Effects of Prey Availability, Land Use and Human Disturbance on Weasel Populations

Research report

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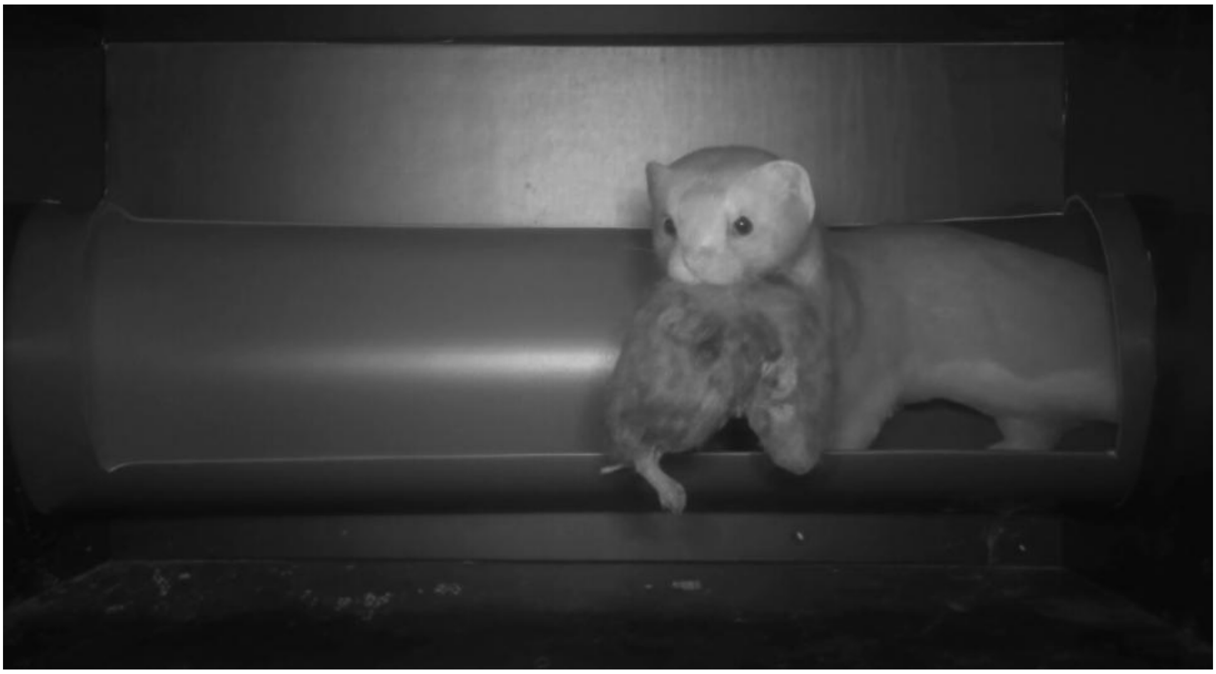

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Abstract

The weasel plays a complex yet important role in ecosystems as it is the smallest carnivores in the Netherlands and therefore the most common specialist involved in rodent population cycles. Due to a limited amount of research it is unclear how different environmental factors such as small rodent abundances, land use and human disturbance, explain the occurrence of weasels (*Mustela nivalis)*. Data was collected in four research areas in the Netherlands using 16 Mustela camera trap boxes from the 28th of April until the 28th of September 2025. Weasels were detected more often at locations with higher bank vole abundances, and their activity overlapped most with bank voles compared to other small rodents. Open fields, pastures, and urban grasslands were positively associated with weasel presence, likely due to higher prey densities. However, the various proxies of human disturbance did not significantly affect weasel activity in this study, neither on a small scale within research areas nor on a larger scale when comparing between those areas. To further refine these findings, future research should study how prey availability and land use shape weasel occurrence at larger spatial scales, and whether human disturbance leads to shifts in space use or temporal activity rather than local habitat avoidance.

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Introduction

Small mammalian carnivores play important roles in ecosystems, influencing ecosystem structure and providing various ecosystem services (Marneweck et al., 2021). However, they are particularly vulnerable to local extinction in fragmented landscapes created by human development due to their relatively large ranges and low numbers (Crooks, 2002; Marneweck et al., 2021). The weasel (*Mustela nivalis*) is the smallest carnivores of the Mustelidae family (King & Powell, 2006). It is widespread and relatively common throughout Europe (King & Powell, 2006). This small mustelid is native to the Netherlands and plays a complex yet important role in ecosystems (Mos & Hofmeester, 2020). Its ecological significance is largely due it being the smallest carnivores in the Netherlands and therefore the most common specialist involved in rodent population cycles (King & Powell, 2006; Norrdahl & Korpimäki, 2000). Recent studies, however, suggest that their population is declining drastically (García & Mateos, 2009; Hellstedt et al., 2006; Torre et al., 2018; Wright et al., 2022). Because of this the weasel was given increased protection across five provinces in the Netherlands in 2017-2019 (Mos & Hofmeester, 2020).

Nevertheless, reliable data regarding the occurrence, habitat preferences and population size of the weasel is still lacking (Croose & Carter, 2019; García & Mateos, 2009; Mos & Hofmeester, 2020). This lack of appropriate data is mainly caused by the difficulties of detecting the weasel (Croose & Carter, 2019; García & Mateos, 2009; Mos & Hofmeester, 2020). Small mustelids are infrequently observed and leave few easily detectable signs in the field, causing a multitude of monitoring techniques to be unsuitable (Croose & Carter, 2019; García & Mateos, 2009; Mos & Hofmeester, 2020). Most data regarding small mustelids is obtained by live trapping, citizens science or using hunting statistics (Croose & Carter, 2019; Mos & Hofmeester, 2020), all of which are either invasive, pose risks to the animals or can be unreliable. This lack of reliable data does not only cause doubt about the population status of small mustelids, but also results in uncertainties regarding their behavior and ecology. Monitoring the abundance, behavior and distribution of small mustelids is essential for protecting and managing their populations but also for understanding the ecosystem processes they are part of (Graham, 2002; Wilson & Delahay, 2001).

To tackle the monitoring challenges regarding the weasel, the Mustela camera box (hereafter "Mustela box") was designed by the Small Mustelids Foundation (Mos & Hofmeester, 2020). The Mustela box is specifically designed for small mustelids by combining the high detection probability of tracking tunnels and the identification possibilities of a standard camera trap. It can monitor small mustelids in dense undergrowth, where they seek refuge from predators such as red foxes (*Vulpes vulpes*), owls and hawks (Croose & Carter, 2019; García & Mateos, 2009; Mos & Hofmeester, 2020). This spatial predator avoidance behavior significantly shapes the behavior of weasels, leading them to avoid open areas without dense plant cover (Zub et al., 2008). Predator avoidance behavior can also show as temporally distancing, causing prey to be active at a different time as their predators (Dröge et al., 2017). Wildlife species can respond to human disturbances as they would to their natural predators (Ciuti et al., 2012). However, it remains unclear whether small mustelids also react to human disturbances this way. Small mustelids are known for their bold behavior, and therefore it cannot be assumed they actively avoid human disturbances. Due to the limited amount of research on this topic, their actual behavioral response to human disturbances remains unclear. Because of the rapidly growing human population it is crucial to know how small mustelids respond to human disturbances (Beardsley et al., 2009; Niemelä et al., 2010).

The distribution and abundance of small mustelids are known to be strongly influenced by the availability of small rodents. Compared to other mammals, weasels have a relatively high basal metabolic rate, which results in a high energetic demand and a strong dependence on frequent food intake (Erlinge, 1974). Therefore, prey abundance is a critical factor for their survival. The effect of food availability on weasel abundance has been detected in multiple studies (Magrini et al., 2009; Zub et al., 2008; Jedrzejewski et al., 1995). Also, weasel reproduction is known to be dependent on the rodent density in spring (Jedrzejewski et al., 1995). Among rodent species, the bank vole seems to be or particular great importance, as it is the primary prey species of the weasel (Korpela et al., 2014). Therefore, its abundance plays a crucial role in sustaining small mustelid populations (Croose & Carter, 2019; Graham, 2002; Mos & Hofmeester, 2020). Because of the great dependence of weasels on bank vole abundance, small mustelids are thought to only occur in habitats where bank voles are present in large enough numbers.

Because of their high energetic demands, small mustelids require habitats with high prey densities. Therefore, weasels show clear land use preferences. Open and cultivated fields generally support high abundances of small rodent prey (Magrini et al., 2009). However, weasels are themselves vulnerable to predation in such environment. Predators impose a high predation risk for small mustelids when moving through open fields (Epps et al., 2017; Jedrzejewski et al., 1995). Therefore, small mustelids use densely structured habitats to remain hidden from predators (Magrini et al., 2009). As a result, the combined pressures of high food requirements and predation risk lead weasels to use open habitats with natural edges (Magrini et al., 2009; Zub et al., 2008).

