

Across Time and Territory: Spatio-temporal occurrence of mesopredators in Dutch protected meadow bird areas



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Abstract

Mesopredators, small to mid-size carnivores ranking in the middle of the foodweb, play a critical role in balancing the ecosystem through predation. The decline of biodiversity and apex predators has changed mesopredator-prey dynamics. Land-use intensification and landscape homogenization have reduced abundance of prey, among which meadow birds. The reduced abundance of prey species has intensified competition between mesopredators, particularly those with high diet similarities. In this study, we aimed to gain insight into the spatial and temporal co-occurrence of mesopredators in protected meadowbird areas. A grid of 30 wildlife cameras was set up in two different locations in the north of the Netherlands, and monitored for 3 months during the breeding season, circa March to June. We found high spatial and temporal overlap between 5 different mesopredator species (weasel, stoat, European polecat, stone marten and domestic cat) with overlap exceeding the 50th percentile for most species pairs. Smaller species (weasel, stoat) adjusted their activity patterns to that of larger species (European polecat, stone marten), by exhibiting two activity peaks instead of one, except for the domestic cat (*Felis catus*). Most species pairs had high spatial overlap, except for three species pairs (marten-weasel, cat-stoat, cat-weasel) with large differences in body size. However, for these pairs spatial avoidance was not significant. The high spatial and temporal overlap between species pairs are likely influenced by the absence of large predators (such as the red fox), variations in prey availability and niche differentiation, all of which allow mesopredators to coexist. The results of this study offer insights for nature management, contributing to the conservation of meadow bird species and their predators by improving predictions of management outcomes in the context of predator community shifts.

Introduction

Predator interactions

Predators at high trophic levels play a crucial role in ecosystem dynamics, where trophic cascades and complex interspecific interactions intensify their influence on prey populations (Ritchie & Johnson, 2009; Tsunoda et al., 2020). Interspecific interactions among predators of the same trophic level occur when they compete for limited resources, potentially reducing the fitness of one species due to negative impact of the other (De Boer & Prins, 1990; Zanni et al., 2021). To mitigate competition risks, species partition their activity in space, time or dietary niche to reduce direct interactions (Bu et al., 2016; Remonti et al., 2012; Zalewska et al., 2021). Understanding how ecologically similar predator species coexist, can aid in conservation and management efforts, especially in communities where apex predators are absent. In these environments, mesopredators often experience population increases, intensifying their interactions with both prey and other predators (Ritchie & Johnson, 2009). Insights into these interactions can inform management strategies to balance predator-prey dynamics, supporting biodiversity and the conservation of vulnerable species.

Mesopredators

Over recent centuries, apex predator populations across the world have declined and disappeared due to human-driven suppression and habitat destruction (Estes et al., 2011; Gittleman, 2001; Wang et al., 2015). The decline of apex predators has resulted in the mesopredator release effect, altering mesopredator density, distribution and behaviour (Crooks & Soulé, 1999; Prugh et al., 2009). Mesopredators are defined as small to mid-sized mammalian carnivores with a bodyweight under 15 kg, that occupy an intermediate position in the food web (Prugh et al., 2009; Roemer et al., 2009). As mesopredators are subordinate to apex predators and primarily predate on smaller animals such as small mammals, birds and invertebrates, they play a critical role in balancing the ecosystem through predation (Ritchie & Johnson, 2009). Apex predators regulate mesopredator populations through predation and fear effects (Prugh et al., 2009; Wang et al., 2015). Their disappearance and reappearance in certain areas, however, influences mesopredator dynamics. With the mesopredator release effect, mesopredator abundance increases, intensifying predation pressure and sometimes causing local prey declines or extinctions (Gittleman, 2001; Prugh et al., 2009; Ritchie & Johnson, 2009). While mesopredators show higher diversity in species, ecology and behaviour, they have been relatively understudied compared to apex predators, as mesopredators are often seen as less charismatic and regarded more as resources or pests (Roemer et al., 2009). This higher species diversity increases the potential for interspecific competition.

Competition

In intensive agricultural fields, prey populations are declining, leading to intensified competition between mesopredator species (Prugh et al., 2009). Due to the reduced prey abundance in many agricultural and urbanized landscapes, mesopredators are attracted to more scarcely available natural habitat, where they will need to share a smaller area. Besides indirect competition for the same prey here, mesopredators might also have a higher chance of direct encounters with other mesopredator species. Direct competition may lead to negative social interactions, including aggressive behaviours, as individuals defend scarce resources (Krauze-Gryz et al., 2012; Zalewska et al., 2021; Zanni et al., 2021). Competition can lead to interspecific killing, where larger or more dominant predator species actively kill smaller competitors to reduce competition (Zalewska et al., 2021). Also referred to as intraguild predation, this behaviour creates a landscape of fear for subordinate species as they face predation risk from other mesopredators (Palomares & Caro, 1999; Roemer et al., 2009). Body-size differences and trophic overlap are known to be predictors of lethal interaction strength (Palomares & Caro, 1999). These aggressive interactions could result in competitive exclusion, where the less competitive species is pushed out of preferred habitats (Remonti et al., 2012).

Spatio-temporal partitioning

One way mesopredators cope with competition, is by altering their activity through space and time to minimize encounters with competitors (Zalewska et al., 2021). This behaviour, known as spatio-temporal partitioning, allows species to coexist in competitive landscapes by minimizing overlap in area or time of activity (Remonti et al., 2012; Zalewska et al., 2021). Animals exhibit a range of circadian activity patterns, shaped by a complex balance between optimal foraging/survival strategies, social behaviours and environmental limitations (Pyke,

1984; Zanni et al., 2021). This results in some species being mainly active at night, such as the European polecat (*Mustela putorius*), whereas others, for example domestic cats (*Felis catus*), are most active during twilight hours of the day (S. Horn et al., 2021; Lode, 1995). Predators adjust their temporal activity patterns, where species optimize their activity to be similar to that of their prey, or subordinate species adjust it to avoid potential negative interactions with larger predators (Zalewska et al., 2021; Zanni et al., 2021). Alternatively, individuals can adjust their spatial distributions, centering activity around prey-rich areas or by avoiding areas dominated by larger carnivores (Krauze-Gryz et al., 2012; Ritchie & Johnson, 2009; Zalewska et al., 2021). For example, Krauze-Gryz et al., (2012) found that the presence of cats and foxes was linked, where cats were observed less frequently in areas where foxes were present. This suggests that species spatially and temporally avoid each other to prevent direct encounters.

These spatio-temporal adjustments help species coexist, by limiting their overlap in space and time, therefore allowing them to share the same area without direct competition. Such behavior enhances survival for smaller or less dominant predators by helping them avoid larger competitors or potential predators. Insights into these dynamics are essential in understanding and predicting community changes, which in turn can aid in conservation strategies for vulnerable species like meadowbirds. For instance, knowing how different predator species partition their time, space and resources could reveal potential areas or times at which meadowbirds face higher predation risk.

Meadowbird areas

In this study, we investigated the role of spatial and temporal partitioning in the coexistence of five mesocarnivore species - the domestic cat, stone marten, European polecat, weasel and stoat - living in Dutch protected meadowbird areas. The Netherlands is an important breeding area for meadow birds, making it an essential region for the survival of species such as the Eurasian oystercatcher (*Haematopus ostralegus*), black-tailed Godwit (*Limosa limosa*) and northern Lapwing (*Vanellus vanellus*) (de Boer, 2011). However, populations of these meadowbird species have decreased since the 1960's. Some species have seen population declines of up to 70% since 1990 (Roodbergen & Teunissen, 2014). These declines are mainly due to intensification of agriculture and its associated practices. In order to conserve meadowbirds and their critical habitats, certain grassland areas have been designated as protected meadow bird areas. By restricting harmful agricultural practices in these areas, nature organizations aim to conserve important meadow bird populations. Management practices can involve delayed mowing to protect meadowbird nests, resulting in higher densities of meadowbirds and other species such as voles (*Microtus arvalis*) (Otte, 2021). The higher prey availability and reduced human disturbance in protected areas also attract mesopredator species, especially compared to intensive agricultural grasslands. This mesopredator attraction is further increased by habitat fragmentation from agriculture and urban development, which may concentrate mesopredator populations in these protected zones where prey density remains relatively high (Wilcox & Murphy, 1985). However, this high predator density threatens meadowbirds as nestpredation by terrestrial predators is one of the main reasons for low hatching success (Dekker & Jonge Poerink, 2020; Oosterveld, 2022). In response, conservation organizations implement predator control measures, such as trapping and culling, to reduce predation on vulnerable meadowbird chicks (Loonstra et al., 2024). This high concentration of predators, combined with fluctuating prey populations

provides an interesting system for studying spatial and temporal dynamics of mesopredators.

