=0.38$), and was therefore dropped from the model. This means the interaction between season and species group did not have a significant effect on the number of avian predators; i.e. the effect of season on avian predator counts was not significantly different between the species groups. A model without this interaction, but with season as fixed effect was significantly better than a model without both "season" as interaction and season as fixed effect. Thus, the fixed effect of "season" was significant (table 4). The pairwise comparison showed the number of avian predators was significantly lower in both spring and chick-phase compared to winter, while the number of predators did not differ between spring and the chick phase (table 5 and fig. 6).

Table 5. Post hoc results of the pairwise comparison between seasons

Contrast	Estimate	SE	df	z.ratio	p.value	Sign. codes
chick - spring	-0.227	0.171	Inf	-1.325	0.3811	
chick - winter	-0.932	0.159	Inf	-5.849	<.0001	***
spring - winter	-0.705	0.153	Inf	-4.609	<.0001	***

Signif. codes: '***' 0.001, '**' 0.01, '*' 0.05, '.' 0.1

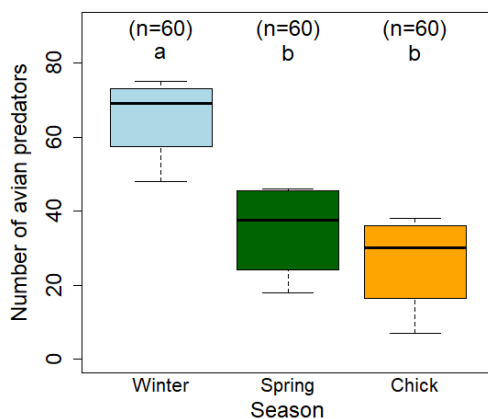


Figure 6. Counts of avian predators per season. Letters indicate which seasons differed significantly between each other.

The relationship between avian predators and LUI

The comparison between a model with the fixed effect of LUI as interaction with species groups was significantly better than a model without this interaction (table 4). Thus, the interaction between LUI and species groups had a significant effect on the number of avian predators. This means the effect of LUI on avian predator counts differed significantly between the species groups (fig. 7). A post hoc test was performed to determine differences in the effect of LUI between the species groups. This showed that raptor numbers declined with an increase in LUI, while the other species groups showed a positive trend in their relationship

with LUI. When examined in detail, the raptor numbers differed significantly in their relationship with LUI from crows and herons (table 6).

Table 6. Post hoc results of the pairwise comparison between avian predator species groups

Contrast	Estimate	SE	df	z.ratio	p.value	Signif. codes
Crow - Herons	1.62	3.50	Inf	0.464	0.9669	
Crow - LB_Gull	4.66	3.79	Inf	1.230	0.6074	
Crow - Raptors	12.69	3.41	Inf	3.721	0.0011	**
Herons - LB_Gull	3.04	3.84	Inf	0.792	0.8582	
Herons - Raptors	11.06	3.46	Inf	3.195	0.0076	**
LB_Gull - Raptors	8.03	3.75	Inf	2.138	0.1410	

Signif. codes: '***' 0.001, '**' 0.01, '*' 0.05, '.' 0.1

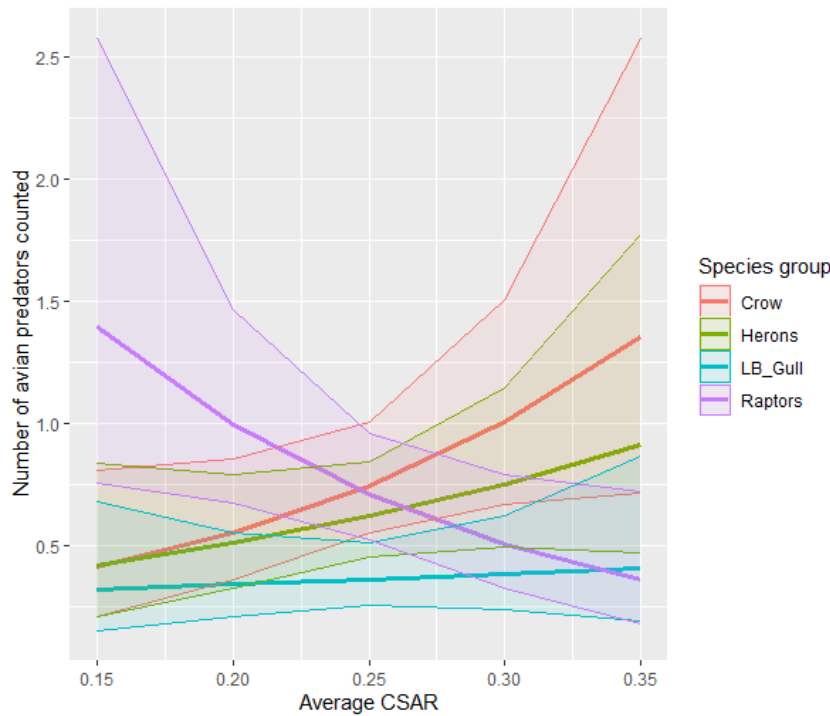


Figure 7. The effect of LUI on the number of avian predators in different species groups. LUI ranges from 0.158 (low LUI) to 0.339 (high LUI). The coloured ribbons indicate the upper and lower limits of the 95% confidence interval.

The relationship between mammalian predators, season and LUI

The comparison between a model including "season" as interaction with mammalian "species group" and a model without this interaction, showed the model with this interaction was not significantly better ($X^2=1.91$, $df=6$, $p=0.93$), and was therefore dropped from the model. This means that the interaction between season and species group did not have a significant effect on the number of mammalian predators, i.e. the effect of season on mammalian predator counts was not significantly different between the species groups. A model without this interaction, but with season as fixed effect was not significantly better than a model without season ($X^2= 0.10$, $df=1$, $p=0.75$). Thus, the fixed effect of season was not significant either, and therefore dropped from the model. The comparison between a model including LUI as interaction with mammalian species group and a model without this interaction, showed the model with this interaction was significantly better (table 9). This means the interaction between LUI and species group had a significant effect on the number of mammalian predators; i.e. the effect of LUI on mammalian predator counts was significantly different between the mammalian species groups (fig. 8). When examined in detail with a post hoc test, badger occurrence differed significantly in its relationship with LUI from beech martens, polecats, and brown rats, in which badgers showed a positive relation to LUI. Domestic cats showed a positive trend with LUI, and differed from beech martens, polecats, and brown rats as well (table 10).