In this study I researched how different environmental factors: small rodent abundances, land use and human disturbance, explain the occurrence of weasels (*Mustela nivalis*) in four nearby research areas in the Netherlands. This was done on the basis of the following research questions and hypotheses. First, I researched whether human disturbance influenced the activity of weasels at both a small spatial scale (average distance between measurement points: ± 500 m) and at the scale of entire research areas (2.5-5.6 km^2). I predicted that the weasel is less active and more nocturnal (under the assumption of relatively low human activity at night) near human activity and more active and more diurnal in areas further away from human disturbance. This pattern was expected to be seen at both spatial scales as mammals are known to spatially and temporally avoid their natural predators. I predicted that small mammals would react to humans in the same way they do to their natural predators. Secondly, I researched if there is a relation between the abundances of the different small rodent species and the number of small mustelids detected at both a small spatial scale and at the scale of entire research areas. It was expected that only bank vole abundance would have a positive effect on the number of weasel detections on both small scale and on the scale of entire research areas. Because the bank vole is the main prey species of weasels, higher small mustelid activity was expected in areas with higher bank vole densities. Lastly, it was researched which land use types predict the occurrence of weasels and how these patterns explain differences in small mustelid activity between the four research areas. This was done using species distribution modelling (SDM, using Maxent software) based on reported occurrences in the Netherlands. I hypothesized that land use types that increase the availability of open habitat with natural edges would positively affect small mustelid abundance. Therefore pasture and agriculture land use types were expected to positively predict the occurrence of weasels, whereas forest and urban land use types were expected to have a negative effect. Because of the similar land uses between the research areas, I expected that there was no meaningful difference in small mustelid occurrences between the four research areas.

Research methods

Study areas

The research was carried out at four sites selected through convenience sampling: 'Hagebeemd', 'Markdal', 'Broek/Strijbeekse heide' and 'Merkske' in the Netherlands (Figure 1).

Hagebeemd has the most observations of weasels around Breda since 2020 (Waarneming.nl, n.d.). It is a nature and recreation area with herb-and faunal-rich grassland, wet hay meadows, marsh and wet scrubland (Vierde Bergboezem Breda, n.d.). Hagebeemd has a size of 3.9 km².

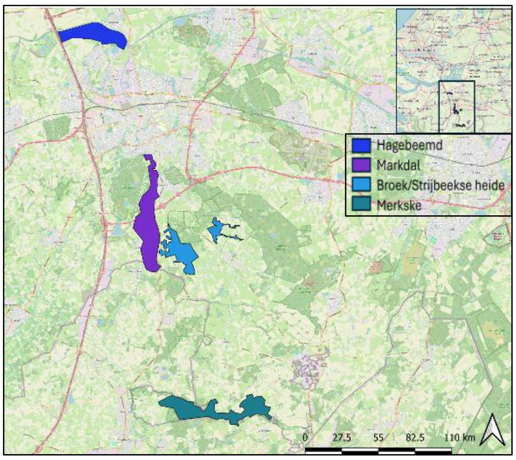

Figure 1: The locations of research areas 'Hagebeemd', 'Markdal', 'Broek/Strijbeekse heide' and 'Merkske'

Markdal has the second highest number of observations of weasels around Breda since 2020 (Waarneming.nl, n.d.). Markdal is a nature, recreation and farming area. Markdal therefore has a varied landscape of pastures, trails and nature and is a typical stream valley landscape (Vereniging Markdal, 2019). This area has a size of 2.6 km²

Broek and Strijbeekse heide (hereafter "Strijbeekse heide") are two identical small scale cultural landscapes and are part of nature area 'Chaamse beek'. They consist of hedgerows, species-rich grasslands, and creeks flowing through the area (Natuurmonumenten, n.d.). They have a jointly size of 2.5 km²

Merkske is a nature area featuring a diverse ecosystem of woodlands, bramble walls and species-rich grasslands along the creek 'Merkske' (Staatsbosbeheer, n.d.). Merkske has a size of 5.6 km²

Data collection

Small mustelids and rodent species

The Mustela box was used for the data collection (Appendix 1, Figure 2, Stichting Kleine Marters, 2025). The Mustela box is designed to capture footage of small mustelids by combining a regular camera trap with the high observation rate of a tracking tunnel (diameter of 8 cm). The Mustela box was made of 12 mm concrete plywood and the camera used in the Mustela box was the Reconyx Hyperfire 2 HF2X.

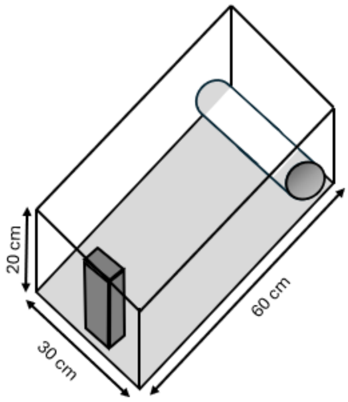

Figure 2: A schematic drawing of the 'Mustela camera box'. The Mustela camera box has a length of 60 cm, a width of 30 cm and the height of 20 cm.

Species occurrence data was gathered from small mustelids and small rodents in four study sites at a total of 69 measuring locations. The data collection period lasted 154 days, starting at the 28th of April and ending at the 28th of September (Appendix 2 and 3). The first 13 weeks and 4 days each of the four research areas had a total of four Mustela boxes. The Mustela boxes were moved to other measuring points within their respective study areas every four weeks. After the first 13 weeks, all the sixteen Mustela boxes were moved to research area Hagebeemd, to increase the number of sightings, as most sightings were in Hagebeemd. Some of the Mustela boxes continued to be relocated every four weeks, however not all boxes were moved each month because in Hagebeemd, there were not enough measuring locations to relocate all sixteen Mustela boxes simultaneously. At each relocation, the SD card and batteries were replaced. The average distance between neighboring measuring points was 495 meters (SD = 160, min = 370, max = 1631, n = 69).

Land use

A SDM analysis was conducted with MaxEnt version 3.4.4 (Steven et al., 2025) on *Mustela nivalis* occurrence data from GBIF from 2023 till November 2025 (GBIF.org, 2025). A total of 2696 detections were filtered for duplicates, coordinate errors and spatial sampling bias. Duplicate records were removed using dplyr, and coordinate errors were filtered using the CoordinateCleaner package with standard tests (capitals, centroids, equal coordinates, GBIF headquarters, institutions, seas and zero coordinates). Spatial sampling bias was addressed by spatial thinning using the terra package, where one occurrence was randomly retained per 0.05° grid cell. This resuted in 793 valid occurrences used for the analysis (Hijmans, 2020; Wickham et al., 2023; Zizka et al., 2019). Land use data was downloaded from LGN from the year 2023 and aggregated from the original five meter resolution to a hundred meter resolution using modal. Also the data was transformed to binary data (Appendix 4) (Hazeu et al., 2025).

Human disturbance

The human disturbance at each measuring point was estimated as the distance of the measuring point to structures that create human disturbance. The structures that create human disturbance were 0-30 km/hour roads, 40-60 km/hour roads, 70-90 km/hour roads, highways, bicycle lanes, footpaths and urban areas. Nearest distance to these structures where calculated using QGIS (QGIS.org, 2025).

Data processing and storage

The camera footages were uploaded to Agouti (Casaer et al., 2019). Here images were clustered into one sequence when the time differences between images was less than 120 seconds. For the different small rodent species, the number of sequences was used to predict their abundance. For weasels, there was a smaller number of individuals, making it possible to distinguish between individuals. Overall, weasels revisited the Mustela box daily, and I assumed this was the same individual, unless clear external differences were seen such as size or coat patterns. When the Mustela box was moved and later replaced back to the original location, the first new observation was counted as a new individual. Also, a less conservative counting was done, to compare the results with other studies. Using this counting, detections occurring 60 minutes apart were considered to be independent weasel individuals.

When all the camera footage was processed, files with every sequence were noted in an Excel file. This Excel file was stored in a OneDrive cloud to ensure the FAIR data principles of data storage, namely that the data should be findable, accessible, interoperable and reusable.

Data analysis

All statistical analysis were executed using R-studio version 4.4.1 (RStudio Team, 2021). Statistical significance was assessed at an alpha level of 0.05.

Small mustelids and rodent species

The differences in number of weasel individuals per day and bank vole sequences per day between research areas was tested with a Kruskal-Wallis test, and a Bonferroni post-hoc test. The package used was: dunn.test (Dinno, 2014).