Research objective

This study aims to investigate the spatial and temporal distribution of mesopredators in Dutch protected meadowbird areas. Specifically, we are interested in how different mesopredator species avoid competition, either through spatial or temporal partitioning.

Body size difference is a strong predictor of lethal interaction risk, with the smaller species typically avoiding high-density areas of the larger, dominant species as part of a landscape of fear (Zanni et al., 2021). Species with larger body size are therefore expected to show low overlap with smaller species in both space and time, where *H1*) species with similar diets are expected to have high temporal overlap with each other as their activity patterns likely align with that of their (shared) prey (Remonti et al., 2012; Zalewska et al., 2021). *H2*) smaller, subordinate species are expected to have low spatial overlap with larger species as they center their activity around prey-rich areas and avoid areas where dominant predators are active, to reduce the risk of aggressive encounters (Krauze-Gryz et al., 2012; Ritchie & Johnson, 2009; Zalewska et al., 2021).

Overall, we predict that body size and dietary overlap influence spatial and temporal partitioning of mesopredators. To test these hypotheses, we used wildlife camera-traps to monitor the spatial and temporal activity of mesopredators in Dutch meadowbird areas.

Methods

Study area

This study was conducted in two agricultural areas in the north of the Netherlands (Figure 1). The study area in Soarremoarre (1), is mainly owned and managed by farmers from “het Boerencollectief”, other parts are managed by nature organization “It Fryske Gea”. Together, it covers around 40 hectares of meadowbird conservation area. The Study area in Heksum (2), consists of a combination of agricultural fields managed by nature organization “Het Groninger Landschap” with the main purpose of meadowbird conservation. The remaining part are private owned agricultural fields with main purpose of dairy farming, and the total area covers about 159 ha. Meadowbird conservation areas are old cultural landscapes and consist of irregular shaped herb-rich grasslands, separated by water-filled ditches and connected by small dykes. In both areas livestock was used for grazing in parts of the area, creating more heterogeneity in the landscape. Livestock such as sheep and cattle were used for grazing in one third of the fields in Heksum, the rest of the fields were left and only mowed after the meadowbird breeding season. In Soarremoarre cattle was used for a grazing mosaic and water table was kept high throughout the breeding season.



Figure 1: Locations of the study areas in the Northern part of the Netherlands. Study area 1 is in Soarremoarre, Friesland (53.0677°, 5.8705°), Study area 2 is located in Heksum, Groningen (53.2873°, 6.5158°).

In the areas, meadowbird species like the oystercatcher (*Haematopus ostralegus*), black-tailed godwit (*Limosa limosa*) and Northern lapwing (*Vanellus vanellus*) are present during the breeding season (de Boer, 2011). As are other bird species such as ducks, geese and coots. Both areas contain terrestrial predators such as red foxes (*Vulpes vulpes*), domestic cats (*Felis catus*), stone martens (*Martes fiona*) and small mustelids, including weasels (*Mustela nivalis*), stoats (*Mustela erminea*) and European polecats (*Mustela putorius*). There are also avian predators present, such as the common buzzard (*Buteo buteo*) and marsh harrier (*Circus aeruginosus*). Both areas have predator management ongoing. For Heksum this consists of culling red foxes and in Soarremoarre management is culling red foxes, stone martens and feral cats (Dekker & Jonge Poerink, 2020).

Camera trapping

The study was conducted using wildlife camera-traps during the breeding season of meadowbirds in 2023 and 2024. A systematic grid (Figure 2) of 30 wildlife camera traps was set up in both Heksum and Soarremoarre. Each grid was made up of cells of 250 by 250 metres, covering both farmland and meadowbird areas. Fields were separated from each other by water-filled ditches and only connected by small dykes. Camera traps were placed at dykes, field entrances and planks that were placed over ditches, as predators are most likely to use these dry, linear structures to get around the fields (Magrini et al., 2009; Rondinini et al., 2006). The cell of the grid in which the first camera was placed, was chosen randomly. Inside the cell, the field entrance, plank or dyke located closest to the upper-left corner was selected as the camera-trap location. Each location had to follow two conditions: the location was at least 100 m away from buildings and roads to minimize human disturbance; and at least 100 m away from the nearest camera-trap. If a location did not meet both conditions, one field entrance or dyke further was chosen. The camera-traps were set up for 3 consecutive months during the breeding season of meadow birds, approximately from the 15th of March to the 15th of June.

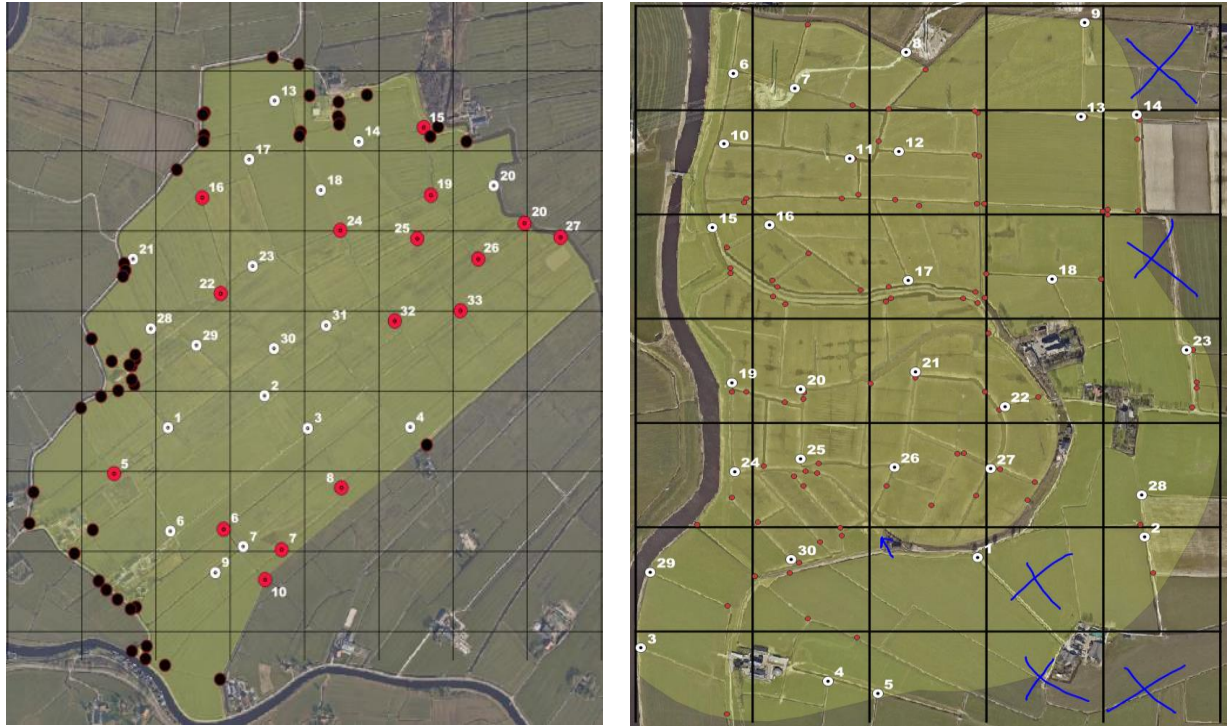


Figure 2: Camera grid used for the study area in Soarremoarre (Friesland). Red and white dots represent camera locations in previous years. Black dots indicate locations unsuitable for camera traps, as they are too close to roads and buildings. Each cell contains 1 camera-trap, camera traps need to be at least 100 m away from each other, roads and buildings.