Table 9. Fixed effects of the final selected model

	Estimate	Std. Error	df	Chisq	Pr(>Chisq)	Sign. codes
(Intercept)	-13.014	1.931				
Species_groupMartes foina	5.625	2.548				
Species_groupMeles meles	-5.833	3.263				
Species_groupMustela_E/N	0.275	2.586				
Species_groupMustela putorius	5.453	2.638				
Species_groupRattus norvegicus	5.819	2.619				
Species_groupVulpes vulpes	3.047	2.514				
LUI_continuous	17.557	7.345				
Species_group:LUI_continuous			6	24.065	0.0005082	***
Species_groupMartes foina:LUI_continuous	-27.774	9.893				
Species_groupMeles meles:LUI_continuous	12.461	12.06				
Species_groupMustela_E/N:LUI_continuous	-20.888	10.029				
Species_groupMustela putorius:LUI_continuous	-28.866	10.291				
Species_groupRattus norvegicus:LUI_continuous	-28.668	10.221				
Species_groupVulpes vulpes:LUI_continuous	-12.947	9.643				

Rejected terms: Species_groups:Season, Season

Signif. codes: '***' 0.001, '**' 0.01, '*' 0.05, '.' 0.1

Table 10. Post hoc results of the pairwise comparisons between mammalian species groups

Contrast	Estimate	SE	df	z.ratio	p.value	Sign. codes
Felis catus - Martes foina	27.774	9.89	Inf	2.808	0.0740	.
Felis catus - Meles meles	-12.461	12.06	Inf	-1.033	0.9464	
Felis catus - (Mustela_E/N)	20.888	10.03	Inf	2.083	0.3629	
Felis catus - Mustela putorius	28.866	10.29	Inf	2.805	0.0746	.
Felis catus - Rattus norvegicus	28.668	10.22	Inf	2.805	0.0746	.
Felis catus - Vulpes vulpes	12.947	9.64	Inf	1.343	0.8318	
Martes foina - Meles meles	-40.235	12.08	Inf	-3.330	0.0152	*
Martes foina - (Mustela_E/N)	-6.887	9.98	Inf	-0.690	0.9932	
Martes foina - Mustela putorius	1.092	10.19	Inf	0.107	1	
Martes foina - Rattus norvegicus	0.893	10.06	Inf	0.089	1	
Martes foina - Vulpes vulpes	-14.828	9.57	Inf	-1.549	0.7147	
Meles meles - (Mustela_E/N)	33.348	12.14	Inf	2.748	0.0868	.
Meles meles - Mustela putorius	41.327	12.38	Inf	3.337	0.0148	*
Meles meles - Rattus norvegicus	41.128	12.29	Inf	3.347	0.0143	*
Meles meles - Vulpes vulpes	25.407	11.81	Inf	2.152	0.3223	
(Mustela_E/N) - Mustela putorius	7.978	10.35	Inf	0.771	0.9877	
(Mustela_E/N) - Rattus norvegicus	7.78	10.23	Inf	0.760	0.9886	
(Mustela_E/N) - Vulpes vulpes	-7.941	9.7	Inf	-0.819	0.9831	
Mustela putorius - Rattus norvegicus	-0.198	10.44	Inf	-0.019	1	
Mustela putorius - Vulpes vulpes	-15.919	9.97	Inf	-1.597	0.6845	
Rattus norvegicus - Vulpes vulpes	-15.721	9.85	Inf	-1.596	0.6851	

Signif. codes: '***' 0.001, '**' 0.01, '*' 0.05, '.' 0.1

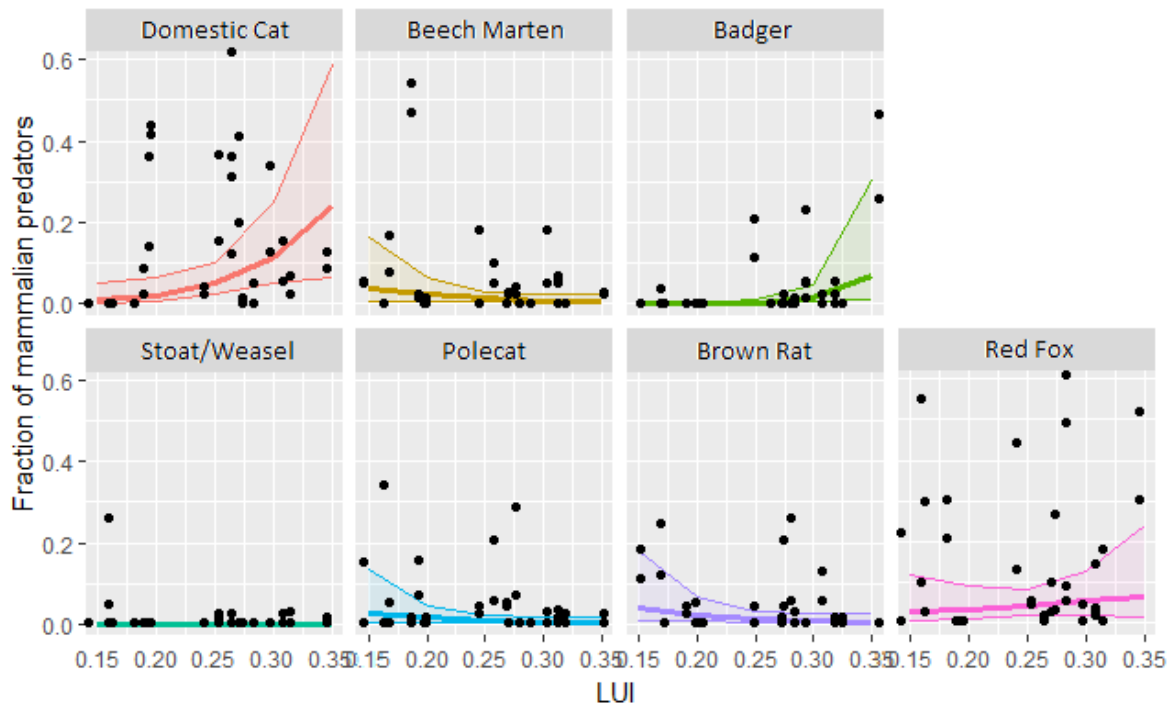


Figure 8. The effect of LUI on the number of mammalian predators in different species groups. Black dots show the observed data, colours indicate predicted lines with confidence intervals. Badgers differed significantly from beech martens, polecats, and brown rats; and domestic cats showed a positive trend with LUI, that differed from beech martens, polecats, and brown rats as well.

