UNIVERSITY OF GRONINGEN

MSC ECOLOGY & CONSERVATION RESEARCH PROJECT

Predicting spatial densities of feral cats on the island of Schiermonnikoog using spatially explicit capture recapture

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Abstract

Introduced feral domestic cats (*Felis catus*) can have large negative impacts on local wildlife, both directly and indirectly, especially on island populations. Successful eradication of feral cats (from islands) requires them to encounter traps, hunters or poison, and thus information on their spatial distribution and population sizes are essential. In a camera trapping study, I studied feral cat spatial distribution and population sizes on the Dutch barrier island of Schiermonnikoog using spatially explicit capture recapture (SECR) methods. I constructed various models to predict feral cat spatial densities, using four data sets (for both a conservative and more liberal identification method, and both a habitat classification including and excluding farmland) and five different ecological predictors: distance to road, distance to village, terrain type, average vegetation height, and average vegetation standard deviation. Due to a lack of adequate data, I had to drop the distance to road and terrain type variable. The population of feral cats consisted of 47-51 individuals for to conservative identification method, and up to 62-79 for the liberal method. Distance to village was a significant predictor for all four datasets, with the highest predicted cat density around 3000m from the village. Both vegetation variables were also significant, but only for the liberal identification method including farmland as a habitat. The ecological explanations for these results, failed results, as well as suggestions for future research are discussed. In conclusion, the feral cat population on Schiermonnikoog appeared to be relatively stable, with distance to village being the best spatial density predictor, but many interesting avenues for future research still remain.

Introduction

Domestic cats (*Felis catus*) have been introduced as pets and pest control by humans around the world, ranging from subarctic and tropical regions, to deserts and forests (Long 2003, Doherty et al. 2014). As generalist predators, cats can have severe negative impacts on local wildlife. In fact, cats are listed as one of the 100 worst invasive species (Lowe et al. 2000), and have contributed to at least 63 (26%) of recent worldwide bird, mammal and reptile extinctions, and threaten an additional 367 species at risk of extinction (Doherty et al. 2016). Feral cats, which are cats descended from domestic ancestors, but are now free-living and no longer dependent on anthropogenic resources, have substantially higher impacts on native fauna, with quadruple the kill rate of domestic cats (Loss et al. 2013, Legge et al. 2020). While the number of feral cats is relatively small compared to their domestic counterparts, their presence is natural environments may still have severe consequences. For example, in the United States alone, feral cats are responsible for majority of cat-killed wildlife, killing an estimated 2.4 billion birds and 11.3 billion mammals annually (Loss et al. 2013). Moreover, feral cats also have non-lethal effects through, for example, hybridisation, disease transmission, and anti-predator behaviour (Doherty et al. 2014, Legge et al. 2020). One of the most well-known examples of anti-predator behaviour is the ecology of fear, where risk avoidance from prey leads to altered ranging, feeding, and breeding behaviours (Laundre et al. 2010, Legge et al. 2020). Such indirect effects can lead to population declines, even under low levels of predation (Bonnington et al. 2013, Legge et al. 2020).

The destructive effects of feral cats on the environment call for conservation measures. One approach in feral cat population management is trap-neuter-return (TNR), in which cats are captured, sterilized, checked and/or vaccinated for disease, and then released back into the wild (Zaunbrecher and Smith 1993). However, TNR is a controversial method, as it is resource and time intensive, and places the cats back into the wild, while scientific evidence for its success remains quite limited (Longcore et al. 2009). Alternatively, cats can be eradicated entirely through, for example, hunting or trapping, after which wildlife can recover (Prior et al. 2018). For example, the removal of cats from Natidivad Island, Mexico, using trapping and hunting led to a 90% decrease in seabird mortality, providing massive improvements to long-term viability of the island's seabird population (Tershy 2002, Keitt and Tershy 2003). Substantial effort has already been put in the eradication of feral cats (Nogales et al. 2004), which is especially relevant for islands where local wildlife often lack defences from mammalian predators (Medina et al. 2011). Cats have been eradicated from over 100 small and intermediate islands across the world ("Database of Island Invasive Species Eradications" 2022), However, these islands are only a fraction of the estimated 5% of 179 000 of small and intermediate sized islands where cats have been introduced (Medina et al. 2011). To successfully eradicate cats, information on cat spatial distribution is crucial, especially for trapping, which may be the preferred method of cat eradication considering the presumably low societal support for cat killing.

Four main mechanisms are suggested to determine habitat use of feral cats (in order of importance): predation and/or competition from other predators, prey availability, human resource subsidies, and shelter (Doherty et al. 2014). As a result, cats generally prefer structurally complex habitats, such as shrubland or woodland, providing cats with a mixture of cover and open areas, which can be used for travel, hunting and shelter (Doherty et al. 2014). Moreover, more complex habitats tend to support a greater number and diversity of prey (Tews et al. 2004). As a result, cats favour certain, more complex habitat components (infrastructure, riparian, shrub/heathland, forest, woodland), while avoiding more simple ones (grassland, agricultural land) (Graham et al. 2012, Doherty et al. 2014). However, the evidence of these ecological predictors for cat densities still remain somewhat weak (Doherty et al. 2014). Moreover, research on feral cats is mostly focussed around relatively sparsely human populated regions in specific geographic regions (Doherty et al. 2014, Bengsen et al. 2016). And yet, feral cats pose a very real threat in much more densely populated regions as well. For example, in the Netherlands, feral cats kill an estimated 141 million animals annually, including 38% of the bird summer population which contain many vulnerable species (Knol 2015). Therefore, there is a need to expand our knowledge on abundance and distribution of feral cats in other areas of interest, such as the Netherlands.

In this study, I used camera trap data to estimate population size on the Dutch island of Schiermonnikoog, and I predicted spatial cat density based on a variety of ecological predictors. Schiermonnikoog contains a variety of habitats (also see Figure 1), and cats are the only relatively large predators on the island. Since cats prefer structurally complex habitats (Doherty et al. 2014), I hypothesize that feral cats will be concentrated near road verges and other areas with high vegetation diversity. In the absence of natural enemies and interspecific competitors, I expect shelter and human resource subsidies to play an important role in feral cat distribution, so cats may be found close to roads, buildings, and high (sheltering) vegetation. I estimated population sizes and spatial densities using spatially explicit capture recaptures (SECR) methods, as this is a robust alternative to more traditional capture-recapture methods which allows for more advanced spatial analysis (Borchers and Efford 2008). Predicting the number and spatial distribution of feral cats might provide valuable information for scientists and conservation managers, and can be used for designing and executing (camera) trapping projects and monitoring programmes to minimize damage of feral cats on the local ecosystem of Schiermonnikoog and similar locations.

Methods

Study area

Schiermonnikoog (53°30′ N, 6°10′ E) is the easternmost of the five inhabited Dutch Waddensea barrier islands, positioned approximately seven kilometres off the Dutch mainland (Figure 1). The island has a land surface area of about 4000ha. A village with 954 inhabitants can be found on the western side of the island, and is surrounded by a polder with several farms. The other habitats on the island are quite heterogeneous, and include dune valleys, a planted forest, mudflats and salt marshes. The entire island and the adjacent parts of the North Sea and Wadden Sea, with the exception of the village, is part of Schiermonnikoog National Park (5400ha). The Natura-2000 site "Duinen Schiermonnikoog" (1042ha) is located within the National Park, surrounding the village. The adjacent Wadden Sea is a UNESCO World Heritage site.

Figure 1: Satellite map of Schiermonnikoog. The southwestern part of the island is a polder with farmland and a salt marsh. North of the polder is the village, which is surrounded by dunes and forest. The middle and western part of the island consists of salt marsh, grassland and dune valleys.

Schiermonnikoog is home to a variety of wildlife, including many species of mammals and birds. As of 2018, over 100 breeding species of birds were observed on the island, of which 20 are on the Dutch list of threatened species ("Rode Lijst") (Kleefstra and Klemann 2018). Moreover, the Dutch barrier islands are a key site for millions of migratory birds along the East Atlantic Flyway (Roomen et al. 2005). Schiermonnikoog harbours a population of hares, with a density of approximately 70 individuals per km2 (Van Wieren et al. 2006). Rabbits, hedgehogs, brown rats, and a variety of mice, shrew and voles inhabit the island as well, for which no scientific population estimates exist. Except for introduced cats, there are no other large mammalian predators (foxes, martens, etc.). As mentioned previously, island species, such as ground breeders, are especially vulnerable to predation, and cat predation may thus threaten local wildlife (Medina et al. 2011, van der Ende 2015a).

Study species

A population of feral cats (hereafter, cats) inhabited the island, descended from abandoned or escaped village or tourist cats. The cat population, outside of the village and surrounding rural lands, was estimated to consist of 34 individuals in 1984 (Langeveld 1987), and 50 individuals in the most recent estimate in 2011 (Op de Hoek et al. 2013). Cats were hunted in the past, but since 1994 there is a no-hunting policy in the natural parts of the island. The population is known to reproduce in the wild

(Langeveld 1987), and it is unknown whether the population has grown since 2011. Cat diet consists mostly of voles, but other mammals and birds are consumed as well (Op de Hoek et al. 2013).

Camera trap deployment

In order to estimate feral cat density, a large part of Schiermonnikoog (Figure 2) was surveyed for cat presence from July 14th to November 23rd 2021 using 17 Reconyx Hyperfire HC600 cameras. This camera type takes multiple pictures when its motion sensor is activated, and thanks to its infrared LEDs, it allows for night pictures to be taken as well. Cameras were placed on poles, 50cm above the ground at 68 different sites, mostly along various (game) trails containing cat droppings to maximize camera capture rate. Traps were deployed away from the village and agricultural lands , as the focus of this study was on feral population living in the natural parts of the island, and to reduce to risk of capturing domestic cats from the village on camera (Figure 1, 2). Moreover, the forest was not monitored as well, since the field crew did not expect cats to be present there (Figure 1, 2). Cameras were moved across the island over time. From July 14th to September 8th, the Eastern part of the island was sampled in three sessions at 36 locations. From September 23rd to November 2nd, the Western part of the island was sampled in two sessions at 18 locations, and from November 1st to November 23rd, the middle part of the island was sampled in a single session at 14 locations. Some of the sessions overlap as some cameras were moved over the course of several days. Camera trap locations were recorded using GPS. GPS coordinates from six camera trap locations were in unrealistic locations (like the middle of a road) due to small measurement inaccuracies. I have manually modified these coordinates (up to ~2m) to prevent complications in further analysis.