Camera set-up

The cameras were placed in the field attached to steel poles or onto wooden fenceposts with adjustable tension straps (Figure 3), at 40 cm height and tilted slightly downwards. This ensures maximum capture opportunity for medium sized predators such as red foxes, stone martens and domestic cats, as well as for smaller species like common weasels and stoats. Reconyx hyperfire 2 wildlife cameras were used and set to take 10 photos with each detected movement. A timelapse photo was taken once an hour, to ensure proper working of the camera, even when nothing is captured. Cameras were equipped with passive infrared motion detectors and infrared illuminators for nighttime operation. See table 1 for additional camera settings.



Figure 3: Cameras were attached to fenceposts or placed on steel poles on the edge of dykes and general field entrances.

Table 1: Camera trap settings

Active time	24 hours/day
Mode	Photo only
Sensitivity	High to Very high sensitivity
Speed	Rapid fire
Photos per trigger	10
Delay between triggers	No delay
Time lapse photo	1 photo/hour

Once a week, camera positions in the field were checked. The correct date and time, battery fullness and SD card fullness were assessed. Batteries were changed when lower than 50% charge and SD cards were replaced when 50% full or higher. Vegetation around the cameras was shortened to prevent view obstruction and minimize false triggers as much as possible. Cameras were moved or removed in case of flooding or wildlife and livestock interference. These cameras were later placed back or moved to a nearby location, where the closest dyke within the same grid cell was selected as the new location. Locations and reference photos were saved in the program Mergin Maps, to make navigation in the field run smoothly.

Data processing

After data collection, camera-trap images were uploaded into Agouti Artificial Intelligence Software (Casaer et al., 2019). The software extracts metadata from images, organizes images into sequences, filters out blank images, and uses the AI model Western Europe v4a for automatic species classification. Images were grouped into sequences, each starting with 10 images from the first camera trigger and including any subsequent triggers within 120 seconds. A species spotted within a sequence was counted as one observation of that species. Agouti classified all images, only unclassified (~ 25%) and unusual observations were checked and scored manually. All mammal observations were filtered in the software and double checked by hand to ensure scoring accuracy of the study species, as previous study years found high percentages of incorrect annotations for predators (Turlier, 2023). Unclear images were classified as the highest taxa we could determine with certainty. Due to time constraints, only data from Soarremoarre 2023 was analyzed and used for statistical analysis.

Statistical analysis

All statistical analyses were conducted using R version (4.4.1) in R studio (2024.04.2 + 764) (R Core Team, 2024; R studio team, 2024)

Temporal activity

For the temporal analysis, daily activity of 5 mesopredator species was estimated using the timestamp of each observation. Time data (00:00 - 23:59) was transformed to circular data (0 - 2π), to reflect the cyclical nature of time data. The range 0- 2π represents circular data in mathematical terms, where 0 marks the starting point and 2π represents a full circle. Using this circular framework, mesopredator activity was analyzed using Kernel density estimates (Ridout & Linkie, 2009). To determine temporal overlap between the different study species, coefficient of overlap was calculated for each species pair (Table 4). This overlap coefficient ranges from 0, indicating no overlap between species, to 1, indicating complete overlap. Dhat1 is commonly used for sample sizes below 50. Since our study had 30 camera locations, we chose to use this method (Meredith et al., 2024; Ridout & Linkie, 2009). For this analysis we also included sunrise and sunset data to compare day and night observations. For this, the first and last sunset and sunrise of the study period were taken and mean sunrise and sunset times were calculated. To assess time of darkness, we used the length of twilight, based on the time of year. For the study period, this was 36 minutes after sunset and 36 min before sunrise (KNMI, 2014), where sunset and sunrise times were based on the mean for the entire study period.

The overlap coefficient is a descriptive approach, so to evaluate the similarity between the activity peaks of each species pair, Watson's two-sample test was used, a statistical test for circular data (Pewsey et al., 2013; Tsunoda et al., 2020). The test statistic U^2 is used to measure the difference between two circular distributions. Consistent with previous studies (Monterroso et al., 2020; Torretta et al., 2016; Tsunoda et al., 2020), overlap was categorized as "high" when above the 75th percentile, "moderate" between the 50th and 75th percentiles, and "low" when below the 50th percentile. For these analyses, R packages "overlap" and "circular" were used (Lund & Agostinelli, 2004; Meredith et al., 2024; Ridout & Linkie, 2009).

Spatial activity

For the spatial analysis we assessed spatial overlap between species pairs, using the Sørensen Similarity Index (Sørensen, 1948)), as this index gives a straightforward overview per camera location and works well for lower sample sizes. The index calculates overlap as a number between 0 and 1, where 1 is complete overlap and 0 is no overlap, or complete partitioning. Spatial activity was based on the camera location data and predator presence was marked as present (1 or more observations) or absent (0 observations). The Sørensen similarity index (SSI) was calculated with the following formula:

$$SSI_{ij} = \frac{2a_{ij}}{2a_{ij} + b_{ij} + c_{ij}}$$

Where a_{ij} represents the number of camera locations where both species i and j were observed (at least once). b_{ij} and c_{ij} represent the number of camera locations where only one of the species was observed. Spatial overlap was categorized as "high" when above the 75th percentile, "moderate" between the 50th and 75th percentiles, and "low" when below the 50th percentile.

As the *SSI* does not account for observation densities at the camera locations, the capture rate of each species at each location was included as well. The capture rate was calculated as the number of observations (of a species) divided by the number of days the camera was working. To explore potential spatial partitioning among species pairs, linear models based on capture rate were constructed. The larger species was taken as independent variable and the smaller species as the dependent variable, as we expect the distribution of the larger species to predict the distribution of the smaller species.

To account for potential location-based bias due to differences in location type, we explored detection probabilities. We used occupancy models to calculate the detection probability of the different species at camera locations, with differing levels based on the presence of a dyke, plank or fence. This was done in R using packages “unmarked” and “MuMIn”.

Results

Camera trap data

Camera traps in Soarremoarre were active from 26th of March until the 7th of June, 2023, accumulating a total of 2,022 trap nights across 30 sites (mean = 67.4 days per camera, min= 31.1 days, max= 74.6 days). From a total of 1.409.149 images, 48.582 timelapse images were identified, the remaining 1.36 million photos grouped into 44.683 sequences. Among the remaining sequences, 18.5 % were blank images, 79.2% captured animals, 1.38% were human observations and 0.48% included vehicles. Additionally, 0.32% of sequences were marked as “unknown”, due to the lack of identifiable features. Out of the 35,433 animal observation sequences, 782 (2.05%) were mammalian predators, while the remaining 34,705 sequences captures non-predator species (see table 2). A total of 5 mesopredator species were observed, unclear observations were included in two categories of higher taxon levels (Appendix, fig. 1). Stone martens were the most frequently observed, while weasels were the least recorded species (Table 3). For analysis purposes, sequences labeled “unknown small mustelids” and “unknown mustelids” were excluded to focus only on observations confidently identified to species. This left 589 observations across 30 camera locations for the analysis.

To get insight into species distribution across the study area over the entire study period, an occupancy matrix was created. All dates of the study period are shown on the x-axis and camera locations on the y-axis (Figure 4). This matrix is based on binary data, with “1” indicating at least one predator observation on that day at a given location and “0” indicating no predator observations. Days when a camera trap malfunctioned (e.g. due to a dead battery, full SD card, technical failure, view obstruction, or removal from the field), were marked as “downtime”, indicated as a red box in the occupancy matrix, providing a direct overview of trapnights during the study period. Predators were observed on every camera during the study period. Camera SK20 captured predator activity only on 3 days, while camera SK19 captured predator activity on 62 days.

The spatial distribution of observations is displayed on the map in figure 5, showing variation between camera locations. Some locations had high observation rates, with the most visited

location recording 143 observations (SK19), while the least visited locations had 5 observations (SK17 & SK20).

Table 2: non-predator species observations in Soarremoarre 2023, one observation is one sequence.

Species	Observations
<u>Rabbits and hares</u>	23.390
<u>Birds</u>	9.414
<u>Humans</u>	616
<u>Cattle</u>	558
Roe deer	468
<u>Rodents</u>	243
Otters	18

Table 3: Total observations for individual predator species on all cameras combined.