The relationship between LUI and prey presence

The relationship between LUI and voles

LUI had a significant effect on the number of voles, with vole numbers decreasing with an increase in LUI (table 11 and fig. 9a). The numbers of voles also differed significantly between LUI when LUI was included as a categorical variable (table 11 and fig. 9b). The number of voles was greater on parcels with a low LUI than on high LUI parcels, and greater on intermediate LUI parcels than on high LUI parcels (table 12).

Table 11. Coefficients of the model with the continuous LUI variable as predictor

Model with LUI_continuous as predictor variable	Estimate	Std. Error	df	F value	Pr(>F)	Sign. codes
(Intercept)	3.733	0.322				
LUI_continuous	-2.812	1.324	1	4.6611	0.03184	*
Model with LUI_categorical as predictor variable	Estimate	Std. Error	df	F value	Pr(>F)	Sign. codes
(Intercept)	2.3478	0.2916				
LUI_categorical			2	5.7287	0.003712	**
LUI_categorical Intermediate	1.0543	0.3409				
LUI_categorical Low	0.8355	0.3449				

Signif. codes: '****' 0.001, '***' 0.01, '**' 0.05, '.' 0.1

Table 12. Post hoc results of the pairwise comparisons between LUI categories

Contrast	Ratio	SE	df	z.ratio	p.value	Sign. codes
High - Intermediate	0.348	0.119	Inf	-3.092	0.0056	**
High - Low	0.434	0.150	Inf	-2.422	0.0408	*
Intermediate - Low	1.245	0.318	Inf	0.857	0.6672	

Signif. codes: '****' 0.001, '***' 0.01, '**' 0.05, '.' 0.1

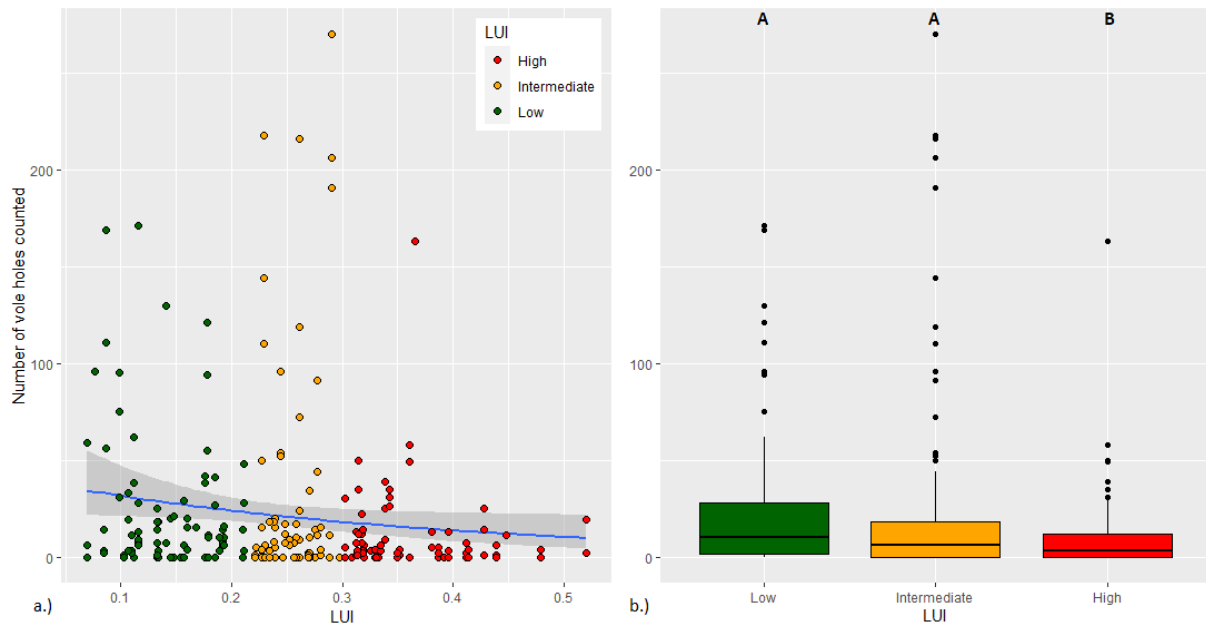


Figure 9(a) The number of vole holes counted along an LUI gradient (CSAR). The negative relation between the number of voles and LUI was significant ($p < 0.05$). (b) Boxplots of the number of voles per LUI category. Letters indicate which LUI categories differed significantly between each other.

The relationship between LUI and godwit breeding pairs

LUI had a significant effect on the number of godwit breeding pairs, with the number of breeding pairs decreasing with an increase in LUI (fig. 10a and table 13). The numbers of godwit breeding pairs differed significantly between the LUI categories (fig. 10b and table 13), where the number of godwit breeding pairs was greater on fields with low LUI than on fields with high LUI (table 14).