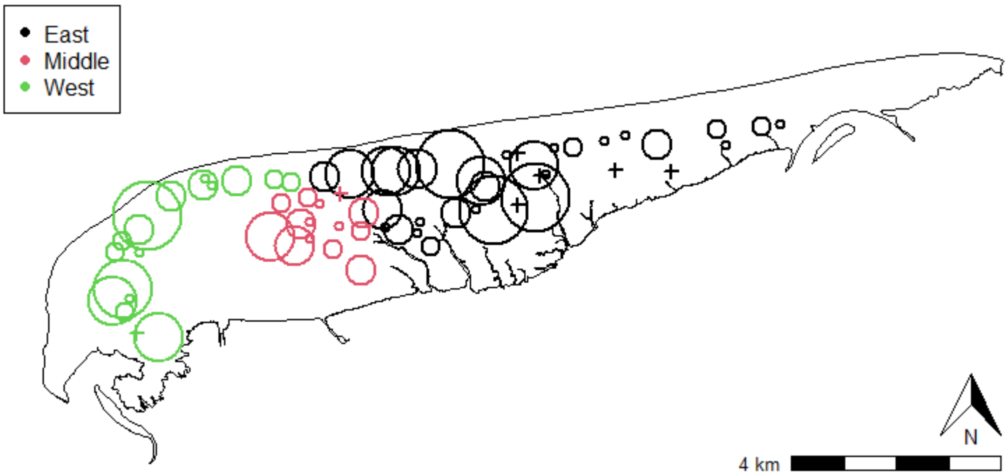


Figure 2: Overview of camera trap placement on Schiermonnikoog. Camera traps were placed around trails as to maximize capture probability (also see Figure 4). Different colours represent the different parts of the island where traps were placed. Circles represent functioning traps, with size indicating the number of individuals captured (conservative estimate, see "Cat identification"), ranging from zero to six individuals. Crosses represent failed camera trapping sites.

Table 1: Overview of camera deployments on Schiermonnikoog. Camera traps were deployed on three parts of the island (East, West and middle) at various sites during multiple sessions. Some failed sites were dropped from the analysis, for example because of stolen SD-cards, or broken cameras. (*) An additional two cameras were placed in front of moving vegetation, continuously triggering the camera. These two sites were still included in the analysis, but were active for less than 24 hours because of full memory. (**) Four additional cameras had failed, but were successfully redeployed in a later session.

Location	Period (2021)	Sites	Failed	Sites with cat
East	July 4 – September 8	36	6*	19
West	September 23 – November 2	18	1**	13
Middle	November 1 – November 23	14	1	9

Camera trap effort

Not all individual camera traps were used equally for the different locations, for example due to malfunctions, or asymmetrical sampling effort (Table 1). To incorporate this variability in usage (and the resulting variability in cat detection opportunities) in the analysis, I included an effort variable in future analysis, describing how long all camera traps were used for all camera trap locations, for the entire duration of the study. Camera traps that were active at a location for an entire day (24 hours) were given a value of 1 for that day and location. Camera traps that were only partially active during a day, were given a corresponding lower value. For example, a camera trap that was placed at 7:00 AM, will only be active roughly 70.8% of the day (the remaining 17 out of 24 hours), and would thus be given an effort value of 0.708 for that day and location. When a camera trap was not active at a location, either due to malfunction or having been moved to another location, the camera trap was given a value of 0 for those days and sites (Table 1). These camera trapping effort values can then be used in future analysis in SECR methods to yield more precise density estimates as described by (Efford 2022c).

Image analysis

All camera trap images were scanned by hand by one observer for cat presence. Photographs from failed sessions (e.g., stolen SD-cards, malfunctions, incorrectly placed cameras) were not examined (Table 1). Photographs from failed sessions (e.g., a lot of moving vegetation, unreliable triggering) were unexamined or only briefly scanned unexamined. Since the camera traps can take multiple photos of the same cat in a short timespan, a cat photo was classified as new sighting when at least five minutes had passed between that and the last photo of that individual.

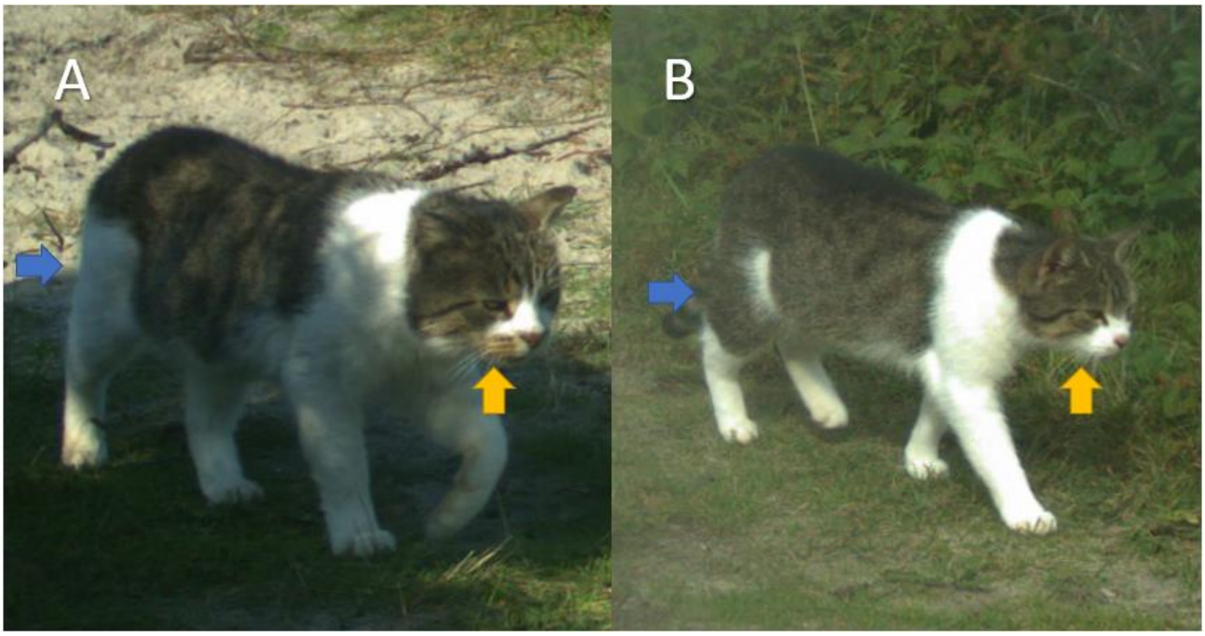


Figure 3: Example of high-quality camera trap photographs of two individuals at the same camera trap site. At first glance, these cats appear to be the same individual, but it is possible to distinguish the two through some of their characteristic markings and colourations: a differently coloured thigh (blue arrow) and differently coloured check (yellow arrow).

Cat identification

All cats from sightings were subsequently identified using characteristic markings and colourations (Figure 3) by two different independent observers. All cat photographs were checked against all previously identified individuals, and were given a new ID when cat appearance did not match any of the previously identified cats. Afterwards, cat identifications from the two independent observers were compared, and inter-observer discrepancies were adjusted following discussion. Since some pictures were of poor quality (Figure 4), it was sometimes difficult to identify individuals with confidence, even after discussion. Therefore, I decided to create two identification lists. The first is a conservative estimate, where individuals that were difficult to identify were classified as the most plausible already existing individual, based on colour, markings, location, and time of sighting. For example, a poor-quality picture of a cat may be classified as a similar-looking cat that has been sighted at the same location several hours prior. The second list is a liberal estimate, where every cat that could not be identified with confidence was identified as a “new” individual (i.e., an individual that has not been sighted before). These conservative and liberal identifications were analysed separately. For both lists, completely unidentifiable images and kittens were excluded from the analysis, as they could not confidently identified.

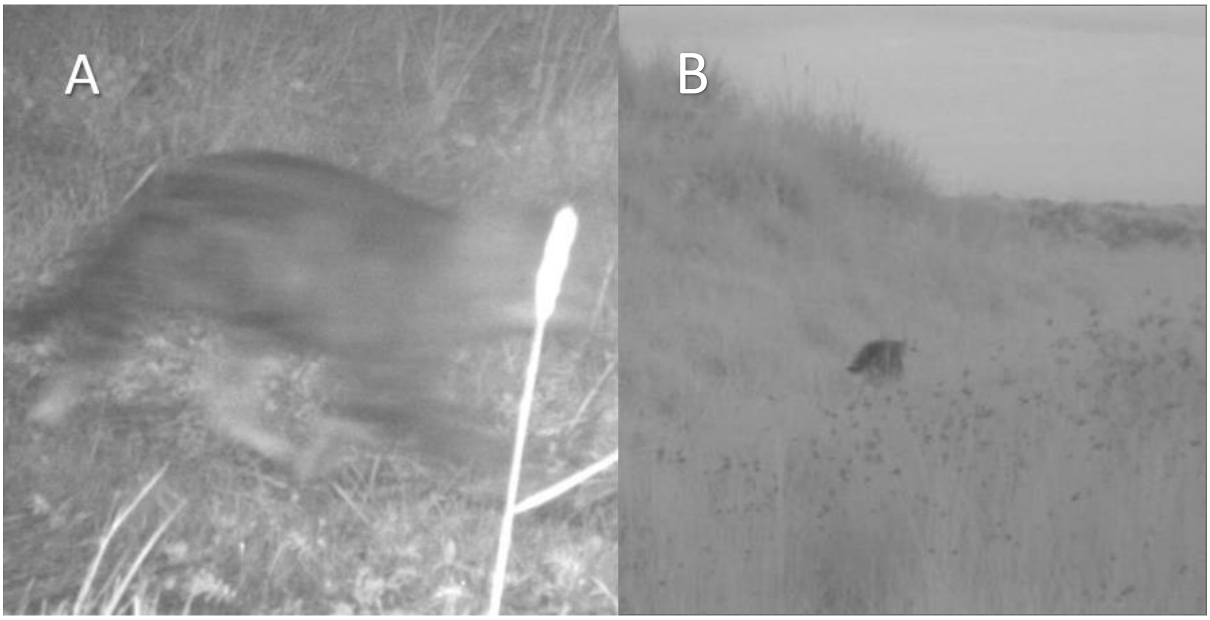


Figure 4: Example of some poor-quality pictures, taken at two different locations. The picture on the left (A), though blurry, could still be assigned to an individual. When cats could not be confidently identified, cats were given a conservative (existing individual) and a liberal (new individual) identification, analysed separately in models. Because of its common and non-distinctive brown colouration, I have identified this individual as a similar-looking individual when using conservative identification, but as a new individual when using when the liberal identification. The picture on the right (B) is an example of an unidentifiable individual, and was excluded from further analysis.