Also, activity patterns were analyzed using the sequences made by Agouti for both weasels and small rodents per week. Daily activity (diel) patterns of weasels and all small rodent species were studied by converting the time of detection into time (hours) relative to sunrise. Pairwise temporal overlap between species was calculated using the coefficient $\hat{D}_1$. The following packages were used in R studio: dplyr 1.1.4 (Wickham et al., 2023), lubridate 1.9.4 (Grolemund & Wickham, 2011), suncalc 0.5.1 (Thieurmel & Elmarhraoui, 2022) and overlap 0.3.9 (Meredith et al., 2024). Also, weasels seasonal variation was analyzed. This was done by summarizing the number of indidviduals per month and research area. A negative binomial mixed model was used to determine if there were a significant differences between the months, with month as fixed factor, research area as random factor and a correction for the number of Mustela boxes per research areas. For the bank vole, the same was done, using the Agouti sequences instead of individuals. The following packages were used in R studio: dplyr (Wickham et al., 2023), lubridate (Grolemund & Wickham, 2011) and glmmTMB (Brooks et al., 2017).

Land Use

In MaxEnt the random test percentage was put to 30, output format as logistic, the land use data as categorical and a resampling of 10 (Steven et al., 2025). The most important variables predicting weasel abundance were determined using the jackknife produced by MaxEnt. Climatic variables (Bioclim) were not included, as meaningful differences were not expected given the small spatial scale of the study.

Human disturbances

To study the impact of human disturbances on weasel individuals, a binominal generalized linear model was used. The human disturbances were standardized (mean=0, SD=1) and a logit link function was used for the binomial family. Also, a generalized linear mixed model was done, including research area as random effect. The following packages were used in R studio: tidyverse 2.0.0 (Wickham et al., 2019) and lme4 1.1.37 (Bates et al., 2015). A zero inflated binominal GLMM could not be performed as it was too complex a model for the limited amount of data.

Due to a small sampling size, differences in distances to human disturbances between measuring points with and without small mustelid detections were compared using A Mann-Whitney U test. The following packages were used in R studio: dplyr 1.1.4 (Wickham et al., 2023) and car 3.1.3 (Fox & Weisberg, 2019).

The influence of human disturbance on the nocturnality of weasels could not be measured due to a small sample size.

Results

General findings

Small mustelids and rodent species

A total of 5209 sequences were recorded during 154 trap days using 16 Mustela boxes. Of these sequences, 104 were mustelid sequences, representing 19 individual weasels (*Mustela nivalis*). No stoats (Mustela erminea) were observed. Of all weasel sequences, 96% percent, representing 16 individuals, was observed in Hagebeemd, while none were found in Merkske. The weasels were observed at a total of 12 different measuring points, 9 of which were located within Hagebeemd. At four of the measuring locations within Hagebeemd, two different individuals were detected. The overall trap rate was 0.03 weasels per trap day. When using the less conservative counting of Mos & Hofmeester (2020) 78 weasel individuals were detected, resulting in an overall trap rate of 0.12 weasels per trap day.

A total of 3422 mouse sequences were detected, of which 1989 wood mouse (*Apodemus sylvaticus*) sequences, 1111 common bank vole (*Myodes glareolus*) sequences and 322 White-toothed Shrews (*Crocidura russula*) sequences. For all the three rodent species, 70 percent or more was detected in Hagebeemd (Table 1). Besides small rodents and weasels, also non-target species were detected in the Mustela boxes: Common toad *(Bufo bufo)* (one sequence), Red fox (*Vulpes vulpes*) (one sequence), Great tit (*Parus major*) (six sequences), True frog (*Pelophylax*) (seven sequences) and Brown rat (*Rattus norvegicus*) (sixteen sequences).

Tabel 1: Average number of sequences per day of the target species detected in the Mustela boxes in the four different research areas.

Species	Hagebeemd	Markdal	Merkske	Strijbeekse heide
Apodemus sylvaticus	1.331	0.883	0.412	0.562
Myodes glareolus	0.919	0.250	0.115	0.093
Crocidura russula	0.215	0.049	0.249	0.006
Mustela nivalis	0.095	0.003	0.000	0.009

The number of detection per month differed per species. The number of weasel individuals detected seemed to increase over the months, but this trend was not significant (GLMM, nbinom2, estimate=0.20, SE=0.19, z=1.08,p=0.28). Also the bank vole sequences increased over time, this trend is significant (GLMM, nbinom2, estimate= 0.61, SE=0.21, z=2.97, p=0.003).

Human disturbance

The average distance to a type of human disturbance differs per research area (Table 2). On average, Merkske seems to be farthest away from most human disturbances while Markdal is closest to most human disturbances.

Tabel 2: Average distance to the different kinds of human disturbances per research area.

Human disturbances	Hagebeemd	Markdal	Strijbeekse heide	Merkske
Highway	1816	1452	3406	9717
70-90 km/h road	1856	1991	1151	3295
40-60 km/h road	504	376	1049	555
0-30 km/h road	412	204	386	567
Urban area	697	243	625	1174
Bicycle lane	168	89	635	312
Footpath	140	66	229	98
Agricultural plot	26	132	181	200

Human disturbances and small rodents

Human disturbance, mouse species and bank vole abundance did not influence the presence of weasels at measuring locations (binomials GLMs, p> 0.1, Appendix 5). However, locations where weasels were detected had significantly more bank voles then locations without weasels (Wilcoxon rank-sum test, W=207.5, n0= 57, n1=12, p=0.021).

The weasel sequences showed a diurnal activity pattern. Contrary, the mouse species were most active during the night, showing a nocturnal activity pattern. However, the weasel activity did overlap most with that of the bank vole (Activity overlap, Dhat1= 0.56) (Figure 3) compared to the wood mouse and white-tooted shrew (Activity overlap, Dhat1= 0.27 and 0.31, respectively).

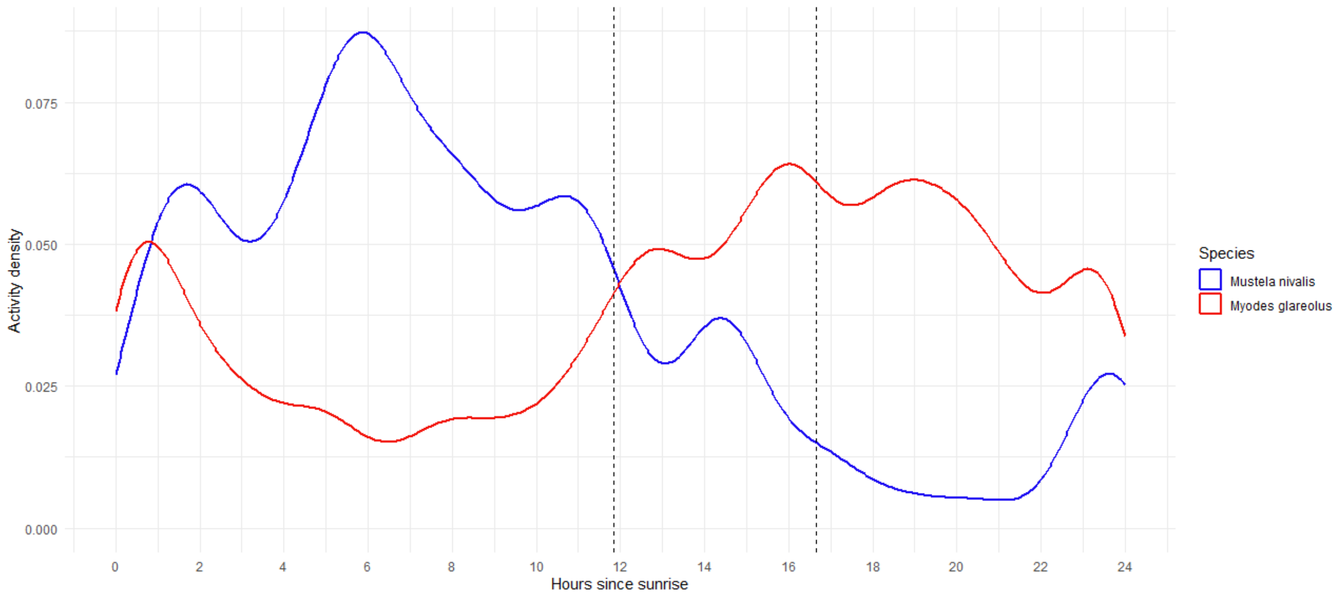

Figure 3: Number of sequences per hour after sunrise (hour 0) of weasels and bank vole detected in the Mustela boxes per week during the data collection. The first vertical line shows the earliest sunset during this research, and the second vertical line shows the latest sunset during this research.

Land use

The MaxEnt analysis showed that “pasture”, “grass in urban”, “salt water” and “agriculture” were the four most important predictors of weasel activity (Figure 4). Salt water had a clear negative impact on the weasel occurrence. In contrast, the other three variables had a positive impact on the weasel occurrences (Appendix 6). The average test AUC for the replicate runs was 0.728, and the standard deviation was 0.011.