Table 13. Coefficients of both models

Model with LUI_continuous as predictor variable	Estimate	Std. Error	df	F value	Pr(>F)	Sign. codes
(Intercept)	1.46753	0.08119				
LUI_continuous	-1.27875	0.35344	1	12.098	0.0005371	***
Model with LUI_categorical as predictor variable	Estimate	Std. Error	df	F value	Pr(>F)	Sign. codes
(Intercept)	0.94288	0.09905				
LUI_categorical			2	6.898	0.001082	**
LUI_categorical Intermediate	0.18829	0.13394				
LUI_categorical Low	0.37904	0.11044				

Signif. codes: '***' 0.001, '**' 0.01, '*' 0.05, '.' 0.1

Table 14. Post hoc results of the pairwise comparisons between LUI categories

Contrast	Ratio	SE	df	z.ratio	p.value	Sign. codes
High - Intermediate	0.828	0.1110	Inf	-1.406	0.3379	
High - Low	0.685	0.0756	Inf	-3.432	0.0017	**
Intermediate - Low	0.826	0.0847	Inf	-1.860	0.1504	

Signif. codes: '***' 0.001, '**' 0.01, '*' 0.05, '.' 0.1

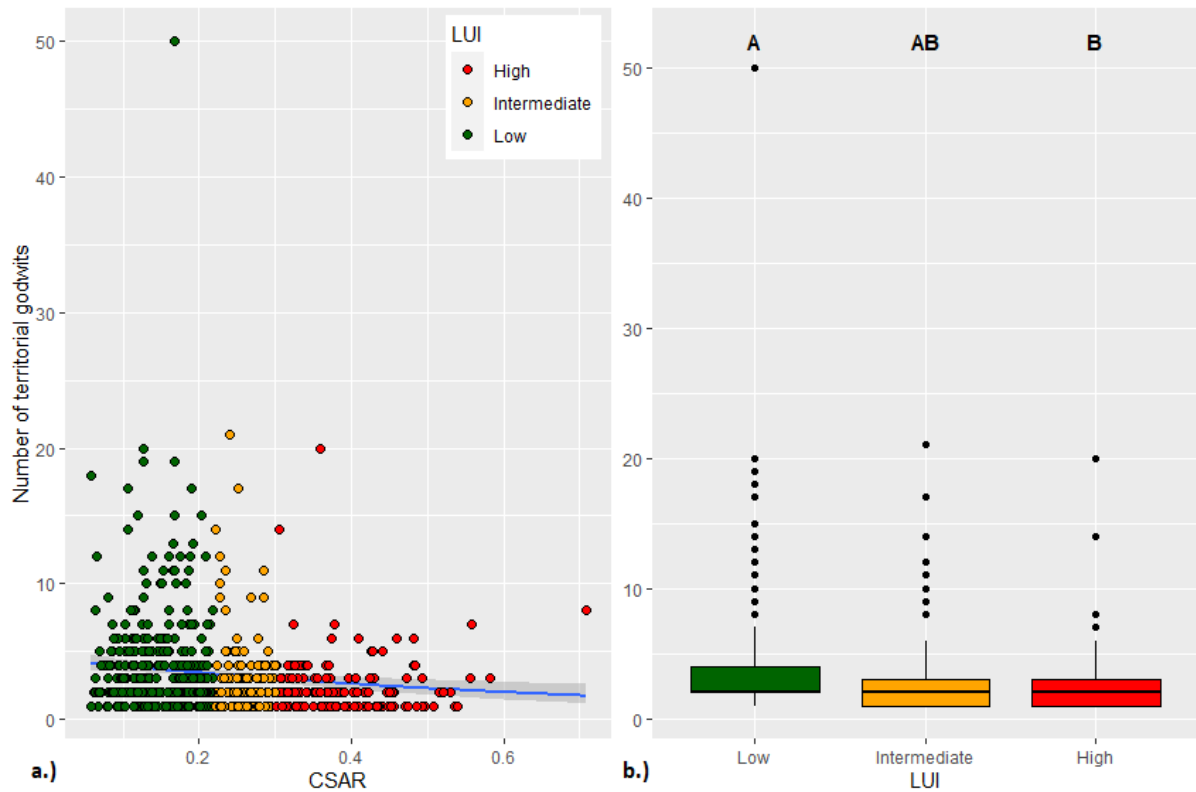


Figure 10(a) The number of godwits breeding pairs along an LUI gradient. The negative relation between the number of godwit breeding pairs and LUI was significant ($p < 0.001$). (b) Boxplots of the number of godwit breeding pairs per LUI category. Letters indicate which LUI categories differed significantly between each other.

The relationship between LUI and godwit families

LUI had a significant effect on the number of godwit families, with the number of godwit families decreasing with an increase in LUI (fig. 11a and table 15). The numbers of godwit families differed significantly between the LUI categories (fig. 11b and table 15), where the number of godwit families was greater on parcels with low LUI than on parcels with both high LUI and intermediate LUI. The number of godwit families was also greater on intermediate LUI parcels than on parcels with high LUI (table 16).

Table 15. Coefficients of both models

Model with LUI_continuous as predictor variable	Estimate	Std. Error	df	LR Chisq	Pr(>Chisq)	Sign. codes
(Intercept)	-0.2451	0.1061				
LUI_continuous	-7.3489	0.5081	1	256.12	< 2.2e-16	***
Model with LUI_categorical as predictor variable	Estimate	Std. Error	df	LR Chisq	Pr(>Chisq)	Sign. codes
(Intercept)	-3.2673	0.1474				
LUI_categorical			2	246.2	< 2.2e-16	***
LUI_categorical Intermediate	1.2082	1.1784				
LUI_categorical Low	1.9624	0.1570				

Signif. codes: '***' 0.001, '**' 0.01, '*' 0.05, '.' 0.1

Table 16. Post hoc results of the pairwise comparisons between LUI categories

Contrast	Ratio	SE	df	z.ratio	p.value	Sign. codes
High - Intermediate	0.299	0.0533	Inf	-6.771	<.0001	***
High - Low	0.141	0.0221	Inf	-12.496	<.0001	***
Intermediate - Low	0.470	0.0537	Inf	-6.608	<.0001	***