Density estimates using SECR

To obtain a density estimate of the total population of feral cats on Schiermonnikoog, based on camera trap images, I used a spatially explicit capture-recapture (SECR) model using the "secr" package version 4.5.4 (Efford 2022b) in R version 4.2.0. SECR is a set of methods that can be used to estimate densities that has several advantages over more traditional capture-mark-recapture methods, generally performing better than simple capture-recapture methods (Sollmann 2018, Davis et al. 2020), and have been successfully used in previous ecological studies (e.g., Boulanger et al. 2018). SECR models work with the assumption that base detection probability (g0) decreases with increasing distance by spatial parameter σ from an individual's activity centre (representing the centroid of an individual's home range): the so-called detection functions (Efford 2004; Figure 5). Without radiotelemetry, information on the precise locations of these activity centres is usually unknown, but with data on where individuals have been (re-)sighted and their probability of detection, it is possible to obtain some (imperfect) estimates. The distribution of activity centres usually follows a homogenous Poisson point process (Borchers and Efford 2008), meaning that all activity centres of individuals that could have been exposed to sampling are included in the so-called state space – the area in which activity centres can be located. Consequently, when the state space is large enough (i.e., containing enough activity centres), further increases in state space do not affect density estimates. Activity centres of feral cats may not actually be distributed according to homogenous Poisson process, especially since feral cat home range size overlap and can differ between sexes and seasons (Recio and Seddon 2013). However, as long as camera trap deployment is not biased towards or away from activity centres, non-uniformities are expected to average out (Borchers and Efford 2008, Mcgregor et al. 2015). By dividing the number of activity centres in the state space over the sampling area, it is possible to obtain a density estimate.

Mask

SECR methods work with a mask, which is a grid of square cells that cover the trapping grid and all the surrounding area which might contain home ranges of the sampled population. The outer limit of this mask is determined by the buffer, which extends the mask by "buffer" meters around all detectors. The buffer should be sufficiently large as to not influence density estimates, and was set to 4000m after analysis of a mask buffer diagnostic plot created with the esa.plot function from the secr package, using the data from Figure 2. The mask can then be clipped by natural boundaries, and areas of non-habitat can be removed. For this, I used ESRI-shapefiles from the *Basisregistratie Topografie* (BRT; Base registration topography). More specifically, I used the TOP10NL topographic map of Schiermonnikoog (Rijkswaterstaat, Ministerie van Infrastructuur en Waterstaat 2022a). For viewing and manipulation of this and all subsequent spatial data (see Density models), I used QGIS v.3.10.11. I manually removed sandbanks around the island, as these get inundated regularly, making them unsuitable habitat for cats. Since it is unclear whether cats use the island's agricultural areas as habitat (Figure 1), I created two masks, one in which I classified both the village and the surrounding farmlands as non-habitat, and one where I only classified the village as non-habitat (both in addition to other areas of non-habitat, such as bodies of water). Grid cell size of the mask should fall around or below the spatial parameter σ to provide a safety margin against biased density estimates, and (Efford 2022a), and was set to 200m after preliminary analysis (also see Table 3).

Detection function

Next, I fitted models with various detection functions, describing how the chance of detecting an individual changes with increasing distance from its activity centre, influencing density estimates (Figure 5). SECR has a total of twenty detection functions, most of which are rather unconventional or used for specific data types (such as audio signals). After excluding these options, three function forms remained: half-normal (HN), negative exponential (EX), and hazard rate (HR) (Figure 5). I constructed models with these detection functions, and compared their AIC-values, and chose HR to use in further modelling, as this function had the lowest AIC-value. HR follows the formula $g(x) = g0\ (1 - exp(- (x / \sigma)^{(-z)}))$, where g(x) is the chance of detection of an individual x meters from its home range centre, g0 is the base detection rate, σ is the spatial parameter in meters, and z is a variable describing the length of the detection probability 'plateau' at short distances from the activity centre (Figure 5). The values of g0, σ and z are given for significant models in Table 3. Note that the use of HR is usually discouraged, because of its sensitivity out to very large distances, requiring very large buffers which would slow down the models. However, since I'm working with an island with natural boundaries, this should not pose much of a problem.

Population size estimates

SECR has built-in functions for estimating population sizes in the sampled region, using spatially fitted capture-recapture models, by discrete summation of every point in the fitted density surfaces. As an alternative to this more classical expected population size, the realised population size often yields similar results, but is considered to be more robust and has more adequate confidence intervals (Efford and Fewster 2013). The realised population size is calculated using slightly different methods, by excluding spatial process variance (see Johnson et al. 2010, Efford and Fewster 2013). I will base my results and conclusions based off realised population estimates, as theses do not estimate the population sizes below the actual number of observed individuals, and are more robust in general. I still included expected population sizes for comprehensiveness.

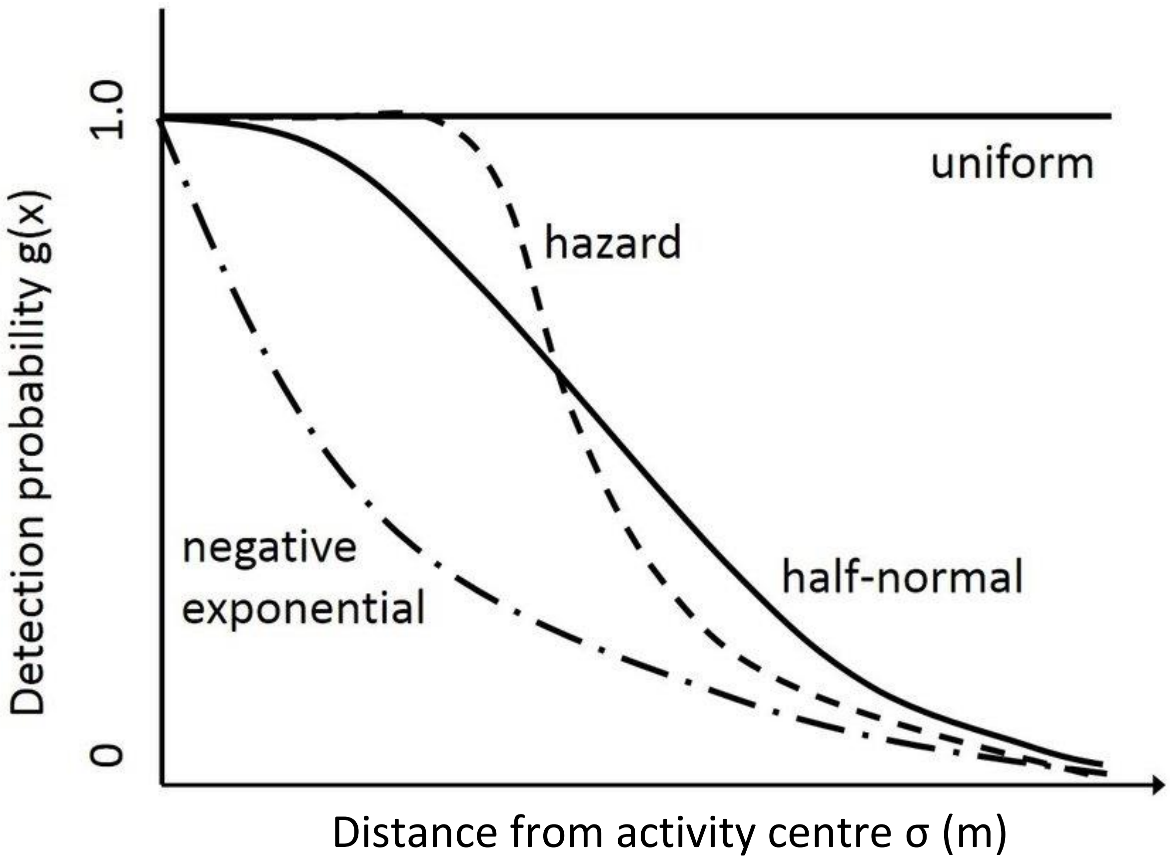


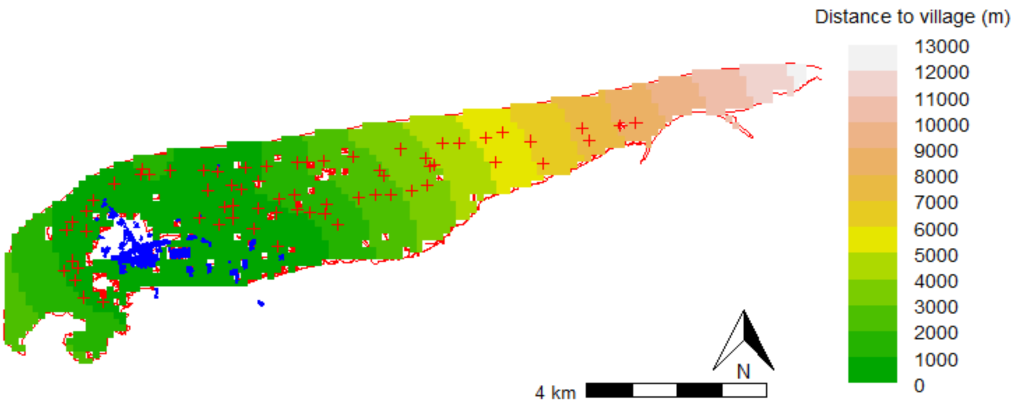
Figure 5: The most used detection functions in SECR. Detection functions describe how detection probability g(x) declines with increase distance σ from activity centres (home ranges or territories). For this study, I used the hazard rate function, as this function fitted my data the best. Note that the base detection g0 here is 1.0, but this is usually not the case in practice.

Covariates

To explain possible variation in cat density throughout the island by ecological predictors, I used five different covariates in my models: distance to road (DTR), distance to village (DTV), terrain, vegetation mean height (VMH), and standard deviation of vegetation height (VSD), which I calculated using topographic and remote sensing data, explained in more detail below. These ecological predictors were then added to the mask for further analysis.

