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Habitat Selection and Prey Choice in the House Cat (*Felis silvestris catus*)

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Ecology

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Abstract

The domestic cat's effect on wildlife, especially as a predator on birds, has been increasingly debated in later years. Most studies that examine predation by cats have recorded home-brought prey or analyzed stomach contents of shot feral cats. In this study, a collar with both a camera and a GPS device was mounted on domestic cats to better record home range, habitat selection, activity, prey choice and capture rate. The recorded 95 % kernel home range size from this study was c. 3.6 ha on average, and was significantly influenced by the cats' age. Cat sex, body mass and the presence of cat-flaps in the cat's home had no effect on home range size. Time of day and cat sex were the most important effects on the level of general activity, i.e. distance moved per hour block. The cats showed a nocturnal diel pattern with highest activity in the darkest hours. Males had higher activity than females, but this effect was non-significant. The cats preferred to spend time in deciduous and mixed forest types, while they avoided coniferous forest. They also spent more time in agricultural land and in close proximity to building structures than would be expected by random choice. The probability of a plot being a cat GPS fix rather than random point increased with distance from the cat's home. This indicates that the cats moved in a decisive manner towards their preferred hunting grounds. Hunting and prey capture activity were correlated with general activity, showing the same diel pattern. The observed capture rate was low, compared to other studies, and the cats captured few avian and mammalian prey. Insects were by far the most commonly captured prey. The cats moved their avian and mammalian prey far more often than they moved their insect prey, but did not present any prey item for the cat owner. This study is the first to mount camera and GPS device on domestic cats to determine habitat selection and capture rate, and suggests that recording home-brought prey underestimates actual capture rate.

Sammendrag

Huskattens påvirkning på dyreliv, spesielt som fuglejeger, har blitt stadig mer debattert i senere år. De fleste studier som undersøker kattens jaktvaner har fokusert på å dokumentere hjem-brakt bytte og mageinnhold hos skutte villkatter. I denne studien ble et halsbånd med påmontert kamera og GPS-sender festet på huskatter og brukt til å bedre dokumentere hjemmeområde, habitat-seleksjon, aktivitet, byttedyrvalg og fangstrate. Det registrerte 95% kernel hjemmeområde fra denne studien var bare 3.6 ha i gjennomsnitt, og var signifikant påvirket av kattens alder. Kattens kjønn, kroppsvekt og tilgang på katteluke hadde ingen effekt på størrelsen av hjemmeområde. Tid på døgnet og kattens kjønn var de viktigste effektene på generelt aktivitetsnivå, dvs. forflytningsdistanse per timesblokk. Kattene viste en nattlig døgnrytme med høyest aktivitet i de mørkeste timene. Hanner hadde høyere generell aktivitet enn hunner. Jakt og bytte-fangst aktivitet var korrelert med generell aktivitet, og viste det samme døgnrytme-mønsteret. Kattene foretrakk å tilbringe tid i løvskog og blandingsskog, mens de unngikk barskog. De tilbrakte også mer tid i fulldyrka jord og i nærheten av bygningsstrukturer enn man ville forvente ut fra tilfeldig valg. Sannsynligheten for at et registret punkt var en katt-GPS-fiksering, istedenfor et tilfeldig punkt, økte med avstand fra kattens hjem. Dette indikerer at kattene bevegde seg på en bestemt måte mot sine foretrukne jaktområder. Den observerte jaktraten var lav, sammenlignet med andre studier, og kattene fanget få fugler og pattedyr. Insekter var et langt mer vanlig fanget bytte. Kattene flyttet sine fugle- og pattedyrsbytter langt oftere enn sine insektbytter, men presenterte ingen byttedyr for katteieren. Denne studien er den første som fester kamera og GPS-sensor på huskatter for å bestemme habitatvalg og fangstrate, og slik indikerer at dokumentasjon av hjembrakte byttedyr gir et underestimat av faktisk fangstrate.

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1. Introduction

The most widespread terrestrial carnivore, the domestic cat (*Felis catus*), inhabits climate zones ranging from subarctic to desert (Konecny 1987), and are known to prey on several wildlife species (Turner & Bateson 2000). It can cause steep declines in populations of birds (Crooks et al. 2001), small mammals, and even herptiles (Baker et al. 2005). On islands, the cat's effect on wildlife may drive populations to extinction (Loss et al. 2013). Many bird populations around the world are declining (Saino et al. 2011), and domestic cats may have a negative effect on both migratory birds and backyard birdlife (Loyd et al. 2013). Even though the focus has been on feral domestic cats, the influence of owned domestic cats (*Felis silvestris catus*) should not be ignored, as they may also cause problems to wildlife (Lenth et al. 2008; Loyd et al. 2013). Cats are popular pets because they meet the requirements many people have to a pet, and require little space and care. They are also wanted as a predator on pest species. Consequently, domestic cats have been introduced on a global scale (Lenth et al. 2008). Domestics cats hunt a wide range of prey, and because they have been selected on their skills as a predator, they are quite successful (Braastad 2012). The extent of the predation, however, remains a topic of debate (Turner & Bateson 2000; Braastad 2012).

A great share of the studies on the domestic cat's effect on wildlife populations has been done in areas with endemic species with few anti-predatory defense-mechanisms against introduced domestic cats (Turner & Bateson 2000). Some studies suggest that cats have a great effect on wildlife populations (Konecny 1987; Turner & Bateson 2000). Medina et al. (2011) found that feral cats on islands have been responsible for at least 14% of global bird, mammal, and reptile extinctions, and that they are the principal threat to 8% of critically endangered birds, mammals, and reptiles. Studies done on Pacific islands and in Oceania may not be transferable to other environments with different species composition.

In Norway, the domestic cat is the most popular pet, and the estimated number of cats in the country is 767 000, spread out on 400 000 households ((FEDIAF, The Pet Food Industry 2014)). With the number still increasing, it is conceivable that cats might have an effect on potential prey species in Norway as well. Habitat selection and predation habits in domestic cats have not been studied in Scandinavia (Turner & Bateson 2000).

Understanding where and how the cat spends its time provides an essential basis for understanding the predation effect domestic cats pose on wildlife populations. Cats' home range sizes have been shown to differ greatly within and between areas (Turner & Bateson 2000), and are affected by cat-population density, food abundance and sex (Langham & Porter 1991; Turner & Bateson 2000). Few studies have included the effect of age and body mass on home range size.

Study of habitat selection in domestic cats have shown that cats prefer forest areas (Klar et al. 2008). These studies often focus on the amount of cover (Oehler & Litvaitis 1996; Crooks & Soulé 1999; Marks & Duncan 2009), but to my knowledge, none have included the differences between forest types. Furthermore, no studies, to my knowledge, have included buildings as a separate habitat structure. Domestic cats have been found to prefer to move along habitat components that offer cover (Barratt 1997), and may as well choose to move along building structures when walking back and forth between hunting grounds and home.

The domestic cat's general activity seem to be correlated with predation activity, and is therefore important to understand in order to assess capture rate (Barratt 1997; Turner & Bateson 2000). However, the observed diel patterns differ between areas and studies (Konecny 1987; Langham & Porter 1991; Turner & Bateson 2000).

Most studies on the domestic cat's prey choice and capture rate have been done by examining stomach contents in shot feral cats and recording home-brought prey items in house- and feral cats (Turner & Bateson 2000). The latter method would depend greatly on the proportion if prey items that are brought home, which may differ greatly between cats; depending on sex, age, body mass, reproductive state, and prey type (Turner & Bateson 2000) . Capture rate and prey choice have been found to differ greatly between studies (Warner 1985; Turner & Bateson 2000).

To estimate the domestic cat's effect on wildlife populations in Norway, it is essential to do studies in Norwegian conditions. In this study, I used a camera and a GPS-device mounted on the cat. This made it possible to assess if the number of home-brought prey items is a good proxy for how many prey the cats actually capture, allowing an estimation of what type of prey is potentially not brought home. The combination of camera and GPS-device allow information on time and location of prey captures to be recorded. To my knowledge, my study is the first to incorporate this method to study habitat selection and prey choice in domestic cats.

My study aimed to answer the following questions: i) How large home range size does house cats have, and which cat traits explain differences in home range sizes? ii) Do cats prefer some habitats over others, and do they hunt in the areas in which they spend the most time? iii) When, in the course of a day, is the cat the most active? Is general activity and predation activity correlated? iv) What is the domestic cat's hunting and capture rate? v) Is home-brought prey a sufficient estimate of cat predation on wildlife?

2. Method

2.1 Study Area

The study was conducted in Ås municipality in Akershus County, in southeast Norway (59°40’ N, 10°47’ E, approximately 100 m elevation). Located close to Oslo, the population in Ås is relatively concentrated, with approximately 19000 inhabitants spread over 103 km^2. The area is dominated by agricultural landscape and small hills covered with forest (Bratli 2000). Forested areas have been utilized in forestry for centuries, and both the forested areas and agricultural landscape are highly affected by human encroachment and intense exploitation. Because of forestry, deciduous species have, to a large extent, been replaced by coniferous species (Bratli 2000).

The cat owners participating in this study all lived in residential areas within 3 km from downtown Ås (figure 1). The distance between the cat owners differed as a result of the recruitment method described below, with nine living in close proximity of each other, and the last two more than 1 km away from any other cat included in the study (figure 1).

The fieldwork was executed between 6 June and 29 July in 2015. Only recordings made before 23 July were included in the study, due to time constraints and the large amount of data that had to be analyzed. The average time of solar midday during the study period was 13.21 hours. Average time for sunrise and sunset was 04.00 and 22.41 hours, respectively. Solar data for Oslo (c. 30 km north of Ås) was used in the analysis.

According to the database eKlima (2015), the normal temperature for Ås in June and July is 14.8° and 16.1° (2015 eKlima), respectively. In 2015 the average temperature for June and July was 13.4 ° and 15.6 °. The normal total precipitation for June and July is 68.0 mm and 81.0 mm, respectively. In 2015, the total precipitation for June and July was 59.9 mm and 151.7 mm, respectively (2015 eKlima). All data on precipitation and temperature were obtained from the climate database eKlima (2015) of the Norwegian Metrological Institute. The chosen metrological station was Ås, Kjerringjordet (17850), as this station lies 2.0 km from the most distant cat home.

Passerine birds, bank vole (*Myodes glareolus*), field vole (*Microtus agrestis*), wood mouse (*Apodemus sylvaticus*), and common shrew (*Sorex araneus*) are common in the study area, and are potential prey for domestic cats. In 2015, the population of bank field vole and wood mouse in Ås were relatively high, while there is little data on the population of field vole and common shrew in the area (G. A. Sonerud, pers. comm.). A great variety of insect prey species was available in the study period, including butterflies and moths (Lepidopterans) and crane flies (Tipuloidae).

