Habitat selection of beech martens (*Martes foina*) in relation to prey availability and habitat characteristics in an agricultural landscape

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Keywords: Beech marten, habitat selection, predation, prey selection, meadow-birds, habitat characteristics, intensification of agriculture, conservation.

Meadow breeding bird populations have shown a strong decrease in the recent decades caused by intensification of agriculture. Despite conservation efforts to decrease the negative effect of agriculture on meadow-bird populations, the decline continues rapidly due to increased predation by generalist predators. Previous research has focussed on identification and impact of predator species. However, little is known about the ecology of predators of meadow-birds. This study focusses on habitat preference of one predator of meadow-birds, the beech marten (*Martes foina*), in a landscape with a mosaic of intensively farmed parcels and parcels where different types of measures for meadow birds are taken, creating spatiotemporal variation in the occurrence of prey species (breeding meadow-birds and common voles *Microtus arvalis*). In 2020 and 2021, in total six different beech martens were GPS-tracked during the breeding season of meadow-birds. Weekly field measurements such as vegetation height and water table height, were taken in fields with different levels of meadow-bird conservation measures in the home range of the martens. In addition, prey availability was determined by monitoring vole activity and meadow-bird presence (nests and chicks). In both study years it was found that voles prefer intensive grasslands whereas meadow-birds prefer fields with meadow-bird conservation measures. Four out of six tracked martens showed preference for meadow-bird habitats, one marten preferred intense grasslands and one inhabited urban habitat. These findings imply that beech martens actively select for habitats where meadow-birds are abundant instead of habitats where alternative prey such as voles are present. Therefore, successful conservation of meadow-birds is dependent on reducing predation pressure of beech martens.

Introduction

Iconic meadow-bird species of the Dutch dairy farming landscape such as the black tailed godwit (*Limosa limosa*) and the northern lapwing (*Vanellus vanellus*) decreased dramatically since the last quarter of the 20th century (Donald *et al.* 2001; Newton 2004; Kentie *et al.* 2013, 2015). Declines in productivity and increased chick mortality have been identified as key contributors to the population decline of these ground nesting meadow-birds (Peach *et al.* 1994; Plard *et al.* 2020).

Since the middle of the last decade agriculture has intensified to increase its productivity (Groen *et al.* 2012). Decrease in soil moisture, decrease in grassland vegetation complexity, increased chemical use such as pesticides and fertilisers and change of mowing and harvesting regimes are all consequences of the intensification of agriculture (Donald *et al.* 2006; Verhulst *et al.* 2007; Bos *et al.* 2013). As a result agriculture has become an increasing driver for loss of biodiversity (Erisman *et al.* 2016). Intensive agricultural management has led to declines of meadow-bird populations (Newton 2004). Practices such as earlier mowing regimes are known to contribute to nest loss and chick mortality and reduced soil wetness has a negative effect on foraging success of meadow-birds (Kleijn & van Zuijlen 2004; Broyer *et al.* 2016). Furthermore, decrease of herbaceous plant species in intensified grasslands decreases food availability for chicks (Schekkerman & Beintema 2007).

To counteract these negative population trends, measures have been applied to conserve meadow-bird populations. Delayed mowing and grazing, reduced use of chemicals such as fertilizers and rising of the water table are examples of measures applied to improve breeding habitat and promote chick survival (Henderson *et al.* 2009; Franks *et al.* 2018). In addition, grassland monocultures are diversified by creating mosaic landscape or creating set aside field strips with higher vegetation diversity to increase food availability (Henderson *et al.* 2009). The aim of mosaic landscapes is creating suitable habitats for a variety of meadow-birds during all stages of the breeding season (Oosterveld *et al.* 2011). An example of this type of management are wet grassland patches, in Dutch "*plasdras*". Habitats which attract breeding meadow-birds as it is a more suitable breeding ground with high food availability for adults and chicks (Natural England 2009; Franks *et al.* 2018). High water tables in combination with postponed mowing provides a more diverse vegetation and therefore increased and diverse food supply, such as insects, for chicks (Melman *et al.* 2020). Despite these efforts taken by meadow-bird conservation and farmer collectives, and changes made in management to conserve meadow-birds, populations continue to decline (Kleijn & van Zuijlen 2004).

Low productivity of meadow-bird populations has, as previously stated, a large impact on population dynamics (Plard *et al.* 2020). A factor contributing to this low productivity, beside intensification of agriculture, is increased nest and chick predation by mammalian predators such as red fox (*Vulpes vulpes*), cat (*Felis catus*), and several *Mustelidae* species such as stoat (*Mustela erminea*) and avian predators such as carrion crow (*Corvus corone*) and marsh harrier (*Circus aeruginosus*) (Teunissen *et al.* 2008; Kentie *et al.* 2015). Predation as a limiting factor for prey populations is a well-studied subject within ecology (Roos *et al.* 2018). Predation of meadow-birds increased over the last 40 years in western Europe and are caused by an increase in densities of smaller generalist predators, or mesopredators, such as beech marten and red fox (Roodbergen *et al.* 2012; Ainsworth *et al.* 2016). The presence of such mammalian predators in high densities prevent declining meadow-bird populations to recover (Hay 2009; Malpas *et al.* 2013).

Reduced predator control and lack of top predators can cause mesopredator species to increase in numbers, consequently increasing predation pressure on their prey. (Rogers & Heard 2000; Roos *et al.* 2018). In addition, land-use changes due to agricultural intensification are suggested to increase predation rates of meadow-birds. For example, reduction of vegetation height by early mowing increases nest visibility, making nests more susceptible to predation (Evans 2004). Moreover, isolation of breeding reserves in a fragmented landscape is hypothesised to increase predation efficiency by generalist predators (Evans 2004; Newton 2004). Thus, increasing predator populations in an agricultural habitat with little alternative prey due to low biodiversity, poses as a significant threat for meadow-birds (Rogers & Heard 2000; McKinnon *et al.* 2014).

Current research on predation of meadow-birds focusses mainly on identification of predator species and the impact predation has on meadow-bird populations (Roos *et al.* 2018; Plard *et al.* 2020). These studies have identified which predator species commonly predate on eggs or chicks, how the occurrence of predator species differs between study sites and how different types of meadow-bird management impacts predation risk (Schekkerman *et al.* 2008; Teunissen *et al.* 2008). Exclusion experiments where predators are kept out of meadow-bird breeding sites through electrical fences have shown a positive increase of hatching success and nest survival (Smith *et al.* 2011; Malpas *et al.* 2013). However, fencing can only be done on a relative small scale, has high maintenance and can be costly (Smith *et al.* 2011; Franks *et al.* 2018). Similar results are found when predators are removed by culling, but this method is controversial due to ethical concerns (Smith *et al.* 2010). Little research has been done on the ecology and behaviour of predators of meadow-birds in the Netherlands. Insight prey selection and behaviour of these predators will prove useful in developing new and more sustainable management.

This study focusses on foraging behaviour and habitat selection of one specific predator of meadow-birds in the Netherlands, the beech marten. Since beech martens have been increasing in numbers in the Netherlands since the 1950's they propose an increasing problem for meadow-bird populations (van den Berge 2016). Feeding habits of beech martens vary across habitats and seasons with a high diversity of food categories, such as: fruits, insects, small mammals, birds and eggs (Lode 1994; Papakosta *et al.* 2014). This generalist predator switches diet seasonally, depending on food availability (Ben-David *et al.* 1997). Increasing populations of beech martens are known to limit populations of prey species, as was found for a certain tortoise species (Vilardell *et al.* 2012). Due the flexibility in diet and hunting behaviour, the beech marten is able to settle in a range of different habitat types, including urban and agricultural areas (Toth *et al.* 2009). Despite the diversity in diet, beech martens show a preference for specific types of prey. Small mammals, such as the voles of the genus *Microtus* are preyed upon throughout the year and birds when seasonally available (Lode 1994; Ben-David *et al.* 1997; Hisano *et al.* 2016). Models to investigate how prey populations respond to generalist predators, show that predation pressure of generalist predators on prey species is larger when no alternative prey is present and vice versa (Matthiopoulos *et al.* 2007). However, little research on prey switching behaviour is available from field situations, and in particular in relation to the issue of meadow-bird predation. Hence, we poorly understand the impact of beech martens on meadow-birds, and whether meadow-birds are a preferred prey even when alternative prey species, such as common voles, are present.

This research aims to describe the habitat use of beech martens through GPS tracking in a dairy farming agricultural landscape in the north of the Netherlands. Habitat selection is linked to differences in habitat characteristics and possible prey abundance across areas with different management regarding meadow-bird conservation. Previous studies have shown that the main prey of beech martens, meadow-birds and the common vole, have different habitat preferences (Bertolino *et al.* 2015; Melman *et al.* 2020; Prieur & Swihart 2020). While meadow-birds show a preference for wet grasslands, common voles prefer dryer grasslands (Bertolino *et al.* 2015; Franks *et al.* 2018; Prieur & Swihart 2020). Habitat preference of beech martens can therefore be linked to prey selection. Therefore, this research includes a sub question regarding if fields of different types of management contain different common vole and meadow-bird densities, due to a difference in habitat preference by both prey.

The first part of the study aims to identify the difference in nesting meadow-birds and common vole densities between fields without meadow-bird management, fields with limited meadow-bird management and fields where the management is completely devoted to meadow-bird conservation. Prey abundance is also linked to habitat characteristics such as vegetation height and water table level. In addition to meadow-birds and common vole, the presence of breeding waterbird species like Eurasian coot (*Fulica atra*) is documented as it might form a third alternative prey (Zschille *et al.* 2014). The second part of the study aims to find out whether beech martens show a preference for fields with a specific type of management which is subsequently related to a certain prey type. I.e. do martens prefer the wet areas where meadow-birds presumably are most abundant, or do they prefer drained, intensively managed areas where voles are presumed to be more abundant? An additional factor taken into account is the time of mowing, as mowing is one of the dominant ‘events’ in the study area and might affect the selection of fields and thus habitat selection, independently of the occurrence of prey.

Common voles and meadow-birds are expected to prefer different habitats. Where meadow-birds show a preference for wet grasslands, common voles show a preference for more dry habitats (Bertolino *et al.* 2015; Franks *et al.* 2018; Prieur & Swihart 2020). Both meadow-birds and common voles prefer high vegetation (Breeuwer *et al.* 2009; Smink *et al.* 2018). However, due to the drainage in monocultures, common voles are expected to be more abundant in areas with agriculture as main purpose, whereas meadow-birds are expected to be less abundant in these fields. A study area with different types of management harbouring different prey will provide a landscape in which beech martens can select for one specific prey, thus providing a unique opportunity to study their habitat preference and thus prey selection. Optimal foraging theory suggest that predators decide which prey to hunt based on relative cost of catching one type of prey in comparison to an alternative prey type (Price & Banks 2016). Therefore, it is expected that beech martens will show a preference for habitat with the most accessible prey which can be the easiest to catch or the most abundant. This is expected to be common vole habitat when meadow-birds are absent in the study area, such as early in the season before the breeding season. After meadow-birds arrive in the study area it is expected that a shift in habitat selection will be observed if meadow-birds are more abundant in the area in comparison to common voles. In case common vole are more abundant, a continued preference for common voles is expected. Previous research has shown that beech martens prefer habitat with high vegetation (Rondinini & Boitani 2002). Therefore, mowing of fields is expected to have a negative effect on habitat selection of beech martens.