Distance to roads and village

Although feral cats are not necessarily dependent on humans for their survival, they may still make use of anthropogenic resources. The village and paths on the island may be sources of anthropogenic resources, for example in the form of leftover food from hiking tourists, or restaurants with garbage bins. Moreover, as mentioned previously, cats may prefer using roads and road verges for easy travel, and hunting or shelter opportunities (Doherty et al. 2014). However, cats may also perceive humans as dangerous, and might therefore avoid the village and some of the busier paths. To measure whether cats made use of roads and paths and possible anthropogenic resources around them, I used the "Wegdeel" (road sections) layer from the TOP10NL topographical maps, containing main roads, as well as smaller roads and (bicycle/hiking) paths. The distinction between major and minor roads was somewhat arbitrary, with some dirt paths being classified as main roads and some paved roads classified as minor paths. Therefore, I chose to combine both of these into one dataset. In the secr-package it is possible to calculate the distance of various points to the nearest camera trap by using the "distancetotraps" function. So, by converting the spatial road data into points, I could easily calculate the distances from traps from roads (DTR; Figure 6). I calculated the distance from traps to the village (DTV) in a similar fashion, by selecting the polygons that made up the buildings from the “Terrein” (terrain) layer of the TOP10NL topographical maps and converting them into points, and then using the “distancetotraps” function (Figure 6). During preliminary analysis, models containing the DTR-variable were highly significant (Appendix A), but also unrealistically extrapolated population estimates over the island (for example Appendix B3), and were thus excluded from the final analysis.



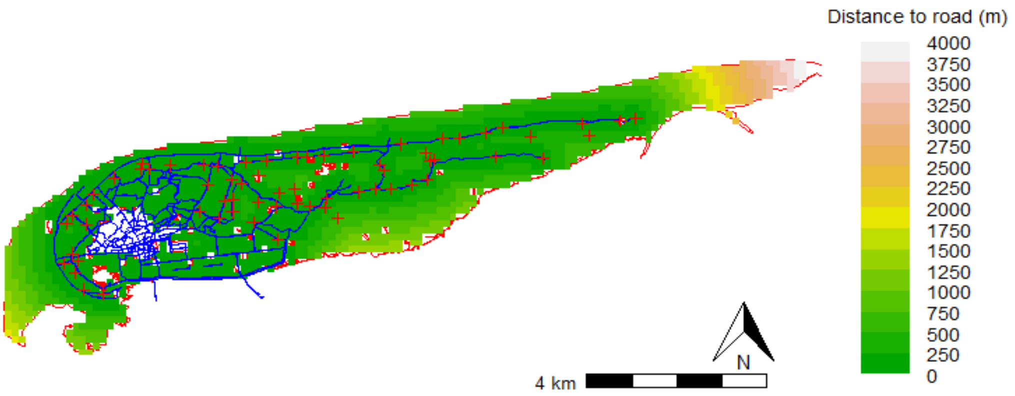


Figure 6: The distance to village (DTV; top) and distance to road covariates (DTR; bottom) used in SECR density models, plotted in the farmland mask. Buildings and roads are included in blue in their corresponding plot. Both these variables were calculated using a built-in function in SECR, and could thus only be plotted within an SECR-mask. Red crosses are trap locations.

Terrain

As mentioned previously, structurally complex habitats are preferred by cats due to their hunting and shelter opportunities (Doherty et al. 2014). Schiermonnikoog contains various terrain types with varying degrees of complexity, ranging from dunes to forests (Figure 1). To investigate whether habitats can explain possible differences in cat density on the island, I included a terrain variable in the analysis. Again, I used the terrain layer from the TOP10NL topographical maps. This data could be added straight to the mask, as "unsuitable" terrain (such as buildings or water) is already cropped out from habitat masks. The terrains from this map consisted of various broad categories, including sand (beaches), dune, grassland, forest (deciduous, coniferous, mixed) and cropland. However, during preliminary analysis, models using this this terrain covariate had trouble fitting, and were thus excluded from further analysis (represented, for example, by NA's when estimating population densities, also see appendix B3 and B4).

Vegetation height and standard deviation

Vegetation height and standard deviation may also be good ecological predictors for cat presence. High vegetation may provide good shelter opportunities for cats. Vegetation standard deviation can be used as a proxy for structural complexity. Since available detailed vegetation maps were likely outdated, as the island is constantly changing (Bakker et al. 2003), I decided to estimate the vegetation height and standard deviation myself with more recent data using remote sensing. By subtracting a digital terrain model (DTM; the elevation of Earth's surface, without buildings or vegetation) from a digital surface model (DSM; the elevation of tallest surface, including buildings and vegetation) it is possible to obtain an estimate of vegetation height. DTM and DSM for Schiermonnikoog are available in Het Actueel Hoogtebestand Nederland (AHN3; Current Dutch Elevation), where through laser altimetry a raster of DTM and DSM at a 5m resolution is obtained (Rijkswaterstaat, Ministerie van Infrastructuur en Waterstaat 2022b). As DSM does not distinguish between buildings and vegetation, structures are still included, but since I excluded the village from the mask, this should only minimally influence the results. Because these are estimates, some degree of error remains. For example, there were a small number of negative values for vegetation height, which I have manually set to 0 in QGIS. As I am interested in the vegetation height in an area around the traps, and not necessarily the vegetation height at the trap itself, I calculated the vegetation mean height (VMH) around a 150m radius for all cells in the raster using a moving window (Figure 7). This value was based off the HR detection function I selected earlier, suggesting that cats were most likely to be seen in a ~150m radius around the activity centre, thus making it an area of particular interest. In a similar fashion, vegetation standard deviation (VSD; representing heterogeneity/complexity) around all raster cells can be calculated with a moving window (Figure 7). After performing these calculations, the data was added to the mask for future analysis.

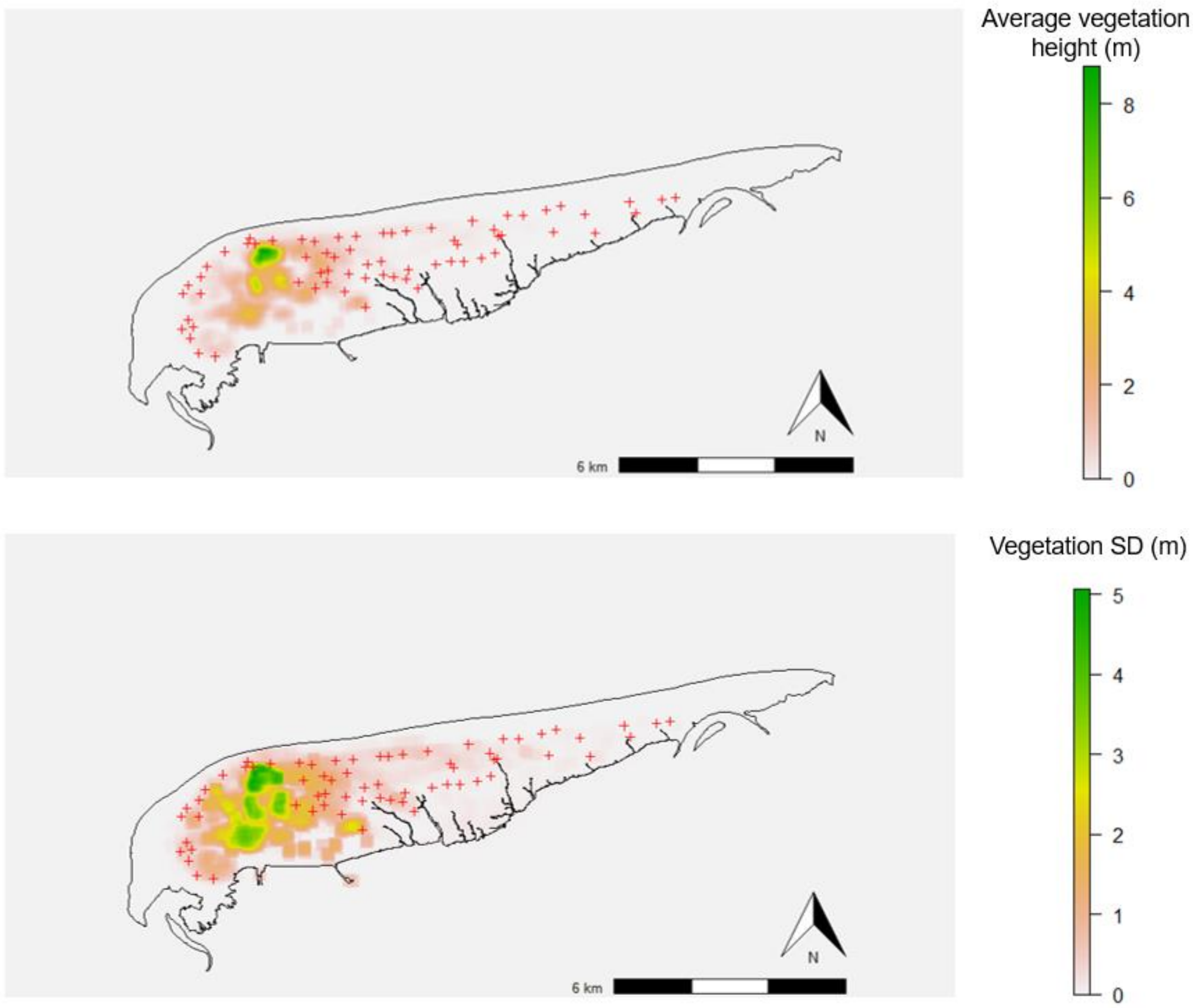


Figure 7: The average vegetation height (top) and vegetation standard deviation (bottom) of a 150m radius moving window, used as covariates in SECR density modelling. Vegetation height was calculated using remote sensing techniques that could not distinguish between vegetation and buildings, but since the village is excluded from the SECR mask, this should not pose a problem.

Final density models

With the above covariates, I created various maximum likelihood models using SECR to explain possible variance in density over the island for both habitat masks (with and without agricultural land) and identification lists (conservative and liberal). I used both conventional models, as well as regression splines for continuous variables (all variables but terrain, as terrain is not a continuous variable), which are a flexible alternative to polynomials in spatial trend analysis (Efford 2022d). Smoothness of the curve is determined by the number of knots, which I have set to three, as indicated in covariate names (e.g., DTV3 is the distance to village covariate, but using regression splines instead of conventional methods). When models had trouble fitting, I changed the method and link arguments until I found the most reliable fit, as suggested by (Efford 2022d). By comparing AICc-values, I could select the models (and thus covariates) that explained possible variation in cat density throughout the island significantly better than the null model (homogenous density throughout the island), which I used in further analysis and visualization. A model was considered significantly better than the null model when its AICc-value was at least 2 points lower than the null model.