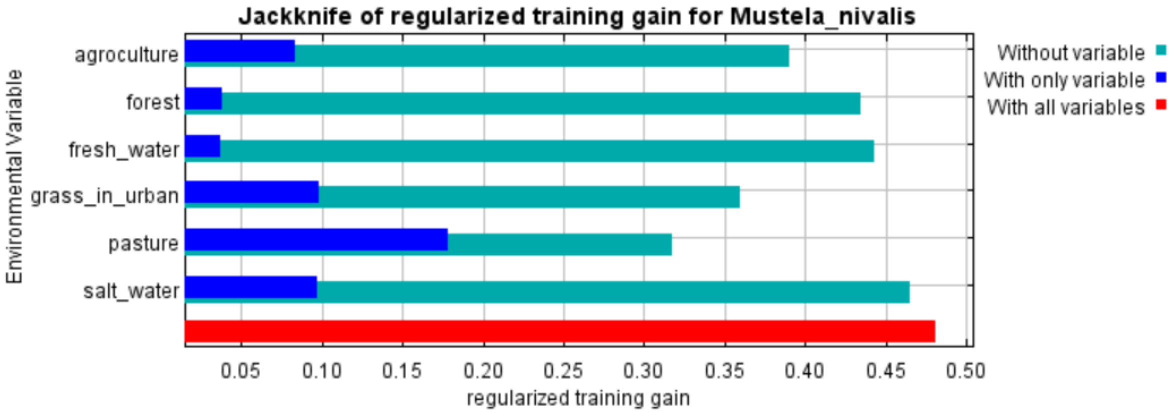

Figure 4: Jackknife of regularized training gain showing the variables agroculture, grass in urban, pasture and salt to be the four most important in predicting weasel occurences.

Differences between research areas

Daily probability of detecting a weasel individual per measuring location per day differed significantly among research areas. (KW test, χ^2= 12.74, df= 3, p= 0.01). Post-hoc tests (Bonferroni-corrected) showed significant differences between Hagebeemd and Markdal (p= 0.021) and Hagebeemd and Merkske (p= 0.003) (Figure 5).

Also, a significant difference was found for the number of bank vole sequences per day between the four research area’s (Kruskal-Wallis rank sum test, χ^2= 10.97, df= 3, p= 0.012). Post-hoc Dunn tests (Bonferroni-corrected) showed significant higher bank vole occurrences per day in Hagebeemd compared to Merkse and Strijbeekse heide (0.014 and 0.018 respectively) (Appendix 7). For all the small rodents combined there was a higher abundance in Hagebeemd than in Merkske (p= 0.037).

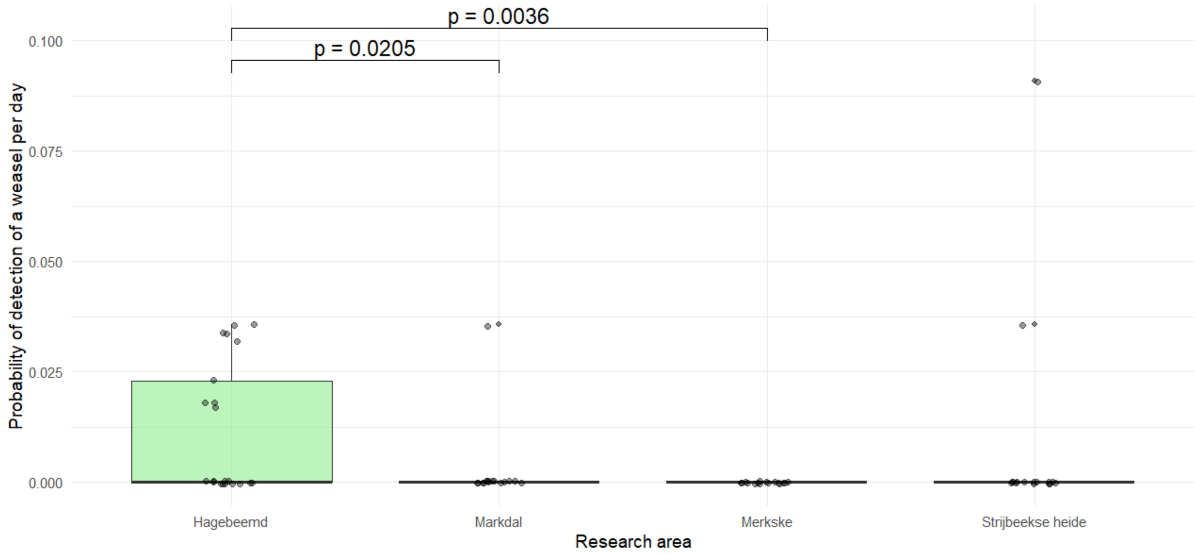

Figure 5: Kruskal Wallis test on the probability of detecting weasel individuals per measuring location per day between the four different research area's: Hagebeemd, Markdal, Merkske, Strijbeekse heide. There a significant higher propabalility of detecting a weasel individual at measuring locations in Hagebeemd then there was in Markdal and Merkske.

Discussion

In this research I studied how different environmental factors: small rodent abundances, land use and human disturbance, explain the occurrence of weasels (*Mustela nivalis)* in four research areas in the Netherlands. This study shows that weasel occurrence is strongly influenced by prey availability and habitat structure. Weasels were detected more often at locations with higher bank vole abundances, and their activity overlapped most with bank voles compared to other small rodents. Open fields, pastures, and urban grasslands were positively associated with weasel presence, likely due to higher prey densities. Most weasel sequences were recorded in Hagebeemd, where habitat characteristics matched the key variables identified in the MaxEnt analysis, highlighting the importance of land use for weasel distribution.

Bank voles are probably influencing weasel behavior and and habitat choice. This is because measuring locations where weasels occurred had significantly higher bank vole densities than measuring locations where weasels were not detected. Also, there were significantly more weasel detections in Hagebeemd than in Markdal and Merkske, while no significant difference was found between Hagebeemd and Strijbeekse heide. Similarly, bank vole numbers were significantly higher in Hagebeemd than in Merkske and Strijbeekse heide, while no significant difference was found between Hagebeemd and Markdal. These findings suggest that weasels adjust their movement and habitat selection based on the abundance of their main prey species. This corresponds with literature, where weasels adjust the size and placement of their territory according to the prey densities (Magrini et al., 2009; van Vuurde & van der Grift, 2005; Zub et al., 2008). It is known that predators want to shrink the available spatio-temporal space where their prey are distributing themselves in (de Matos Dias et al., 2018). Thus, besides weasels adjusting their spatial movements to increase their overlap with bank voles, they could also adjust their temporal activity. In my research this was supported by the observation that weasel activity overlapped most strongly with the bank vole compared to the other small rodent species. However, it should be noted that this support is relatively weak as the sample size of this study is rather small. Therefore it would be interesting to research in more detail if weasels are trying to close the spatio-temporal activity difference with their main species, and how strongly they adjust their habitat choice based on bank vole abundances.

Weasels have a strong preference for habitats with open fields and natural edges (Magrini et al., 2009; Zub et al., 2008), as their prey is relatively abundant in open field while they can hide from predators within the natural edges. The MaxEnt analysis showed that the variables ‘pasture’, ‘agriculture’ and ‘grass in urban’ had clear positive effects on weasel abundance. Probably because open and cultivated fields support high abundances of small mammal prey (Magrini et al., 2009). The high prey density is probably the reason for weasels to be mostly present in Hagebeemd, where habitat characteristics broadly align with the explaining variables in the Maxent analysis. Remarkably, the MaxEnt analysis also showed ‘forest’ to have a small but positive impact on weasel abundance, whereas in the literature an actual avoidance of forested habitats is found (Magrini et al., 2009; Zub et al., 2008). At present, no clear explanation for this result can be provided. It may reflect context dependent habitat use, limitations of the dataset, or landscape specific structural features. Lastly ‘salt water’ had a clear negative impact on weasel abundance, which is expected given that saline environments generally provide unsuitable conditions for the species. Because the most important land use variables correspond with the research area in which 96% of all weasel sequences were detected, land use appears to play an important role in determining weasel abundance.

I did not observe that the various proxies of human disturbances affected weasel activity, neither on a small scale within research areas nor on a larger scale when comparing those areas. In literature however, it is known that members of the mustelid family are influenced by human disturbance. For example, habitat suitability for the Eurasian otter (*Lutra lutra)* is negatively impacted by human disturbance (Ali et al., 2010) and the Stone marten (*Martes foina)* prefers less disturbed areas as resting sites (Santos & Santos-Reis, 2010). This makes it plausible that the weasel is also impacted by human disturbance, even though this is not found in my research. Besides the small sample size (only 19 weasels observed), the lack of significance may be explained by the large size of weasel territories, which can range from 8 up to 216 ha, which is much larger than the spatial scales used in my research (Gehring & Swihart, 1996; Jedrzejewski et al., 1995). If a weasel's territory is much larger than the research area, the effects of human disturbance may be overlooked. Weasels may use the measured area because of factors such as prey availability, while most of their territory remains relatively undisturbed by humans. As a result, avoidance of human disturbance at the territory level may not be detected when only a small portion is studied. Since human disturbance is known to affect mammals at larger spatial scales (Cavada et al., 2019; Defries et al., 2010), future research should consider the entire territory of weasels to better assess their true response to human presence.