Species	Total observations
Stone marten (<i>Martes fiona</i>)	173
Unknown small mustelids (<i>Mustela nivalis/erminea</i>)	167
Stoat (<i>Mustela erminea</i>)	130
European polecat (<i>Mustela putorius</i>)	121
Domestic cat (<i>Felis catus</i>)	88
Common weasel (<i>Mustela nivalis</i>)	77
Unkown mustelids (<i>Mustelidae</i>)	26

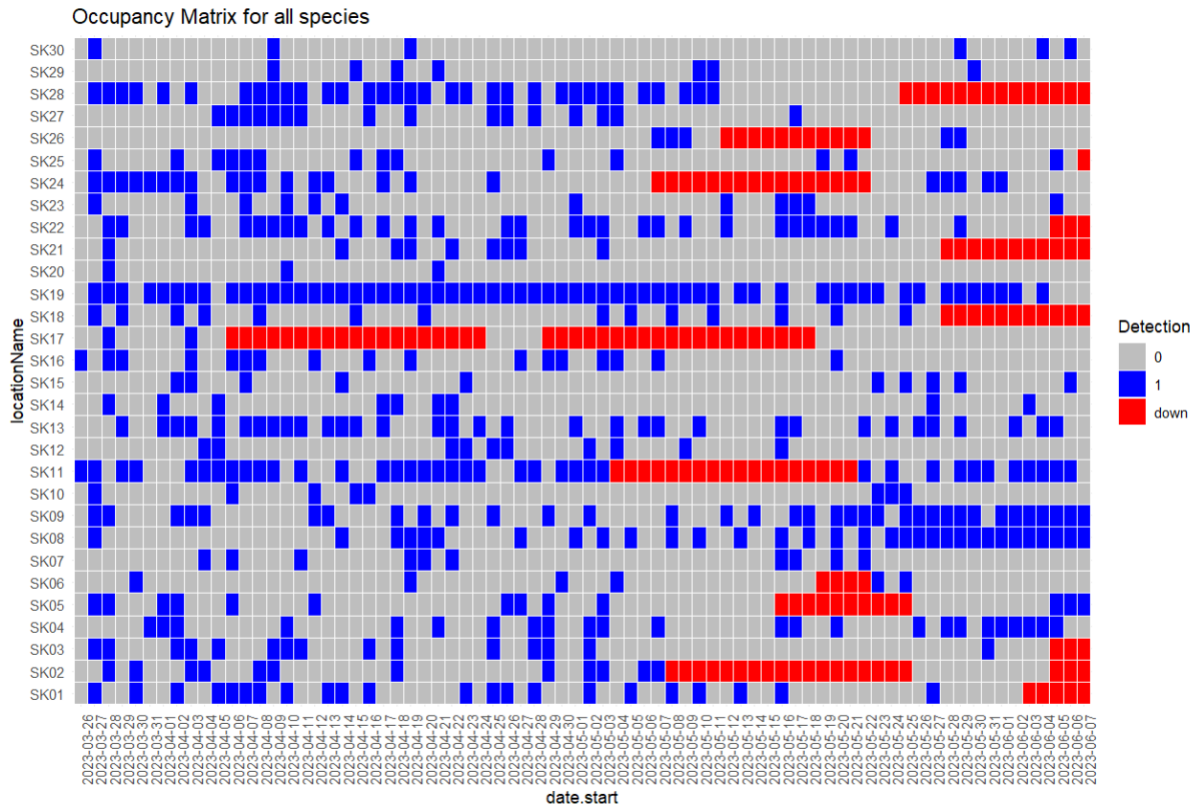


Figure 4: Occupancy matrix showing predator observations per day at each camera location. Blue cells indicate days with at least one predator observation, red cells mark days where cameras malfunctioned, and grey cells represent functioning cameras with no predator detections.

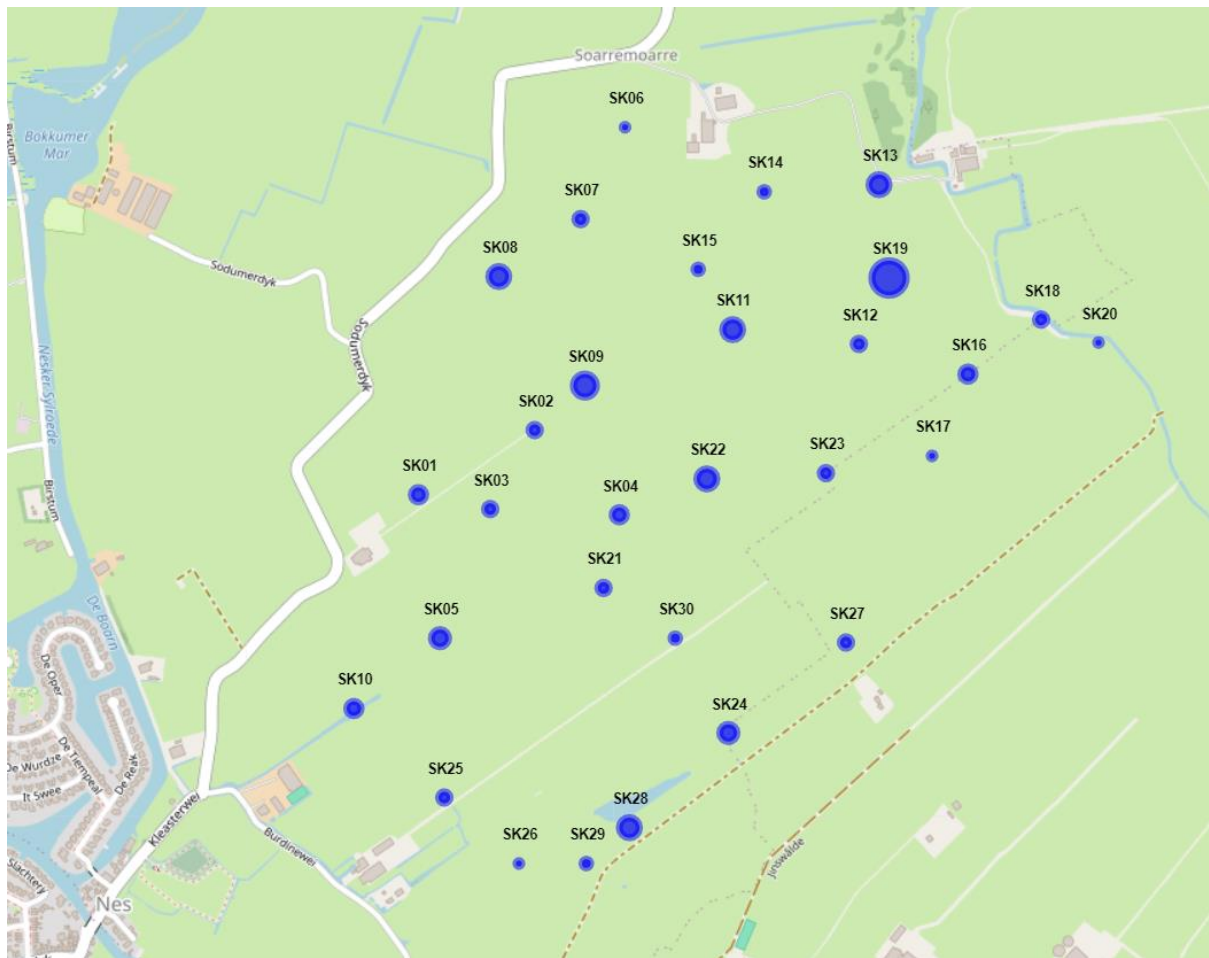


Figure 5: Number of observations per camera location for all predator species combined. Dot size is related to amount of observations. Highest total observations per location was 143 (SK19), lowest total observations per location was 5 (SK17 & SK20).

Temporal activity

Temporal overlap was quantified using the temporal overlap coefficient (Dhat), with results indicating moderate (Dhat 0.5 - 0.75) to high temporal overlap (Dhat > 0.75) among most species pairs (Table 4). Watson's two sample test (U) revealed significant differences in peaks for all species pairs, except for the cat-weasel pair (Table 4). All species were exclusively nocturnal or crepuscular, except for the stoat, which was also recorded as active during the daytime, though still had peaks in activity at nighttime (Figure 6). Notable is that weasels, stoats and domestic cats have two peaks that roughly coincide, around sunset and in the early morning. Polecats and stone martens have only one peak, primarily after sunset. Overall, similar sized species showed more temporal overlap than species with large size differences, except for the cat, which showed high overlap with both weasels and stoats.