Density surfaces

I used density surfaces to visualize the expected heterogeneity in density. The models selected above can be used to predict densities for every raster point of the mask (Borchers and Kidney 2014). I plotted these expected densities over the mask for all models that were significantly better than the null model (with a “flat” density surface) for all different datasets, both in the mask, and in graph form showing how densities are expected to change with an increasing value of covariate, as described by (Efford 2022d).

Results

Camera trapping results

Cameras were operational for trapping 1413 days, during which a total of 482.690 photographs were taken. Of these photographs, 1981 contained at least one cat at 41 sites (62% of all sites) over 343 different sightings, 335 of which were usable by the investigators (Figure 1). As mentioned above, identifications were split up into a conservative (43 identified individuals) and liberal estimate dataset (58 identified individuals). Individuals were resighted on average 8.10 ± 2.33 and 6.33 ± 2.03 (mean ± SE) times for the conservative and liberal dataset respectively with 21% and 33% of individuals having been sighted only once, and one individual having been resighted 93 times (conservative dataset). The number of cats resighted between the western and eastern part of the island were very limited (see Appendix C).

Population size estimates

Realised population size was estimated at 45-51 individuals for both significant conservative models, and 62-79 individuals for significant liberal models, where the lower and upper limits differed slightly between the different covariates for the latter. As mentioned previously, the DTR and terrain covariables was excluded from the analysis due to unrealistic extrapolation and unreliable model fits. After exclusion of DTR and terrain, DTV(3), VMH(3) and VSD(3) remained as covariates. For both the conservative and liberal data, estimated realised population sizes were practically identical between masks, independent of the significant covariate. A full overview of estimated population sizes, both realised and expected, can be found in Table 2.

Table 2: Overview of realised and expected estimated feral cat population size for all significant models of all datasets. Covariates include distance to village (DTV), vegetation mean height (VMH) and vegetation height standard deviation (VSD). The use of regression splines is indicated by a "3" after the variable name, after the number of knots.

Dataset	Covariate	Population	SE Estimate	LCL	UCL
Realised					
Conservative – Farms	DTV3	47.60344	1.529540	45.44136	51.68024
Conservative – No Farms	DTV3	47.76898	1.506146	45.60592	51.72749
Liberal – Farms	VMH	66.58303	4.295742	61.39778	79.68137
	DTV3	66.51544	2.399040	62.95409	72.63695
	VMH3	66.58316	4.298136	61.39630	79.69146
	VSD	66.56160	4.304621	61.37645	79.7095
Liberal – No Farms	DTV3	66.44788	2.334735	62.96383	72.37734
Expected					
Conservative – Farms	DTV3	45.09152	6.887018	33.48390	60.72307
Conservative – No Farms	DTV3	45.03499	6.877751	33.44282	60.64530
Liberal – Farms	VMH	70.70194	9.442210	54.48235	91.75016
	DTV3	62.78788	8.279087	48.54242	81.21389
	VMH3	70.70245	9.443327	54.48117	91.75345
	VSD	70.78036	9.450403	54.54617	91.8462
Liberal – No Farms	DTV3	62.55809	8.246761	48.36779	80.91158

Density surface models

Heterogeneous density surface models were more supported than models assuming homogenous density (null models) for all datasets, with an average density range of 0.0181-0.0278 cats/ha (Table 3), depending on identification methods, mask, and model. A summary of the most suitable models after model selection can be found in Table 3.

The DTV3 covariate model explained differences in cat density over the island significantly better than the homogenous null model for all datasets (conservative and liberal estimates, with and without farmland). Interestingly, these models were only more supported when using regression splines, indicating that the relationship between distance to the village and feral cat densities may be relatively complex, as it apparently cannot be well-described by a conventional polynomial. Density surface predictions suggested that cat density on the island resembles a partial bell-shaped curve, with a relatively high cat density around the village, gradually increasing with increasing distance from the village, up to around 3000m, from which cat density declines again (Figure 8).

Table 3: Summary of model selection results of feral cat monitoring on Schiermonnikoog (July – November 2021) for all datasets (conservative and liberal estimates; with and without farms as a potential habitat). D is feral density (cats/ha) on the island, and g0, σ and z are detection function parameters. Models were considered significantly better when they were at least 2 AIC_c-units less than the null model. Various covariates were used in analysis, including distance to village buildings (DTV), mean vegetation height around camera traps (VMH), and standard deviation of vegetation height around camera traps (VSD). More flexible regression splines were also used as an alternative to the standard polynomials (indicated by a 3 following the covariate name, representing the number of knots). An overview of all models can be found in Appendix A.

Dataset	Covariate	D (± SE)	g0	σ	z	AICc-Weight
Conservative Farms	DTV3	0.0181 (±0.0041)	0.4853	278.1	2.630	0.5575
Conservative No Farms	DTV3	0.0196 (±0.0042)	0.5133	263.1	2.594	0.6950
Liberal Farms	VMH	0.0266 (±0.0045)	0.9998	188.6	2.603	0.5040
	DTV3	0.0240 (±0.0051)	0.4971	258.4	2.754	0.1768
	VMH3	0.0266 (±0.0045)	0.7564	216.5	2.644	0.1564
	VSD	0.0227 (±0.0030)	0.8242	206.7	2.623	0.0340
Liberal No Farms	DTV3	0.0278 (±0.0056)	0.5297	243.3	2.701	0.7795

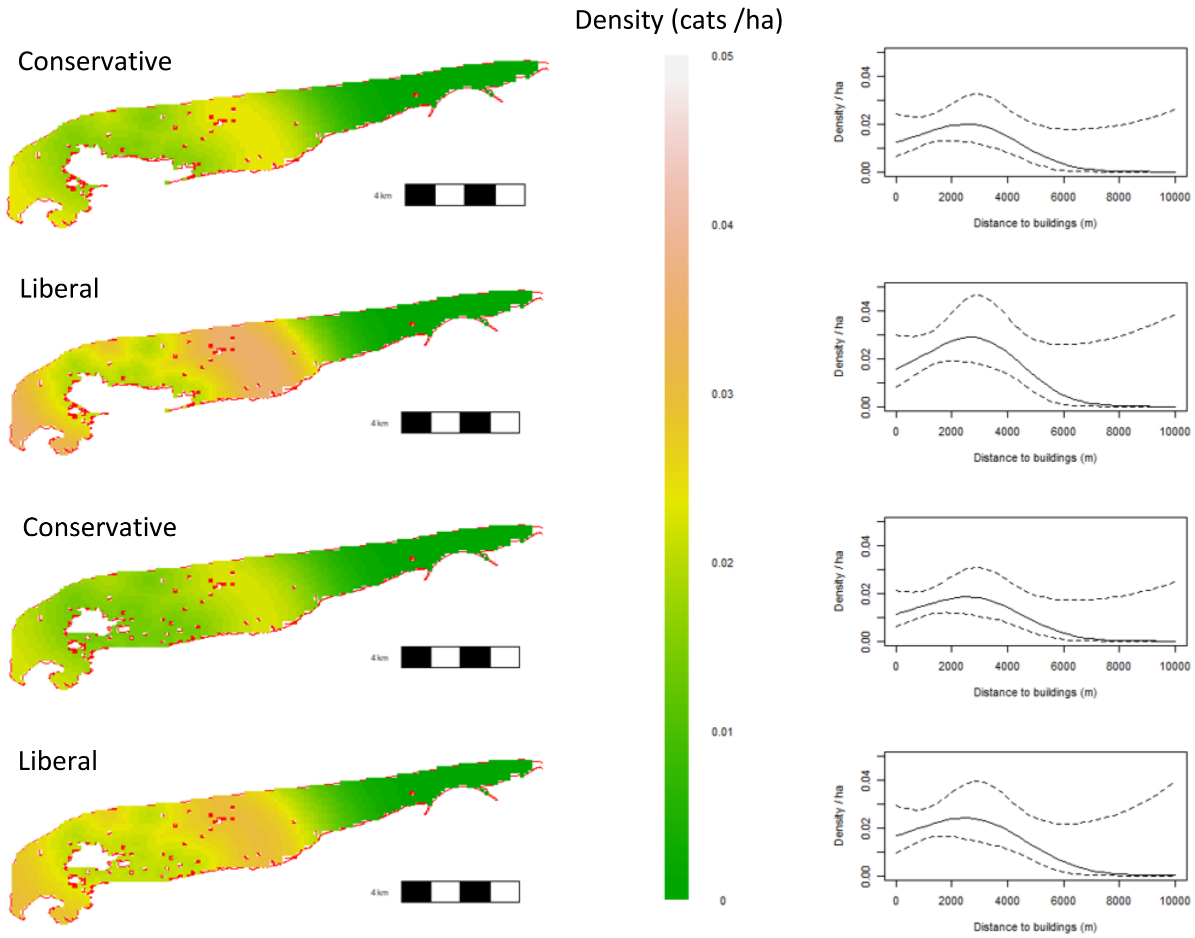


Figure 8: Mean expected density surface plots (left) and predicted densities with increasing distance to the village (right; mean and 95% confidence limits) from the DTV3 (distance to village; regression splines) models, both without farmland (top plots) and with farmland (bottom plots) for both the conservative and liberal identification methods, as indicated by the text.

Interestingly, the liberal farmland dataset was the only dataset that had other covariates as significantly better predictors for spatial differences in cat density. In addition to the DTV3 model, the predicted densities from the VMH, VMH3 and VSD models were also significantly better than the null model for the liberal estimate with farmland (Table 3). The VMH covariate was an even better predictor for density than DTV3, even though the predicted densities looked more similar to less significant VMH3 and VSD models (Figure 9). These vegetation models suggest that cats are mostly found around areas with low (< 1m) and homogenous vegetation, as predicted densities quickly decline to zero with increasing mean vegetation height and standard deviation (Figure 9).