Another explanation for the lack of a spatial response of weasels to human disturbance in their habitat could be because they are temporarily separating themselves instead. Because humans are mostly active during the day, the pressure of disturbance is lower at night. As a result, mammalian species have adapted to the human pressure by shifting their behavior more towards a nocturnal lifestyle (Gaynor et al., 2018). Because of this clear pattern for mammals across the world, it is plausible that weasels react to human disturbance in the same way. In my research, there were not enough weasel occurrences detected to test for increased nocturnal activity near human disturbances. However, when examining the study area used by Mos & Hofmeester (2020), it shows that their site was located closer to all sources of human disturbance compared to Hagebeemd. In their research weasel activity followed a clear crepuscular pattern, while in my research a Diurnal weasel activity was found. This may suggest that weasels are temporally separating themselves when human disturbance increases. However, this interpretation should be treated cautiously, because it based on only two sites and without a comparison with relatively undisturbed sites. It would thus be interesting for future research to further investigate temporal separation of weasels as a response to human disturbance.

Besides possible changes in their diel activity, the type of human disturbance measured also greatly impacts the results. In my research, distance to human disturbance was measured. However, besides distance no distinction was made according to the intensity of the disturbance. Because of that, a footpath can be very busy or barely used but still be treated the same in the analysis. It would be useful for further research to look into the actual intensity of disturbance instead of only the distance to the disturbance. Besides the intensity of disturbance, the type of human disturbance measured is also of great importance. This research focused on disruption by humans because of their presence. But larger scale disturbances such as habitat fragmentation and degradation should also be taken into account. Because of small mustelid's narrow diet and their specific habitat preferences, these kind of disturbances to their habitat could greatly impact their population size (Crooks, 2002). While small mustelids prefer typical cultural landscapes with natural corridors, these kinds of landscapes are rapidly being replaced by more efficiently managed agriculture (Schmitz & Herrero-Jáuregui, 2021), with less space for natural corridors and therefore wildlife. Because of this change, agriculture is one of the main causes of habitat fragmentation and degradation (Magrini et al., 2009). For future research, it would be interesting to differentiate between extensively and intensively managed agriculture.

Due to sample size limitations many of the results were inconclusive. This raises the question whether the research design could be improved to increase the number of detections. An improvement that has shown to significantly increase the number of detections is using a ten cm tube in the Mustela box instead of an eight cm tube (Mos & Hofmeester, 2020). However, eight centimeter tubes were used in this study to ensure comparability with previous research employing similar Mustela box designs. Importantly, an increase in tube diameter does not necessarily reflect a higher number of individual weasels, but may instead result from a higher number of detection events, potentially caused by repeated visits of the same individual. This distinction is crucial because Mos & Hofmeester (2020) used different criteria to define independent detections then I did. While Mos & Hofmeester (2020) considered detections occurring more than 60 minutes apart to represent independent individuals, detections in my study were only classified as separate individuals when clear morphological differences were observed or when the Mustela box was removed from the specific measuring location and redeployed after a period of one month or longer. As a result, increasing tube size could lead to more visits by the same weasel being counted as separate individuals in the Mos & Hofmeester approach, while in my study these would still be considered the same individual. However, increasing tube diameter could potentially increase the number of stoat detections, as there were none found in my research despite their know presence within the study area (Waarnemingen.nl, 2025). Other studies also detected a far lower trapping rate of stoats then weasels when using the Mustela boxes (Croose & Carter, 2019; Mos & Hofmeester, 2020). An explanation for absence of stoat detections could be their reluctance to enter tracking tunnels (Brown, 1994), which could be due to their larger size. Stoats are heavier and longer then weasels are, this might deter them from entering small tubes. Besides tube size of the Mustela box, research area has proven to greatly impact the number of weasels detected. Therefore, before starting the research period, it would be beneficial to select research areas based on the land use characteristics that were shown to be important in the MaxEnt analysis to increase the trapping rate.

Conclusion

This study aimed to examine how environmental factors, including small rodent abundance, land use and human disturbance, influence the occurrence of weasels (*Mustela nivalis*) in the Netherlands. The results show that weasel occurrence is primarily determined by prey availability, particularly the abundance of bank voles, and the land use. Weasels were more frequently detected at sites with higher bank vole densities, and their activity overlapped most with this species, compared to the other small rodents. This supports the hypothesis that prey availability plays a key role in weasel habitat selection. Additionally, land use, particularly open habitats such as pastures and urban grasslands, was positively associated with weasel occurrence, confirming the importance of habitat structure for weasel distribution.

However, the various proxies of human disturbance did not significantly affect weasel activity in this study, neither on a small scale within research areas nor on a larger scale when comparing between those areas. This could be due to the small sample size and the large territorial ranges of weasels, which might make local effects harder to detect. Weasels may respond to human disturbance at larger spatial scales or through temporal shifts in activity, such as becoming more nocturnal in disturbed areas. Future research should focus on broader spatial scales, incorporating the intensity of human disturbance and the full range of weasel territories, to better understand their response to human presence.

This study addresses the knowledge gap regarding the relative importance of prey availability, land use and human disturbance on weasel occurrence. To further refine these findings, future research should study how prey availability and land use shape weasel occurrence at larger spatial scales, and whether human disturbance leads to shifts in space use or temporal activity rather than local habitat avoidance.

Recommendations

Based on the conclusions of this study, future research should focus on exploring the relative roles of prey availability, land use, and human disturbance at spatial and temporal scales. Future studies could build on this work by conducting a landscape scale study that covers entire weasel territories, rather than smaller research areas, to better capture responses to human disturbance. This would allow testing whether human effects on weasels are primarily spatial (habitat avoidance) or temporal (shifts in diel activity).

Also, human disturbance could be measured more precisely by incorporating both disturbance intensity and type. Differentiating between extensively and intensively managed agricultural areas might also provide a better understanding how human disturbance affects small mustelids.

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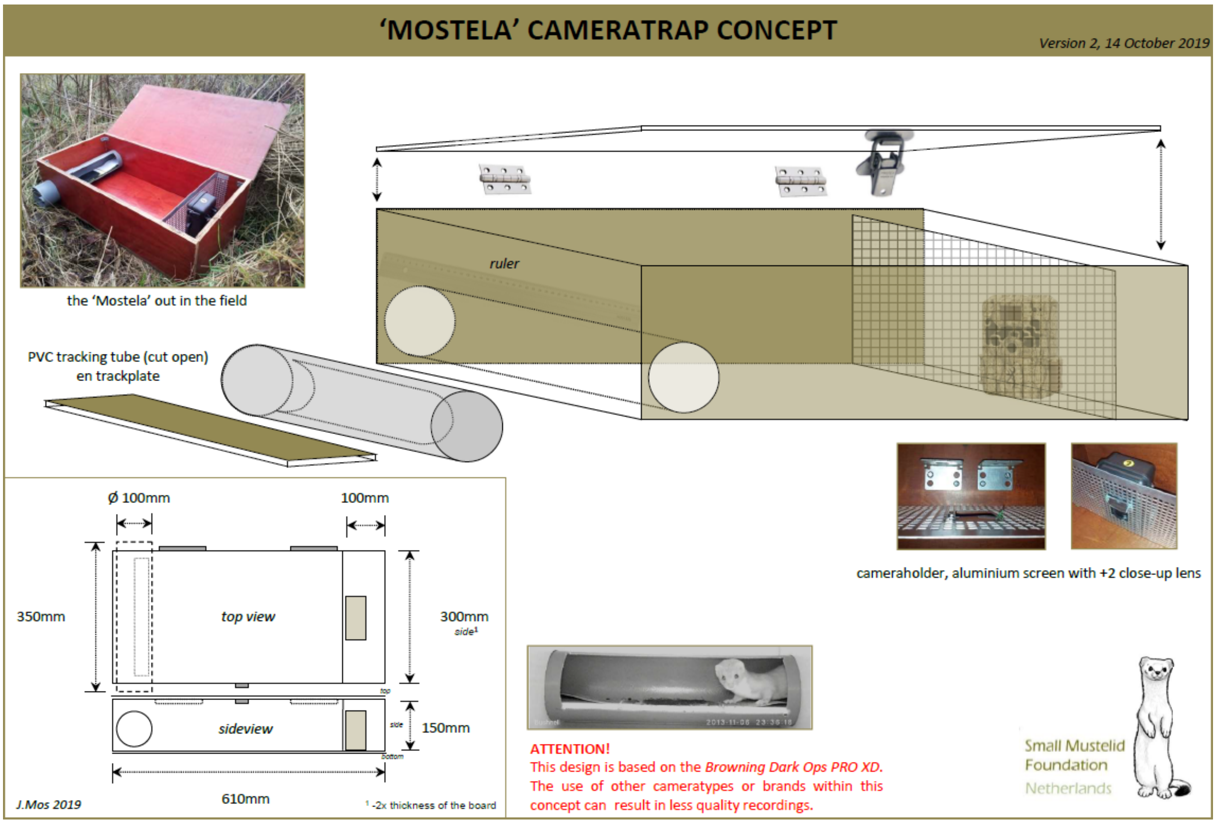
Appendix