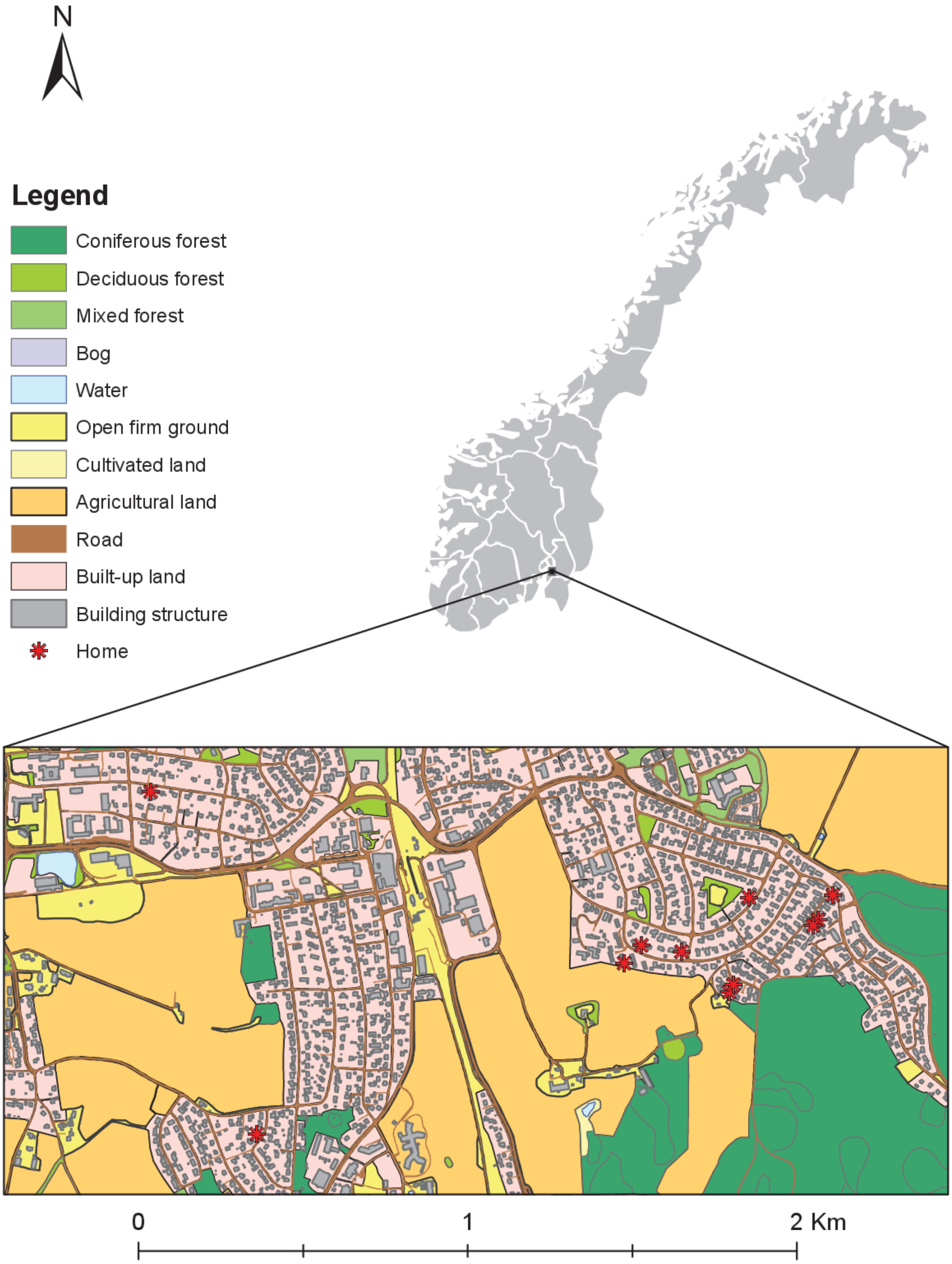

Figure 1. Map of Norway showing counties, with a map of the study area inserted, showing the distribution of the households for each cat in the study. All habitats included in the analysis are listed in the legend. Asterisks marks the house of cat owners.

2.2 Sample

All cats included in the study were 'house cats', i.e. cats spatially bound to a household and regularly fed by their owner. The cats were recruited to join the study by knocking on doors in the Ås municipality, and asking if potential cat owners wanted to join the project. To create a representative selection, I excluded cats that did not fit the following criteria. Firstly, the cats chosen to be included had to be located less than 5 km from the campus of Norwegian University of Life Sciences (NMBU), Ås, to ease the fieldwork. Secondly, cats had to be available for more than at least four of the seven weeks of the study period. Thirdly, only one cat from each household was included in the study. Fourthly, only cats that successfully habituated to wearing a stripped collar (no device mounted), and later to the full collar for the study period (camera and GPS device mounted, hereafter called collar), were included. One recorded cat had to be excluded because it failed this test. All cats included in the study wore a stripped collar for at least a week prior to the actual recording period to allow them to habituate to wearing something around their necks. Consequently, unnecessary stress and discomfort that could influence their behavior during recording was avoided.

A cat bout was defined as the period from when the cat started to wear the collar until the owner removed it (range 4-19 h). Due to technical problems with cameras and GPS devices, not all cat bouts recorded data from both the camera and the GPS device. Only cat bouts that consisted of both data sources were included. The data set for this study consisted of 90 cat bouts with a total of 1002 h covered. A total of twelve cats were included in the field work, but one cat was dropped from the analysis because it wore a camera on only one bout before the cut-off date. Thus, eleven cats were included in the analysis (named A to K based on the order of the first bout). The following characteristics were noted for each cat: sex, age, body mass, whether the cat had access to a cat flap (a portal in the door that cats can use to walk in and out of the house when they please), and whether the cat was neutered or not.

All cats were weighed right before their first cat bout. This was done by using a bathroom scale and first weighing a person without the cat, then weighing the same person holding the cat. Afterwards the difference was assigned as the cat's body mass, which was given with a precision of 0.1 kg. Age was rounded to the nearest whole year. Most households had birth certificate with information about the cat, including the age; others gave their best estimate of age. Of the eleven cats, seven were males and four were females. All cats were neutered, which is a common procedure nowadays; as many as 95 % of all house cats in Norway are neutered (Eriksen 2015). Age ranged 3-15 years, and body mass ranged 3.2-8.5 kg. Three cat owners had installed cat flaps that were regularly used by the cat.

2.3 Organization

To decide which cat that should wear the collar at what time (cat sequence), the software R 3.2.2 (R Core Team 2013) was used to randomly choose 11 letters (A-K, each assigned to a cat ID). The cat sequence was drawn for one sequence, with two cats per day, e.g. covering six days. The drawing of sequence was carried out two days before the next sequence started, to make time to communicate and make plans with the cat owners.

In households without cat flap, the owners were also allowed to take the collar off, as long as the collar were mounted and turned on when the cat was let out. Thus, in the analyses, periods within a cat bout lacking GPS signals were treated as periods spent indoors. This was a safe interpretation because the last GPS fix before loss of signal and the first GPS fix after the signal returned was exclusively detected in near proximity of the entrances that the cats regularly used. All movement while indoors was excluded from the analyses.

During the first two weeks of the study, only one bout was done by the cat before it got a rest day. However, to cover more hours per day, two bouts were run after each other per cat for the remaining five weeks of the study period. The recording time was limited to approximately 12 h, depending on the cat's activity; no movement gave no trigging of the video cameras' motion detection and thus no recording. Thus, by swapping cameras, the consecutive recording time was extended to approximately 24 h. The cat got one collar (collar A) for the first bout, and this was swapped with another collar (collar B) when the cat had worn collar A for approximately 12 h. Because both the camera and the GPS device were mounted to the same collar, changing collars meant changing both the camera and the GPS device, even though the battery time of the latter was much longer (up to 90 h, pers. obs.). The data from collars A and B were treated as two separate cat bouts because the swap was typically made indoors when the cat came home to feed, thus making it a natural breakpoint. Although the aim was to cover all 24 hours during a day evenly, the starting point of each bout during the day varied between cat bouts (range 17-55, with the average (± SE) of 36.5 ± 2.5, table 1).

Table 1. The number of hour blocks with both video recordings and GPS data per hour during the day.

Hour of the day	Number of hour blocks with data
0000 - 0100	52
0100 - 0200	49
0200 - 0300	43
0300 - 0400	37
0400 - 0500	32
0500 - 0600	31
0600 - 0700	31
0700 - 0800	21
0800 - 0900	17
0900 - 1000	22
1000 - 1100	21
1100 - 1200	26
1200 - 1300	25
1300 - 1400	29
1400 - 1500	31
1500 - 1600	29
1600 - 1700	36
1700 - 1800	42
1800 - 1900	40
1900 - 2000	49
2000 - 2100	51
2100 - 2200	55
2200 - 2300	53
2300 - 2400	55
Total	877

2.4 Camera and GPS device

To monitor a cat's activity, a 42 g (after manipulation) DVR device (digital video recorder), here called camera (figure 2), was utilized. It contained a PIR (passive infrared sensor) to detect motion. A device with PIR was chosen in order to extend the video recording period by saving battery while the cats rested. The camera included eight IR (infrared) night vision LEDs (light emitting diodes) with focal length = 2.8, providing night visibility up to a distance of 5 m. The camera was mounted on a collar, in a 90 degrees angle to the ground, to facilitate prey identification. The cameras were purchased from Ebay.com. No brand name or information about the manufacturer was obtainable. The cameras were produced and shipped from China. The camera was fitted with a 32 GB micro SD card, and had, primarily, a battery lifetime allowing 5 h continuous recording. However, this battery (3.7 V, 800 mAh) was replaced with a more efficient polymer lithium battery (3.7 V, 1200 mAh). In addition, motion detection mode greatly extended the total video recording period per bout (maximum in this study was 19 h covered). The recordings were cut into a minimum of 30 s sequences, so that when triggered, the camera recorded video files of 30-300 s length, depending on the motion's duration. A GPS ™ route logger from Canmore Electronics, Canada was used to track the cats. The logger weighed 15 g and had a USB adapter, which made data transfer straightforward. The accuracy was 2.5 m. The device was set to record one fix every 20 s. The Canway data-logger program was used to read the GPS logs, before the data was exported to CSV (comma separated values) files and opened in Excel (2013).

Figure 2. The collar used in the study. The GPS device mounted above the neck, and the camera below. The matchbox is included in the image to give a size reference (L x W x D = 80 mm x 40 mm x 25 mm).

2.5 Video analysis

To respect people's right to privacy, all video clips were seen by me first. Because video recordings showing humans were of no interest in this study, video recordings including humans were watched at high speed (8 times normal speed). All video recordings including persons were deleted immediately. The software VLC media player was used to view the video recordings. In total, the entire period of study resulted in 542 h video recordings, covering a video monitoring period of 1152 h, due to the motion detectors. The cut-off reduced this to 485 h, covering 1002 h. This were the data making up the basis of all analyses. To make it manageable to review, viewing in fast-forwarding speed was necessary. However, to reduce the chance of missing out on predation events, and assess if fasting forward affected detection rate, video recordings from a chosen percentage of the cat bouts (33%) were viewed more thoroughly, hereafter called thorough viewing method (TVM). In TVM, up to 4 times normal speed was allowed. The only exception was video recordings made indoors, which I viewed on 16 times normal speed. With 4 times normal speed, VLC media player still play the sounds from the recordings. The other 66 % was viewed in a less thorough way, hereafter called superficial viewing method (SVM). In SVM, fasting forward speed was chosen according to situation, ranging from normal speed and up to 32 times normal speed. I still examined every possible predation event carefully, but allowed fast speeds when the cats were lying still or staying indoors. Events included in SVM were predation events, meetings with other cats, and whether the cat was indoors or outdoors. The listing of when the cat went in- and outdoors was used to decide which fixes should be included in the analyses. Events included in TVM were the same events as in SVM, but also including alarm calls by birds, identified to species if possible, and vocal noises made by the cat in relation to the specific situation in which they were made. Due to time constraints, neither alarm calls or vocal noise by the cat were analyzed further.

By comparing SVM and TVM, the probability of failed detection using SVM was predicted. Of the 130 predation events, 46 were detected in SVM (35 %), with the expectation of 33 %, no difference was detected between the methods. Consequently, TVM seemed to be as reliable a method as SVM, and materials from both methods were managed in the same way.