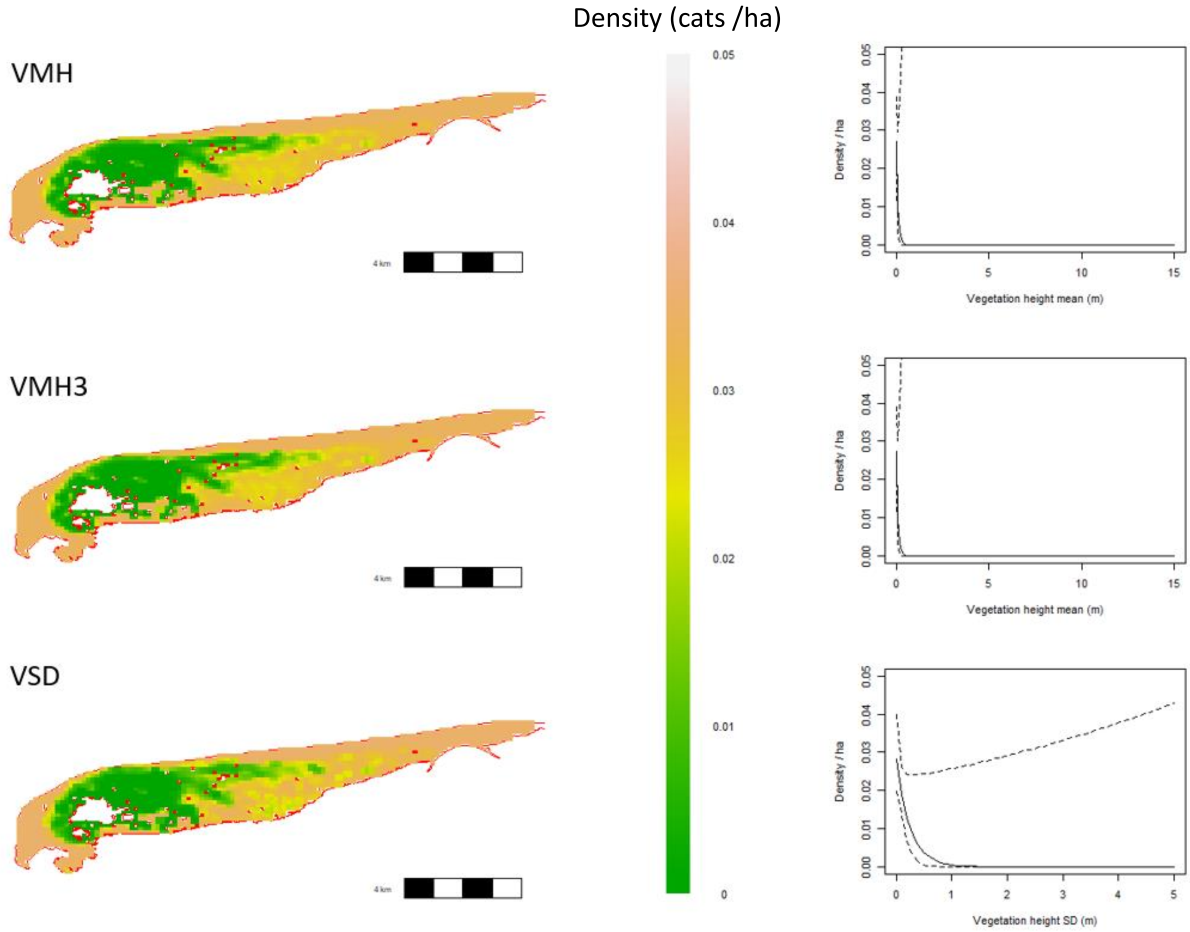


Figure 9: Mean expected density surface plots (left) and predicted densities with increasing vegetation mean height or standard deviation (right; mean and 95% confidence limits) from VMH (vegetation mean height), VMH3 (vegetation mean height; regression spline) and VSD (vegetation height standard deviation) models (as indicated by text) for the liberal, farmland mask dataset.

Discussion

Using images from a camera trapping study on Schiermonnikoog, I found that a population of 45-51 (62-79 using the liberal estimate) cats inhabits the island, which is in line with previous estimates of 34 and 50 cats in 1984 and 2011 respectively (Langeveld 1987, Op de Hoek et al. 2013). As expected, cats were heterogeneously distributed across the island. The distance to village ecological predictor suggested that cat density was highest around 3000m from the village. Vegetation height and standard deviation were also significant ecological predictors for the liberal farmland dataset, and predicted that cats made use of mostly homogenous low vegetation. This is surprising, as previous research has suggested cats prefer the use more structurally complex habitats (Doherty et al. 2014). Studies that investigate spatial distributions of animals using SECR are still relatively scarce, and to the best of my knowledge, this is the first study to model differences in densities using density surfaces for feral cats in The Netherlands. Since spatial density studies can prove useful for capture or monitoring programmes of damaging invasive species (Green et al. 2020), larger and more extensive studies on spatial densities of such species should be a high priority.

Depending on the identification method, Schiermonnikoog is home to between 45-79 feral cats. Since camera trapping studies are notorious for overestimating population sizes due to identification errors (Johansson et al. 2020), the conservative estimate of 45-51 individuals is likely to be the most reliable. The cat population on Schiermonnikoog is thus probably relatively stable, compared to the latest estimate from 2011 of 50 individuals (Op de Hoek et al. 2013). The population of feral cats may actually consist of two separate populations, as indicated by the low number of resightings between the east and west of the island, with the village acting as a barrier. With a density of roughly 0.02 cats/ha, Schiermonnikoog has a relatively low density compared to more tropical islands, where densities of 0.5 cats/ha are not unheard of (Nogales et al. 2004). Despite these seemingly low densities, predation by feral cats can still threaten vulnerable bird and mammal populations on the island (Op de Hoek et al. 2013, Schrama et al. 2015, Kleefstra and Klemann 2018, Dekker and van Norren 2021), especially in places where feral cat abundance is highest. Identification of cats turned out to be quite difficult at times. The use of DNA-identification, such as hair traps (Boulanger et al. 2018), may be a better, though possibly more time-consuming alternative to camera trapping and likely yields the most accurate (spatial) densities. As mentioned previously, the liberal identification method most likely leads to overestimations of population size (Johansson et al. 2020). While for the sake of completeness it might be desirable to include both a liberal and conservative estimate, simply using the conservative identification list may be sufficient as well, if the proper methods are used (Choo et al. 2020).

Distance to village was the best ecological predictor for cat presence, as this covariate was significant for the widest range of models. The relatively high estimated cat density around the village (0.01-0.02 cats/ha, Figure 8) suggest that some cats may make use of anthropogenic resources of the village. Previous research has demonstrated that feral cats may indeed make use of anthropogenic resources (Doherty et al. 2014, Hand 2019), and it has been shown that animal densities can be affected by these resources (Liberg et al. 2000, Hubert et al. 2011). However, cat density was highest around 3000m from the village. Since home ranges of feral cats on Schiermonnikoog only span a few hundred ha at most (van der Ende 2015b), most cats would have to go out of their way to visit the village. Moreover, a prior diet analysis of cats on the island has revealed that scat does not contain anthropogenic food sources, but mostly voles (van der Ende 2015b), the densities of which tend to be lower in urban environments (Gortat et al. 2014). This suggests that cats would not make use of anthropogenic resources. Since no actual camera traps were placed in close proximity of the village, the relatively high predicted cat densities around the village may simply be the result of an extrapolation error. The high cat density around 3000m from the village may be the result of the prevalence of shorter vegetation (Figure 7), which provide a suitable habitat for voles (Jacob et al. 2014), but this does not explain the low cat densities in the eastern part of the island. Without additional data on prey availability and vegetation, the precise ecological mechanisms behind this high density remain speculative.

Vegetation height and heterogeneity were also a significant ecological predictor for cat distribution, but only for the liberal farmland dataset. These models suggested that cats made use of mostly homogenous low vegetation habitats, which is surprising, considering previous research predicted the use of more structurally complex habitats (Doherty et al. 2014). Again, the likely high prevalence of voles in lower, more homogenous habitats may explain the higher densities of cats in these areas (Jacob et al. 2014). However, one would still expect cats to make use of higher vegetation for shelter. The use of vegetation height for shelter alone may not be sufficient for predicting cat densities, as shelter use is variable. For example, cats mostly take shelter in high and dense vegetation (such as forests) during periods of bad weather (Harper 2007). Moreover, cats activity varies throughout the day (Langeveld 1987, van der Ende 2015b), with cats sheltering in patches of higher vegetation during rest, and using prey-rich heterogeneous vegetation patches while active (Doherty et al. 2014). In future analysis, it would thus be interesting to include interactions between vegetation height and heterogeneity, and temporal or meteorological covariates.

It should be noted that the validity of the vegetation models may be questionable. The confidence limits in Figure 9 rapidly grew with increasing vegetation height and standard deviation, suggesting that the model predictions are not very precise. Possibly, the remote sensing data may not be accurate enough, as demonstrated by the negative vegetation height values mentioned in the methods. Additionally, areas with higher vegetation (such as the forest north of the village, Figure 5), were not monitored, while it is known that cats make use of, and often prefer woodland habitats (Bengsen et al. 2016). This lack of monitoring in such areas can lead to unreliable extrapolation of the data. Moreover, the fact that most the vegetation covariates were only significant for one of the datasets, as opposed to the DTV covariate, may indicate that the significance of these models may be the result of some methodological artifact, which I will discuss in more detail below.

Unreliable results due to data extrapolation and inadequate data led to frequent complications in the analysis. For example, the arbitrary definition of major and minor roads led me to combine both into one variable, while there are pronounced differences between the two. Also, since all camera traps were placed near roads (Figure 4) and paths to maximize capture probability, the extrapolation of data led to unreliable results. The lack of monitoring in certain habitats not only led to extrapolation of the data, but also led me to analyse the data with two different masks. The extra area in the farmland may allow for estimated activity centres to be located in other areas, leading to altered density estimates. This is nicely illustrated by the difference in significance of the vegetation models for the different masks. More systematic deployment of camera traps can solve the problem of having to use multiple masks and extrapolation errors, as the entire island would be sampled. Previous research has shown that density estimates from a reduced number of systematically placed camera traps are comparable to those from a greater number specially selected camera trap sites, given enough detections (Després-Einspenner et al. 2017). Clustered sampling, where a smaller subset of areas is more intensively sampled, may also be an interesting alternative for large study areas, as these methods seem reliable while reducing required sampling effort (Efford and Fewster 2013, Clark 2019). For future research, I would thus recommend the use of more systematic sampling methods.

In conclusion, I found that the population of feral cats on Schiermonnikoog consists of an estimated 47-51 individuals, which are heterogeneously distributed throughout the island, with distance to village being the best predictor. However, the lack of adequate data prevented me from further investigating the ecological processes behind the spatial differences in cat densities, leaving open many interesting avenues for future research. My results highlight the importance of carefully considering the methods to employ in these types of studies, both for camera trapping (e.g., systematic sampling) and analysis (e.g., identification methods). Nevertheless, SECR is a robust and versatile tool in any ecologist's arsenal, and should yield promising results in future studies.