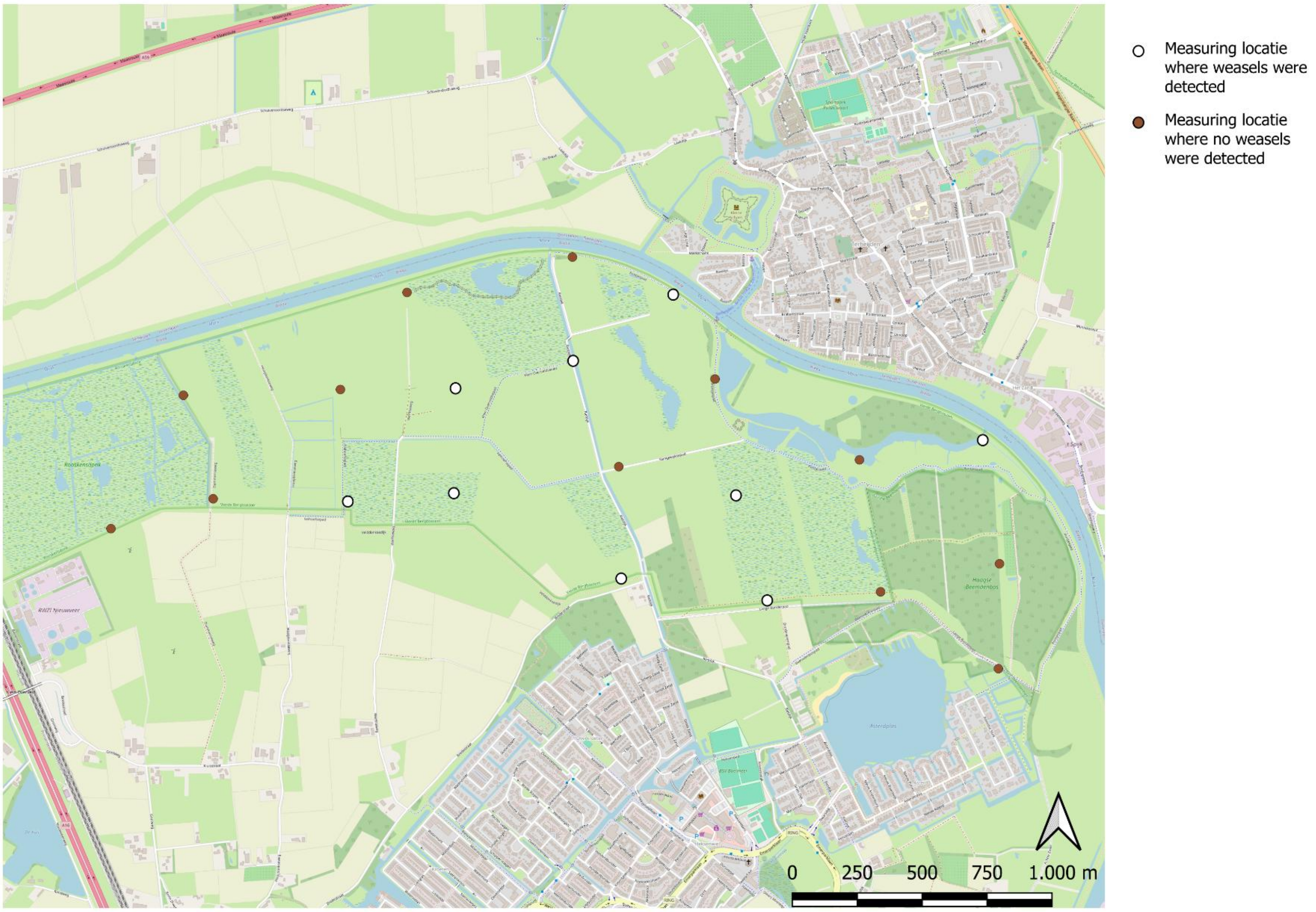
Appendix 1

Blueprint of the Mustela camera box from the Small Mustelid Foundation Netherlands (Stichting Kleine Marters, 2025). A= the short sides, 30 cm x 20 cm, B= 30 cm x 20 cm with a hole for the camera, C= camera, D= the long sides, 60 cm x 20 cm, E= the flooring and roof, 60 cm x 30 cm, F= the opening in footprint tracking tunnel, G= the footprint tracking tunnel with a diameter of 8 cm.



Appendix 2

Locations of different measuring points in the research areas Hagebeemd, Markdal, Strijbeekse heide and Merkske.




Measuring location where weasels were detected
Measuring location where no weasels were detected
0 250500750 1.000 m


Measuring location where weasels were detected
Measuring location where no weasels were detected
0 250 500 750 1,000 m


Measuring location where no weasels were detected
0 250 500 750 1.000 m

Appendix 3

Trap effort per measuring point

Measuring point	Research area	Trap effort
1	Hagebeemd	56
2	Hagebeemd	59
3	Hagebeemd	0
4	Hagebeemd	31
5	Hagebeemd	31
6	Hagebeemd	56
7	Hagebeemd	28
8	Hagebeemd	87
9	Hagebeemd	59
10	Hagebeemd	87
11	Hagebeemd	59
12	Hagebeemd	56
13	Hagebeemd	59
14	Hagebeemd	31
15	Hagebeemd	56
16	Hagebeemd	59
17	Hagebeemd	59
18	Hagebeemd	59
19	Hagebeemd	0
20	Hagebeemd	59
21	Hagebeemd	59
22	Markdal	28
23	Markdal	28
24	Markdal	28
25	Markdal	0
26	Markdal	28
27	Markdal	28
28	Markdal	28
29	Markdal	28
30	Markdal	28
31	Markdal	11
32	Markdal	28
33	Markdal	28
35	Markdal	11
38	Markdal	11
39	Markdal	11
47	Markdal	0
51	Strijbeekse heide	28
52	Strijbeekse heide	28
53	Strijbeekse heide	11
55	Strijbeekse heide	11

60	Strijbeekse heide	28
62	Strijbeekse heide	28
63	Strijbeekse heide	28
64	Strijbeekse heide	28
65	Merkskse	28
66	Merkskse	28
67	Merkskse	28
69	Merkskse	0
70	Merkskse	28
71	Merkskse	28
72	Merkskse	28
73	Merkskse	28
74	Merkskse	28
75	Merkskse	0
76	Merkskse	0
77	Merkskse	28
78	Merkskse	28
79	Merkskse	11
85	Strijbeekse heide	28
87	Strijbeekse heide	0
88	Strijbeekse heide	28
89	Strijbeekse heide	11
90	Strijbeekse heide	28
91	Strijbeekse heide	28
92	Strijbeekse heide	0
93	Strijbeekse heide	0
100	Merkske	11
103	Merkske	11

Appendix 4

LGN layers definition used in the MaxEnt analysis.

Class	**Combined class name in this analysis**
Pasture	Pasture
Maize	Agroculture
Potato	
Beetroot	
Grain	
Other agriculture	
Greenhous horticulture	
Orchards	
Flower Bulbs	
Deciduous forest	Forest
Coniferous forest	
Fresh water	Fresh water
Salt water	Salt water
Buildings in primary built-up area	Urban area
Buildings in secondary built-up area	
Forest in built-up areas	Forest in urban area
Forest in secondary built-up area	
Grass in primary built-up area	Grass in urban area
Buildings in rural areas	Buildings in rural areas
Other land use in rural areas	Other
Grass in secondary built-up areas	Grass in urban area
Solar parks	Solarpark
Salt marshes	Salt marshes
Open sand in coastal area	Opens sand in coastal area
Dunes with low vegetation	Dunes
Dunes with tall vegetation	
Dune heath	
Open drifting san and/or river sand	Open drifting san and/or river sand
Heather	Heath
Moderately grassed heath	
Heavily grassed heath	
Raised bog	Raised bog
Forest in the raised moor area	Forest
Other swamp vegetation	Swamp
Reed vegetation	Reed vegetation
Forest in swamp area	Forest
Naturally managed agricultural grasslands	NMGA
Grass in coastal area	Grass in coastal area
Other grass	Other grass
Tree nurseries	Nurseries
Fruit farms	
Main infrastructure and railway body	Roads

Semi-paved roads, slow traffic infrastructure and other infrastructure	
Narrow roads	
Shrub vegetation in raised bog areas low	Bushes
Shrub vegetation in swamp area low	
Other shrub vegetation low	
Shrub vegetation in high moorland	
Shrub vegetation in swamp area high	
Other shrub vegetation high	