The results of this study will provide insight on habitat use of a proposed threat of the already declining meadow-birds. More information on beech martens can consequently be used in sustainable predator management to conserve meadow-birds.

Method

This study was conducted over two years, 2020 and 2021. Measurements taken in 2020 were done by Seljee (2021). Measurements for 2021 were conducted by myself. Data from both years were combined and analysed alike.

Study area

In both years measurements were taken in agricultural landscapes in the north of the Netherlands. Agriculture in this area has a main purpose of dairy farming and the landscape consists mainly of permanent grasslands. The 2020 study was executed in fields between the villages of Winsum and Wetsinge (Seljee 2021). The study conducted in 2021 was executed near the village of Hekkum. Both areas contain conservation habitats that provide breeding gound for several meadow-birds species such as the northern lapwing, black tailed godwit and Eurasian oystercatcher (*Haematopus ostralegus*), etc. (de Boer 2011). The areas are managed by nature organisation “Groninger landschap” and consist of pasture plots surrounded by water from old and new waterways. Several parcels are grazed by livestock owned by farmers which lease parcels from the management organisation. The remaining fields in the study areas consist of pasture plots with dairy farming as main purpose. In a selection of these fields meadow-bird conservation management is applied such as delayed mowing and active pumping of water into the fields. However, the majority of the fields consist of intensive grassland. Therefore, fields are categorised in three categories according to management (table 1.).

Field score	*Description*
A	Field with main purpose of meadow-bird conservation. Mowing regimes and water table levels are adjusted to create ideal meadow-bird breeding grounds.
B	Farmer owned dairy grasslands where some form of meadow-bird conservation management is applied such as postponed mowing, nest protection or actively pumping of water into the field.
C	Intensive dairy grasslands with the main purpose grass production for dairy farming. In some fields meadow-bird nests are protected to prevent trampling by cattle.

Table 1:Meadow-bird management categories as used in this study.

GPS tracking

Adult beech martens were captured using baited walk-in traps, and fitted with GPS tracking collars (E-OBS, model 1C). Loggers were programmed to record coordinates during the night since beech martens are nocturnal animals (Vilella *et al.* 2020). Loggers were set to automatically activate one hour after dusk and shut off one hour before dawn. These are accelerometer-informed GPS loggers, which means that the device will only log the location of an individual when it is active (as based on accelerometer data) with an interval of 5 minutes by default. During certain periods loggers where set to intensive sampling with logging intervals of 1 minute.

Field observations

Duration

Field work in 2020 and 2021 took place in weeks 17 -24 and weeks 18 – 26 respectively (Seljee 2021). These periods have been selected due to the breeding season of meadow-bird species in the Netherlands, which starts around the end of April (Musters *et al.* 2010). Duration of GPS tracking of the individual martens was dependant on trapping dates. Martens were captured from the end of march until mid may. In 2021 tracking was continued until the first of July.

In-field measurements

All measurements were weekly conducted in a total of 30 and 15 focal fields in 2020 and 2021 respectively (Seljee 2021). Focal fields were selected based on GPS tracking data of each individual marten to ensure focal fields were within the home range and visited on a regular basis by the martens. In addition, selection was based on meadow-bird conservation management so that a comparison could be made between different types of management. Measurements taken were: vegetation height, water table height, signs of vole activity, bird presence (only in 2021) and estimation of mowing date.

Vole abundance within fields was measured and expressed as VSI (vole sign index). The method used to calculated VSI is as described by Smink *et al.* (2018). This method is based on visual indicators of vole activity such as burrows, grass clippings or grazing and droppings. Droppings of common voles are easy to distinguish from droppings of other mammals and are therefore a good indication of common vole presence (Delattre *et al.* 1996). Burrows remain intact over a long period of time causing them to be less reliable for the current vole density and are therefore dropped as visual indicator (Gervais 2010). Therefore, this research only uses droppings and signs of grazing or clippings to establish vole abundance. Signs of vole activity are a comparable method to trapping methods and are therefore considered reliable (Jareño *et al.* 2014). In 2020, VSI was determined by using a 100x100cm square plot to search for signs of vole activity. A transect of 10 plots was traversed with 5 meters between each plot. The starting point would be different each time a field was visited to gain a comprehensive view of a field at the end of the field-measurement (Seljee 2021). In 2021, plots of 25 cm^2 were placed every 10 meters while walking a 100m transect. This was done 3 times to form a triangle, where one side of the triangle was parallel to the ditch of the focal field (see appendix A). Each time a field was measured a different part of a parcel was selected to get a complete picture of each parcel. For both 2020 and 2021, visual indication of vole activity within a plot was logged giving information on signs of activity (+/-). Afterwards, the average activity throughout all transects of a field visit was calculated. This gave the VSI for each field on the day of visiting ranging from 0, no activity at all, to 1, signs of activity in all plots.

Vegetation height was measured during field observation since vegetation height has an effect on habitat selection of beech martens, meadow-birds and common voles. Vegetation height is measured during the VSI transect measurements. In 2020, this was done at the 2nd, 4th, 6th and 8th plot (Seljee 2021). In 2021, in each 5th plot of a transect the vegetation height was measured. Measuring was done by holding the vegetation upright along a ruler, and the maximum height was recorded. For each field visit the average (maximum) vegetation height was calculated. Water table height was measured in 2020 by measuring the height difference between the ground and the water within a ditch at all 4 sides of each field. In 2021 water table was measured at the first point of the transect alongside the ditch, this was only measured once during the study period.

In 2021, the number of black-tailed godwits, northern lapwings, Eurasian oystercatcher and redshank (*Tringa totanus*) in addition to 'other' bird species was documented during each field visit. The 'other' category consist of other birds present at the time such as waterfowl species. Bird surveys were conducted before entering the field.

In both years, nests were mapped throughout the study area by experienced nest searchers. Nest surveys were conducted within the nature reserves as well as at the regular farmland. In 2021, mapping of nests outside the nature reserve were mainly restricted to parcels with conservation measures. Thus, in 2021 the coverage of the nest survey was incomplete.

Field monitoring

In addition to in-field measurements, the status of the different fields throughout the study area were monitored. First it was noted whether a field was part of a nature reserve (property of Het Groninger Landschap) or not (regular farmland owned by farmers). For farmland it was subsequently noted whether conservation measures were in place (delayed mowing, inundation), or whether it was farmed regularly. In 2021, every week it was checked whether a field was mown. A field was given of score of -1 when a field was not mown, 0 in the week a field was mown and a 1 for the week after mowing.

Analyses

Data and statistical analyses were conducted using R, version 4.0.5 (R Core Team 2020), in RStudio (RStudio Team 2020).

Field analysis

The measurements of both years taken in the focal fields (vegetation height, water table, vole sign index, and bird / nest density) were modelled in a liner model with week and field score as explaining variables. Vegetation, vole sign index, bird and nest data were square root, cube root, square root and log transformed respectively to meet model assumptions. Non-significant variables were dropped from the model accordingly. Differences between fields scores were determined by a Tukey's posthoc test using the R add-on package multcomp (Hothorn *et al.* 2008).

Tracking data analysis

Intensive sampling (1 minute interval) tracking data was removed from the data as this could present a bias in the results. By overlaying the tracking data on a map of the study area (Basisregistratie Percelen 2019) every location was linked to a particular field. From this, for every marten, the number of GPS fixes per field per week were calculated. By dividing by field area, densities of GPS fixes were obtained. Furthermore, for every field the distance to the nearest daytime roost was determined. Roosting sites were derived from the tracking data, and were locations where a marten stayed during the day, as indicated by the last position of the night and the first position on the next morning coming from the same site. These calculations were done for each marten and for both 2020 and 2021.

The home range or minimum convex polygon (MCP) of each individual beech marten was calculated using the R add-on package adehabitatHR (Calenge 2019). Home range of an individual is defined by the area in which an individual rests and forages (Burt 1943). For beech martens home range can vary over time and is determined by other martens and habitat (Skirnisson 1986). For this study the MCP with 95% of the locations was calculated using all GPS data of the whole tracking period.

Habitat preference can be expressed in multiple ways. A simple method is the amount of time an individual has spent in a certain habitat with respect to time spent in other habitats (Barany & Kis 2009). For example, a shift in habitat preference over time, common vole rich habitats prior to meadow-bird arrival and meadow-bird rich habitat after meadow-bird arrival, can be analysed by comparing the number of observations or GPS points in a certain habitat and testing the difference using a chi-squared test (Goszczyński *et al.* 2007). Note that preference in habitat studies is a relative term expressed in “little” preference and “strong” preference for a certain habitat (Aebischer *et al.* 1993). For this study the density of points within a certain field and IVLEV’s electivity index was used as a measure for habitat selection (Jacobs 1974).

The home range of individual beech martens was used in habitat selection analysis using IVLEV’s electivity index (Jacobs 1974; Martinoli *et al.* 2006). Positive values of the index indicate a preference for a certain habitat, negative values show that the habitat is avoided and value of 0 indicates that the habitat is used according to availability (Lechowicz 1982) IVLEV’s electivity index is calculated by:

$$E_i = (u_i - a_i)/\,(u_i + a_i)$$

where u_i is the proportion of observations of the individual in a certain habitat (i) and a_i is the proportion of available habitat (i) within the home range (Manly *et al.* 1993; Martinoli *et al.* 2006). These variables were calculated as the relative proportion of GPS points of each field score (u_i) and relative proportion of habitat of each field score within the home range (a_i). For each field score IVLEV's electivity index was calculated over time. The calculated electivity index is fitted into a linear mixed model using the R add-on packages Lme4 and lmerTest with field score and week as fixed factors and marten ID as random factor (Bates *et al.* 2015; Kuznetsova *et al.* 2017). To test for an effect of distance from the day roost on the use of fields, a separate linear mixed model was constructed with point density of fields as response variable, field score and minimal distance as fixed factors and marten ID as random factor.

Finally, the nearest distance of each GPS point to the border of the field was calculated. To test whether the distribution of distances differed from random, i.e. whether the martens tended to walk more often along edges or in the middle of the field, also distances to the field edge were calculated for random points. These random distributions were obtained by rotating the track using a random angle. Rotation has the advantage that the internal track geometry is preserved. Distance was log transformed to meet model assumptions. Differences between the observed and random distribution were tested using a Wilcoxon signed-rank test.