References

Bakker, J. P., D. Bos, and Y. de Vries. 2003. To graze or not to graze, that is the question. Pages 67–88 Proceedings of the 10th International Scientific Wadden Sea Symposium.

Bengsen, A. J., D. Algar, G. Ballard, T. Buckmaster, S. Comer, P. J. S. Fleming, J. A. Friend, M. Johnston, H. McGregor, K. Moseby, and F. Zewe. 2016. Feral cat home-range size varies predictably with landscape productivity and population density. Journal of Zoology 298:112–120.

Bonnington, C., K. J. Gaston, and K. L. Evans. 2013. Fearing the feline: domestic cats reduce avian fecundity through trait-mediated indirect effects that increase nest predation by other species. Journal of Applied Ecology 50:15–24.

Borchers, D. L., and M. G. Efford. 2008. Spatially Explicit Maximum Likelihood Methods for Capture-Recapture Studies. Biometrics 64:377–385.

Borchers, D. L., and D. Kidney. 2014. Flexible density surface estimation for spatially explicit capture-recapture surveys. CREEM Technical Report 2014–1:16.

Boulanger, J., S. E. Nielsen, and G. B. Stenhouse. 2018. Using spatial mark-recapture for conservation monitoring of grizzly bear populations in Alberta. Scientific Reports 8:5204.

Choo, Y. R., E. P. Kudavidanage, T. R. Amarasinghe, T. Nimalrathna, M. A. H. Chua, and E. L. Webb. 2020. Best practices for reporting individual identification using camera trap photographs. Global Ecology and Conservation 24:e01294.

Clark, J. D. 2019. Comparing clustered sampling designs for spatially explicit estimation of population density. Population Ecology 61:93–101.

Database of Island Invasive Species Eradications. 2022, March 7. . http://diise.islandconservation.org/.

Davis, A. J., D. A. Keiter, E. M. Kierepka, C. Slootmaker, A. J. Piaggio, J. C. Beasley, and K. M. Pepin. 2020. A comparison of cost and quality of three methods for estimating density for wild pig (Sus scrofa). Scientific Reports 10:2047.

Dekker, J., and E. van Norren. 2021. Achteruitgang van haas en konijn sinds 1950, oorzaken en beschermingsmogelijkheden. Zoogdiervereniging Rapport 2020.24:28.

Després-Einspenner, M.-L., E. J. Howe, P. Drapeau, and H. S. Kühl. 2017. An empirical evaluation of camera trapping and spatially explicit capture-recapture models for estimating chimpanzee density. American Journal of Primatology 79:e22647.

Doherty, T., A. Bengsen, and R. Davis. 2014. A critical review of habitat use by feral cats and key directions for future research and management. Wildlife Research 41:435–446.

Doherty, T. S., A. S. Glen, D. G. Nimmo, E. G. Ritchie, and C. R. Dickman. 2016. Invasive predators and global biodiversity loss. Proceedings of the National Academy of Sciences 113:11261–11265.

Efford, M. 2004. Density estimation in live-trapping studies. Oikos 106:598–610.

Efford, M. 2022a. Habitat masks in the package secr:18.

Efford, M. 2022b, February 13. secr: Spatially Explicit Capture-Recapture.

Efford, M. G. 2022c. Adjustment for varying effort in secr 4.5:6.

Efford, M. G. 2022d. Density surfaces in secr 4.5:16.

Efford, M. G., and R. M. Fewster. 2013. Estimating population size by spatially explicit capture–recapture. Oikos 122:918–928.

van der Ende, J. M. 2015a. thesis-Spatial ecology and prey choice of tagged feral cats on Schiermonnikoog. PhD Thesis, Vrije Universiteit van Amsterdam.

van der Ende, J. M. 2015b. Spatial ecology and prey choice of tagged feral cats on Schiermonnikoog. Lutra 60:73–91.

Gortat, T., M. Barkowska, A. G.-S. Tkowska, A. Pieniążek, A. Kozakiewicz, and M. Kozakiewicz. 2014. The Effects of Urbanization — Small Mammal Communities in a Gradient of Human Pressure in Warsaw City, Poland. Polish Journal of Ecology 62:163–172.

Graham, C. A., M. Maron, and C. A. McAlpine. 2012. Influence of landscape structure on invasive predators: feral cats and red foxes in the brigalow landscapes, Queensland, Australia. Wildlife Research 39:661.

Green, A. M., M. W. Chynoweth, and Ç. H. Şekercioğlu. 2020. Spatially Explicit Capture-Recapture Through Camera Trapping: A Review of Benchmark Analyses for Wildlife Density Estimation. Frontiers in Ecology and Evolution 8.

Hand, A. 2019. Estimating feral cat densities using distance sampling in an urban environment. Ecology and Evolution 9:2699–2705.

Harper, G. A. 2007. Habitat selection of feral cats (Felis catus) on a temperate, forested island. Austral Ecology 32:305–314.

Hubert, P., R. Julliard, S. Biagianti, and M.-L. Poulle. 2011. Ecological factors driving the higher hedgehog (Erinaceus europeaus) density in an urban area compared to the adjacent rural area. Landscape and Urban Planning 103:34–43.

Jacob, J., P. Manson, R. Barfknecht, and T. Fredricks. 2014. Common vole (Microtus arvalis) ecology and management: implications for risk assessment of plant protection products. Pest Management Science 70:869–878.

Johansson, Ö., G. Samelius, E. Wikberg, G. Chapron, C. Mishra, and M. Low. 2020. Identification errors in camera-trap studies result in systematic population overestimation. Scientific Reports 10:6393.

Johnson, D. S., J. L. Laake, and J. M. Ver Hoef. 2010. A Model-Based Approach for Making Ecological Inference from Distance Sampling Data. Biometrics 66:310–318.

Keitt, B. S., and B. R. Tershy. 2003. Cat eradication significantly decreases shearwater mortality. Animal Conservation 6:307–308.

Kleefstra, R., and M. Klemann. 2018. De broedvogels van Schiermonnikoog in 2018:39.

Knol, W. 2015. Verwilderde huiskatten: effecten op de natuur in Nederland. Koninklijke Nederlandse Jagersvereniging, Amersfoort, the Netherlands.

Langeveld, M. J. 1987. Veldkatten (Felis catus L.) op Schiermonnikoog. Een gedragsecologisch onderzoek met behulp van radiotelemetrie. Rijksuniversiteit Groningen, Groningen.

Laundre, J. W., L. Hernandez, and W. J. Ripple. 2010. The Landscape of Fear: Ecological Implications of Being Afraid~!2009-09-09~!2009-11-16~!2010-02-02~! The Open Ecology Journal 3:1–7.

Legge, S., J. C. Z. Woinarski, C. R. Dickman, B. P. Murphy, L.-A. Woolley, and M. C. Calver. 2020. We need to worry about Bella and Charlie: the impacts of pet cats on Australian wildlife. Wildlife Research 47:523–539.

Liberg, O., M. Sandell, D. Pontier, and E. Natoli. 2000. Density spatial organisation and reproductive tactics in the domestic cat and other felids. undefined.

Long, J. L. 2003. Introduced mammals of the world: their history, distribution & influence. CSIRO Publishing, Melbourne.

Longcore, T., C. Rich, and L. M. Sullivan. 2009. Critical Assessment of Claims Regarding Management of Feral Cats by Trap–Neuter–Return. Conservation Biology 23:887–894.

Loss, S. R., T. Will, and P. P. Marra. 2013. The impact of free-ranging domestic cats on wildlife of the United States. Nature Communications 4:1396.

Lowe, S. M., M. Browne, S. Boudjelas, and M. De Poorter. 2000. 100 of the World's Worst Invasive Alien Species: A Selection From the Global Invasive Species Database. Published by The Invasive Species Specialist Group (ISSG) a specialist group of the Species Survival Commission (SSC) of the World Conservation Union (IUCN), 12pp. First published as special lift-out in Aliens 12.

Mcgregor, H., S. Legge, J. Potts, M. Jones, and C. Johnson. 2015. Density and home range of feral cats in north-western Australia. Wildlife Research 42.

Medina, F. M., E. Bonnaud, E. Vidal, B. R. Tershy, E. S. Zavaleta, C. Josh Donlan, B. S. Keitt, M. Corre, S. V. Horwath, and M. Nogales. 2011. A global review of the impacts of invasive cats on island endangered vertebrates. Global Change Biology 17:3503–3510.

Nogales, M., A. Martín, B. R. Tershy, C. J. Donlan, D. Veitch, N. Puerta, B. Wood, and J. Alonso. 2004. A review of feral cat eradication on islands. Conservation Biology 18:310–319.

Op de Hoek, T., M. J. J. Schrama, and C. Smit. 2013. Verwilderde katten op Schiermonnikoog. De levende natuur 114:4–8.

Prior, K. M., D. C. Adams, K. D. Klepzig, and J. Hulcr. 2018. When does invasive species removal lead to ecological recovery? Implications for management success. Biological Invasions 20:267–283.

Recio, M. R., and P. J. Seddon. 2013. Understanding determinants of home range behaviour of feral cats as introduced apex predators in insular ecosystems: a spatial approach. Behavioral Ecology and Sociobiology 67:1971–1981.

Rijkswaterstaat, Ministerie van Infrastructuur en Waterstaat. 2022a, July 4. Dataset: Basisregistratie Topografie (BRT) TOPNL. PDOK. https://www.pdok.nl/introductie/-/article/basisregistratie-topografie-brt-topnl.

Rijkswaterstaat, Ministerie van Infrastructuur en Waterstaat. 2022b, July 4. Dataset: Actueel Hoogtebestand Nederland (AHN3). https://www.pdok.nl/downloads/-/article/actueel-hoogtebestand-nederland-ahn3-.

Roomen, M., C. van Turnhout, E. Winden, B. J. Koks, P. Goedhart, M. Leopold, and C. Smit. 2005. Trends in benthivorous waterbirds in the Dutch Wadden Sea 1975-2002: Large differences between shellfish-eaters and worm-eaters. Limosa 78:21–38.

Schrama, M., D. Kuijper, R. Veeneklaas, and J. Bakker. 2015. Long-Term Decline in a Salt Marsh Hare Population Largely Driven by Bottom-Up Factors. Ecoscience.