Appendix 5

Binominal GLM R studio output

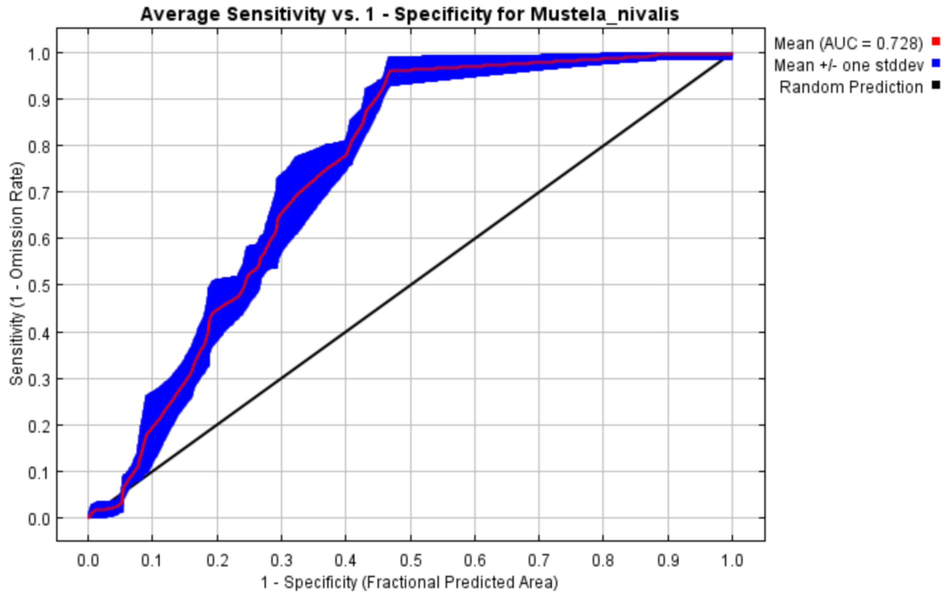
```
Call:
glm(formula = marter_aanwezig ~ `kans op woelmuis per dag` +
    `kans op spitsmuis per dag` + `kans op bosmuis per dag` +
    `afstand tot snelweg (meter)` + `afstand tot 70-90 weg` +
    `afstand tot 40-60 weg` + `afstand tot 0-30 weg` + `afstand tot bebouwde kom` +
    `afstand tot fietspad` + `afstand tot wandelpad` + `afstand tot agrarische percelen`,
    family = binomial(link = "logit"), data = data)

Coefficients:
                                   Estimate Std. Error z value Pr(>|z|)
(Intercept)                       7.786e-01  1.168e+00   0.666    0.505
`kans op woelmuis per dag`       -8.154e-02  5.674e-01  -0.144    0.886
`kans op spitsmuis per dag`       8.214e-01  1.783e+00   0.461    0.645
`kans op bosmuis per dag`        -4.193e-01  3.657e-01  -1.147    0.252
`afstand tot snelweg (meter)`    -3.792e-07  2.457e-07  -1.543    0.123
`afstand tot 70-90 weg`          -2.384e-07  4.509e-07  -0.529    0.597
`afstand tot 40-60 weg`           3.019e-07  1.380e-06   0.219    0.827
`afstand tot 0-30 weg`           -3.271e-06  2.414e-06  -1.355    0.176
`afstand tot bebouwde kom`        1.223e-06  1.093e-06   1.119    0.263
`afstand tot fietspad`           -4.296e-07  2.247e-06  -0.191    0.848
`afstand tot wandelpad`          -5.226e-06  4.937e-06  -1.058    0.290
`afstand tot agrarische percelen`  1.006e-06  2.336e-06   0.431    0.667

(Dispersion parameter for binomial family taken to be 1)

    Null deviance: 63.761  on 68  degrees of freedom
Residual deviance: 49.146  on 57  degrees of freedom
AIC: 73.146

Number of Fisher Scoring iterations: 6
```

Binominal GLMM R studio output

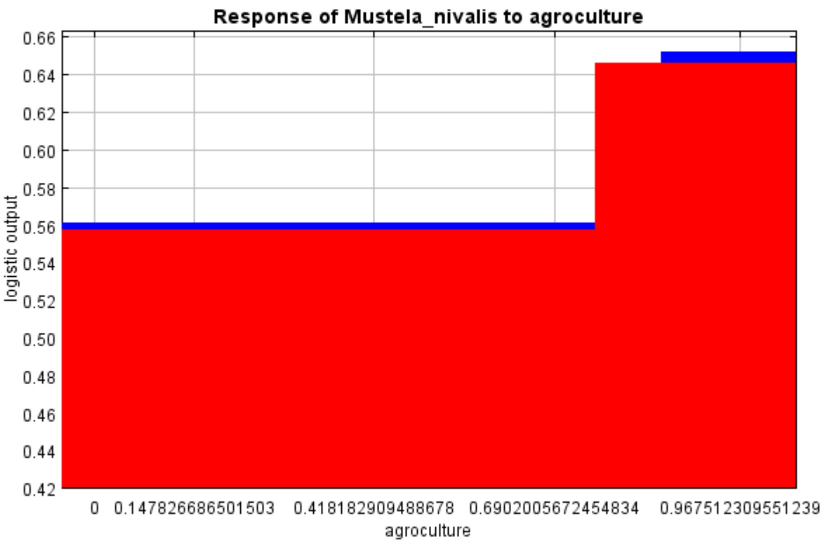
```
Generalized linear mixed model fit by maximum likelihood (Laplace Approximation) ['glmerMod']
 Family: binomial  ( logit )
Formula: marter_aanwezig ~ `kans op woelmuis per dag` + `kans op spitsmuis per dag` +
    `kans op bosmuis per dag` + `afstand tot snelweg (meter)` +
    `afstand tot 70-90 weg` + `afstand tot 40-60 weg` + `afstand tot 0-30 weg` +
    `afstand tot bebouwde kom` + `afstand tot fietspad` + `afstand tot wandelpad` +
    `afstand tot agrarische percelen` + (1 | Onderzoeksgebied)
   Data: data
Control: glmerControl(optimizer = "bobyqa", optCtrl = list(maxfun = 2e+05))

      AIC       BIC    logLik -2*log(L)  df.resid
     70.8      99.8     -22.4      44.8        56

Scaled residuals:
     Min       1Q   Median       3Q      Max
-1.88695 -0.29557 -0.13949 -0.01473  2.59979

Random effects:
 Groups           Name        Variance Std.Dev.
 Onderzoeksgebied (Intercept) 3.106    1.762
Number of obs: 69, groups:  Onderzoeksgebied, 4

Fixed effects:
                                  Estimate Std. Error z value Pr(>|z|)
(Intercept)                       -3.56683    1.58243  -2.254   0.0242 *
`kans op woelmuis per dag`        -0.04199    0.47357  -0.089   0.9294
`kans op spitsmuis per dag`       -0.02780    0.48221  -0.058   0.9540
`kans op bosmuis per dag`         -0.30848    0.46072  -0.670   0.5031
`afstand tot snelweg (meter)`     -2.14920    1.93488  -1.111   0.2667
`afstand tot 70-90 weg`           -0.15801    0.75025  -0.211   0.8332
`afstand tot 40-60 weg`           -0.46335    0.75931  -0.610   0.5417
`afstand tot 0-30 weg`            -1.60646    0.97751  -1.643   0.1003
`afstand tot bebouwde kom`         0.04987    1.00404   0.050   0.9604
`afstand tot fietspad`             0.50333    0.86955   0.579   0.5627
`afstand tot wandelpad`           -0.76515    0.93156  -0.821   0.4114
`afstand tot agrarische percelen`  0.97230    0.68723   1.415   0.1571
---
Signif. codes:  0 ‘***’ 0.001 ‘**’ 0.01 ‘*’ 0.05 ‘.’ 0.1 ‘ ’ 1

Correlation of Fixed Effects:
            (Intr) `owpd` `ospd` `obpd` `ts()` `t70-w `t40-w `t0-3w `tbkm` `tfts` `twnd`
`knsopwpdg`  0.035
`knsopspdg`  0.167  0.233
`knsopbpdg`  0.151  0.154  0.164
`fsts(mtr)`  0.622  0.132  0.170  0.145
`ft70-90wg` -0.008 -0.236 -0.229 -0.189 -0.039
`ft40-60wg`  0.274 -0.379  0.221 -0.132  0.305  0.064
`fst0-30wg`  0.274  0.076  0.348  0.110  0.055  0.137  0.231
`fstndtbkm`  0.255  0.102 -0.074  0.117  0.316 -0.459 -0.066 -0.284
`fsttftspd` -0.204  0.214 -0.235  0.100 -0.183 -0.063 -0.640 -0.333  0.188
`fstwndlpd`  0.077 -0.372 -0.081 -0.007  0.009 -0.048  0.336 -0.110 -0.253 -0.379
`fstaprcln` -0.519 -0.060 -0.242 -0.126 -0.463  0.231 -0.285 -0.378 -0.501  0.245  0.182
```