Results

Environmental conditions
Average measured temperatures in spring in the Netherlands were 10.3 °C and 8.1 °C for 2020 and 2021 respectively (KNMI 2021). Average precipitation was 77 mm and 178 mm for 2020 and 2021 respectively (KNMI 2021).

Martens tracked
In both 2020 as 2021 a total of 3 martens were captured and GPS tracked (table 2).

Year	*ID*	*Sex*	*First week of tracking*	*Last week of tracking*
2020	Freerk	m	14	20
2020	Anne-Jan	m	12	20
2020	Eddie	m	9	22
2021	Trudy	f	10	27
2021	Marco	m	15	27
2021	Omgo	m	19	27

Table 2: Overview of all captured and tagged martens used for this study (n=6).

Field data
In 2020 the proportion of habitat of category A, B and C were respectively 0.10, 0.10 and 0.80 within a total area of 335.3 ha. In 2021 the proportion for category A, B and C were respectively 0.11, 0.08 and 0.82 within a total area of 568.8 ha.

Mean water table height in fields of field score A were significantly lower in comparison to both field scores B & C (figure 1.a) ($p < 0.005$, appendix B: model 1). Field scores B & C do not differ in mean water table height ($p=0.54$) Water table height in all field scores did not change significantly over time ($p=0.184$). Average vegetation height increased over time in all three field scores (figure 1.b) ($p=0.003$, appendix B: model 2), Average vegetation height was lower in fields of field scores C in comparison to A ($p=0.04$, appendix B: model 2a) and B (p=0.001, appendix B: model 2a). Fields of category A & B did not differ significantly in vegetation heigh (p=0.29, appendix B: model 2a).

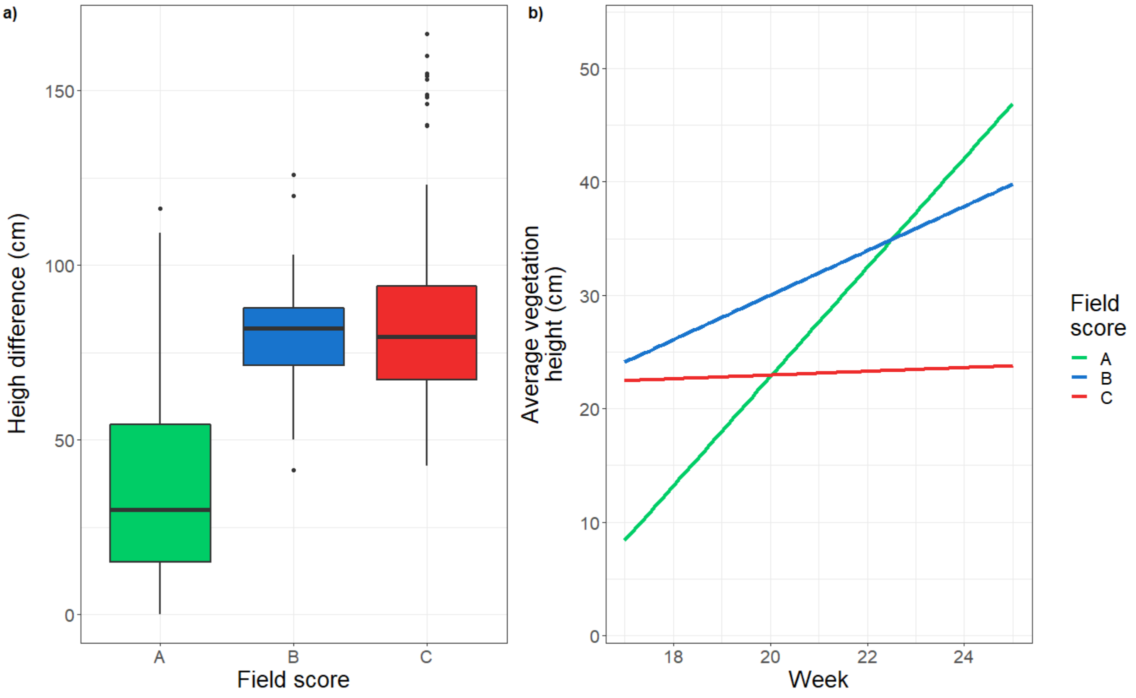

Figure 1: a) Height difference between ground and water level for all field scores, e.g. low height difference means high water table. Water table was higher in fields of category A than in fields of category B (p<0.001) and category C (p<0.001). b) Average vegetation heigh all field scores over time. Vegetation in all field scores changed over time in varying degrees (R^2=0.17, p=0.005). Overall average vegetation height was lower in category C than in A (p=0.04) and B (p=0.001).

VSI significantly increased in successive field scores from A to C (figure 1) (p < 0.005). Fields of category A showed an overall lower VSI in comparison to fields of score B & C. Fields B & C did not differ in VSI on average. VSI was lower across all field scores in 2021 in comparison to 2020 (p <0.005). VSI increased with increasing vegetation and decreases with in increasing water table height (P<0.05).

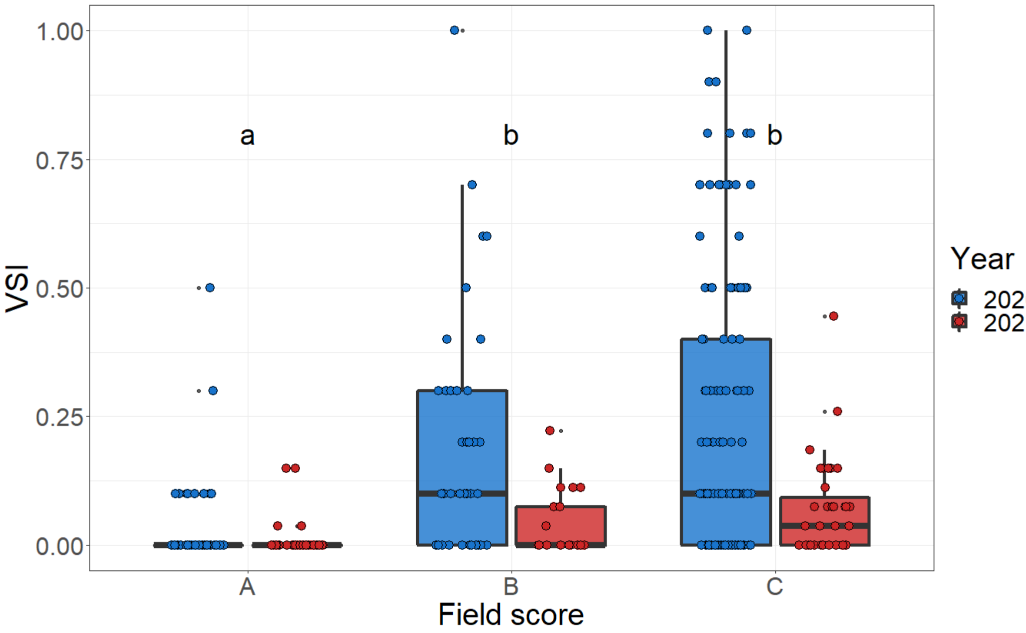

Figure 2: Fields of field score A contain significantly less voles in comparison of fields of score B (p<0.001) & C (p < 0.001). Labels above each fields score depict which fields are grouped together and which fields differ. Overall vole densities were lower in 2021 than in 2020 (p < 0.001).

In 2020 fewer nests were found in fields of category C than in fields of category A ($p<0.001$, appendix B: model 5a) and B ($p=0.008$, appendix B: model 5a) (figure 3. A). In 2021 no significant difference in the number of nests between field scores was found ($p=0.39$, appendix B: model 6) (figure 3, B). However, the number of birds counted in fields of the different field scores differed and significantly increased over time ($p<0.001$, appendix B: model 7), with highest numbers in field score A ($p < 0.001$, appendix B: model 7a), fewer birds in field score B ($p < 0.001$, appendix B: model 7a) and the least in field score C ($p < 0.001$, appendix B: model 7a) (figure 3, C). In 2021 significantly more nests were found than in 2020 ($p<0.005$, appendix B: model 8).

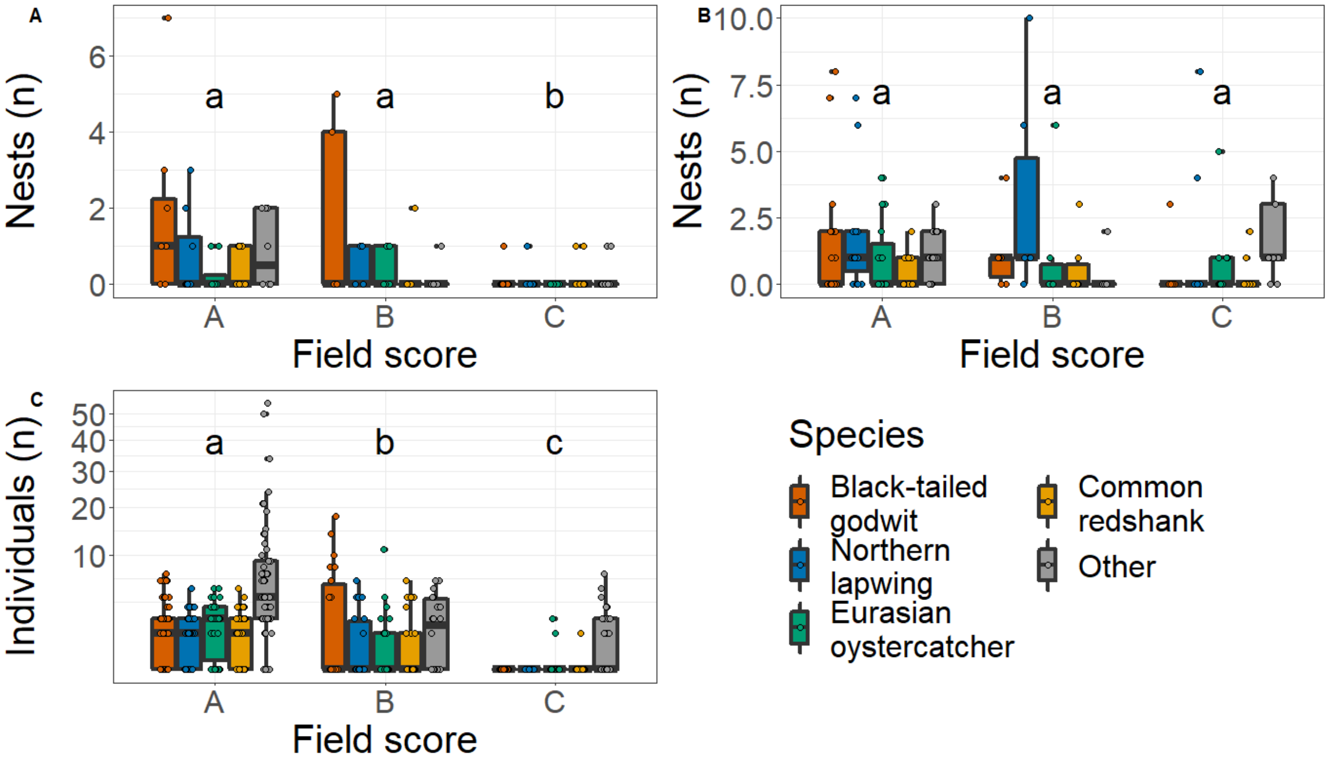

Figure 3: Boxplots depicting the difference in counted nests in 2020 and counted nests and individuals in 2021 between fields of different field scores. Labels within each plot show which field scores differ. A) In 2020 counted nests was lower in category C in comparison to A & B ($p<0.05$). B) In 2021 no difference in counted nests was found between different field scores ($p > 0.05$). C) Counted individuals did differ between all categories in 2021 ($p<0.05$).