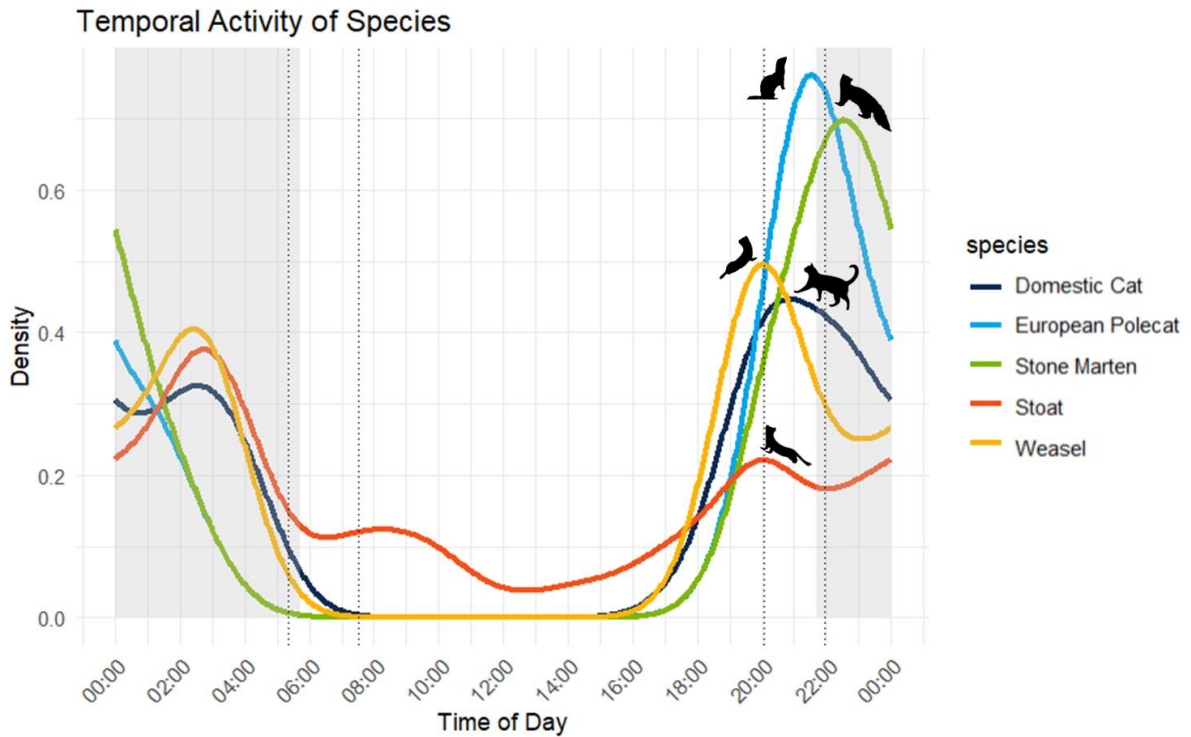


Figure 6: Temporal activity plot of all predator observations on all cameras. Peaks in densities indicate peaks in activity levels at that time of day. Dotted lines are the first and last sunset and sunrise times during the study period. Shaded areas are the parts of the day where it is completely dark. For the study period, this was 36 minutes after sunset and 36 min before sunrise. Sunset and sunrise times were based on the mean time for the entire 3 month period, set at: sunrise 6:20, sunset 21:05.

Table 4: Temporal overlap patterns between each mesopredator species pair expressed as the temporal overlap coefficient (Dhat1) and tested for significant differences with Watson’s two sample test (U^2). Higher Dhat1 indicates more temporal overlap between species, whereas a higher U^2 indicates a greater difference between temporal activity peaks of two species.

Larger sp.	Smaller sp.	Dhat1	U^2	P-value
<i>Domestic cat</i>	<i>Stone marten</i>	0.695	0.829	< 0.001
	<i>European polecat</i>	0.691	0.841	< 0.001
	<i>Stoat</i>	0.704	0.621	< 0.001
	<i>Weasel</i>	0.830	0.092	> 0.10
<i>Stone Marten</i>	<i>European polecat</i>	0.829	0.497	< 0.001
	<i>Stoat</i>	0.453	2.958	< 0.001
	<i>Weasel</i>	0.582	1.463	< 0.001
<i>European Polecat</i>	<i>Stoat</i>	0.448	2.651	< 0.001
	<i>Weasel</i>	0.589	1.436	< 0.001
<i>Stoat</i>	<i>Weasel</i>	0.684	0.491	< 0.001

Spatial activity

Spatial overlap was quantified using the SSI, where most species demonstrated moderate (SSI 0.5 - 0.75) to high overlap (SSI > 0.75) , with the exception of 3 species pairs (Figure 7). The marten - weasel pair showed low overlap with an index of 0.43, while the cat-weasel pair and cat-stoat pair had overlaps of 0.48 and 0.53, respectively (Table 5).

To represent spatial distributions, capture rate was also included in the spatial analysis. Capture rates were plotted by species across all locations (Figure 8). This plot indicates that only three locations observed all five study species, while most locations captured two to three different species. Some spatial patterns appear, where domestic cats are primarily observed around the western edge of the area, weasels more frequently in the northeastern part and stone martens and European polecats are observed mainly in the core and northern part of the area (Figure 8).

Using linear models for spatial partitioning, no evidence was found for a negative linear relationship between the five predator species (Appendix, table 1). Two of the models indicated significant positive relationships between the marten-stoat ($\beta = 0.65$, $SE = 0.27$, $t = 2.33$, $p = 0.02$, $R^2 = 0.163$) and marten-weasel pairs ($\beta = 0.19$, $SE = 0.06$, $t = 3.46$, $p = 0.002$, $R^2 = 0.299$) (Appendix, fig. 2). This positive relationship appears driven by a single outlier skewing the data upwards. When this outlier was removed, the trend turned negative and was no longer significant for both marten-stoat ($\beta = -0.23$, $SE = 0.23$, $t = -1.03$, $p = 0.31$, $R^2 = 0.038$) and marten-weasel ($\beta = -0.08$, $SE = 0.07$, $t = -1.08$, $p = 0.29$, $R^2 = 0.041$) pairs. The multiple R-squared of the models is lower after outlier removal, indicating a reduced fit of the model.

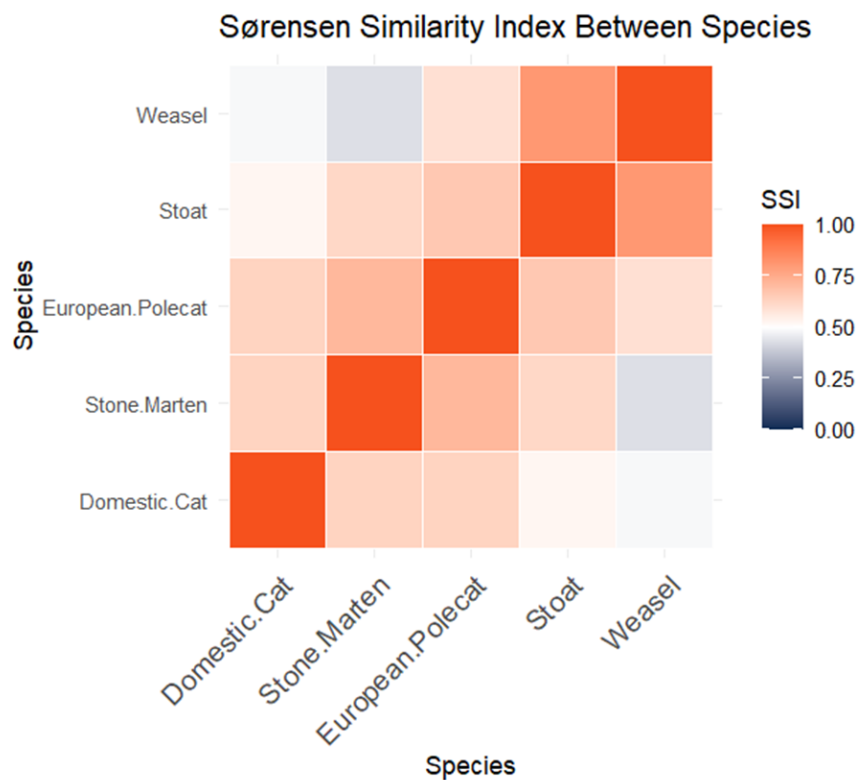


Figure 7: Matrix with the Sørensen Similarity Index. The SSI measures the similarity between the presence of two species, measuring the co-occurrence between locations. 1 means the species are always present in the exact same locations. 0 means the species are never co-occurring in the same locations. The more red in the figure, the higher the spatial overlap between species.