Sollmann, R. 2018. A gentle introduction to camera-trap data analysis. African Journal of Ecology 56:740–749.

Tershy, B. 2002. Removing cats from islands in north-west Mexico. Turning the tide: the ….

Tews, J., U. Brose, V. Grimm, K. Tielbörger, M. C. Wichmann, M. Schwager, and F. Jeltsch. 2004. Animal species diversity driven by habitat heterogeneity/diversity: the importance of keystone structures. Journal of Biogeography 31:79–92.

Van Wieren, S., M. Wiersma, and H. Prins. 2006. Climatic factors affecting a brown hare (Lepus europaeus) population. Lutra 49 (2006) 2 49.

Zaunbrecher, K. I., and R. E. Smith. 1993. Neutering of feral cats as an alternative to eradication programs. Journal of the American Veterinary Medical Association 203:449–452.

Appendix A: Complete model selection results

Appendix A: Full model selection results from both identification methods and both masks, where N is the number of parameters. I ran models with five covariates: distance to road (DTR), distance to village (DTV), terrain type (Terrain), mean vegetation height (VMH) and standard deviation (VSD) 150m around the camera trap. I used both conventional polynomial methods, as well as regression splines (denoted by covariate name followed by a "3", after the number of knots used). Models were significantly better when AICc-values were at least 2 AIC_C-units lower than the null model. I ended up excluding the Terrain and DTR covariates as they had unrealistic density estimates and had unreliable model fits. For that reason, model weights here and in Table 2 do not match.

Appendix A1: Conservative

Conservative	N	LogLik	AICc	ΔAICc	Weight
With farmland					
DTR3	6	-629.146	1272.626	0	0.4302
DTR	5	-630.52	1272.661	0.035	0.4228
DTV3	6	-630.805	1275.942	3.316	0.082
Null	4	-634.495	1278.043	5.417	0.0287
VMH	5	-633.741	1279.104	6.478	0.0169
VSD	5	-634.273	1280.167	7.541	0.0099
VSD3	6	-633.548	1281.429	8.803	0.0053
VMH3	6	-633.741	1281.815	9.189	0.0043
DTV	5	-724.086	1459.794	187.168	0
Terrain	11	-726.849	1484.215	211.589	0
Without farmland					
DTR	5	-635.101	1281.824	0	0.6362
DTR3	6	-634.484	1283.301	1.477	0.304
DTV3	6	-636.32	1286.974	5.15	0.0484
Null	4	-640.407	1289.866	8.042	0.0114
VMH	5	-640.288	1292.197	10.373	0
VSD	5	-640.376	1292.374	10.55	0
VSD3	6	-639.452	1293.237	11.413	0
VMH3	6	-640.277	1294.887	13.063	0
Terrain	10	-638.551	1303.977	22.153	0
DTV	5	-731.911	1475.444	193.62	0

Appendix A2: Liberal

Liberal	N	LogLik	AICc	ΔAICc	Weight
With farmland					
DTR	5	-615.487	1242.129	0	0.6289
DTR3	6	-614.768	1243.184	1.055	0.3711
Terrain	11	-616.034	1259.807	17.678	0
VMH	5	-625.624	1262.402	20.273	0
DTV3	6	-625.425	1264.497	22.368	0
VMH3	6	-625.547	1264.742	22.613	0
VSD	5	-627.262	1265.679	23.55	0
Null	4	-629.521	1267.796	25.667	0
VSD3	6	-627.168	1267.984	25.855	0
DTV	5	-743.717	1498.587	256.458	0
Without farmland					
DTR	5	-617.991	1247.135	0	0.7209
DTR3	6	-617.693	1249.033	1.898	0.2791
DTV3	6	-632.314	1278.275	31.14	0
Terrain	10	-626.832	1278.346	31.211	0
VSD3	6	-634.451	1282.549	35.414	0
Null	4	-637.225	1283.205	36.07	0
VSD	5	-636.715	1284.584	37.449	0
VMH	5	-637.203	1285.561	38.426	0
VMH3	6	-636.818	1287.283	40.148	0
DTV	5	-753.763	1518.68	271.545	0

Appendix B: Population estimates for all models

Appendix B: Full list of population estimates, both expected and realised around the island for all datasets and covariates. Terrain models could not always estimate al parameters, which is an indication of bad model fits, and were thus excluded from the analysis. DTR and DTR3 models wildly extrapolated population estimates, and were also excluded.

Appendix B1: Conservative Farmland

Conservative, Farms	Estimate	SE Estimate	LCL	UCL
Null				
Expected	47.81977	7.350898	35.44242	64.51961
Realised	47.72166	2.493175	44.78636	55.48016
Terrain				
Expected	43.80710	NA	NA	NA
Realised	49.76806	NA	NA	NA
DTR				
Expected	80.04480	18.19264	51.55873	124.2693
Realised	50.13545	15.84069	43.52222	140.4961
DTV				
Expected	38.12615	6.671575	27.12662	53.58588
Realised	48.75092	2.526610	45.52432	56.10179
VMH				
Expected	49.23269	7.585783	36.46438	66.47193
Realised	47.63414	2.882953	44.51043	57.21800
VSD				
Estimate	48.20934	7.396354	35.75175	65.00774
Realised	47.70349	2.548866	44.73980	55.71572
DTR3				
Expected	111.57989	39.59416	56.81290	219.1416
Realised	53.16243	38.15911	43.40229	299.7175
DTV3				
Expected	45.09152	6.887018	33.48390	60.72307
Realised	47.60344	1.529540	45.44136	51.68024
VSD3				
Expected	48.68186	7.476250	36.09160	65.66413
Realised	47.72956	2.685603	44.67814	56.32943
VMH3				
Expected	49.23201	7.58634	36.46280	66.47298
Realised	47.63419	2.88783	44.50955	57.22663

Appendix B2: Conservative No Farmland

Conservative, Without farms	Estimate	SE Estimate	LCL	UCL
Null				
Expected	48.01772	7.380253	35.59066	64.78390
Realised	47.92575	2.539767	44.90188	55.75742
Terrain				
Expected	47.76708	7.709163	34.88468	65.40675
Realised	47.75137	3.415277	44.34112	59.83329
DTR				
Expected	85.74969	19.71308	54.96207	133.7834
Realised	50.92060	17.40275	43.58706	149.8643
DTV				
Expected	37.66878	6.564338	26.83832	52.86983
Realised	48.56742	2.328465	45.53455	55.22943
VMH				
Expected	47.86994	7.320170	35.53452	64.48748
Realised	47.94492	2.390596	45.01400	55.14114
VSD				
Estimate	47.90680	7.333683	35.55062	64.55757
Realised	47.93597	2.424067	44.98477	55.27534
DTR3				
Expected	108.70079	38.58951	55.33143	213.5470
Realised	53.29503	37.15440	43.42597	291.8169
DTV3				
Expected	45.03499	6.877751	33.44282	60.64530
Realised	47.76898	1.506146	45.60592	51.72749
VSD3				
Expected	48.50889	7.441759	35.97468	65.41023
Realised	47.93219	2.621237	44.85562	56.10963
VMH3				
Expected	47.91353	7.332966	35.55810	64.56210
Realised	47.94316	2.420508	44.99243	55.26383

Appendix B3: Liberal No Farmland

Liberal, Without farms	Estimate	SE Estimate	LCL	UCL
Null				
Expected	67.01728	8.881253	51.74574	86.79585
Realised	66.86246	3.443744	62.24967	76.48220
Terrain				
Expected	74.71543	NA	NA	NA
Realised	67.72416	NA	NA	NA
DTR				
Expected	219.26351	48.71321	142.60352	337.1339
Realised	80.95581	46.40812	59.88476	337.5942
DTV				
Expected	53.24216	8.091411	39.59434	71.59427
Realised	68.61499	3.496966	63.65840	77.91339
VMH				
Expected	67.11598	8.869676	51.85880	86.86193
Realised	66.81561	3.399290	62.24949	76.28809
VSD				
Estimate	68.04286	9.148898	52.34125	88.45472
Realised	66.44295	3.957206	61.52510	78.22166
DTR3				
Expected	258.10894	86.10045	136.55690	487.8569
Realised	85.35206	84.58829	59.34913	612.5300
DTV3				
Expected	62.55809	8.246761	48.36779	80.91158
Realised	66.44788	2.334735	62.96383	72.37734
VSD3				
Expected	69.37508	9.239279	53.49825	89.96374
Realised	66.47106	3.998650	61.51697	78.40363
VMH3				
Expected	67.55744	8.980426	52.12162	87.56458
Realised	66.52170	3.618094	61.83702	76.92595

Appendix B4: Liberal Farmland

Liberal, Farms	Estimate	SE Estimate	LCL	UCL
Null				
Expected	67.04107	8.888894	51.75740	86.83791
Realised	66.86830	3.459968	62.24068	76.54578
Terrain				
Expected	74.04104	NA	NA	NA
Realised	67.31918	NA	NA	NA
DTR				
Expected	209.40670	46.44866	136.28476	321.7613
Realised	79.58347	44.13696	59.74719	324.6255
DTV				
Expected	54.50158	8.307861	40.49505	73.35272
Realised	69.33398	3.810378	63.96818	79.52399
VMH				
Expected	70.70194	9.442210	54.48235	91.75016
Realised	66.58303	4.295742	61.39778	79.68137
VSD				
Estimate	70.78036	9.450403	54.54617	91.8462
Realised	66.56160	4.304621	61.37645	79.7095
DTR3				
Expected	264.99344	89.19494	139.4372	503.6068
Realised	85.78561	87.69689	59.3387	634.7074
DTV3				
Expected	62.78788	8.279087	48.54242	81.21389
Realised	66.51544	2.399040	62.95409	72.63695
VSD3				
Expected	70.50781	9.48610	54.22881	91.67363
Realised	66.57963	4.41342	61.31924	80.17683
VMH3				
Expected	70.70245	9.443327	54.48117	91.75345
Realised	66.58316	4.298136	61.39630	79.69146

Appendix C: Spatial recaptures

Appendix C: An overview of spatial recaptures for both the conservative (top) and liberal (bottom) identification methods. Coloured dots represent traps where cats have been sighted, and red crosses are trapping locations without any cat sightings. Lines represent spatial recaptures, meaning that one individual has been sighted at multiple locations. Colours have been reused, and a single colour may thus represent multiple individuals.