Habitat selection

Home ranges in 2020 for Freerk, Anne-Jan and Eddie were 116.2, 197.7 and 86.6 ha respectively. For Trudy, Marco and Omgo in 2021 this was respectively 165.6, 382.6 and 277.1 ha. The percentage of GPS fixes within fields of either category A, B or C were 58.2, 43.4 and 56.2 % for Freerk, Anne-Jan and Eddie respectively. In 2021 they were 37.3, 36.3 and 16.0 % for Trudy, Marco and Omgo respectively.

In 2020 the martens showed a preference for fields of either category A or B and little preference for fields of category C. A different pattern was seen in 2021. Then, female Trudy showed an overall high preference for fields of category A & B throughout the whole season. Whereas Marco showed a continues preference for fields of category C and avoidance for fields of category A & B, except at the end of the study period in week 24 – 27 when fields of category A and B were preferred. Omgo, who spend most time in urban areas, showed some preference for either category B or C (figure 4), but the time spent on fields was small. Altogether, from the 6 martens, 3 individuals (Freerk, Anne-Jan and Trudy) showed a highest preference for category A, one (Anne-Jan) for category B, one (Marco) for category C, and the pattern for one (Omgo) was unclear because of a low sample size (figure 5, table 3). Due to this large variation between individuals and years, no significant effect of either week of field score was found to explain the variation in habitat selection (p=0.65, appendix B: model 8).

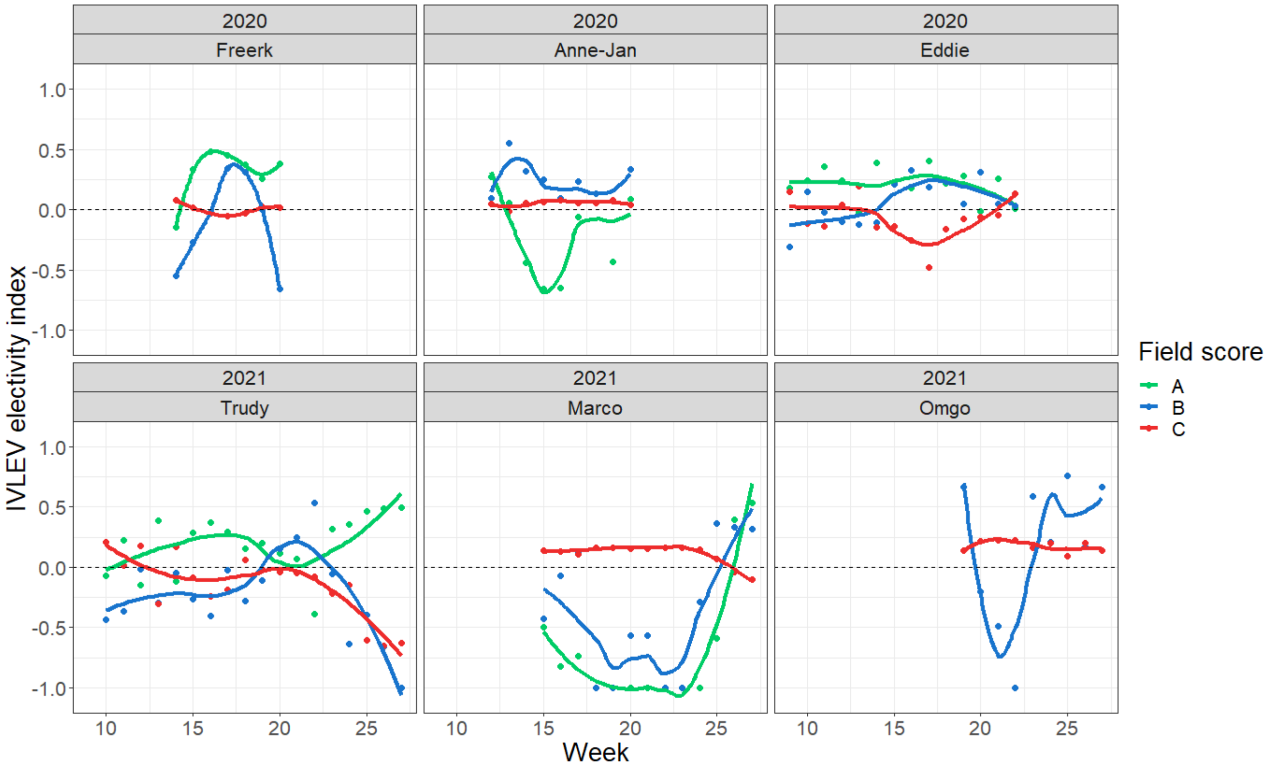

Figure 4: IVLEV's electivity index over time for each individua marten (n = 6). Positive values indicate a preference for fields of a certain category, negative values indicate avoidance of fields of a certain habitat.

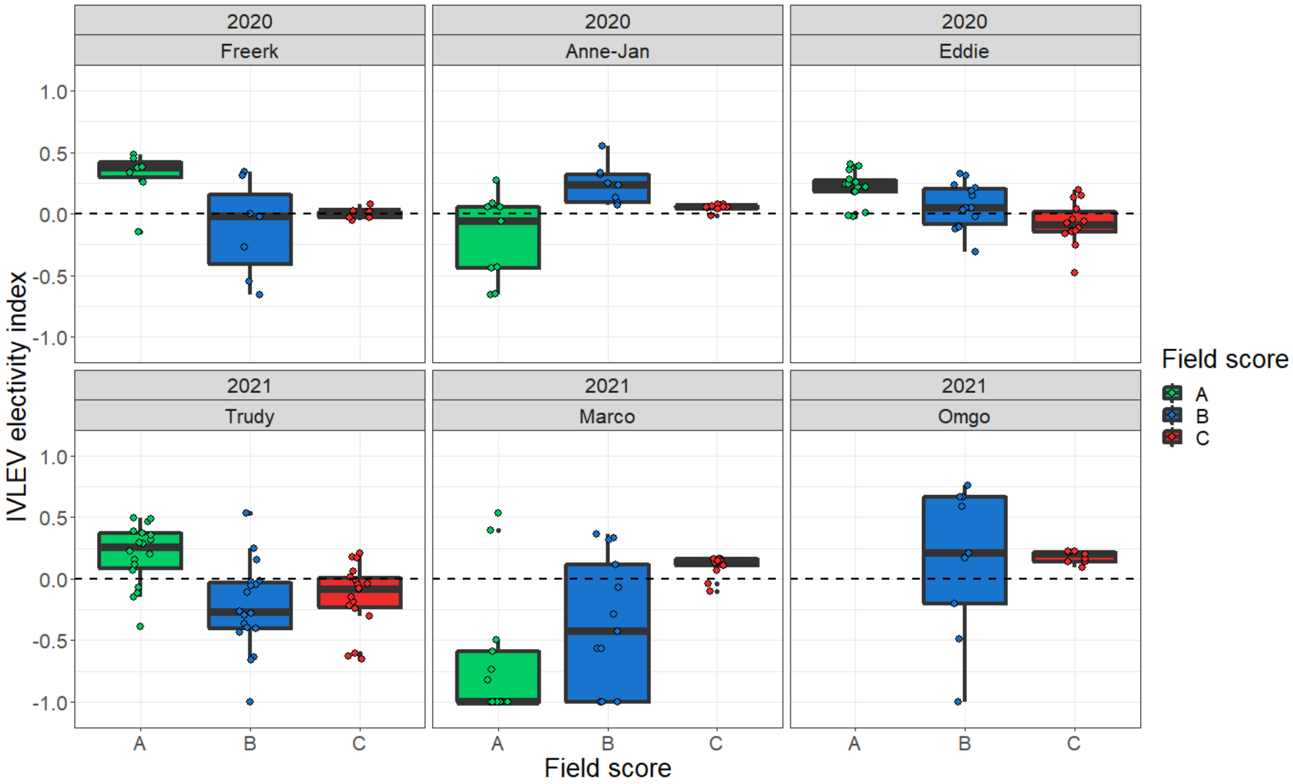

Figure 5: Boxplot showing the difference in overall IVLEV's electivity index per marten in both 2020 & 2021.

			Week																		
Year	*Marten*	*Fieldscore*	*9*	*10*	*11*	*12*	*13*	*14*	*15*	*16*	*17*	*18*	*19*	*20*	*21*	*22*	*23*	*24*	*25*	*26*	*27*
2020	Freerk	A						-0.15	0.34	0.48	0.45	0.37	0.26	0.38							
		B						-0.55	-0.27	-0.02	0.35	0.31	0.00	-0.66							
		C						0.08	0.02	-0.03	-0.06	-0.03	0.02	0.02							
	Anne-Jan	A				0.27	0.05	-0.44	-0.66	-0.65	-0.06	0.06	-0.44	0.08							
		B				0.09	0.55	0.32	0.25	0.09	0.23	0.14	0.07	0.33							
		C				0.05	-0.01	0.05	0.07	0.08	0.05	0.06	0.08	0.04							
	Eddie	A	0.18	0.25	0.35	0.24	-0.02	0.39	0.22	0.18	0.40	0.22	0.28	-0.01	0.26	0.01					
		B	-0.31	0.15	-0.02	-0.10	-0.12	-0.11	0.21	0.33	0.19	0.23	0.05	0.31	0.05	0.03					
		C	0.15	-0.11	-0.14	0.04	0.19	-0.15	-0.13	-0.26	-0.48	-0.16	-0.07	-0.06	-0.05	0.13					
2021	Trudy	A		-0.07	0.22	-0.14	0.39	-0.12	0.28	0.37	0.29	0.16	0.20	0.12	0.07	-0.38	0.32	0.36	0.46	0.49	0.50
		B		-0.43	-0.36	-0.01	-0.30	-0.05	-0.26	-0.40	-0.03	-0.28	-0.11	0.16	0.25	0.53	-0.06	-0.64	-0.40	-0.66	-1.00
		C		0.21	0.01	0.18	-0.30	0.17	-0.09	-0.24	-0.18	0.06	-0.02	-0.04	-0.05	-0.08	-0.22	-0.15	-0.61	-0.66	-0.63
	Marco	A							-0.50	-0.82	-0.74	-1.00	-1.00	-1.00	-1.00	-1.00	-1.00	-1.00	-0.59	0.40	0.54
		B							-0.42	-0.07	0.12	-1.00	-1.00	-0.57	-0.57	-1.00	-1.00	-0.29	0.36	0.33	0.32
		C							0.14	0.13	0.11	0.16	0.16	0.15	0.15	0.16	0.16	0.14	0.07	-0.04	-0.10
	Omgo	B											0.67	-0.20	-0.49	-1.00	0.59	0.21	0.76	0.17	0.66
		C											0.14	0.22	0.22	0.23	0.16	0.20	0.09	0.20	0.14

Table 1: Specific IVLEV's electivity index values per marten per week. Green cells show positive values, red cells show negative values. Positive values show preference whereas negative values show avoidance.