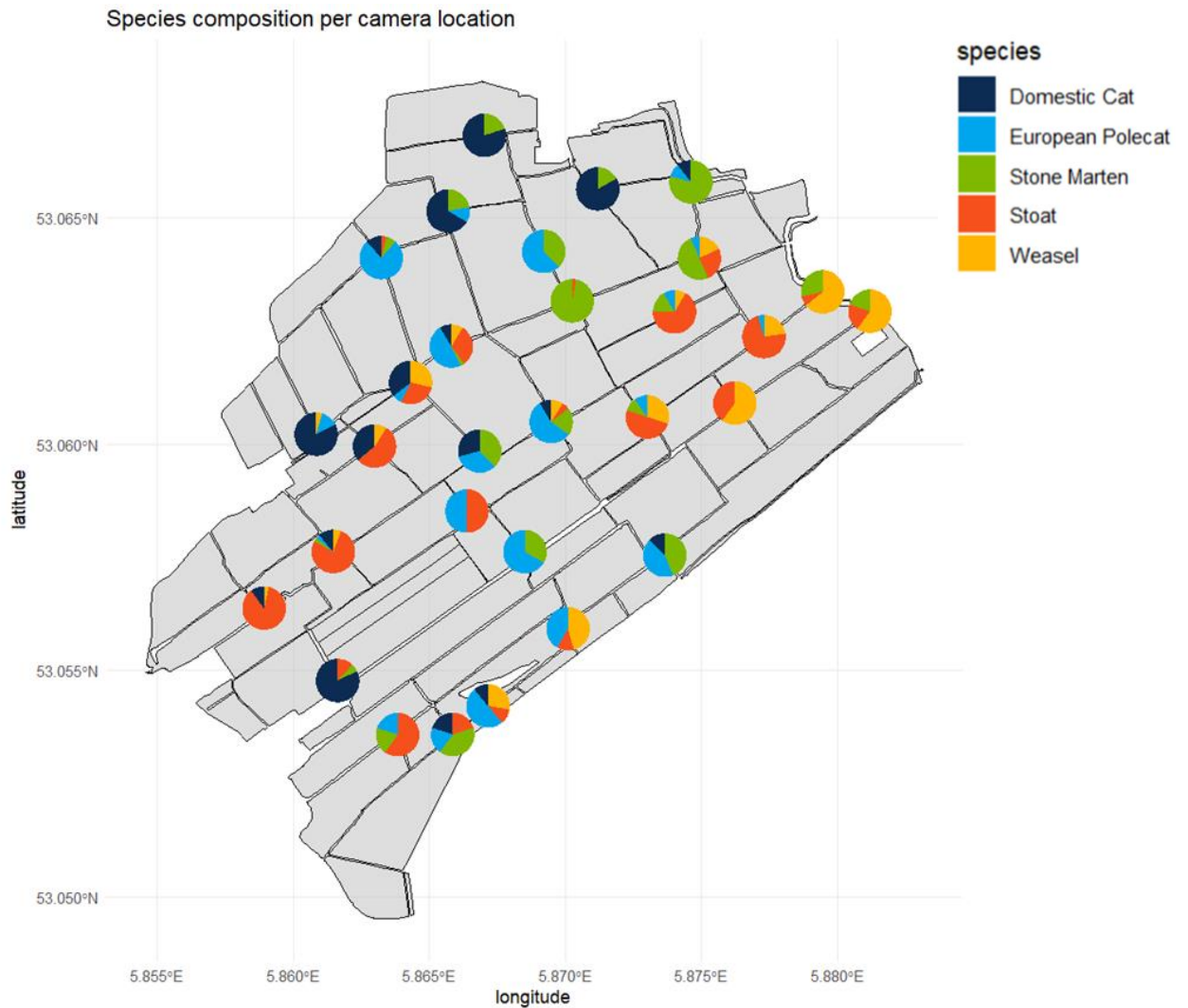


Figure 8: Species composition per camera location based on capture rate. Pie charts representing the relative species densities are plotted over each camera location and visualised on the map of the area.

Table 5: Spatial overlap between predator species pairs based on the Sorensen Similarity Index.

Larger sp.	Smaller sp.	Sorensen Similarity Index
<i>Domestic cat</i>	<i>Marten spp</i>	0.6315789
	<i>European polecat</i>	0.6315789
	<i>Stoat</i>	0.5263158
	<i>Weasel</i>	0.4848485
<i>Stone Marten</i>	<i>European polecat</i>	0.7142857

	<i>Stoat</i>	0.6190476
	<i>Weasel</i>	0.4324324
<i>European Polecat</i>	<i>Stoat</i>	0.6666667
	<i>Weasel</i>	0.5945946
<i>Stoat</i>	<i>Weasel</i>	0.8108108

Detection probability

Daily detection probability differed between species per camera trap placement (dyke/fence/plank). We found the highest detection probability for stone martens, stoats and common weasels by cameras placed at planks (pSM: 0.31, pS: 0.15, pCW: 0.09, table 6). European polecats were best detected on dykes (pEP: 0.09) and domestic cats at fences (pDC: 0.09). The differences in detection probability were minimal (mean difference = 0.0059, table 6), indicating that detection probabilities likely did not influence the spatial patterns we observed. The consistency across species detection implies a reliable representation of spatial overlap in our data.

Table 6: Detection probability per species at different camera placements (dyke, fence and plank).

Species	Placement	Predicted	SE	Lower	Upper
European polecat	dyke	<u>0.09653790</u>	0.010780901	0.07737450	0.11983106
European polecat	fence	<u>0.03267646</u>	0.009237051	0.01869475	0.05651281
European polecat	plank	<u>0.06028357</u>	0.014173376	0.03780083	0.09482059
Stone Marten	dyke	<u>0.07815476</u>	0.008633236	0.06282329	0.09684112
Stone Marten	fence	<u>0.02387814</u>	0.008420203	0.01190668	0.04730989
Stone Marten	plank	<u>0.31081073</u>	0.038044022	0.24150820	0.38978049
Weasel	dyke	<u>0.06146756</u>	0.01218958	0.041489403	0.09016080
Weasel	fence	<u>0.01596319</u>	0.00660748	0.007062939	0.03567599
Weasel	plank	<u>0.09219867</u>	0.01722793	0.063535810	0.13196995
Stoat	dyke	<u>0.03156233</u>	0.00732543	0.01996825	0.04954788

Stoat	fence	<u>0.05600204</u>	0.01166964	0.03706262	0.08377771
Stoat	plank	<u>0.15956314</u>	0.02180692	0.12129766	0.20705564
Domestic Cat	dyke	<u>0.04679360</u>	0.00829427	0.03297267	0.06601228
Domestic Cat	fence	<u>0.08929938</u>	0.01388256	0.06557145	0.12050628
Domestic Cat	plank	<u>0.01405861</u>	0.01309304	0.00223397	0.08325017

Discussion

The aim of this study was to examine the coexistence of mesopredators in a protected meadowbird area, by investigating their spatial and temporal overlap. We captured 589 predator observations across 30 locations during 2.022 trapnights. Our findings suggest slight spatial and temporal interactions between five mesopredator species (domestic cat, stone marten, European polecat, stoat and weasel). We found overlap in temporal activity, with all species displaying primarily nocturnal or crepuscular behavior. Species with similar diets, such as the weasel and stoat, demonstrated more overlapping activity peaks than species with more distinct prey preferences, such as weasel-marten and polecat-stoat pairs. Activity of the domestic cat, stoat and weasel was more spread out over time with two activity peaks, while the stone marten and European polecat displayed only one activity peak at night. As weasel-stoat and polecat-marten pairs have similar body sizes and diets, but cats are much larger than weasels and stoats, these results partially support the hypothesis that species with similar diets and body size have more temporal overlap.