For every predation event, whether the prey item was moved or not, and if it was, the time the prey item was dropped, was registered. In addition, the number of times and duration the cat fed from food bowl, the amount of prey digested, and the handling time of each prey, was recorded but not analyzed due to time constraints.

2.6 Prey identification

Attacks were defined as predation events, including both unsuccessful attacks (hereafter called attempts) and successful attacks (hereafter called captures). Identification of prey items was done to the lowest possible taxonomic group. In cases in which prey identification was particularly difficult, the prey item could only be assigned to insect, bird or mammal. All captures classified as either bird or mammal included a visual confirmation of the prey item on the video. For the classification term insect, such visual cue was not needed (although it was present in most cases), given that the cat's movement strongly suggested that it chased after prey, and noises and jaw movements clearly indicated chewing. Movements of the cat that closely resembled the ones involving a prey item, i.e. rapid change of pace ending in a strike, but did not include any sounds of chewing or movements of the jaws indicating chewing were recorded as attempt.

2.7 GIS (geographic information system)

The total sum of cat GPS fixes recorded were 158377, and varied greatly between cats (table 2) with an average (± SE) of 14394.3 ± 1410.6. Of these, 119187 were recorded outdoors, with an average of 10835.2 (± SE) ± 674.3 per cat. To analyze the habitat selection of the domestic cats, I examined the information about the habitats in the study area using ArcGIS Desktop 10.2 (ESRI 2014). A resource map (AR5), i.e. a detailed national land capability classification system (for Norway) and dataset, provided by The Norwegian Mapping Authority (Bjørkelo et al. 2009) was added. I then converted the latitude and longitude coordinates from the GPS devices into UTM coordinates (UTM_32N), which were subsequently uploaded into ArcMap.

Table 2. Number of total cat GPS fixes and total of cat GPS fixes recorded outdoors for each cat.

Cat ID	Total number of fixes	Number of outdoor-fixes
A	10940	10940
B	18956	13088
C	16061	10035
D	14314	12291
E	21808	10913
F	20018	15218
G	9217	8399
H	9417	7752
I	9488	9488
J	17291	12186
K	10827	8877
Total	158377	119187

The following standard habitat types in the AR5 were included in this study. Bog (bog vegetation and > 30 cm peat layer), water (≥ 0.2 ha water surface), open firm ground (area that is not farm land, forest, built-up or infrastructure), cultivated land (cleared and even ground suitable to farming), agricultural land (area plowed to standard depth), road, built-up land (built-up land in close proximity to residential area), and building structures. Forest land was included (area ≥ 15 trees/ha) and divided into three types of forest, coniferous forest (≥ 50 % coniferous species cover), deciduous forest (< 20 % coniferous species cover), and mixed forest (20-50 % coniferous species cover) (Bjørkelo et al, 2014). Bog and cultivated land were removed from the analysis because none was present in close proximity to any of the eleven cats, the closest GPS fix being 91 m and 90 m from bog and open firm ground cultivated land, respectively.

Making up a different map, the site quality for forest vegetation was added. This consisted of non-relevant (e.g. buildings, roads), high, medium, low, and non-productive forest land. However, these maps are not shown, because as many as 112572 of the 119188 (94 %) GPS fixes were located within non-relevant habitat structure. This is because the latter includes many of the habitats in which the cats spent a great amount of time, such as agricultural land and built-up land. Consequently, the sample was non-balanced, and thus the test did not give any information.

The home variable was generated by drawing a polygon of the house in ArcMap, and including the garage for the cats that repeatedly rested or fed there (cat G used cat flap to access food in the garage). Thus, the distance to home was defined as the shortest distance between a location and the closest part of a wall of the house (or garage) the cat resided in.

The shortest distances between each GPS fix for each cat and all the habitat types, separately, were constructed by using the ‘join and relate’-function in ArcMap. These distances were saved into csv files, which were subsequently merged creating an excel-file containing all the distances from every cat GPS fix for all cats to every habitat structure in the study.

2.8 Statistical analysis

2.8.1 Data

The 24 daily hour blocks were calculated and used as the basis for the analyses of home range, activity, and predation rate. For each cat bout, only hour blocks, and thus the attacks occurring within these, with at least 55 minutes video recording and GPS data coverage, was included in the data analysis. Consequently, the total dataset used in this study consisted of 877 hour blocks recorded for eleven cats (table 1).

2.8.2 Home range

Based on all outdoor GPS fixes for a cat, the 99 % MCP (minimum convex polygon) home range was calculated in R using the 'mcp' function, and the 95 % kernel home ranges was calculated using 'kernel UD' and 'getverticeshr', in the adehabitatHR package (Calenge 2006). Further, the 95 % kernel home ranges were calculated for each cat per cat bout. In addition, 25, 50, 75, and 99 % kernel home ranges were calculated (appendix 1). Home ranges were subsequently exported to ArcMap as CSV files. The area of each home range was calculated using 'calculating geometry' in ArcMap.

The total 95 % kernel home range size for each cat, i.e. overall home range size for all bouts (hereafter called total home range size), was used in the further analysis, as the response variable. A second analysis was made based on the 95 % kernel home range size per bout per cat (hereafter called home range size per bout per cat) as the response variable. In both analyses, the following fixed variables were fitted: sex, age, body mass, and whether the cat owner had cat flap installed or not. Because the residuals of age and body mass were not normally distributed around the mean, non-parametric tests were used. Total 95 % kernel range size was included as response variable and cat flap and sex as explanatory variables in two separate Mann-Whitney tests. Spearman's rank correlation was used to test for the effect of age and body mass on total home range size, in two separate tests. Then, total home range size was log-transformed, giving acceptable normal distributed residuals around the mean for both age and body mass. A linear regression model was fitted using 'lm' function in R, making up the global model for the analysis.

For home range size per cat per bout, log-transformation of the response variable gave acceptable normal distributed residuals around the mean for both age and body mass. Thus, a global model was fitted by linear regression using 'lme' function, in 'nlme' package in R in the latter. Cat ID was included as a random variable to control for individual differences (Pinheiro & Bates 2000). Based on the global model of each analysis, a correlation matrix for the fixed variables was calculated. A correlation more extreme than $r = \pm 0.50$ between two variables were tested by fixing both variables in separate linear models (hereafter called isolated model) using 'lmer' function, in 'lme4' package in R. If the parameter estimates of a given variable changed when both were included in the same linear model, using the same function, the correlation was considered a potential problem. The variable with the highest AIC (Akaike information criterion) value from the isolated model was dropped.

As for all tests in this study, except for the cosinor analysis below, 'dredge', in the package MuMIn, was run, with REML (restricted maximum likelihood) set to false. This returned all possible variations of variable-combinations in the global model, ranked after AICc values (Burnham & Anderson 2004). For analyses with more than ten probable models, the ten models with the lowest AICc value were listed for each analysis. However, the number of parameters (K) was checked for all models within two ΔAICc values of the lowest AICc value in the analysis of concern, and the most parsimonious model within two ΔAICc values of the lowest AICc value was considered the best model. This model was then fitted, with REML=T, and the estimates for all fixed effects were listed in a table. Significant level was defined as $p = 0.05$.

2.8.3 Habitat selection analyses

To get an even distribution of random positions inside the kernel home range, 10 000 points were produced by random. A general linear mixed model was fitted in R using 'lmer', with the probability of a fix being an observation (1) rather than a random point (0) as the response variable, as a function of distance from the different habitat types. In addition to testing for habitat selection based on observation fixes, two other habitat selection analyses were carried out, one including both all successful attacks (captures) and all unsuccessful attacks (attempts), hereafter called hunting habitat selection analysis; and the other only including captures, hereafter called capture habitat selection analysis. These two analyses together are addressed as predation habitat selection.

The location of prey captures were obtained by taking the time for each capture, noted from video recordings, and interpolating the position between the GPS fix immediately before and immediately after the capture time. The GPS devices were set to give one GPS fix every 20 s, but minor signal-problems did occur, giving longer spans between fixes (maximum 76 s). All prey captures with a fix within one minute before or after prey event were included. Only one insect, captured by cat I, had to be discarded.

For the hunting habitat analysis, twelve random points were created for each cat within its 95 % kernel home range, because the dataset comprised 130 attacks with a GPS fix, giving an average of 11.8 GPS fixes per cat. For capture habitat selection, which included 83 captures (mean was 7.5 per cat), eight random points were created within 95 % kernel home range for each cat.

To produce figures of the effect of the habitats in the three habitat analysis, I the used logistic regression formulae,

$$E(y) = \frac{e^{y}}{1+e^{y}} = \beta_0 + \beta_1 x_1 + \ldots + \beta_k x_k$$

Where β_0 is the intercept, β_k are the regression coefficients, and x_k are the predictor variables (Montgomery et al. 2015). The estimates from the best model returned by dredge were put into the formulae. The best model was found and presented by the same procedure as for home range analyses. To produce graphs presenting related variables with more than three dimensions, two dimensional graphs were made while the other habitats were controlled for by being fixed to the average distance m for that habitat.

All combinations of variables was calculated by the use of dredge, and the best model was chosen by the same procedure than for home range analyses.

2.8.4 Activity

Three types of activity (per hour block) were calculated: the predicted numbers of m moved per hour block (hereafter called general activity), probability of attack per hour block (hunting activity), and probability of capturing a prey per hour block (capture activity). Predation activity is used to address these two analyses.

In order to calculate general activity, the distance between each GPS fix was found using the cosine-haversine formulae (Robusto 1957),

(ACOS (COS (RADIANS (90 - Lat1)) * COS (RADIANS (90 - Lat2)) + SIN (RADIANS (90 - Lat1)) * SIN (RADIANS (90 - Lat2)) * COS (RADIANS (Long1 - Long2))) * 6371) * 1000

Where Lat1 and Lat2 is the latitude for the first GPS fix and the GPS fix 20 s later, respectively, and Long1 and Long2 are the correspondingly for longitude, while 9371 is the radius of the Earth. The equation was multiplied with 1000 to convert units into distance in m. Based on the distances and the time registered, a linear mixed-effect model was fitted using 'lme' function in R, with the response variable set to predicted distance moved per hour block. The fixed explanatory variable 'time of the day' was fitted using the cosinor method, with 24 h as the fundamental period combined with three harmonic components (1^{st}, 2^{nd} and 3^{rd}) to modulate the signal (Nelson *et al.* 1979; Pita, Mira & Beja 2011). In addition, sex was added as another fixed variable (table 3). Because the sample only included 11 cats, and thus few data points on the continuous variables age and body mass, the latter could not be included, as they gave a skewed sample not suitable for cosinor analysis. Cat ID was included as a random variable to control for individual differences.

Predation activity (hunting activity and capture activity) was tested by fitting two separate logistic regression models with a binomial distribution (Bates et al. 2014; Montgomery et al. 2015) using the 'glmer' function in the 'lme4' package. For hunting activity, GPS fixes for all attacks were included, and the response variable was defined as whether or not an attack occurred (0/1) within an hour block. For capture activity analysis, the response variable was defined as whether or not a capture event occurred (0/1) within an hour block. Then, global logistic regression models were fitted for both tests. Based on the global models in the three analyses, all possible combinations of variables (the same for the three analyses) were constructed manually (table 3), and the associated models ranked using 'AIC' function in R. The selection of the best model and the process of fitting this was done by the same procedure as for the habitat selection analyses.

Table 3. Models of general activity, hunting activity, and capture activity analysis, representing all combinations of variables, where x represents 'time of day' and Ɛ is the random effect 'cat ID'.