Signif. codes: '***' 0.001, '**' 0.01, '*' 0.05, '.' 0.1

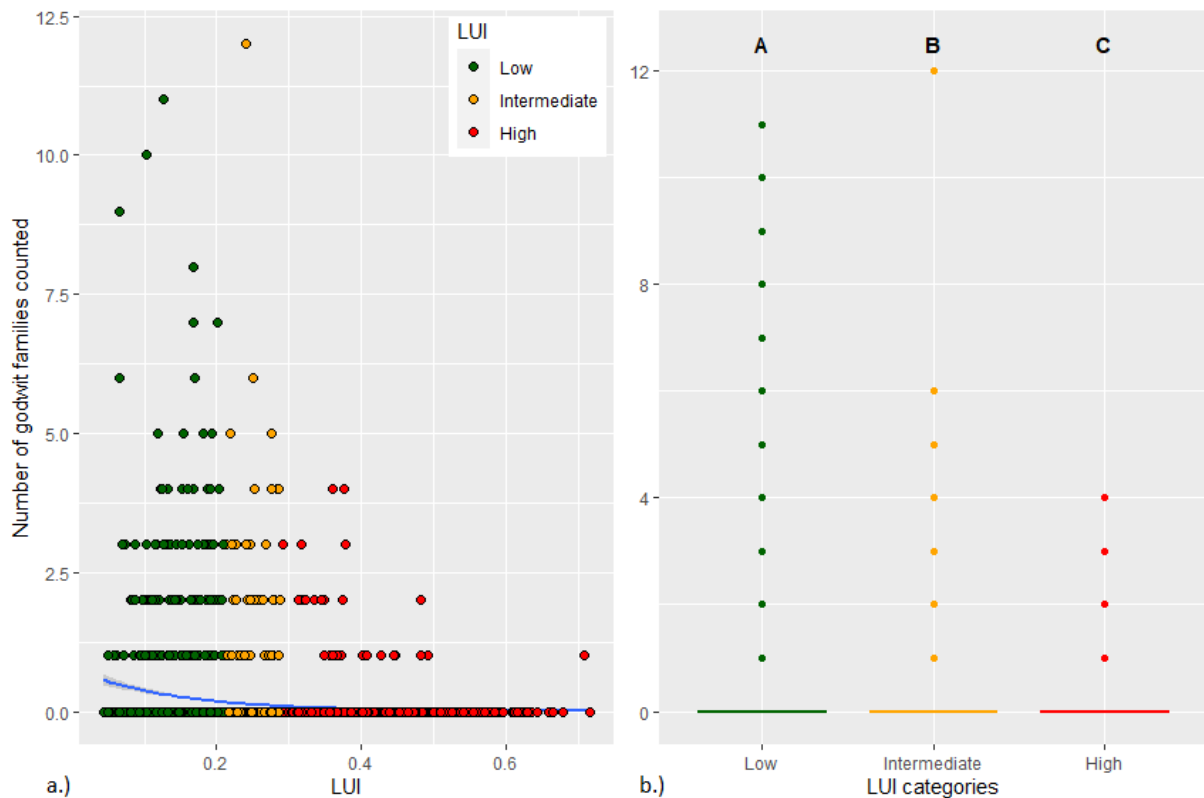


Figure 11(a) The number of godwit families counted, along an LUI gradient. The negative relation between the number of godwit families and LUI was significant ($p < 0.001$). (b) Boxplots of the number of godwit families per LUI category. Letters indicate which LUI categories differed significantly between each other.

The relationship between avian predators and the presence of godwit families

A generalised linear mixed model was used to describe the relationship between the number of predators and the number of godwit families. Initially, I also wanted to include the fixed effects of LUI and voles in this model again, but since LUI and voles proved to be collinear in the previous analyses (of the relationship between the number of predators and LUI, season, the number of voles, and the number of godwit breeding pairs), I dropped voles from the model. Also in this model, godwit families and LUI were collinear (fig. 12), therefore I dropped LUI from the model. I did not include godwit breeding pairs in the model this time, because for this analysis I was interested in the effect of godwits with nests and chicks alone to determine variation in the distribution of predators in relation to the presence of godwit families. Therefore, I only used the data of the chick-phase. The comparison between a model including the number of godwit families as interaction with species group and a model without this interaction, showed the model with this interaction was significantly better (table 7). This means the interaction between the number of godwit families and species group had a significant effect on the number of avian predators, i.e. the effect of godwit families on avian predator counts differed significantly between the avian predator species groups (fig. 13). When examined in detail with a post hoc test, the raptors differed significantly in their relationship with godwit family counts from herons (table 8).

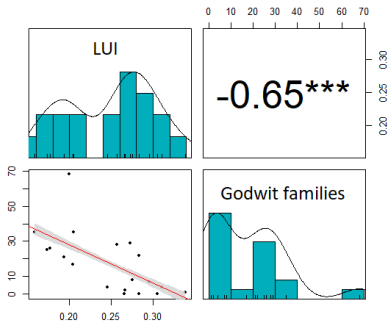


Figure 12. Scatterplot, histograms, and Pearson correlation of the fixed effects LUI and godwit families

Table 7. Fixed effects of the final selected model

	Estimate	Std. Error	Chisq	df	Pr(>Chisq)	Sign. codes
(Intercept)	-6.651958	0.338094				
Species_groupsHérons	-0.048543	0.440851				
Species_groupsLB_Gull	-2.017747	0.683486				
Species_groupsRaptors	-0.737173	0.461267				
AlarmCount	-0.001264	0.014263				
Species_groups:AlarmCount			9.8931	3	0.0195	*
Species_groupsHérons:AlarmCount	-0.015150	0.020686				
Species_groupsLB_Gull:AlarmCount	0.028006	0.022449				
Species_groupsRaptors:AlarmCount	0.037136	0.016957				

Signif. codes: '***' 0.001, '**' 0.01, '*' 0.05, '.' 0.1

Table 8. Post hoc results of the pairwise comparisons between avian predator species groups

Contrast	Estimate	SE	df	z.ratio	p.value	Sign. codes
Crow - Herons	0.01515	0.0207	Inf	0.732	0.8841	
Crow - LB_Gull	-0.02801	0.0224	Inf	-1.248	0.5965	
Crow - Raptors	-0.03714	0.0170	Inf	-2.190	0.1259	
Hérons - LB_Gull	-0.04316	0.0249	Inf	-1.733	0.3062	
Hérons - Raptors	-0.05229	0.0201	Inf	-2.607	0.0451	*
B_Gull - Raptors	0.00913	0.0214	Inf	-0.427	0.9739	