Usage of specific fields decreased with distance from that field to the nearest roosting site ($p<0.005$). Higher densities of GPS points were found in fields near possible roosting sites such as houses or barns. Fields further away showed lower densities of GPS points and were visited less often by all martens.

Mowing of fields in 2021 did not cause the three martens to avoid mowed fields. Between the week before mowing and the week after mowing a small increase in visits frequency and visit duration of these fields was observed (p=0.03, appendix B: model 10a) (figure 5). No difference in field visits was found between the week of mowing and the week before and after mowing (p=0.07, appendix B: model 10a)

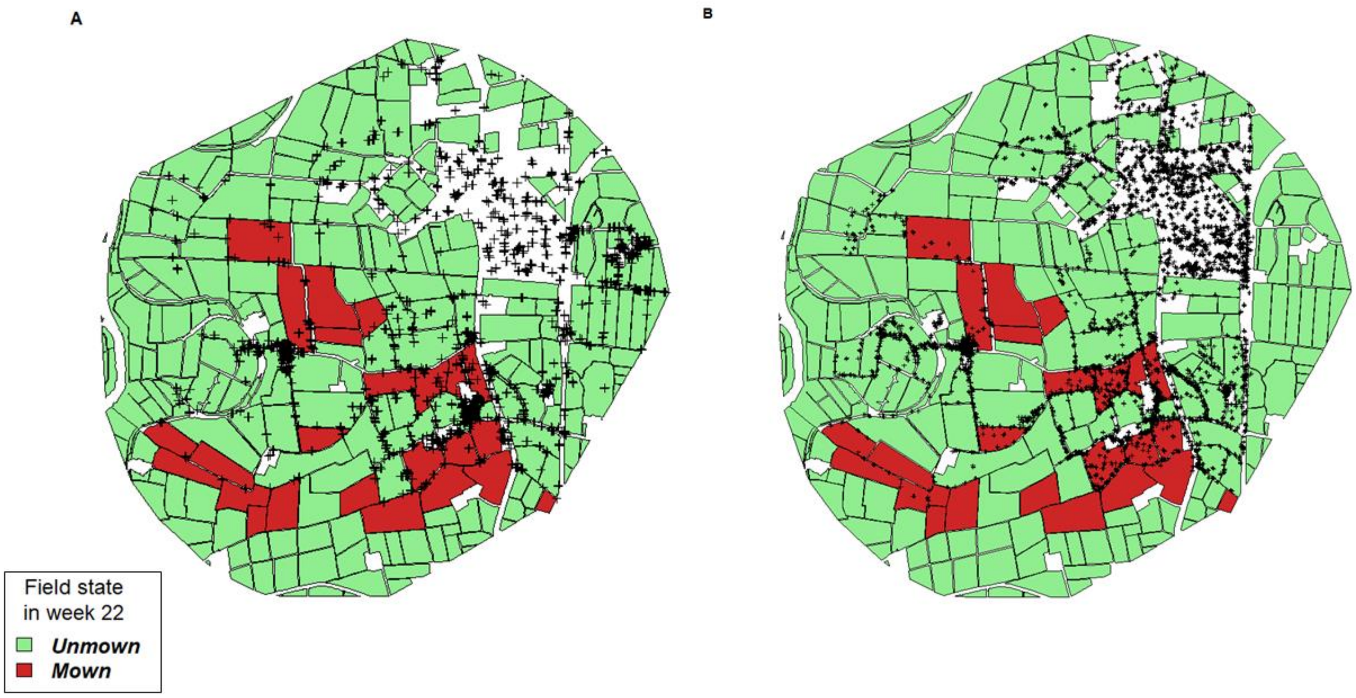

Figure 6: GPS locations of the three martens captured in 2021. Fields in red were mown in week 22. A) GPS locations in week 21, GPS loggers were set to 5 min intervals in this week. B) GPS locations in week 23, GPS loggers were set to 1 min intervals in this week. Field visits in mown fields slightly increased in week 23 in comparison to week 22 (p=0.03).

Distance to border

For all martens, the observed distance to the border of a field was smaller than distances for the random rotated points (p<0.001, appendix C) (figure 5). In 2020 the mean distance to the border were quite similar between individuals, with marten Eddie having a longer mean distance (12.9 m) compared to Freerk (11.1 m) and Anne-Jan (11.8 m) (p<0.001, appendix B: model 11a). In 2021, much larger differences to the field edges were found for marten Trudy (16.5 m) and Omgo (47 m). Marten Marco had a mean distance to the field edge of 9.6 m. All three martens differed in mean distance to border (p<0.001, model 12a).

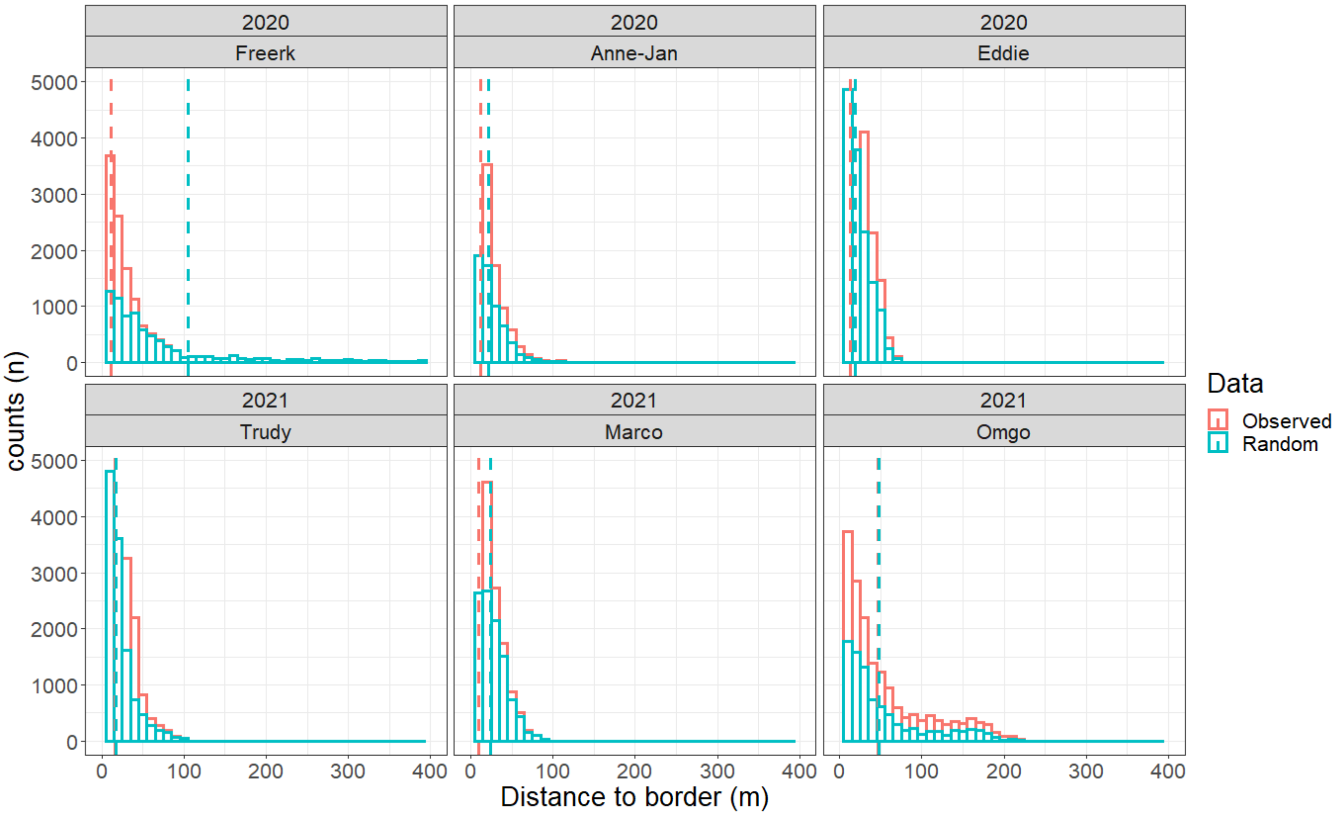

Figure 6: Distance from both observed as random GPS-points to the border of a field for all martens (n = 6). Dashed lines represent the mean distance of the observed or random points per marten. for all martens, the average distance of the observed data was lower than the random data (p<0.001).

Discussion & Conclusions

Field characteristics

This study demonstrates that fields with different levels of meadow-bird conservation management creates an agricultural landscape with different habitat characteristics. Fields of category A, with the main purpose of meadow-bird conservation, have an overall high water table in comparison to other fields in the area where either some (category B), or no meadow-bird conservation is applied (category C). Vegetation height increased faster in fields of category A as well, due to a later mowing date in comparison to fields of category B and C (figure 1). This is expected since postponing mowing and heightening water tables are well known meadow-bird conservation measures (Franks *et al.* 2018; Melman *et al.* 2020). Fields of category B showed relative high vegetation in comparison to category C, but a similar water table. Roughly 80 percent of the fields in the study areas consist of intense grasslands. These fields are characterised by low water tables and early and regular mowing of the grass, thus opposite to meadow bird conservation actions (Donald *et al.* 2001; Bos *et al.* 2013).