Model	Variables
M_0	$f(x) = a_0 + \varepsilon$
M_1	$f(x) = a_0 + \left(a_1 \cos\frac{2\pi x}{24} + b_1 \sin\frac{2\pi x}{24}\right) + \varepsilon$
M_2	$f(x) = a_0 + \left(a_1 \cos\frac{2\pi x}{24} + b_1 \sin\frac{2\pi x}{24}\right) + \left(a_2 \cos\frac{2*2\pi x}{24} + b_2 \sin\frac{2*2\pi x}{24}\right) + \varepsilon$
M_3	$f(x) = a_0 + \left(a_1 \cos\frac{2\pi x}{24} + b_1 \sin\frac{2\pi x}{24}\right) + \left(a_2 \cos\frac{2*2\pi x}{24} + b_2 \sin\frac{2*2\pi x}{24}\right) + \left(a_3 \cos\frac{3*2\pi x}{24} + b_3 \sin\frac{3*2\pi x}{24}\right) + \varepsilon$
M_4	$f(x) = a_0 + \left(a_1 \cos\frac{2\pi x}{24} + b_1 \sin\frac{2\pi x}{24}\right) + Sex + \varepsilon$
M_5	$f(x) = a_0 + \left(a_1 \cos\frac{2\pi x}{24} + b_1 \sin\frac{2\pi x}{24}\right) + \left(a_2 \cos\frac{2*2\pi x}{24} + b_2 \sin\frac{2*2\pi x}{24}\right) + Sex + \varepsilon$
M_6	$f(x) = a_0 + \left(a_1 \cos\frac{2\pi x}{24} + b_1 \sin\frac{2\pi x}{24}\right) + \left(a_2 \cos\frac{2*2\pi x}{24} + b_2 \sin\frac{2*2\pi x}{24}\right) + \left(a_3 \cos\frac{3*2\pi x}{24} + b_3 \sin\frac{3*2\pi x}{24}\right) + Sex + \varepsilon$
M_7	$f(x) = a_0 + Sex + \varepsilon$

2.8.5 Predation rate

The number of attacks per hour block was labelled hunting rate, while capture rate was defined as the number of prey captured per hour block. Because the sample size was fairly small, no particular test of variables was run testing for hunting or capture rate. Success rate for each cat was calculated by dividing number of captures on number of attacks for that cat. Hunting rate and capture rate are together called predation rate.

2.8.6 Home-brought prey

Cat owners were instructed to report all prey items that was captured by their cat during the study period. Only two potential prey items were observed by the owners during the study period, one great tit (*Parus major*) and one eurasian siskin (*Carduelis spinus*). However, none of the mentioned prey were captured during a cat bout, and was therefore not included in the analysis. Home-brought prey was defined as prey presented to the owner, i.e. that the owner reported prey that had been identified in the video recordings.

For all prey items that were moved by the cat, the location of the capture and the location where the prey item was later dropped were registered. The following distances were then calculated: total distance moved, the distance from where the prey was captured to the cat's home, and the distance from where the prey item was dropped to the cat's home. Based on the latter two, the distance moved related to the cat's home was calculated. Cats did not rest while they moved items, thus all distances were total distances, from the capture site to the drop location, in which they left the prey item or fully digested it.

To test the probability of a prey item being moved as an effect of prey type, and thus prey size (i.e. prey size being larger for mammalian and avian prey, as opposed to insect prey items), a logistic regression model using 'lmer' was fitted. The response variable had two outcomes; prey item not moved (0) and prey item moved (1). The prey type was included as a fixed variable, being "insect", "bird" or "mammal". Cat ID was fitted as a random variable. Estimates were presented as mean ± SE.

3. Results

3.1 Home range

3.1.1 Total kernel and MCP home range per cat

Total 95 % kernel and 99 % MCP home range size differed greatly between cats (range 0.16-15.71 ha) with a mean of 3.57 ± 1.43 ha and (range 0.16-1.41 ha) with a mean of 5.41 ± 1.55, respectively (table 4, figures 3, 4)

Table 4. Basic data of the cats studied.

Cat ID	Sex	Age (years)	Body mass (kg)	Cat flap	Home range size (m^2)	
					95 % kernel	99 % MCP
A	Male	3	5.5	Yes	82134	141295
B	Male	13	4.9	No	3554	92712
C	Female	4	4.5	No	8731	15983
D	Male	6	8.5	No	47472	71428
E	Female	15	3.9	No	1639	1626
F	Female	14	3.2	Yes	11543	21664
G	Male	7	5.0	No	157132	136865
H	Male	5	5.2	No	47061	68871
I	Male	5	6.0	No	18736	21944
J	Male	11	5.8	Yes	8495	10577
K	Female	6	4.7	No	6112	12039

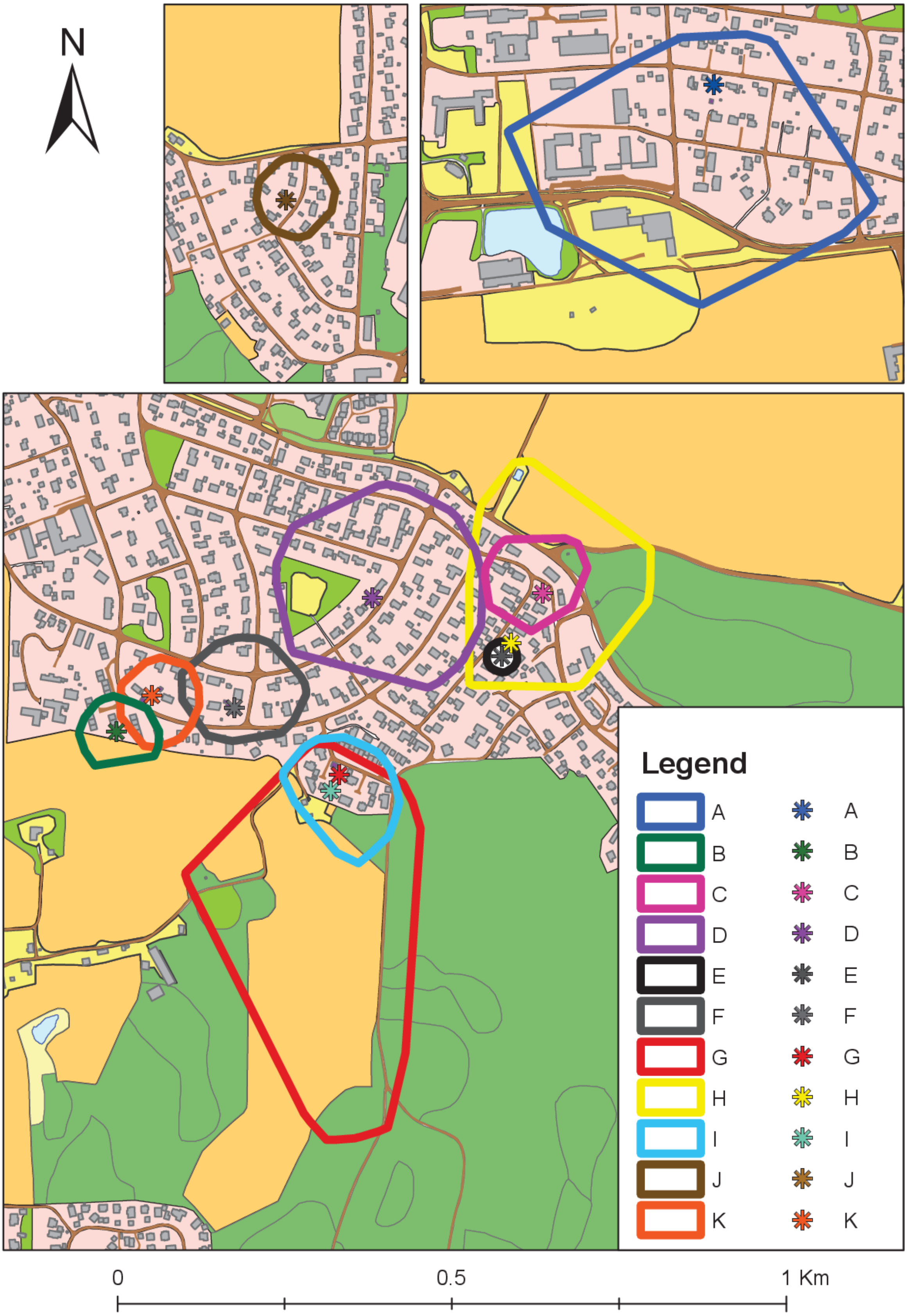

Figure 3. Individual 99 % MCP home range for the 11 cats studied. Asterisk marks the house belonging to the cat owner. The color denotes cat ID. The spatial positions of the home range and home of cat A and cat J are shown in figure 1.

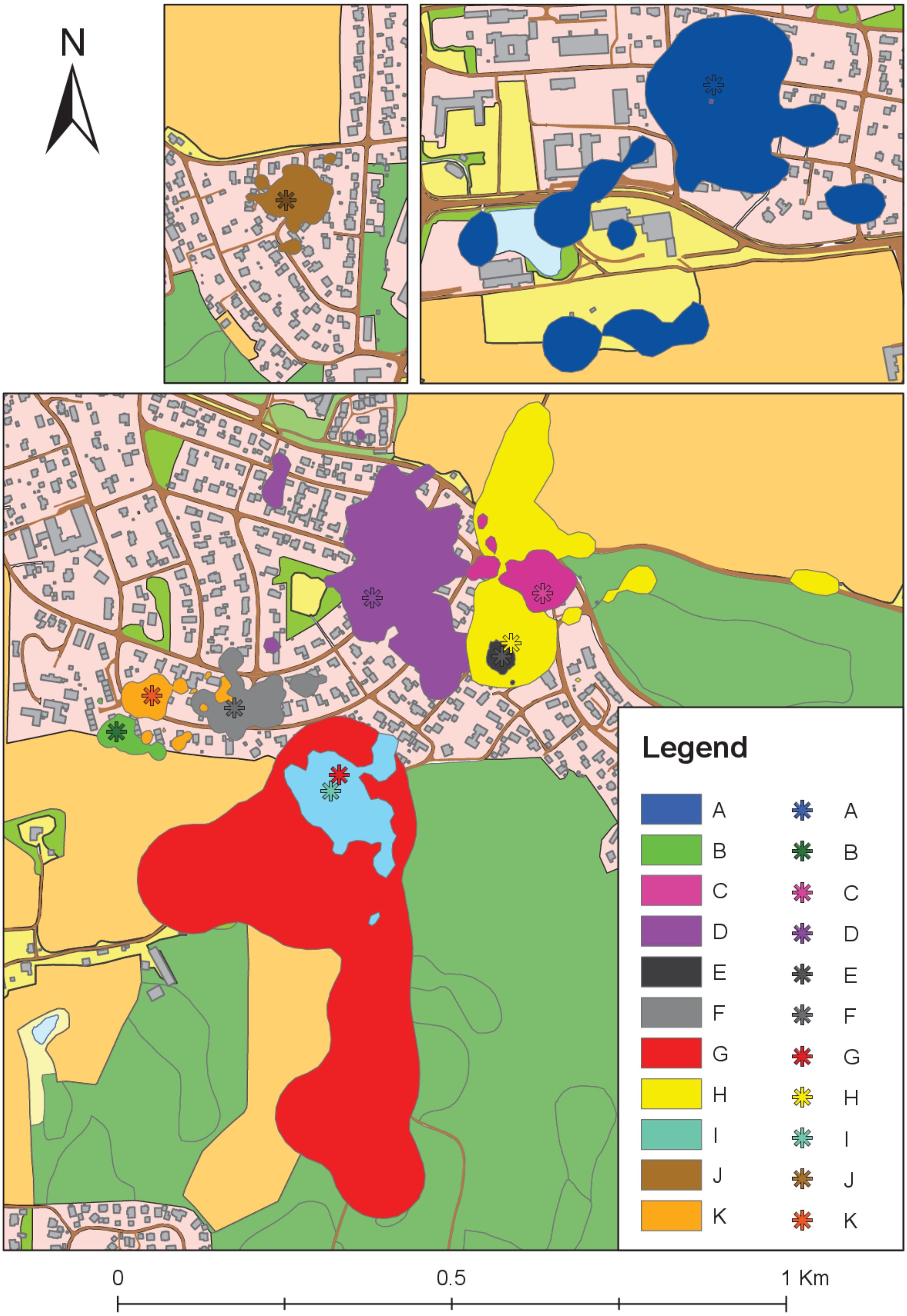

Figure 4. Individual 95 % kernel home ranges for the 11 cats studied. Asterisk marks the house belonging to the cat owner. The color denotes cat ID. The spatial positions of the home range and home of cat A and cat J are shown in figure 1.