Spatial patterns were spread out over the study area, where domestic cats were concentrated at the western edge, weasels in the northeast and stone martens and European polecats mainly in the core and northern part of the area (Figure 8). Spatial analysis indicated moderate to high overlap among most species pairs. Three species pairs with big differences in body size exhibited low spatial overlap (marten-weasel, cat-weasel, cat-stoat, SSI <0.55). This supports the hypothesis that species with larger differences in body size have lower spatial overlap. However, linear models revealed no significant pattern in avoidance. Low mean difference (0.0059) in detection probabilities per camera placement (dyke, plank, fence) between the species was found, indicating that spatial avoidance patterns were not influenced by detection probability.

Temporal activity

Mesopredators in the study area exhibited overlapping temporal activity patterns, with significantly different peaks (Watson's two sample U^2 , $p < 0.001$), except for cat and weasel (U^2 : 0.092, $p > 0.10$). Cats, weasels and stoats exhibited crepuscular activity patterns, with peaks around sunset and early morning (Figure 6), but stoats also showed daytime activity, making its peak activity significantly different from cat and weasel peaks. These bimodal

patterns in cats and stoats align with previous research (J. A. Horn et al., 2011; Sidorovich et al., 2008; Turler, 2023), that observed similar peaks at dusk and dawn. However, domestic cats showed no daytime activity, despite their known tendencies to be active during day (J. A. Horn et al., 2011). This underscores the importance of policy to keep cats inside at night around meadow bird areas during the breeding season. A study by Sidorovich et al. (2008) conducted in forest habitats, recorded weasels to be mainly diurnal, therefore conflicting with the nocturnal patterns that we found. An explanation for this difference is that weasel activity may be influenced by airborne predators, with nocturnal owls posing the highest risk in forests and diurnal raptors in open grasslands (Jędrzejewski et al., 2000; Mougeot et al., 2020). In our study area, the prevalence of diurnal raptors likely drives the weasel's nocturnal behaviour as an adaptation to avoid predation. European polecats and stone martens exhibited single activity peaks between sunset and midnight. While this pattern in polecats is in line with previous findings (Lode, 1995), stone martens were found to be active bimodally in other systems with similar species composition (Roy et al., 2019). This variation might reflect differences in the temporal activity of competing predators and of primary prey species. For instance, the stone marten's main prey in our system are meadow birds and rodents (van den Berge et al., 2021), which may exhibit different temporal patterns than the Woolly hare, its primary prey in other ecosystems (Roy et al., 2019). Additionally, stone martens are very opportunistic and generalist feeders, with a fair amount of their diet including plant materials and household waste (van den Berge et al., 2021) enabling them to alter their activity more easily. Combined with higher human disturbance during daytime from farming, recreation and culling, this may have led to stone martens adapting a nocturnal activity pattern in our study area.

The similarities in temporal activity patterns may stem from the lack of larger predators in the system due to targeted predator management practices. In natural ecosystems, species such as the red fox (*Vulpes vulpes*) would typically be present, however, red foxes are culled during the breeding season in our study area, leading to the absence of the species. Additionally, stone martens and feral cats are culled during the breeding season, maintaining artificially low numbers of larger mesopredators in the area. A study by Tsunoda et al. (2020), found temporal partitioning to be highly influenced by the presence and activity patterns of the largest predator in the system. Three smaller species avoided peak activity times of the largest predator, while showing high temporal overlap with each other, suggesting that body size differences can drive temporal avoidance. The lack of larger predators in our study area may therefore facilitate coexistence between similarly sized mesopredators, reducing the need for temporal partitioning. This concept aligns with other studies on mesopredator release, where reduced large-predator presence has been shown to increase overlap among smaller predators as competition for resources decreases (Prugh et al., 2009).

Competition among mesopredators is higher when prey availability declines, as the risk of negative interactions increases only when the need for food outweighs the risk of injury from interspecific aggression (Lampropoulos et al., 2013). Therefore, competition is dependent on prey availability, which fluctuates throughout the year, as well as between years, influencing spatial and temporal activity (Petersen et al., 2019). The ecological conditions of the study year thus may have shaped the observed spatio-temporal patterns. In 2023, prey availability was relatively high due to increased rodent densities (Bijlsma, 2024), positively affecting predator densities the following year, as higher prey availability results in more survival and

better reproduction (Clermont et al., 2023). Such scarcity of prey combined with higher predator densities could result in higher competition among mesopredators, resulting in stronger spatial and temporal partitioning as a response to intensified resource competition.

Finally, the lack of pronounced temporal partitioning may be due to niche differentiation. Species with similar diets are likely to have comparable temporal activity, as they adapt to activity patterns of their prey. However, subtle differences in prey selection, foraging strategies and hunting abilities may facilitate coexistence between species (Powell & Zielinski, 1983). Remonti et al. (2012) suggest that the coexistence of similar sized mustelids depends on both prey availability and niche differentiation, driven by subtle differences in physiological and behavioural traits. For instance, weasels and stoats have similar habitat preferences, but manage to coexist because of their differences in prey specialization. The smaller weasel mainly feeds on bank voles (*Clethrionomys glareolus*) and moles (*Talpa europaea*) as it can enter their tunnels and runways. In contrast, the slightly larger stoat preys on *Microtus* voles, water voles (*Arvicola terrestris*) as well as birds and lagomorphs, which are too large for weasels (Aunapuu & Oksanen, 2003; Elmeros, 2006).

Spatial activity

Spatial overlap was found to be moderate to high among most species pairs, except for three species pairs with large body size differences (marten-weasel, cat-weasel, cat-stoat, SSI <0.55) (Figure 7). In these pairs, the smaller species face an increased risk of lethal interaction, leading to stronger spatial partitioning with the larger species. This is consistent with previous findings that body size differences can drive spatial segregation in predator communities to minimize direct interactions (Palomares & Caro, 1999). As the species pairs cat-weasel and cat-stoat displayed high temporal overlap, spatial partitioning appears the more prominent mechanism in which they avoid competition or direct encounters. Domestic cats have been documented to prey on small mustelids like weasels and stoats (Flux, 2017; Kauhala et al., 2015), likely contributing to the spatial partitioning between these species pairs. It is important to note that the SSI used to assess spatial overlap provides only a presence-absence measure, without accounting for occupancy or the frequency of observations. Therefore we subsequently used capture rates in linear models account for observation densities as well.

We found no evidence for spatial avoidance in the linear models testing for negative spatial correlations between the three species pairs. This could be partially due to the relatively small sample size of 30 locations, as these species pairs did show a slight negative relationship after omitting an outlier (Appendix fig. 2). Nevertheless, it is likely that variation in spatial occurrence is influenced more strongly by additional factors other than predator presence, such as proximity to humans, vegetation height, prey preference and linear structures (Aunapuu & Oksanen, 2003; Linck et al., 2023; Magrini et al., 2009; Rondinini et al., 2006). Other studies found occupancy of mesocarnivores to be influenced by landscape composition, where heterogeneity in the landscape provides a wider variety of refuge and prey (Linck et al., 2023). As management efforts improve heterogeneity in the landscape, protected areas offer more refuge and prey, enabling coexistence of mesopredators.

Prey availability further plays a significant role in influencing spatial distributions and competition, as prey densities can fluctuate across habitat, seasons and years (Boczulak et

al., 2023). This variation in prey availability can alter patterns of co-occurrence, as higher prey availability often reduces competitive interactions between predators. A study by Petersen et al. (2019), found two mesocarnivore species to only have low spatial overlap when prey availability was low. As prey availability was relatively high in our study year, this may have resulted in less pronounced spatial patterns (Bijlsma, 2024). Additionally, a study by Alipio et al. (2024), found spatial partitioning to be mostly explained by the presence of predators and competitors in the system. As larger predators can be seen as both predator and competitor of the smaller species, it could explain why the smaller species show less spatial overlap with these larger species, similar to the effect large predators have on the temporal partitioning.