Signif. codes: '***' 0.001, '**' 0.01, '*' 0.05, '.' 0.1

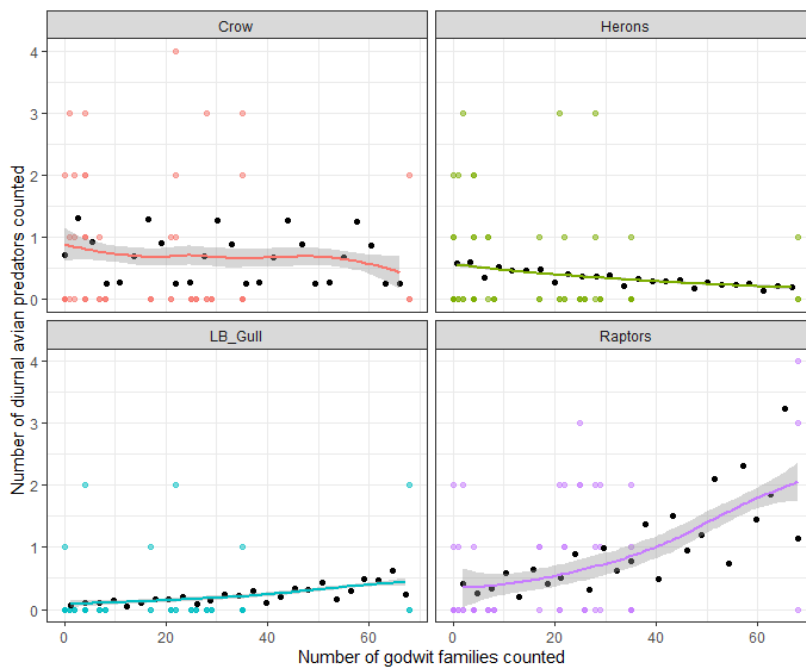


Figure 13. The effect of the presence of godwit families on the number of avian predators in different species groups. Black dots indicate predicted values.

Discussion

The black-tailed godwit, which is seen as a sentinel of sustainable agriculture, is suffering population declines. Besides intensification of agriculture, another factor often mentioned as a cause of the decline of meadow breeding bird populations, is increased nest and chick predation. In this study, I focussed on better understanding these top-down processes in the food-web of the godwit. In particular, I modelled the temporal and spatial variation in the distribution of avian and mammalian predators, in relation to LUI and prey (voles and godwits) presence. Since LUI and prey turned out to be collinear, I dropped the prey variables from these models. However, I was still interested in the effect of the presence of prey, and since this turned out to be strongly related to LUI, I decided to create models to investigate these relationships further, in which I related the separate prey species to LUI. Here, I first discuss the findings of these models, since the distribution of predators is often influenced by the abundance of prey, which in turn appears to be dependent on LUI. Then, I discuss the temporal variation of both avian and mammalian predators, which differed between the seasons for avian predators. After that I discuss the spatial variation of avian and mammalian predators, which both had species-specific relationships with LUI. Lastly, I discuss the consequences for godwit families, by relating the observed avian predator abundance to the number of godwit breeding pairs that successfully managed to produce offspring.

The presence of prey in relation to LUI

The abundance and distribution of the monitored prey, godwits and voles, all seem to be influenced by the agricultural land-use intensity (LUI). Both the number of godwit breeding pairs, and the number of godwit families, decreased with an increase in LUI. This is in accordance with the expectation that godwits select parcels with a low LUI over meadows with a high LUI (Howison et al., 2018). However, godwits are loyal to their nesting site and often return to the nest site of the previous year(s) (van den Brink et al., 2008). Due to changes in management, some sites, which godwits already chose for breeding, have become more extensive. Therefore, it is hard to say whether godwits breeding in these extensive areas selected for low LUI, or whether this is a result of site-faithfulness. To that end, it would be advisable to monitor the choices of newly settling godwits and the smaller site movements of adult godwits. The fact that there were more godwit families in low LUI areas can partly be explained by the higher number of breeding pairs in these areas, since there were more nests in these areas to begin with. Therefore, to determine whether godwit breeding success is greater in areas with low LUI than in high LUI, it would be preferable to measure relative nest success. This can be accomplished by calculating the gross territorial success, which is the number of successful nests, divided by the total number of nests. However, this is not possible on the parcel level (due to movements of the godwits), and therefore not possible within the scope of my research. Nevertheless, the apparent selection for low LUI parcels, could also be explained by the fact that those would be a favourable choice for a nesting site. Factors associated with high LUI parcels, such as dense vegetation, low water tables, lower food availability, and early mowing, have negative consequences for godwit chicks. Consequently, low LUI would be a better habitat for chicks, and would thus be a favourable breeding site. The abundance of voles was also greater in low LUI parcels than in high LUI parcels, which was to be expected as voles are most abundant in undisturbed areas with dense, tall vegetation (Laidlaw et al., 2019). This is also in line with the findings in previous years, where there was a negative trend with LUI (Hooijmeijer et al., 2024).

Temporal and spatial variation in the distribution of predators

Temporal variation

The monitored avian predator species differed in the duration of their presence in the study area and the timing of their breeding season (see table 1) and thus I expected the relative abundance between the different species groups to be different. However, the effect of season on avian predator counts was not significantly different between the species groups. This might be explained by the way I divided the species into groups for analysis purposes. For example, harriers are only present from spring onwards, and great egrets only in winter, but because they are grouped together with other species this is no longer distinguishable. Although there was

not a significant difference in seasonal occurrence between the species groups, the total number of avian predators was significantly lower in both spring and chick-phase compared to winter. Except for great egrets and hen harriers that do not breed in the study area, and Peregrine Falcons who breed in the winter and spring, all other monitored avian predators, breed in the spring and chick phase of the godwits (see table 1). This might explain why more avian predators were counted in winter, since they are not investing time and energy in breeding yet (and therefore neither parent is on the nest), so they can spend more time hunting or foraging, increasing the encounter chance. Another reason could be a possible influx to the study area of individuals that spend the winter, but breed in another area and are therefore no longer seen after the winter. However, the increase in vegetation and vegetation height could have made it more difficult to spot birds who are usually on the ground, in the spring and chick phase, which might have skewed the results in favour of winter. Another point to note is that I did not take variations in daily activity of the avian predators into account. For instance, Tiwari et al (2022) found that the detection chance of raptors such as hen harrier, common buzzard, and common kestrel, was greater around sunrise. Therefore, it would be advisable to randomize the time of day in which the different study locations would be monitored for avian predators, in such a way that each location is visited at different times of the day.