Prey availability

Vole density, expressed as VSI, was overall low in fields of category A in both 2020 and 2021 (figure 1). Higher densities were found in fields of category B and C, again in both years. Differences in vole densities between category A and categories B and C is likely caused by the high water tables or the active pumping of water onto fields where meadow-bird measures were applied, e.g. category A. Common voles inhabit habitat with lower water tables and therefore should prefer habitats of category B & C due to drainage of water for agricultural purposes (Bertolino *et al.* 2015; Smink *et al.* 2018). Common voles would be expected to be most abundant in category B due to low water tables and overall high vegetation, as common voles benefit form tall vegetation as it provides shelter from predators and food (Jacob & Hempel 2003). However, difference in vegetation height between category B & C does not result in a difference in VSI, showing that vegetation height is not the main factor determining vole densities in the study area. Overall vole densities were lower in 2021 in comparison to 2020. Small rodents such as the common vole show yearly population cycles with peaks and crashes (Jánová *et al.* 2003; Pinot *et al.* 2016). It seems that 2021 was a crash year for common vole populations in the study area. However, this is impossible to conclude from the data since vole populations in a fragmentated landscape show a variation in population cycles (Huitu *et al.* 2008).

Both studies conducted in 2020 and 2021 show that meadow-birds such as the black-tailed godwit, northern lapwing, Eurasian oystercatcher and redshank prefer fields where meadow-bird conservation measures were taken (figure 2). In 2020 nests were most abundant in fields of category A & B, whereas the number of nests did not differ between fields of category A, B and C in 2021. It is important to note that searching of nests in 2021 was done in fields where they were expected to be found. Thus, creating a bias for fields of category B & C which might explain the high amount of nests found in these fields. Nevertheless, counts of birds in 2021 show that birds do prefer fields of category A & B over fields of category C. The nest data from 2020 and bird counts from 2021 are in line with the expectations based on literature as the highest amount of birds and nests are found in suitable meadow-bird habitat (Natural England 2009; Franks *et al.* 2018). Birds of category "other", such as waterfowl, in both the nest data and the number of birds data in 2021, seem to be relative abundant in category C.

Results from the vole and bird data show that fields of category A are mainly habited by meadow-birds and very little habited by common voles. The exact opposite is found in fields of category C. Fields of category B are a somewhat hybrid between A & C (figure 1 & 2). Category B could be seen as the most diverse habitat with both meadow-birds as common voles present.

Habitat selection

This study presents evidence that beech martens select for specific habitat in a landscape with different habitats present. Three out of the six martens (Freerk, Anne-Jan and Trudy) showed a preference for fields of category A and one for category B (Anne-Jan). Two other martens, both from 2021, Marco and Omgo did not show this preference. Marco showed preference for category C except for week 24 – 27 when fields of category A & B were preferred. Omgo, who did not visit fields of category A and seemed indifferent to either B or C, spend most of the time in urban areas. Preference of all six martens varied over time and was anything but consistent (figure 3). When habitat preference of beech martens is linked to prey availability, it can be concluded that majority of the beech martens show a preference for habitats with meadow-birds (i.e. selection for category A & B). Even though it is known that birds are an important food source for beech martens, the results are interesting since rodents commonly represent the most important food source in dietary studies (Genovesi *et al.* 1996; Papakosta *et al.* 2014).

Habitat selection in terms of visit frequency is negatively correlated with distance to nearest roosting site. Beech martens adjust their spatial patterns according to several variables such as social interactions and resources (Genovesi *et al.* 1997). In both 2020 and 2021, beech martens visited fields less often when further away from their current roosting site. Mowing showed to have little effect on visit frequency in 2021 and even showed a small increase in visit frequency, although Seljee (2021) found a decrease in visit frequency after mowing in 2020. Increase in visit frequency after mowing is not expected as beech martens prefer high vegetation to seek shelter from possible predators (Rondinini & Boitani 2002; Wereszczuk &

Zalewski 2015). However, very little top predators which pose as a threat for beech martens are present in the study areas of both 2020 and 2021, since foxes are culled. Martens alter their spatial and temporal activity when sympatric with foxes due to predation risk (Lindström *et al.* 1995; Bischof *et al.* 2014). When top predators are absent, as is the case for the study area, beech martens might not need to avoid open spaces and might therefore be less affected by the open grasslands created through mowing.

Since a higher vole density was found in 2020 than in 2021 and in 2021 more nests were found in comparison to 2020, it is expected that martens would have a stronger selection for category A & B than category C in 2021 than in 2020. As martens are opportunistic they will select habitat where food is most abundant (Papakosta *et al.* 2014; Czernik *et al.* 2016; Hisano *et al.* 2016). Despite the difference in prey distribution between 2020 and 2021, this expectation is not met, which is surprising. Only the female, Trudy, showed a strong preference for fields of category A & B, whereas Marco showed preference for category C. Omgo, who showed equal preference for both B & C, spend only 16% of the time in agricultural fields and spend the remaining time foraging in urban habitat. Beech martens are known to successfully inhabit urban regions and live from human resources, marten Omgo seems an example of this (Hisano *et al.* 2016).

The low preference for fields of category C in 2020 and relative high preference in 2021 is a surprising result. As previously stated, small mammals and in specific small rodents make up a large part of the diet of martens during spring (Ben-David *et al.* 1997; Hisano *et al.* 2016). However, diet of martens is highly dependent on seasonal and regional availability of food. Even though voles were abundant in 2020 in the home range of the martens, they still might select for the chicks or eggs of meadow-birds since these are more commonly available within their home-range. Field of category A and B only make up a small part of the total habitat, but contain high densities of nests and breeding meadow-birds. Due to fragmentation and isolation of breeding reserves, meadow-birds and nests are being concentrated in A & B making these area rich and predictable food sources (Evans 2004; Newton 2004). Therefore, according to the optimal foraging theory, category A & B should be selected over category C (Price & Banks 2016). Weasels (*Mustela nivalis*) show a similar pattern where birds become the main prey of weasels when vole densities are low (Tapper 1979). Previous studies found that high vole densities reduces predation pressure of red foxes on waders and waterfowl, suggesting that vole are an important prey for generalist predators when commonly available (Ackerman 2002; Laidlaw *et al.* 2019) Vole abundance in both 2020 and 2021 might be too low for martens to mainly prey on voles causing them to focus on meadow-birds. Conducting a similar research in a year with high vole densities is needed to fully understand this system.

When looking at the mean distance of martens to field borders, Marco shows the smallest average distance (9.6 meter). Which suggests that the main prey, voles, in fields of category C concentrate at the edge of fields. However, as previously stated, birds of category "other" were relatively abundant in category C and consists of waterfowl who breed near water or in reed beds (Fiderer *et al.* 2019). Marco's preference for category C and small distance to field borders could be explained by him mainly preying on waterfowl eggs and chicks, and thus its preference for C seems not related to vole or meadow bird abundance.

In 2020, two out of three martens showed a strong preference for fields of category A, one marten, Anne-Jan, showed little preference for category A. Seljee (2021), stated that this can be explained by occupation of category A by another marten, Freerk, in the same area. Beech martens segregate their home range from martens of the same sex (Genovesi *et al.* 1997; Seljee 2021). Habitat selection is dependent on territories of other beech martens which occupy the same area. Instead of category A, Anne-Jan continued to show a preference for meadow-birds but shifted habitat from category A to B. This theory could as well explain the avoidance of both Marco and Omgo for fields of category A if a untracked male marten occupied these fields. Unfortunately, there is no data to substantiate this for the martens tracked in 2021.

Implications for meadow-bird conservation

Meadow-birds are a preferred prey of beech martens in an agricultural landscape. Whether beech martens prey on meadow-bird eggs, chicks or adults cannot be concluded from this study. Follow-up studies focussing on dietary variation in a similar study area are needed to access their main prey. However, results from this study present a clear preference by beech martens in 2020 and 2021. Repeating this study in a year with high vole densities is needed to fully understand the system and preference of beech martens. Nevertheless, this study confirms the thought that beech martens threaten meadow-bird populations to recover and pose as a possible treat for conservation efforts.

This study indicates that when alternative prey densities are low or absent, beech martens mainly select for habitat where meadow-birds are present. Reducing predation through culling or exclusion are potential methods but are labour intensive, costly and controversial due to ethical concerns (Franks *et al.* 2018; Roos *et al.* 2018) More sustainable management would be to create a landscape with more alternative prey, such as vole rich grasslands, since high vole densities are positively correlated with meadow-bird survival (Beintema & Muskens 1987; Laidlaw *et al.* 2019). Increasing meadow-bird reserves and reducing isolation of breeding grounds will as well lead to a decrease in predation pressure (Seymour *et al.* 2004). These potential methods require more research to test for effectiveness. Despite the results presented here, the decrease in meadow-bird populations remains a complicated problem in need of further research to develop new and effective conservation measures.

Acknowledgement

I would like to thank my supervisor, Raymond Klaassen, for the support, feedback on the report as well as providing me with the opportunity to conduct this research. In addition, I would like to thank Ferdi Seljee for the laid out ground work of this study and for the data gathered in 2020. I thank both Kas Jansma & Christian Stolz for the constructive criticism on the report. Finally I would like to thank 'het groninger landschap' for trusting me to conduct research in their conservation area, Ecosensys for gathering and providing tracking data of the beech martens, the farmers for the trust to give me access to their property to conduct research and all involved volunteers for gathering data, this research could not be done without their help.