Niche differentiation may further explain spatial coexistence of mesopredators, especially for species with similar diets. Selection of different microhabitats, like field edges versus open fields or high vegetation versus low vegetation might allow predators to use different physical spaces within the same landscape (Remonti et al., 2012). For instance, small mustelids strongly prefer edge zones, including the riparian zone and field edges, whereas domestic cats are more likely to stay close to urban areas, farms and within the cover of grasslands (J. A. Horn et al., 2011; Magrini et al., 2009; Rondinini et al., 2006). We see a similar pattern for domestic cats in figure 8, where they appear to be more present in the western edge, close to roads and farms. Specific landscape features, such as proximity to water sources, vegetation structure, and human infrastructure, likely influence habitat selection within this protected area. These variables may act as subtle dividers, facilitating coexistence even when dietary overlap is high, which is especially the case in human-modified landscapes (Torretta et al., 2021).

Lastly, limited spatial availability in small protected areas, such as the 40 ha in our study area, could force mesopredators to coexist more closely than they would in more extensive natural habitats. Outside these protected zones, food availability is often much lower, particularly for specialized predators like small mustelids, confining them to the protected areas. This lack of space available for each species could result in higher spatial overlap, requiring different adaptations to coexist. Larger, undisturbed areas with higher habitat heterogeneity could allow for more spatial partitioning, thereby reducing negative interactions between competing mesopredators (Linck et al., 2023). Expanding protected areas or enhancing connectivity between smaller, existing areas could alleviate mesopredator competition while providing additional space for meadowbird conservation.

Synthesis & Future research

In this study we looked into spatial and temporal partitioning separately, however spatial and temporal behaviors are often linked, with species altering both when and where they are active, in response to perceived risks from other predators (Rees et al., 2024; Tsunoda et al., 2020; Zalewska et al., 2021). Spatio-temporal partitioning patterns in mesopredators may be more pronounced on a micro-scale, where fine-scale reactive behaviours come into play. For example, predators may display avoidance behaviours only when there is a perceived immediate risk of encountering another predator (Zalewska et al., 2021). In this study, we did not examine the combined effects of spatial and temporal dynamics, though these effects are likely interconnected. Studying the spatio-temporal effects in the future could be done by

using occupancy models, time-to-encounter analysis or by conducting scent-marking experiments (Pereira et al., 2024). This is done more easily when working with fewer study species, as 5 species account for 10 pairwise interactions, complicating occupancy modelling.

Future studies would benefit from comparing multiple years of the same study area to better understand the effects of prey availability and ecological variations on the spatial and temporal partitioning. Ideally, these studies incorporate measurements on prey densities as well. Including both study areas with differing management strategies, varying in species compositions and large predator presence, could provide insights into how predator interactions and competition dynamics change across contexts. This ultimately will provide valuable information for management and conservation of both predator and meadowbird populations. Additionally, incorporating different landscape variables such as vegetation height/density, edge-to-area ratio and urbanized areas would be interesting, as studies have shown that predator occupancy is influenced by landscape composition (Linck et al., 2023). Altogether, this might give information on how to design protected areas for optimal predator-prey balance.

Furthermore, extending the study to longer time periods could reveal differences in prey availability throughout the year. A study by Lode (1995), found that temporal activity of the European polecat is variable throughout the seasons. They suggest this may be a result of changes in feeding tactics due to fluctuations in prey availability and prey activity patterns. Seasonal fluctuations may also affect temporal overlap between species, Torretta et al. (2021) observed changes in this between warm and cold seasons, likely due to heightened competition for resources. Extending the study over the entire year may give insight into how prey availability is variable in our study system.

Conclusion

Our study found high spatial and temporal overlap among species, except for a few species pairs, characterized by larger differences in body size and diet. The high spatio-temporal overlap between species pairs could be attributed to the absence of large predators, variations in prey availability and niche differentiation, all of which allow mesopredators to coexist. Studying these spatio-temporal dynamics within protected meadowbird areas offers essential insights for nature management helping to protecting vulnerable meadowbird populations by improving predictions of management outcomes, especially in the context of shifting predator communities.

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Appendix



Figure 1: Camera traps images showing the various mesopredator species recorded in the study area of Soarreemoarre.

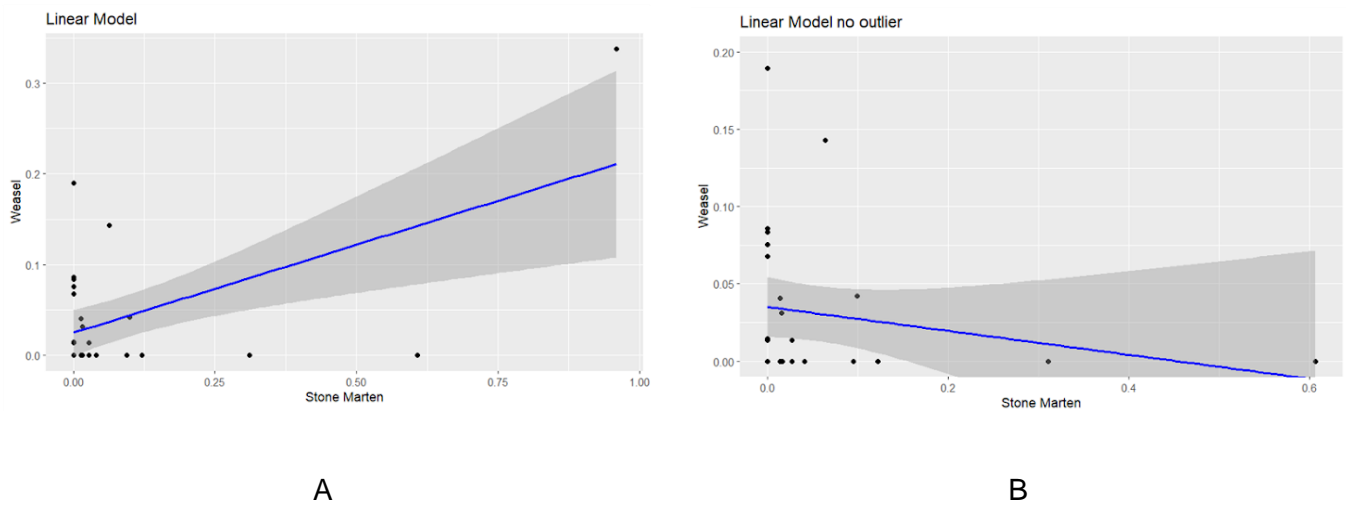


Figure 2: A) Linear model predicting the spatial distribution of the weasel, based on the distribution of the Stone marten. B) Same linear model after removing an outlier.

Table 1: Correlation between species based on capture rates of different camera locations, results of

Larger sp.	Smaller sp.	β	SE	t	p-value	R ²
<i>Domestic cat</i>	<i>Stone marten</i>	-0.05	0.06	-0.97	0.34	0.032
	<i>European polecat</i>	-0.03	0.14	-0.20	0.84	0.001
	<i>Stoat</i>	-0.06	0.09	-0.70	0.49	0.017
	<i>Weasel</i>	-0.20	0.16	-1.31	0.20	0.058
<i>Stone Marten</i>	<i>European polecat</i>	0.24	0.47	0.52	0.61	0.009
	<i>Stoat</i>	0.65	0.27	2.33	0.02	0.163
	<i>Weasel</i>	0.19	0.06	3.46	0.002	0.299
<i>European Polecat</i>	<i>Stoat</i>	0.003	0.12	0.03	0.98	2.672e-05
	<i>Weasel</i>	0.26	0.21	1.26	0.22	0.054
<i>Stoat</i>	<i>Weasel</i>	0.93	0.28	3.31	0.002 **	0.282

linear models.

AI statement

I have made use of the AI tool chatGPT. I primarily used it to rewrite a few sentences I had written that weren't perfect or needed some work. I asked it to rewrite a piece of text I copy pasted into it. I then used its suggestions to make the sentences or piece of text flow better. I also used it to improve code for data analysis and to help me workout errors in code to make data analysis more efficient.

prompts I used:

- *Can you rewrite this piece of text: ...*
- *Can you give me synonyms for ...*
- *I get this error in R ... Can you tell me what is going wrong?*