Male and female home range sizes did not differ significantly, with a mean of 5.2 ± 0.20 ha and 0.7006 ± 0.21 ha respectively (W = 5, p = 0.11). Home range size was marginally non-significantly affected by age (figure 5, S = 339.54, p = 0.084), with decreasing home range size with age. Body mass did not have a significant effect on home range size (figure 6, S= 108, p = 0.11). Neither did home range size differ significantly between cats with cat flap available and cats without cat flap available, with an average home range size of 3.41 ± 2.41 ha, and 3.66 ± 1.85 ha, respectively (W =10, p = 0.78).

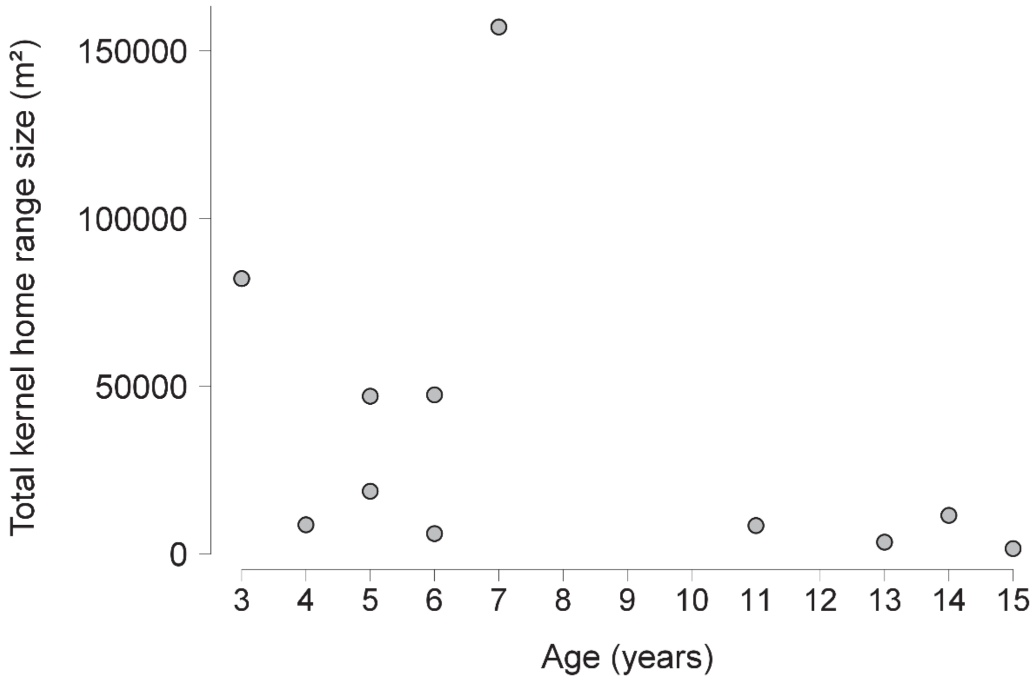

Figure 5. The relationship between total 95 % kernel home range size and cat age for the 11 cats studied.

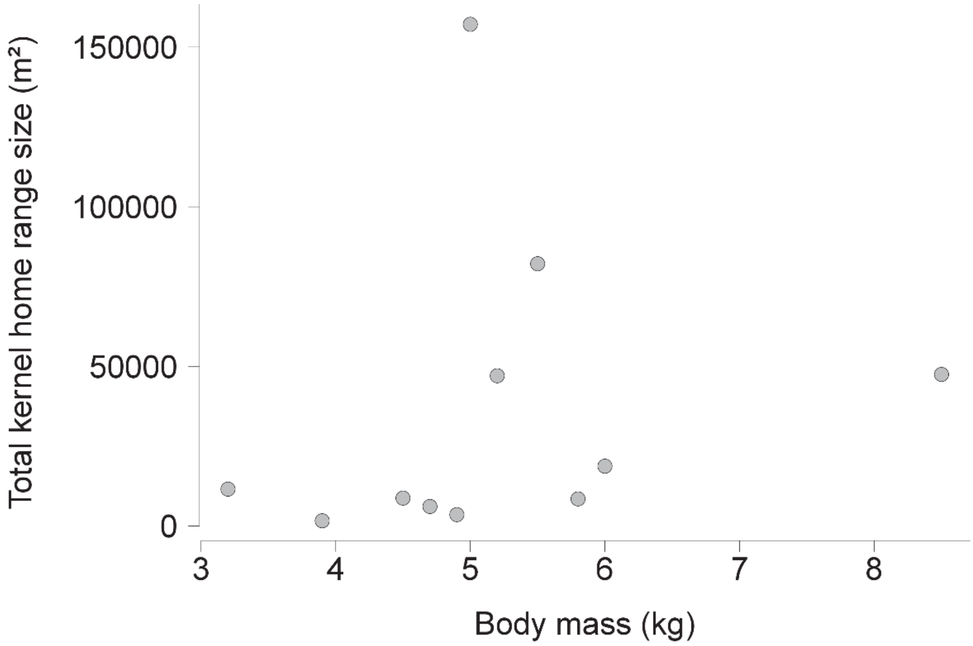

Figure 6. The relationship between total 95 % kernel home range size and cat body mass for the 11 cats studied.

When home range size was log-transformed, the best model, having the lowest AICc value, based on the global model fitting all the four fixed variables, only included age (table 5). The effect of age was significant (table 6), with home range size declining with age (figures 7, 8). The second best model included sex as the only fixed variable (table 7). Sex had a marginally non-significant effect on home range, with males having larger home range size than females (figure 9).

Table 5. The ten best models in the analysis of factors affecting the 95 % kernel total home range size per cat, ranked based on AICc values.

Model	Variables	k	AICc	ΔAICc	AICc weight
1	Age	1	22.54	0.00	0.35
2	Sex	1	23.93	1.39	0.17
3	Age + Sex	2	23.99	1.44	0.17
4	(Null)	0	24.68	2.14	0.12
5	Age + Body mass	2	26.26	3.72	0.05
6	Age + Cat flap	1	26.72	4.17	0.04
7	Age + Body mass	2	27.32	4.78	0.03
8	Cat flap	1	28.48	5.94	0.02
9	Sex + Cat flap	2	29.05	6.51	0.01
10	Sex + Body mass	2	29.08	6.54	0.01

Table 6. Parameter estimates from linear regression with log-transformation, showing the best model explaining kernel home range size.

	Estimate	SE	z	p
(Intercept)	4.94	0.32	15.32	< 0.0001
Age	-0.09	0.05	-2.57	0.031

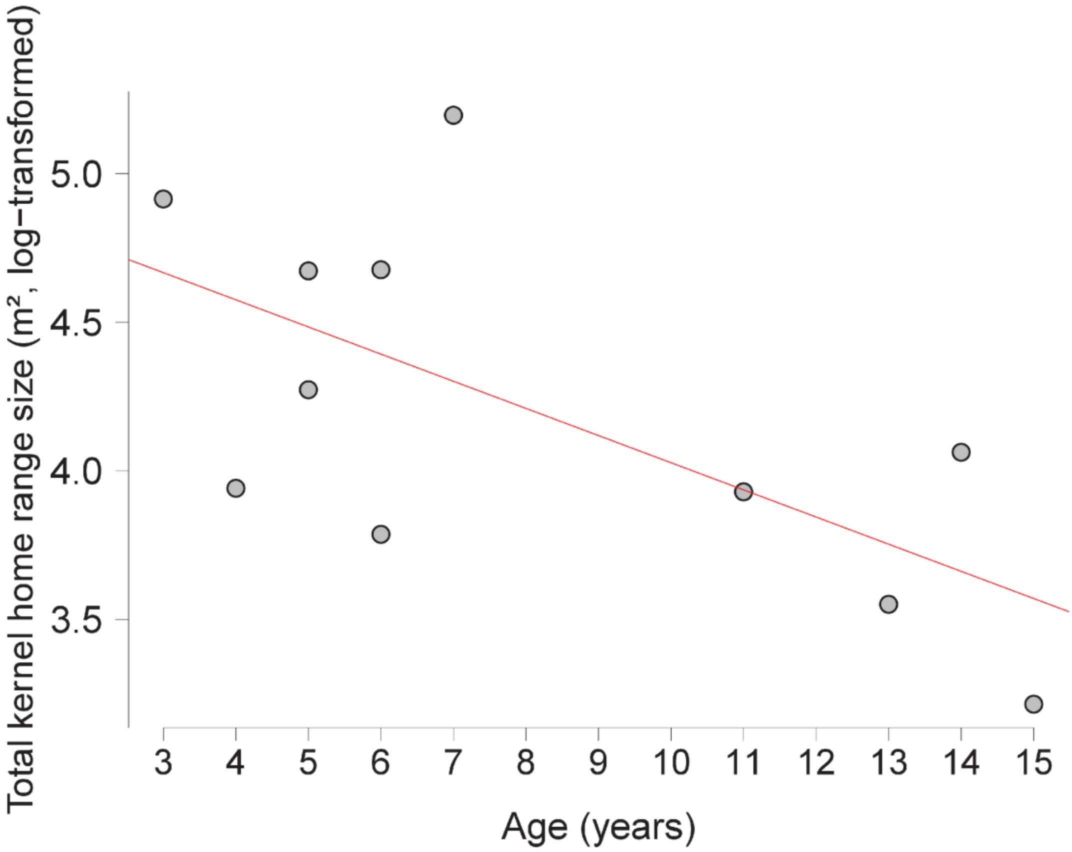

Figure 7. Linear regression fitted to explain total 95 % kernel home range size for each cat as an effect of cat age.

Table 7. Parameter estimates from linear regression with log-transformation, showing the second best model explaining kernel home range size. The estimate for sex is given for males relative to females.

	Estimate	SE	z	p
(Intercept)	3.75	0.26	14.51	< 0.0001
Sex	0.71	0.32	2.14	0.057

Figure 8. Individual total 99 % MCP for the 11 cats studied. Grey scale denotes age, darkness increasing with age. Asterisk marks the house belonging to the cat owner. Polygon outline color indicates cat ID. The spatial positions of the home range and home of cat A and cat J are shown in figure 1.

Overlapping home ranges occurred between males, and between males and females (figure 9). No particular overlapping was observed between females. The sample size was too small to test the effect of sex on home range overlap.