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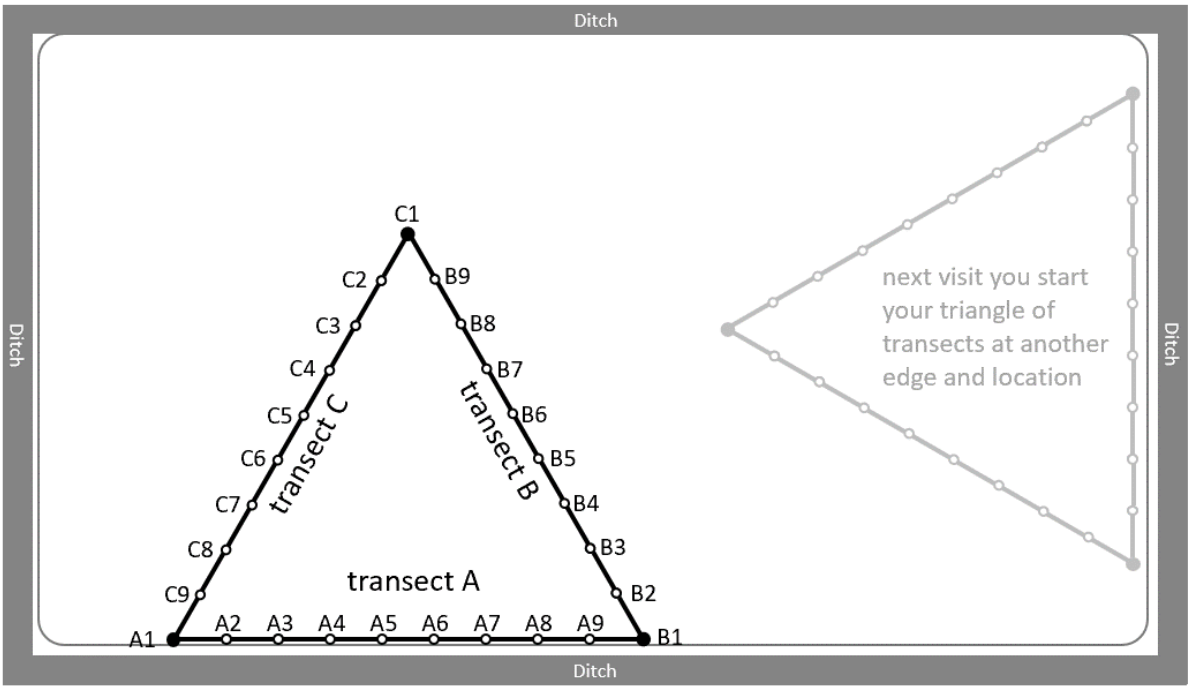
Appendix



Appendix A: protocol for field measurements in 2021
Record start and end point of each transect in Akkermonitor app (transect A: A1-B1, transect B: B1-C1, transect C: C1-A1. Transect A runs alongside the edge of the field. 10 m In between consecutive sampling locations. Note presence (+)/absence(-) of vole signs (fresh droppings, grass clippings) in each plot (25cm*25cm) Record water table height at A1 (difference between ground level and water level in ditch). Record vegetation height at A5, B5 & C5.

Appendix B: Models and statistical outcomes.

Model 1:

```
>m1 <- lm(water ~ fieldscore, data = dat)
> summary(m1)

Call:
lm(formula = water ~ fieldscore, data = dat)

Residuals:
   Min      1Q  Median      3Q     Max
-42.414 -18.349  -3.533  10.717  81.336

Coefficients:
            Estimate Std. Error t value Pr(>|t|)
(Intercept)   39.533      2.573  15.364   <2e-16 ***
fieldscoreB   40.934      4.415   9.271   <2e-16 ***
fieldscoreC   45.381      3.404  13.332   <2e-16 ***
---
Signif. codes:  0 '***' 0.001 '**' 0.01 '*' 0.05 '.' 0.1 ' ' 1

Residual standard error: 26.37 on 296 degrees of freedom
  (32 observations deleted due to missingness)
Multiple R-squared:  0.3935,	Adjusted R-squared:  0.3894
F-statistic: 96.03 on 2 and 296 DF,  p-value: < 2.2e-16
```

Model 1a:

```
> m1a <- glht(m1, linfct= mcp(fieldscore = "Tukey"))
```

```
> summary(m1a)

Simultaneous Tests for General Linear Hypotheses

Multiple Comparisons of Means: Tukey Contrasts


Fit: lm(formula = water ~ fieldscore, data = dat)

Linear Hypotheses:
         Estimate Std. Error t value Pr(>|t|)
B - A == 0  40.934     4.415   9.271  <1e-05 ***
C - A == 0  45.381     3.404  13.332  <1e-05 ***
C - B == 0   4.447     4.224   1.053   0.541
---
Signif. codes:  0 ‘***’ 0.001 ‘**’ 0.01 ‘*’ 0.05 ‘.’ 0.1 ‘ ’ 1
(Adjusted p values reported -- single-step method)
```

Model 2:

```
> m2 <- lm(veg_sqrt ~  week * fieldscore , data = dat)
> summary(m2)

Call:
lm(formula = veg_sqrt ~ week * fieldscore, data = dat)

Residuals:
   Min      1Q  Median      3Q     Max
-3.6597 -1.0237 -0.0869  0.9684  3.8271

Coefficients:
                 Estimate Std. Error t value Pr(>|t|)
(Intercept)      -3.93980    1.19744  -3.290  0.00111 **
week              0.42230    0.05620   7.515 5.65e-13 ***
fieldscoreB       6.17315    2.08655   2.959  0.00332 **
fieldscoreC       8.26028    1.60494   5.147 4.61e-07 ***
week:fieldscoreB -0.27390    0.09737  -2.813  0.00521 **
week:fieldscoreC -0.40605    0.07514  -5.404 1.27e-07 ***
---
Signif. codes:  0 ‘***’ 0.001 ‘**’ 0.01 ‘*’ 0.05 ‘.’ 0.1 ‘ ’ 1

Residual standard error: 1.457 on 323 degrees of freedom
  (2 observations deleted due to missingness)
Multiple R-squared:  0.1815,	Adjusted R-squared:  0.1688
F-statistic: 14.32 on 5 and 323 DF,  p-value: 1.131e-12
```

Model 2a:

```
> m2a <- lm(avg.veg ~ fieldscore, data = dat)
> m2a <- glht(m2a, linfct = mcp(fieldscore = "Tukey"))
> summary(m2a)

	 Simultaneous Tests for General Linear Hypotheses

Multiple Comparisons of Means: Tukey Contrasts


Fit: lm(formula = avg.veg ~ fieldscore, data = dat)

Linear Hypotheses:
           Estimate Std. Error t value Pr(>|t|)
B - A == 0   4.212      2.829   1.489   0.2948
C - A == 0  -5.281      2.173  -2.430   0.0406 *
```

```
C - B == 0  -9.493     2.689  -3.530   0.0013 **
---
Signif. codes:  0 ‘***’ 0.001 ‘**’ 0.01 ‘*’ 0.05 ‘.’ 0.1 ‘ ’ 1
(Adjusted p values reported -- single-step method)
```

Model 3:

```
> m3 <- lm(vsi_cube ~ year + fieldscore, data = dat)
> summary(m3)

Call:
lm(formula = vsi_cube ~ year + fieldscore, data = dat)

Residuals:
    Min       1Q   Median       3Q      Max 
-0.43814 -0.12864  0.01275  0.22769  0.66506 

Coefficients:
            Estimate Std. Error t value Pr(>|t|)    
(Intercept)  0.12864    0.03066   4.196 3.51e-05 ***
year2021    -0.14138    0.03345  -4.227 3.08e-05 ***
fieldscoreB  0.26581    0.04481   5.932 7.67e-09 ***
fieldscoreC  0.30951    0.03539   8.747  < 2e-16 ***
---
Signif. codes:  0 ‘***’ 0.001 ‘**’ 0.01 ‘*’ 0.05 ‘.’ 0.1 ‘ ’ 1

Residual standard error: 0.2781 on 324 degrees of freedom
  (3 observations deleted due to missingness)
Multiple R-squared:  0.2751,	Adjusted R-squared:  0.2684 
F-statistic: 40.99 on 3 and 324 DF,  p-value: < 2.2e-16
```

Model 3a:

```
> m3a <- glht(m3, linfct = mcp(fieldscore = "Tukey"))
> summary(m3a)

	 Simultaneous Tests for General Linear Hypotheses

Multiple Comparisons of Means: Tukey Contrasts


Fit: lm(formula = vsi_cube ~ year + fieldscore, data = dat)

Linear Hypotheses:
           Estimate Std. Error t value Pr(>|t|)    
B - A == 0  0.26581    0.04481   5.932   <1e-05 ***
C - A == 0  0.30951    0.03539   8.747   <1e-05 ***
C - B == 0  0.04370    0.04279   1.021    0.562    
---
Signif. codes:  0 ‘***’ 0.001 ‘**’ 0.01 ‘*’ 0.05 ‘.’ 0.1 ‘ ’ 1
(Adjusted p values reported -- single-step method)
```

Model 4:

```
> m4 <- lm(vsi_cube ~ water + avg.veg, data = dat)
> summary(m4)

Call:
lm(formula = vsi_cube ~ water + avg.veg, data = dat)

Residuals:
    Min       1Q   Median       3Q      Max 
-0.54096 -0.24585 -0.05455  0.22574  0.81454 
```

```
Coefficients:
             Estimate Std. Error t value Pr(>|t|)
(Intercept) -0.0721655  0.0475938  -1.516   0.1305
water        0.0040581  0.0004950   8.199 7.52e-15 ***
avg.veg      0.0020227  0.0009504   2.128   0.0341 *
---
Signif. codes:  0 '***' 0.001 '**' 0.01 '*' 0.05 '.' 0.1 ' ' 1

Residual standard error: 0.2852 on 295 degrees of freedom
  (33 observations deleted due to missingness)
Multiple R-squared:  0.1878,	Adjusted R-squared:  0.1823
F-statistic:  34.1 on 2 and 295 DF,  p-value: 4.758e-14
```

Model 5:

```
> m5 <- lm(n2020_log ~ fieldscore, data = bird.2020.1)
> summary(m5)

Call:
lm(formula = n2020_log ~ fieldscore, data = bird.2020.1)

Residuals:
     Min       1Q   Median       3Q      Max
-0.41459 -0.31862 -0.05708 -0.05708  1.66486

Coefficients:
            Estimate Std. Error t value Pr(>|t|)
(Intercept)  0.41459    0.06062   6.839 1.99e-10 ***
fieldscoreB -0.09596    0.09775  -0.982    0.328
fieldscoreC -0.35750    0.07352  -4.863 2.94e-06 ***
---
Signif. codes:  0 '***' 0.001 '**' 0.01 '*' 0.05 '.' 0.1 ' ' 1

Residual standard error: 0.3834 on 147 degrees of freedom
Multiple R-squared:  0.1538,	Adjusted R-squared:  0.1423
F-statistic: 13.36 on 2 and 147 DF,  p-value: 4.672e-06
```

Model 5a:

```
> m5a <- glht(m5, linfct = mcp(fieldscore = "Tukey"))
> summary(m5a)

	 Simultaneous Tests for General Linear Hypotheses

Multiple Comparisons of Means: Tukey Contrasts


Fit: lm(formula = n2020_log ~ fieldscore, data = bird.2020.1)

Linear Hypotheses:
           Estimate Std. Error t value Pr(>|t|)
B - A == 0 -0.09596    0.09775  -0.982  0.58583
C - A == 0 -0.35750    0.07352  -4.863  < 0.001 ***
C - B == 0 -0.26154    0.08723  -2.998  0.00875 **
---
Signif. codes:  0 '***' 0.001 '**' 0.01 '*' 0.05 '.' 0.1 ' ' 1
(Adjusted p values reported -- single-step method)
```

Model 6:

```
> m6 <- lm(n_log ~ fieldscore, data = nest.dat.2021)
> anova(m6)
Analysis of Variance Table
```

```
Response: n_log
          Df Sum Sq Mean Sq F value Pr(>F)
fieldscore   2  0.717 0.35847  0.9273 0.3976
Residuals  167 64.555 0.38656
```