Food availability in the meadows was likely lower in winter, since many meadow bird species only start breeding from April on, and the number of voles is lower in winter than in spring (Wymenga et al., 2015). Combined with the assumption that mammalian predator species are less active in winter (Noonan et al., 2014; Zoogdierverseniging, 2024), I expected a lower mammalian predator count in winter. However, there were no differences in the relative abundance of mammalian predators between winter and spring. This could be due to the very mild winter we had this year, with a Hellman cold number of 9.6 (based on the daily temperatures from the weather station Stavoren from November 1st 2023 to March 31st 2024) (KNMI, 2021). The Hellman cold number is a cold index which ranges from harsh (>300) to mild winters (<100). Therefore, the activity of both predators and prey might not have been affected as much as a cold winter might have. Furthermore, I also had expected seasonal differences between the mammalian predator species. For instance, the monitored predator species have different timings of their breeding seasons (see table 2). Male mammalian predators are influenced by the breeding seasons in which they usually cover a larger distances to find a mate (Henry et al., 2005), whereas the home range size of females is often reduced during the breeding phase (Travaini et al., 1993). However, the abundance of the different monitored predators did not change between seasons. I would also have expected a difference in abundance of mammalian predators between the winter and spring, and the chick-phase of the godwits, since mammalian predators might be attracted by this new alternative food source (Lima, 2009). However, we removed the camera traps in the chick-phase, due to tall vegetation causing the SD cards to become full. Therefore, we had no usable data on the number of mammalian predators in the chick-phase.

Spatial variation

The abundance of prey is an important driver for the distribution of predators (Carricondo-Sanchez et al., 2016), and since the abundance of both voles and godwits was greater in parcels with a low LUI, I expected predator abundance also to be greater in low LUI parcels. However, for avian predators, this was only the case for raptors. Among the monitored raptors, common buzzard, common kestrel, western marsh harrier and hen harrier, are to a large extent dependent on voles (Wymenga et al., 2015), which could explain the negative relation of raptors with LUI, since vole numbers were significantly higher in low LUI areas. Furthermore, raptors such as common buzzard, common kestrel, and peregrine falcon, are known to hunt from perches (e.g. fence posts) (Vogelbescherming Nederland, 2009) and as (Widén, 1994) et al found, areas with perches are preferred over areas without perches. This could also be a factor in the selection for low LUI areas, since in this study area, low LUI areas hold more perches (personal observations), possibly due to the fact that these areas more often have a dual use and are grazed by livestock before and after the meadow bird breeding season. Whereas much of the intensive areas are used predominantly for grass production and thus fences are not needed. Raptors differed significantly from both crows and herons, which had a positive relation with LUI. Herons in the study area seem to be most abundant near lakes (see fig. 3), which conforms with their habitat needs, for they are dependent on wetland areas and their diet consists mainly of aquatic creatures (Sovon Vogelonderzoek Nederland, 2014; Voslamber et al., 2010). Their positive relation with LUI might also be in line with this, since water levels adjacent to or near high LUI parcels are usually low (Groen et al., 2012; Hooijmeijer et al., 2024), providing the herons with suitable foraging sites (Vogelbescherming Nederland, 2009; Voslamber et al., 2010). Many bird species, including crows, gulls, and herons, are attracted to agricultural activities such as manuring and mowing. Manuring can temporarily increase prey availability, and mowing improves prey accessibility and

availability, and provides better visibility and mobility for foragers (Aguilera et al., 2021; Devereux et al., 2006). Furthermore, birds such as corvids, gulls, and herons are known to switch to voles as their prey when voles are abundant, especially after mowing events (Wymenga et al., 2015). Since the frequency of these agricultural activities is often greater on high LUI parcels, this might explain their (temporal) selection for these areas. However, in contrast to crows and herons, gulls did not show a positive relationship with LUI. This is interesting, as I would have especially expected gulls to have a positive relationship with LUI since their distribution is linked to human activities (Sotillo et al., 2019), and thus I had expected them to be mainly present in high LUI areas. However, the spatial distribution of predators can be influenced by a lot of (ecological) factors, and understanding the (interactions of these) factors is often complex. For further research into the distribution of avian predators within this study area, it would be advisable to take other possible factors into account. For example, many targeted avian predator species (grey heron, carrion crow, common buzzard, northern goshawk) are dependent on wooded habitats for shelter and nesting and perching opportunities (Vogelbescherming Nederland, 2009). This might therefore be an important factor in their distribution, as well as proximity to urban areas and bodies of (fresh) water, and other landscape elements.

For mammalian predators, the effect of LUI was also significantly different between the species groups. Badgers which had a positive relationship with LUI, differed significantly from beech martens, polecats, and brown rats. There was a positive trend of domestic cats with LUI, that also differed from beech martens, polecats, and brown rats. The other species groups did not show a clear relationship with LUI. In contrast to the avian predators, mammalian species groups were more confined to certain areas of the study area (fig. 4). For instance, cats are not found in the far northwest (Workummerwaard) of the study area, where there are no or less farms or other urban settlements. Most of the monitored cats in this study area are thought to be domestic. This might be the reason for their positive relation with LUI, since farms and other urban structures are mostly located near parcels with high LUI management. Badgers are known to prefer sandy or loamy soils to build their burrows (Carter et al., 2012; Centeri et al., 2017), which can mainly be found in the south of the study area (Provincie Fryslân, 2019). Combined with the fact there are more forest areas in the south, could explain badgers only being observed in the south, since they tend to select habitat types that provide coverage for their burrows (Márton et al., 2016; Mori et al., 2014). Furthermore, the positive relation of badgers with LUI might be explained by the greater abundance of earthworms, their primary prey (Mos et al., 2014), in high LUI parcels due to greater fertilization of the soil (Onrust et al., 2019).

Another explanation for the variation in the distribution of mammalian predators is that some species might have to cope with interspecific predation. For example, domestic cats are mostly observed in the northeast part, and red foxes in the southwest. This seemingly spatial separation of the two species might be (partly) caused by avoidance in space. Interspecific predation might also occur between the other targeted mammalian predator species. For instance, red foxes and beech martens are known to kill other mustelids (Bischof et al., 2014). On the other hand, predator species might also cope with interspecific predation by avoidance in time. For example, domestic cats and stoats can be active during both day and night, while beech martens, badgers, and polecats are nocturnal, red foxes are nocturnal and crepuscular, and least weasels are diurnal (Zoogdierverseniging, 2024). Bischof et al (2013) even suggested that weasels show diurnal activity in contrast to the activity of beech marten and red fox, to avoid them in time. Furthermore, the activity window and patterns might differ between the various predator species (Basting, 2024).