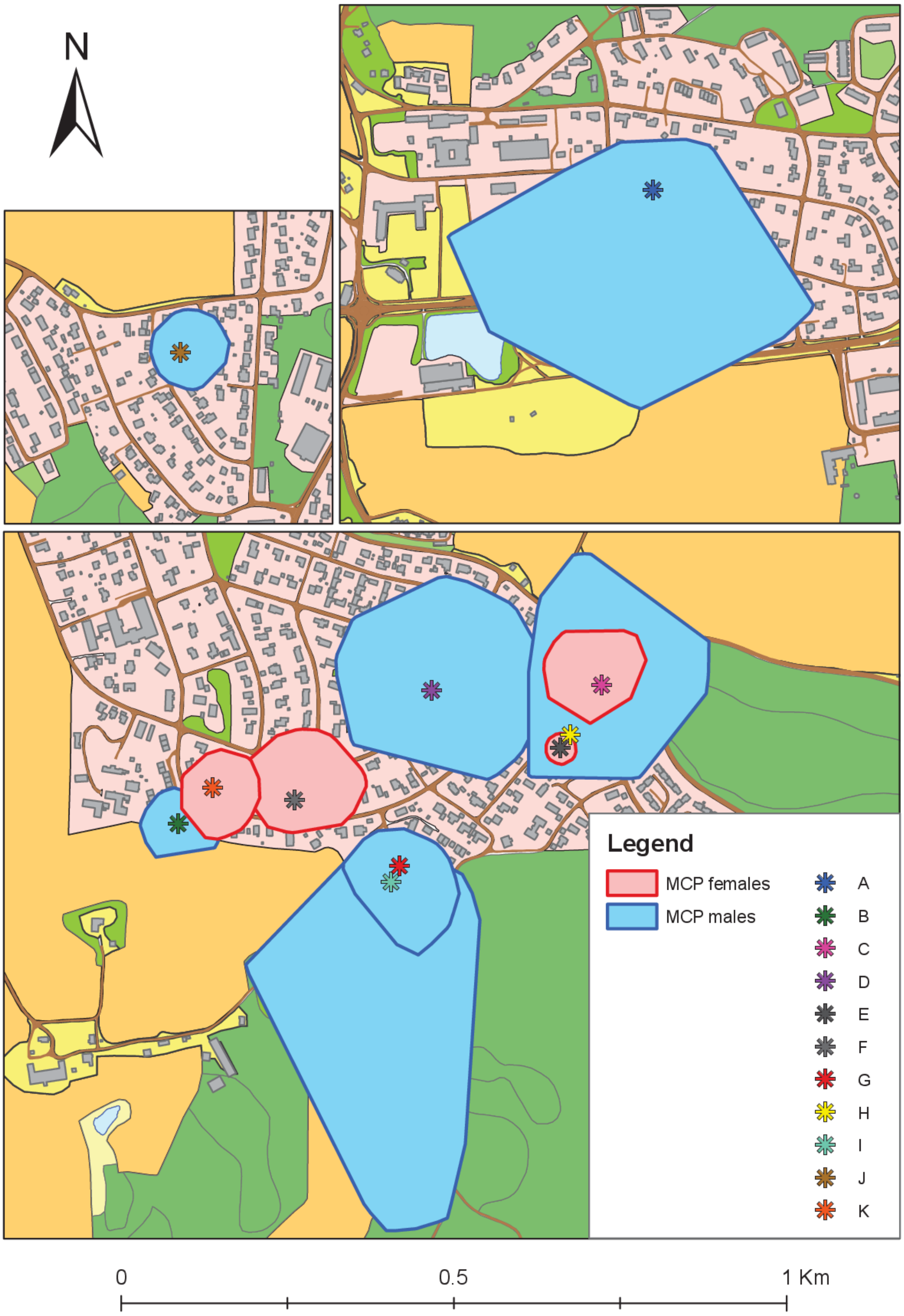

Figure 9. Individual total 99 % MCP for the 11 cats, separated into males (blue) and females (red). Asterisk marks the house belonging to the cat owner. The spatial positions of the home range and home of cat A and cat J are shown in figure 1.

3.1.2 Kernel home range per bout per cat

The effect of age on log-transformed kernel home range size per bout per cat was marginally non-significant (t = -1.95, p = 0.083), with home range size declining with age (figure 10). Body mass did not have any effect (figure 11, t = 0.70, p = 0.50) on log-transformed kernel home range size per bout per cat

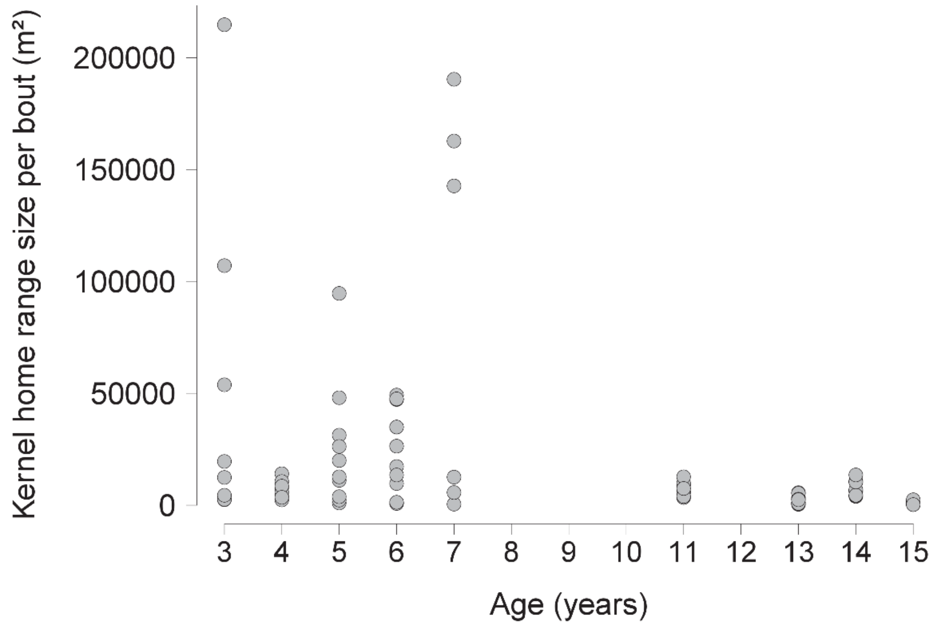

Figure 10. The relationship between 95 % kernel home range size per bout and cat age for the 11 cats studied.

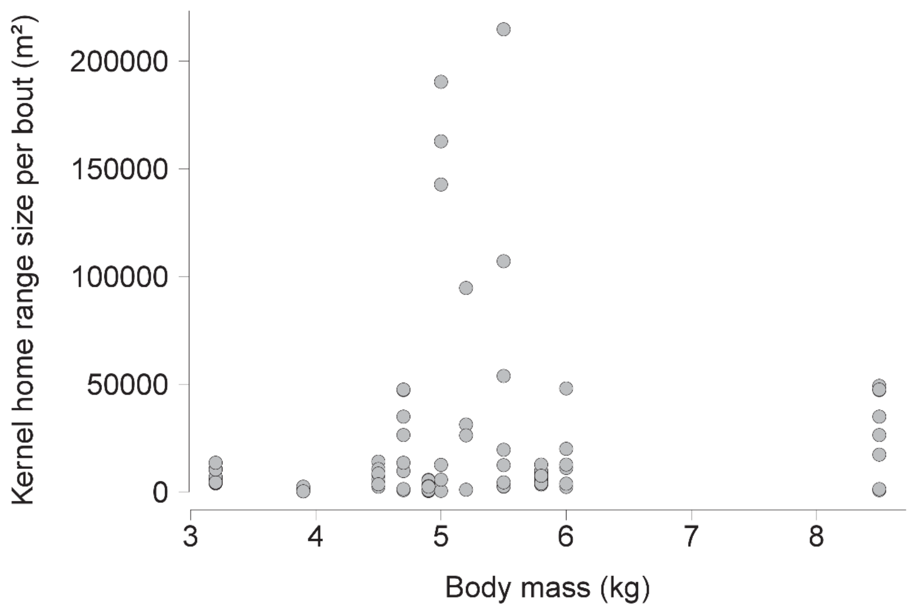

Figure 11. The relationship between 95 % kernel home range size per bout and cat body mass for the 11 cats studied.

A correlation table (appendix 2) showed that the most extreme correlation was between sex and body mass (r = -0.65). However, fitting kernel home range size with each variable in separate models, and then in the same model, gave no change in signs. Thus, both variables were kept in the global model. The best model, based on AICc values and the principle of parsimony, included age, while the second best model included one more variable, cat flap (table 8). In the best model, age was significant (table 9), and kernel home range size per bout declined with cat age (figure 12).

Table 8. The ten best models in the analysis of factors affecting the 95 % kernel home range size per bout per cat, ranked based on AICc values. K includes the random variable cat ID.

Model	Variables	k	AICc	ΔAICc	AICc weight
1	Age + Cat flap	3	163.67	0.00	0.29
2	Age	2	163.80	0.12	0.28
3	Age + Sex	3	165.75	2.08	0.10
4	Age + Sex + Cat flap	4	166.05	2.38	0.09
5	Age + Body mass + Cat flap	4	166.18	2.51	0.05
6	Age + Body mass	3	166.22	2.55	0.08
7	Age + Sex + Body mass	4	168.38	4.71	0.08
8	Age + Sex + Body mass + Cat flap	5	169.03	5.36	0.03
9	(Null)	1	170.92	7.24	0.02
10	Body mass	2	171.28	7.61	0.01

Table 9. Best model based on AIC values and the principle of parsimony, from the analysis of home range size per bout per cat.

	Estimate	SE	z	p
(Intercept)	4.51	0.21	21.20	< 0.0001
Age	0.08	0.03	-3.53	0.0064

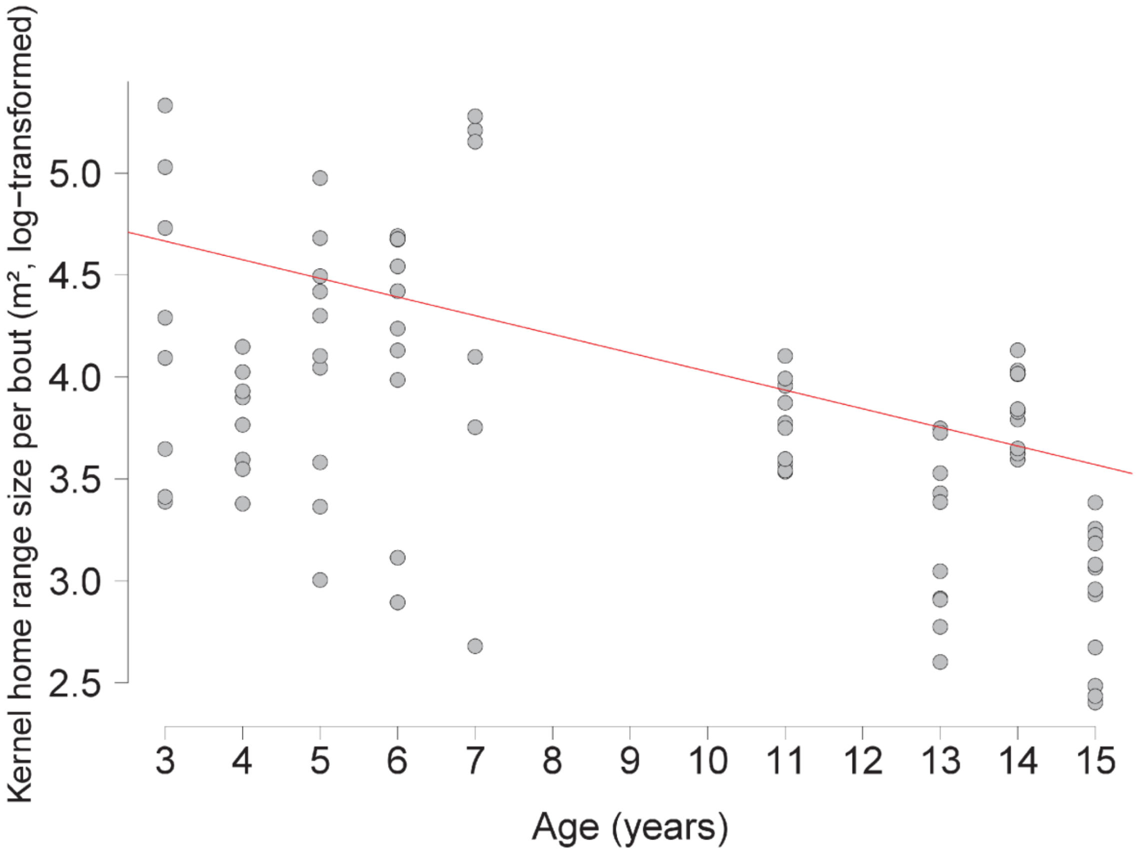

Figure 12. General linear model fitted to explain 95 % kernel home range size per bout as an effect of cat age.