Model 7:

```
> m7 <- lm(sum_sqrt ~ fieldscore + week, data = bird.2021)
> summary(m7)

Call:
lm(formula = sum_sqrt ~ fieldscore + week, data = bird.2021)

Residuals:
   Min      1Q  Median      3Q     Max
-2.8970 -0.6954 -0.0852  0.6062  4.2065

Coefficients:
          Estimate Std. Error t value Pr(>|t|)
(Intercept)  6.89376    0.44359  15.541  < 2e-16 ***
fieldscoreB -1.26308    0.14288  -8.840  < 2e-16 ***
fieldscoreC -2.66071    0.12289 -21.650  < 2e-16 ***
week       -0.16080    0.02081  -7.729 5.16e-14 ***
---
Signif. codes:  0 '***' 0.001 '**' 0.01 '*' 0.05 '.' 0.1 ' ' 1

Residual standard error: 1.26 on 551 degrees of freedom
Multiple R-squared:  0.5084,      Adjusted R-squared:  0.5057
F-statistic: 189.9 on 3 and 551 DF,  p-value: < 2.2e-16
```

Model 7a:

```
> m7a <- glht(m7, linfct = mcp(fieldscore = "Tukey"))
> summary(m7a)

             Simultaneous Tests for General Linear Hypotheses

Multiple Comparisons of Means: Tukey Contrasts


Fit: lm(formula = sum_sqrt ~ fieldscore + week, data = bird.2021)

Linear Hypotheses:
         Estimate Std. Error t value Pr(>|t|)
B - A == 0  -1.2631     0.1429  -8.840   <2e-16 ***
C - A == 0  -2.6607     0.1229 -21.650   <2e-16 ***
C - B == 0  -1.3976     0.1534  -9.112   <2e-16 ***
---
Signif. codes:  0 '***' 0.001 '**' 0.01 '*' 0.05 '.' 0.1 ' ' 1
(Adjusted p values reported -- single-step method)
```

Model 8:

```
> m8 <- lm(n_log ~ year, data = nest.tot)
> summary(m7)

Call:
lm(formula = n_log ~ year, data = nest.tot)

Residuals:
   Min      1Q  Median      3Q     Max
-0.5078 -0.5078 -0.1960  0.1854  1.8901

Coefficients:
```

```
            Estimate Std. Error t value Pr(>|t|)
(Intercept)  0.19601    0.04363   4.492 9.87e-06 ***
year2021     0.31175    0.05986   5.208 3.44e-07 ***
---
Signif. codes:  0 ‘***’ 0.001 ‘**’ 0.01 ‘*’ 0.05 ‘.’ 0.1 ‘ ’ 1

Residual standard error: 0.5344 on 318 degrees of freedom
Multiple R-squared:  0.07858,    Adjusted R-squared:  0.07568
F-statistic: 27.12 on 1 and 318 DF,  p-value: 3.441e-07
```

Model 9:

```
> m9 <- lmer(ivlev ~ fieldscore * week + (1|marten), data = data.ivlev)
> summary(m1)
Linear mixed model fit by REML. t-tests use Satterthwaite's method ['lmerModLmerTest']
Formula: ivlev ~ fieldscore * week + (1 | marten)
   Data: data.ivlev

REML criterion at convergence: 204.6

Scaled residuals: 
     Min       1Q   Median       3Q      Max 
-2.99341 -0.47138  0.05565  0.71251  2.07055 

Random effects:
 Groups   Name        Variance Std.Dev.
 marten   (Intercept) 0.02492  0.1579  
 Residual             0.13368  0.3656  
Number of obs: 201, groups:  marten, 6

Fixed effects:
                  Estimate Std. Error         df t value Pr(>|t|)
(Intercept)     -6.697e-02  2.083e-01  1.389e+02  -0.322    0.748
fieldscoreB     -8.196e-02  2.644e-01  1.916e+02  -0.310    0.757
fieldscoreC      9.053e-02  2.644e-01  1.916e+02   0.342    0.732
week             4.243e-03  1.078e-02  1.936e+02   0.394    0.694
fieldscoreB:week  6.317e-04  1.425e-02  1.926e+02   0.044    0.965
fieldscoreC:week -4.741e-03  1.425e-02  1.926e+02  -0.333    0.740

Correlation of Fixed Effects:
            (Intr) fldscB fldscC week   fldsB:
fieldscoreB -0.659                            
fieldscoreC -0.659  0.539                     
week        -0.921  0.682  0.682              
fildscrB:wk  0.644 -0.969 -0.533 -0.711       
fildscrC:wk  0.644 -0.533 -0.969 -0.711  0.562
```

Model 10:

```
> m10 <- lm(sqrt_n ~ mowscore, data = dat.mow.3)
> summary(m10)

Call:
lm(formula = sqrt_n ~ mowscore, data = dat.mow.3)

Residuals:
    Min      1Q  Median      3Q     Max 
-3.6596 -1.7593 -0.0264  1.3802  5.8811 

Coefficients:
            Estimate Std. Error t value Pr(>|t|)    
(Intercept)   2.5911     0.2998   8.644 6.13e-15 ***
mowscore0     0.1301     0.4239   0.307   0.7593    
```

```
mowscore1    1.0685    0.4239   2.521   0.0127 *
---
Signif. codes:  0 ‘***’ 0.001 ‘**’ 0.01 ‘*’ 0.05 ‘.’ 0.1 ‘ ’ 1

Residual standard error: 2.182 on 156 degrees of freedom
Multiple R-squared:  0.04625,    Adjusted R-squared:  0.03402
F-statistic: 3.782 on 2 and 156 DF,  p-value: 0.02488
```

Model 10a:

```
> m10a <- glht(m1, linfct = mcp(mowscore = "Tukey"))
> summary(m10a)

          Simultaneous Tests for General Linear Hypotheses

Multiple Comparisons of Means: Tukey Contrasts


Fit: lm(formula = sqrt_n ~ mowscore, data = dat.mow.3)

Linear Hypotheses:
        Estimate Std. Error t value Pr(>|t|)
0 - -1 == 0   0.1301    0.4239   0.307   0.9494
1 - -1 == 0   1.0685    0.4239   2.521   0.0339 *
1 - 0 == 0    0.9384    0.4239   2.214   0.0720 .
---
Signif. codes:  0 ‘***’ 0.001 ‘**’ 0.01 ‘*’ 0.05 ‘.’ 0.1 ‘ ’ 1
(Adjusted p values reported -- single-step method)
```

Model 11:

```
> m11 <- lm(dat.2020$log_dist ~ marten, data = dat.2020)
> anova(m11)
Analysis of Variance Table

Response: dat.2020$log_dist
          Df Sum Sq Mean Sq F value    Pr(>F)
marten       2    179  89.641  80.834 < 2.2e-16 ***
Residuals 41301  45801   1.109
---
Signif. codes:  0 ‘***’ 0.001 ‘**’ 0.01 ‘*’ 0.05 ‘.’ 0.1 ‘ ’ 1
```

Model 11a

```
> m11a <- glht(m1, linfct = mcp(marten = "Tukey"))
> summary(m11a)

          Simultaneous Tests for General Linear Hypotheses

Multiple Comparisons of Means: Tukey Contrasts


Fit: lm(formula = dat.2020$log_dist ~ marten, data = dat.2020)

Linear Hypotheses:
                  Estimate Std. Error t value Pr(>|t|)
anne-jan - freerk == 0  0.03318    0.01467   2.263   0.0606 .
eddie - freerk == 0     0.14846    0.01328  11.180   <1e-04 ***
eddie - anne-jan == 0   0.11528    0.01216   9.477   <1e-04 ***
---
Signif. codes:  0 ‘***’ 0.001 ‘**’ 0.01 ‘*’ 0.05 ‘.’ 0.1 ‘ ’ 1
(Adjusted p values reported -- single-step method)
```

Model 12:

```
> m12 <- lm(dat.2021$log_dist ~ marten, data = dat.2021)
> anova(m12)
Analysis of Variance Table

Response: dat.2021$log_dist
          Df Sum Sq Mean Sq F value    Pr(>F)
marten       2   9235  4617.6  3847.3 < 2.2e-16 ***
Residuals 39602  47531     1.2
---
Signif. codes:  0 ‘***’ 0.001 ‘**’ 0.01 ‘*’ 0.05 ‘.’ 0.1 ‘ ’ 1
```

Model 12a:

```
> m12a <- glht(m12, linfct = mcp(marten = "Tukey"))
> summary(m12a)

	 Simultaneous Tests for General Linear Hypotheses

Multiple Comparisons of Means: Tukey Contrasts


Fit: lm(formula = dat.2021$log_dist ~ marten, data = dat.2021)

Linear Hypotheses:
                   Estimate Std. Error t value Pr(>|t|)
marco - trudy == 0 -0.54864    0.01287  -42.63   <2e-16 ***
omgo - trudy == 0   0.70430    0.01383   50.92   <2e-16 ***
omgo - marco == 0   1.25294    0.01428   87.72   <2e-16 ***
---
Signif. codes:  0 ‘***’ 0.001 ‘**’ 0.01 ‘*’ 0.05 ‘.’ 0.1 ‘ ’ 1
(Adjusted p values reported -- single-step method)
```

Appendix C: Wilcoxon rank test for distance to border.

```
> wilcox.test(distance ~ sample, data = data)#trudy, p < 0.005

	Wilcoxon rank sum test with continuity correction

data:  distance by sample
W = 126120413, p-value = 0.0002334
alternative hypothesis: true location shift is not equal to 0

> wilcox.test(distance ~ sample, data = data.1)#marco, p < 0.005

	Wilcoxon rank sum test with continuity correction

data:  distance by sample
W = 126513362, p-value < 2.2e-16
alternative hypothesis: true location shift is not equal to 0

> wilcox.test(distance ~ sample, data = data.2)#omgo, p < 0.005

	Wilcoxon rank sum test with continuity correction

data:  distance by sample
W = 54803290, p-value = 3.954e-10
alternative hypothesis: true location shift is not equal to 0

> wilcox.test(distance ~ sample, data = data.3)#freerk, p < 0.005

	Wilcoxon rank sum test with continuity correction
```

```
data:  distance by sample
W = 72403282, p-value < 2.2e-16
alternative hypothesis: true location shift is not equal to 0

> wilcox.test(distance ~ sample, data = data.4)#anne-jan, p < 0.005

	Wilcoxon rank sum test with continuity correction

data:  distance by sample
W = 59585006, p-value < 2.2e-16
alternative hypothesis: true location shift is not equal to 0

> wilcox.test(distance ~ sample, data = data.5)#eddie, p < 0.005

	Wilcoxon rank sum test with continuity correction

data:  distance by sample
W = 220287138, p-value < 2.2e-16
alternative hypothesis: true location shift is not equal to 0
```