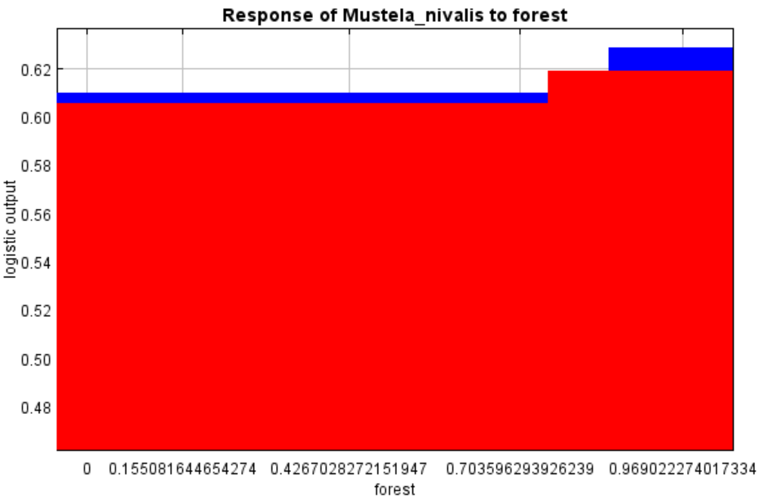
Appendix 6

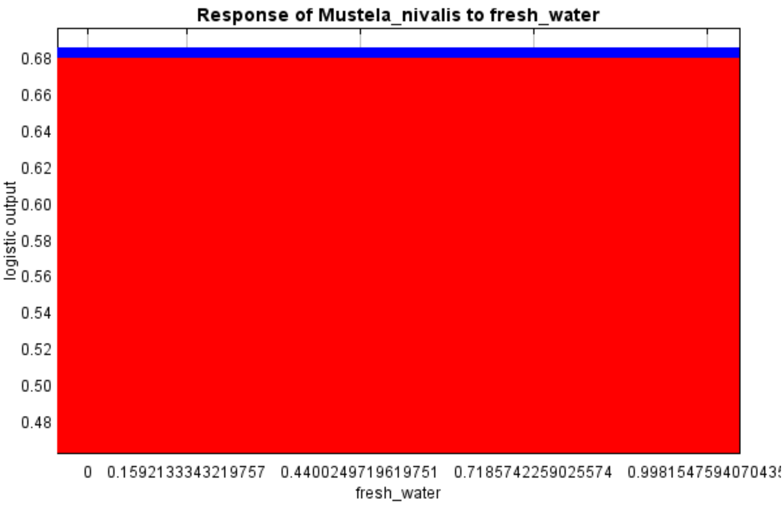
The average test AUC for the replicate runs.

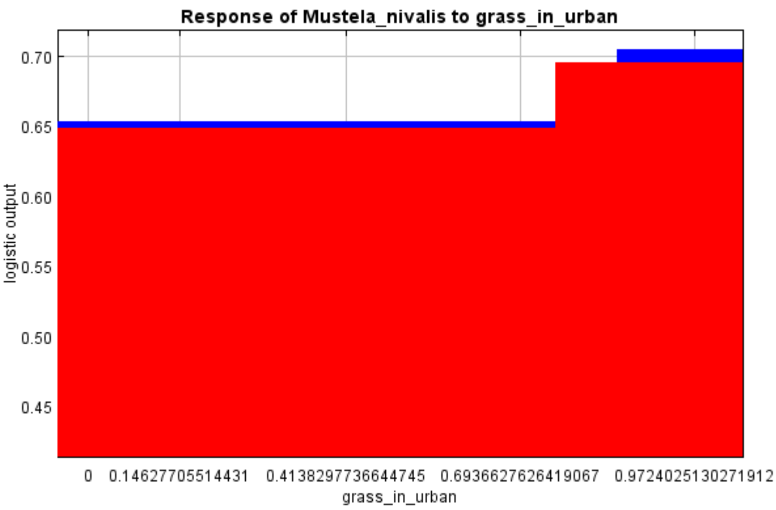


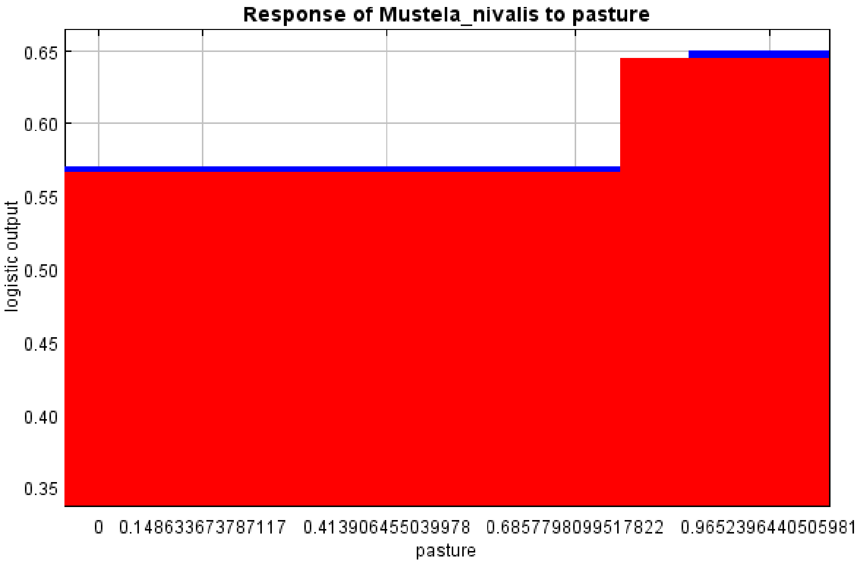
Each of the following curves represents a different model, namely, a Maxent model created using only the corresponding variable. These plots reflect the dependence of predicted suitability both on the selected variable and on dependencies induced by correlations between the selected variable and other variables.

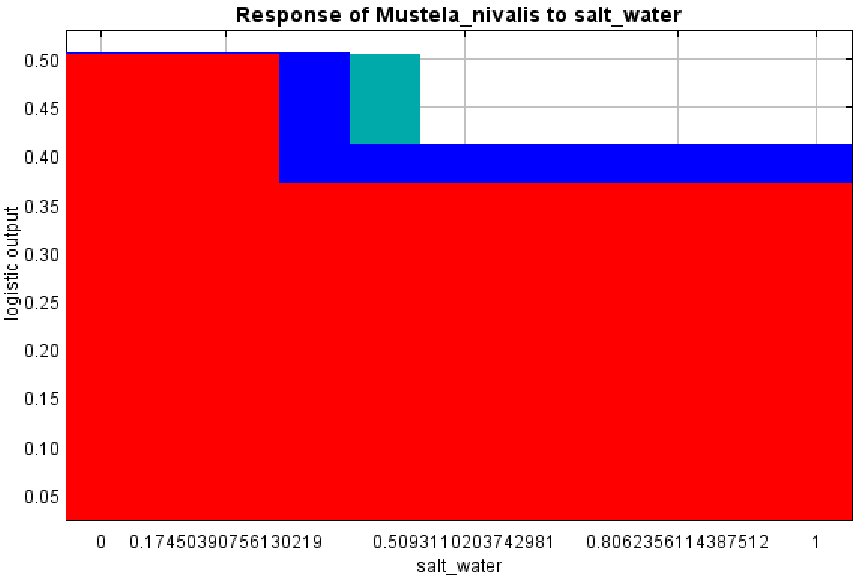



Response of Mustela_nivalis to forest
0.62
0.60
0.58
0.56
0.54
0.52
0.50
0.48
logistic output
0 0.155081644654274 0.4267028272151947 0.703596293926239 0.969022274017334
forest


Response of Mustela_nivalis to fresh_water
0.68
0.66
0.64
0.62
0.60
0.58
0.56
0.54
0.52
0.50
0.48
logistic output
0 0.1592133343219757 0.4400249719619751 0.7185742259025574
fresh_water


Response of Mustela_nivalis to grass_in_urban
0.70
0.65
0.60
0.55
0.50
0.45
logistic output
0 0.14627705514431 0.4138297736644745 0.6936627626419067 0.9724025130271912
grass_in_urban


Response of Mustela_nivalis to pasture
0.65
0.60
0.55
0.50
0.45
0.40
0.35
logistic output
0
0.148633673787117
0.413906455039978
0.6857798099517822
0.9652396440505981
pasture


Response of Mustela_nivalis to salt_water
0.50
0.45
0.40
0.35
0.30
0.25
0.20
0.15
0.10
0.05
logistic output
0
0.17450390756130219
0.5093110203742981
0.8062356114387512
1
salt_water

Appendix 7

Kruskal Wallis test on the number of bank vole sequences per measuring location per day between the four different research area's: Hagebeemd, Markdal, Merkske, Strijbeekse heide.