3.2 Habitat selection analyses

3.2.1 Habitat selection

The correlation matrix from the global model showed that the following pairs of variables had a correlation coefficient (r) more extreme than ± 0.50 (appendix 3): built-up land and building structure, built-up land and home, and agricultural land and open firm ground. The two latter pairs changed signs when tested isolated versus together. Built-up land and open firm ground were dropped from further analysis because they had higher AIC values than the other variable in the pair.

The best model in the habitat analysis (M_2), included the variables coniferous forest, deciduous forest, mixed forest, water, agricultural land, building structure, and home (table 10).

Table 10. The ten best with the lowest AICc values from the analysis of distance to habitat (n = 225453, cats = 11). K includes the random variable cat ID.

Model	Variables	k	AICc	ΔAICc	AICc weight
1	Coniferous forest + Deciduous forest + Mixed forest + Water + Agricultural land + Road+ Building structure + Home	9	274259.6	0.00	0.72
2	Coniferous forest + Deciduous forest + Mixed forest + Water + Agricultural land + Building structure + Home	8	274261.5	1.89	0.28
3	Coniferous forest + Mixed forest + Water + Agricultural land + Building structure + Home	7	274319.5	59.85	0.00
4	Coniferous forest + Mixed forest + Water + Agricultural land + Road + Building structure + Home	8	274320.8	61.18	0.00
5	Coniferous forest + Deciduous forest + Mixed forest + Water + Building structure + Home	7	274353.9	94.31	0.00
6	Coniferous forest + Deciduous forest + Mixed forest + Water + Road + Building structure + Home	9	274354.3	94.73	0.00
7	Coniferous forest + Mixed forest + Water + Building structure + Home	6	274377.0	117.37	0.00
8	Coniferous forest + Mixed forest + Water + Road + Building structure + Home	7	274378.6	119.00	0.00
9	Coniferous forest + Deciduous forest + Mixed forest + Water + Road + Building structure + Home	9	274459.9	200.32	0.00
10	Coniferous forest + Deciduous forest + Mixed forest + Water + Building structure + Home	7	274461.4	201.77	0.00

All variables included in the best model had highly significant effect on distance to habitat (table 11).

Table 11. Parameter estimates and significance tests for the variables in the best model in the analysis of distance to habitats.

Fixed effects	Estimate	SE	z	p
(Intercept)	-1.05	0.27	-3.87	0.00011
Coniferous forest	0.002	0.0001	13.67	< 0.0001
Deciduous forest	-0.001	0.0002	-7.74	< 0.0001
Mixed forest	-0.003	0.0001	-30.39	< 0.0001
Water	0.005	0.0001	38.31	< 0.0001
Agricultural land	-0.001	0.0002	-9.71	< 0.0001
Building structure	-0.011	0.0002	-45.98	< 0.0001
Home	0.013	0.0001	99.78	< 0.0001

The probability of a plot being a cat GPS fix rather than a random plot increased with distance from coniferous forest, water and home. On the other hand, it decreased with increasing distance from deciduous forest, mixed forest, agricultural land, and building structure (figures 13, 14). Many of the GPS fixes occurred within building structures (38 %, appendix 4). Because of low accuracy of the GPS device, these GPS fixes indicated movements that occurred alongside buildings. This was also observed in the video recordings. Based on the distribution of home ranges and observations made by viewing video recordings, cats often followed habitat edges, and seldom used the interior of agricultural land and forest land.

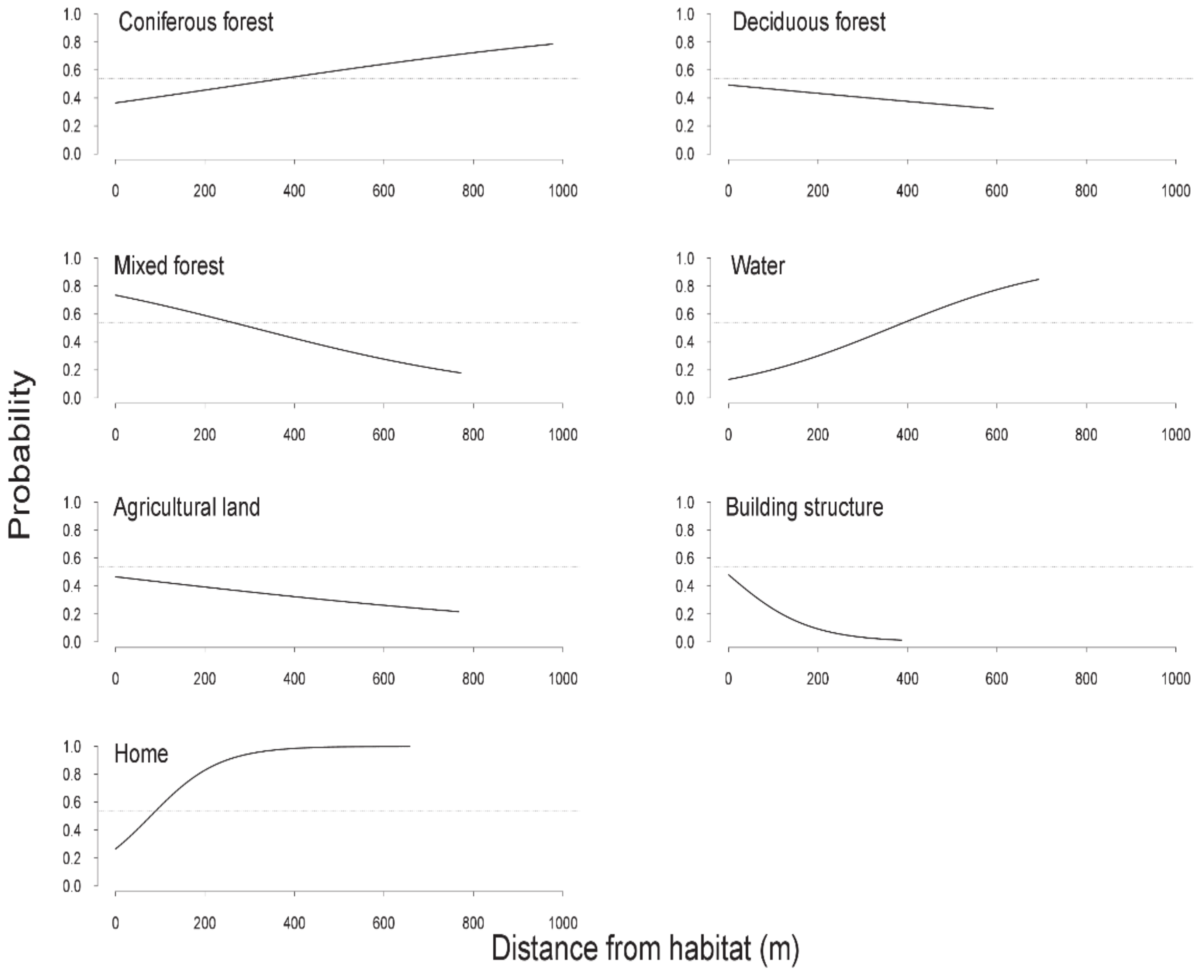

Figure 13. The probability of a plot being a cat GPS fix (1) rather than a random point (0) as a function of distance from habitat, for all the habitats included in the best model. The curves end at the largest distance observed for the particular habitat. The dotted line is the average probability of a plot being a cat GPS fix (0.54).

Figure 14. Map showing habitat distribution based on cat GPS fixes, along with the cats' 95 % kernel home ranges. Only habitats included in the best model are plotted. The spatial positions of the home range and home of cat A and cat J are shown in figure 1.

3.2.2 Hunting habitat selection

Hunting habitat selection included GPS fixes of both failed attacks (attempts) and successful attacks (captures). No strong correlation between variables was found (appendix 5), thus the global model included all ten habitat types (table 12). The best model included only open firm ground. All AIC weight values were very low. No less than 14 models had ΔAICc < 2, and open firm ground was included in all the ten models with lowest AICc value. The best models in the analysis of hunting habitat selection differed greatly from the models in the habitat selection analysis based on all observation fixes, with more parsimonious models generally being better. The probability of a plot being an attack rather than a random plot increased with distance from open firm ground (figures 15, 16). However, the effect of open firm ground on hunting habitat selection was non-significant (table 13). Water was also included in many of the best models, with the probability of a plot being a cat GPS fix increasing with distance from water.

Table 12. The ten models with the lowest AICc values (of the 14 models within ΔAICc < 2) from the analysis of distance from attack locations to habitats (n = 262, cats = 11). K includes the random variable cat ID.

Model	Variables	k	AICc	ΔAICc	AIC weight
1	Coniferous forest + Water + Open firm ground	4	324.5	0.00	0.02
2	Water + Open firm ground	3	324.8	0.30	0.02
3	Deciduous forest + Water + Open firm ground	4	325.0	0.44	0.02
4	Open firm ground	2	325.3	0.80	0.01
5	Coniferous forest + Deciduous forest +Water + Open firm ground	5	325.6	1.05	0.01
6	Coniferous forest + Water + Open firm ground + Home	5	325.8	1.28	0.01
7	Water + Open firm ground + Home	4	326.1	1.53	0.01
8	Coniferous forest + Water + Open firm ground + Building structure +Home	6	326.1	1.54	0.01
9	Open firm ground + Building structure +Home	4	326.2	1.72	0.01
10	Coniferous forest + Open firm ground	3	326.3	1.82	0.01

Table 13. Parameter estimates for variables in the best model of distance between attack locations and open firm ground, the variable included in the best model in the analysis of hunting habitat selection.