A point to note is that the observations of mammalian predators are based on the relative occurrence of species per camera location. Moreover, individuals could not be identified (except for a few individuals with specific mark), and therefore it is not possible to determine absolute numbers. Furthermore, the mammalian species groups can also differ in their detection chance. Home ranges differ considerably between smaller and larger predators (a cat's home range sizes up to 6.6 hectares, while a red fox's can be as large as 7300 hectares) (see table 2), which means there is a greater chance for a larger predator to be captured by multiple cameras. Furthermore, smaller species are more difficult to detect by the camera (Rowcliffe et al., 2011).

Relating avian predator presence to godwit breeding success

In the Netherlands, mammalian predators are thought to be primarily responsible for egg predation (Teunissen et al., 2008). Indeed, in the study area, in 2023 red foxes and badgers were the main culprits, in 2022 red fox

and polecat, and in 2021 beech marten and badger (Hooijmeijer et al., 2022, 2023, 2024). Avian predators on the other hand, are thought to be primarily responsible for chick predation (Teunissen et al., 2008). The analysis of the relationship between avian predators and godwit families, showed that only raptors had a significant positive relationship with the presence of godwit families. This suggests that raptors might indeed be attracted to godwits with chicks. Looking at the nest predation rates of 2023 (figure 3.1.9 in Hooijmeijer et al., 2024), we see that among the avian predators, raptors are the primary nest predators. Since they seem to be attracted by godwits and their nests, it seems likely the same holds true for the presence of chicks. This may have important consequences for the godwits, since the presence of predators can deter godwits. For example, the presence of predators can affect the location choice for their territory or where they move to with their chicks (Hooijmeijer et al., 2024). Godwits are known to move several kilometres to relocate their chicks (Conklin, 2022). Not only do the chicks become vulnerable during this move, to especially avian predation, the new location might potentially put the chicks in even greater risk of predation if (foraging) conditions are worse than in the previous location. Whether the abundance of mammalian predators might also be influenced by the presence of godwit families could not be determined, since high vegetation made it impossible to monitor mammalian species with the camera traps during the chick phase.

Conclusion and future directions

Just like previous years, nest predation was again a considerable limiting factor for the breeding success of godwits during the study year of my project (Hooijmeijer et al., 2024). The abundance of prey is an important driver for the distribution of predators (Carricondo-Sanchez et al., 2016), and while godwit nests might just be an opportunistic “snack” for predators in between searching for their primary prey (often voles), predation may have devastating effects on the godwit population (Bolton et al., 2007). However, in my analyses of the relationship between predators and LUI and prey, there was collinearity between LUI and prey, which made it hard to identify the independent contribution of both effects. Therefore, in future studies, it would be advisable to try to disentangle LUI from prey. For example, by studying fields with different land-use intensities, which also differ in prey composition and abundance. Maybe the implementation of vole fields might help with that, as Schlaich et al (2015) found, where the implementation of such “birdfields” increased the accessibility of voles to avian predators. If for instance, predators would have the choice between such vole fields, and fields where godwits are abundant, it would be interesting to see how this would affect the distribution of the predators. However, an increase in vole abundance could also boost the predator community, which can result in increased predation pressure on an alternative prey such as godwits in the years after, when the primary prey decreases (Breisjøberget et al., 2018; Hooijmeijer et al., 2024; Wymenga et al., 2021). Beside godwits and other meadow birds, predators could also switch to other alternative prey. For example, Angelstam et al (1984) found more hares in the diet of red foxes when there were fewer small rodents. Although it was not possible to directly link predators to prey in relation to LUI, I did find a significant negative relation between the abundance of prey with LUI, and species-specific relationships between predator species and LUI, for both avian and mammalian predators. This shows that although the abundance of prey seems to be greater in low LUI fields, this does not necessarily mean that predators are also most abundant in those areas. To gain a better understanding of the ecology of the mammalian predators and the reasons underlying their distribution, it would be advisable to tag individuals. This would not only improve the comparability of abundance estimates between the different mammalian predator species, it would also improve the estimation of their absolute numbers and the detection chance per species. For instance, Fokkema et al (2024) found that the occurrence of a predator species does not necessarily relate to nest predation; i.e. the predation rates of a species can be smaller or greater than expected based on their presence in the study area. Therefore, by tracking the movements of individuals (within a certain timeframe), it is easier to determine whether they are actually hunting in the area (where they were captured on camera), or just passing through (to get to their roost). In this way information could be acquired about their ranging behaviour and habitat selection, as well as information on (potential) roosting locations. Moreover, it might also be a good idea to study the distribution of the predator species throughout multiple years. In this way, changes in the landscape can be tracked, which could then be linked to alterations in the distribution of the predator community.

Policy implications

In this changing agricultural landscape, where populations of many farmland bird species suffer from dramatic declines, it becomes more and more clear we have to act in order to preserve our meadow birds.

Predation may be a limiting factor in the recovery of these meadow bird populations. However, this study shows that the impact of predation strongly depends on a multitude of factors locally. The distribution of predators varied in space, and for avian predators also over time. Predators had a species-specific relation to LUI, which means that some predator species were seen more in high LUI areas, and others more in low LUI areas. Consequently, godwits locally are exposed to different predator communities. Indeed, not only did nest and chick predation rates vary spatially and temporarily, the composition of predator species responsible for nest and chick predation also varied between the years and locations (Hooijmeijer et al., 2022, 2023, 2024). Therefore, there is no “one size fits all” solution. Several measures that are already being taken, such as the implementation of agri-environmental schemes, and culling of predators, are often shown to be ineffective (Kämmerle et al., 2019; Kleijn et al., 2006). Furthermore, the control of one predator species could lead to an increase in predation pressure by another (Fokkema et al., 2024; Trewby et al., 2008; Van den Berge, 2016). Instead, there is a need for a customized and local approach in the control of predators. For instance, measures to be taken could make use of differences in the encounter chance of various predator species as a guideline. By altering land-use regimes, the presence or absence of certain predator species and the local predator community as a whole, can be regulated, to ensure the protection of godwits and other meadow birds.

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