Variables	Estimate	SE	z	p
(Intercept)	0.18	0.40	0.44	0.66
Open firm ground	0.004	0.002	1.42	0.16

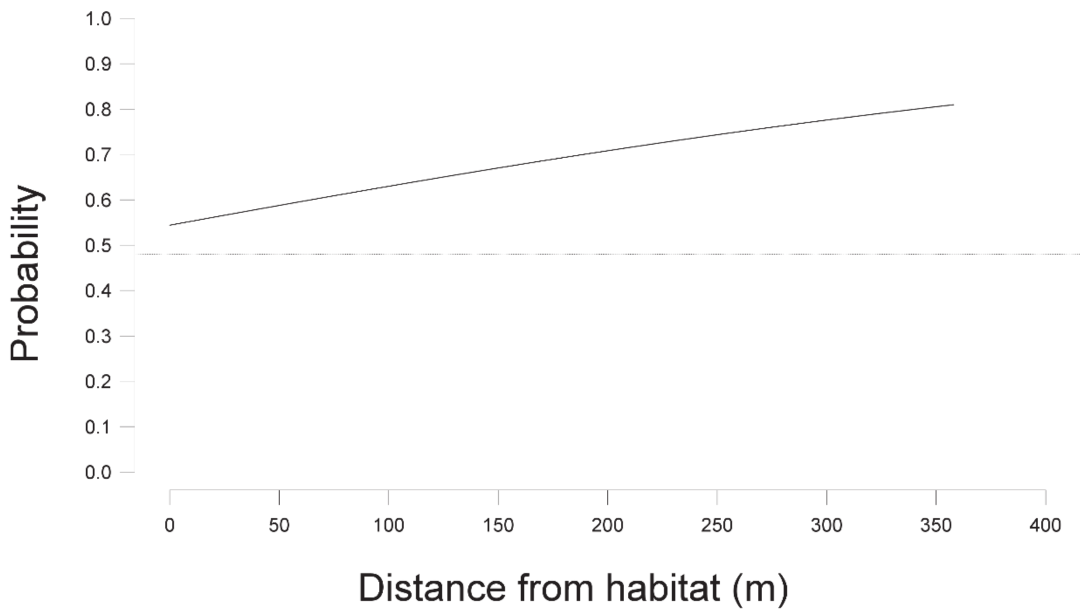

Figure 15. The probability of a plot being an attack GPS fix (1) rather than a random plot (0) as a function of distance from open firm ground. The dotted line is the average probability of a plot being an attack GPS fix (0.48).

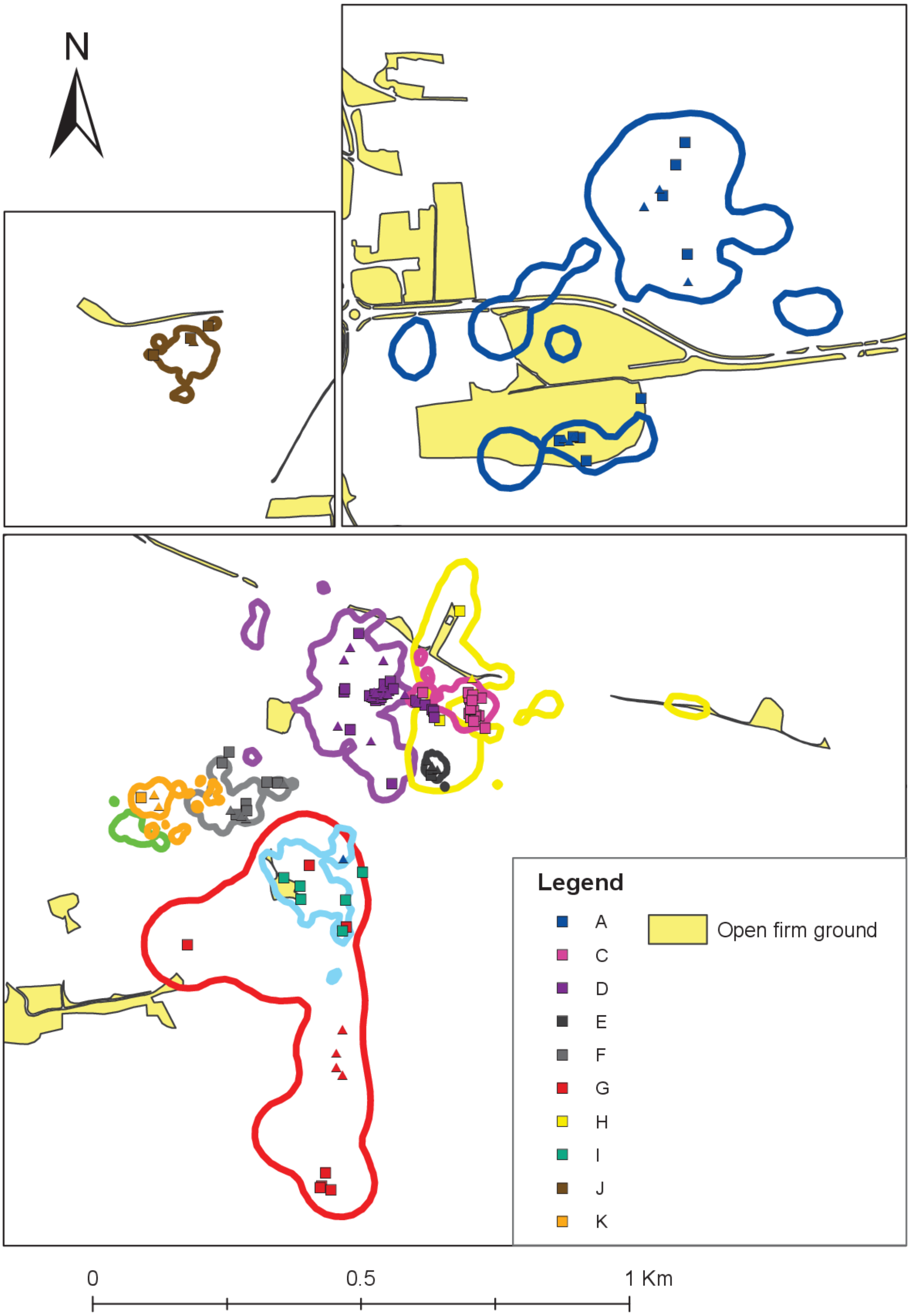

Figure 16. Map showing the location of attempts and captures, and 95 % kernel home ranges, in relation to habitat selection. Only the habitat open firm ground is plotted (the best model). Squares represent capture locations, and triangles represent attempts. The spatial positions of the home range and home of cat A and cat J are shown in figure 1.

Out of the total 130 attacks, 92 of them were located within built-up land habitat (table 14), which was the most utilized habitat type.

Table 14. Number of attacks for each habitat.

Habitat	Number
Coniferous forest	12
Open firm ground	18
Agricultural land	3
Road	5
Built-up land	92
Total	130

No edge habitat was included in this study, but the predation events often seemed to occur on or close to habitat borders, based on predation locations (figure 17) and observations of video recordings.

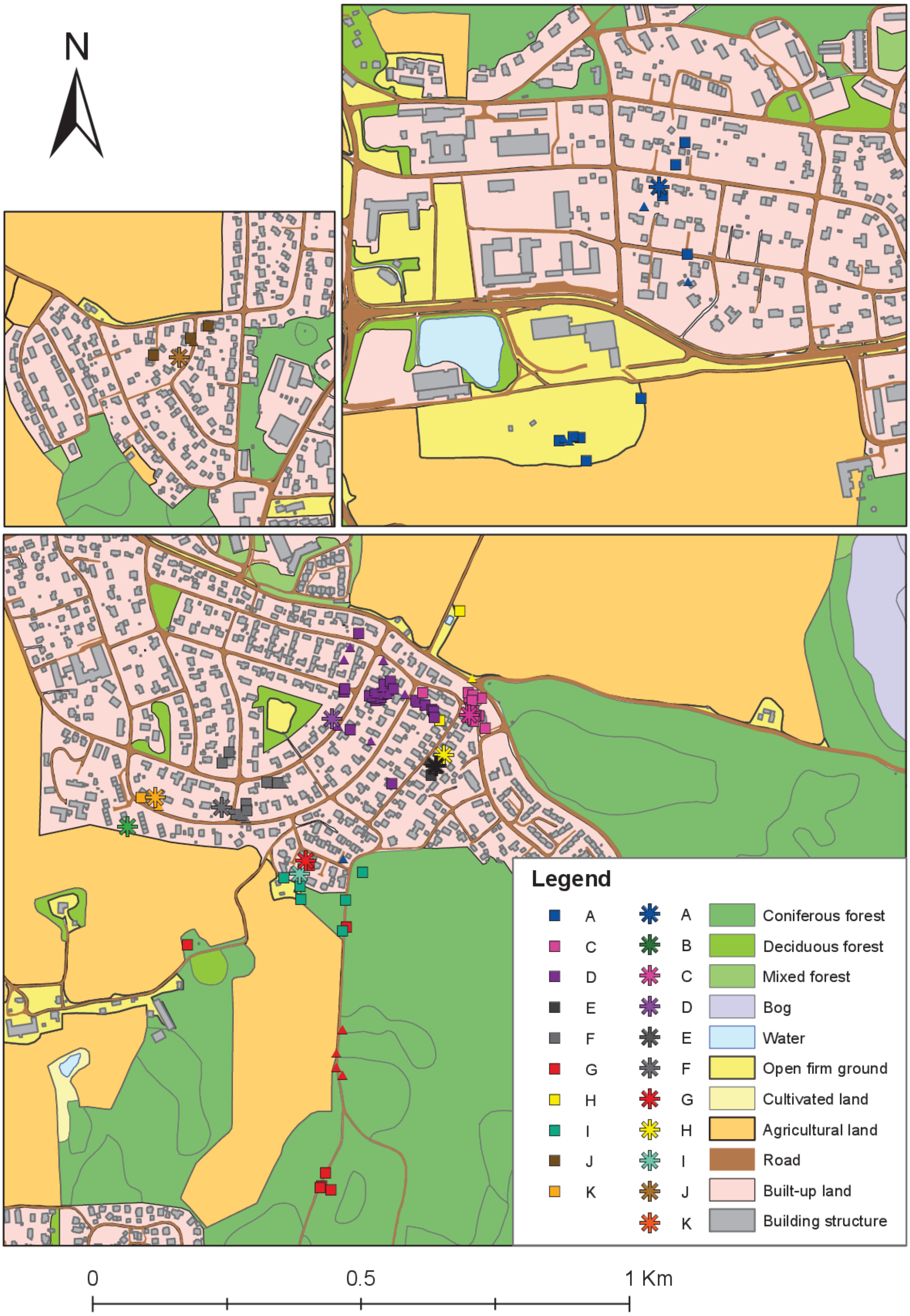

Figure 17. Map showing the location of attempts and captures. All habitats are plotted. Filled squares represent capture locations, and triangles represent attempts. Asterisk marks the house of the cat owners. The spatial positions of the home range and home of cat A and cat J are shown in figure 1.

3.2.3 Capture habitat selection

No strong correlation between variables was found for this analysis (appendix 6), thus the global model included all ten habitat types (table 15). The best model included only the fixed variable open firm ground, i.e. the same variable as for hunting habitat selection. However, for this analysis, open firm ground had a significant effect (table 16). The probability of a plot being a capture rather than a random point increased with distance from open firm ground (figure 18).

Table 15. The ten models with lowest AICc values (of the 32 models within ΔAICc < 2) from the analysis of distance from capture locations to habitats (n = 171, cats = 11). K includes the random variable cat ID.

Model	Variables	k	AICc	ΔAICc	AIC weight
1	Open firm ground	2	264.6	0.00	0.02
2	Building structure + Home + Open firm ground	4	264.8	0.16	0.01
3	Building structure + Coniferous forest + Home + Open firm ground	5	264.8	0.18	0.01
4	Home + Open firm ground	3	264.8	0.18	0.01
5	Coniferous forest + Open firm ground	3	264.9	0.32	0.01
6	Coniferous forest + Open firm + Water	4	265.1	0.55	0.01
7	Coniferous forest + Home + Open firm ground	4	265.5	0.66	0.01
8	Deciduous forest + Open firm ground	3	265.3	0.70	0.01
9	Coniferous forest + Open firm + Home + Water	5	265.5	0.90	0.01
10	Home + Mixed forest + Open firm ground	4	265.6	1.00	0.01

Table 16. Parameter estimates for variables in the best model of distance between capture locations and open firm ground, the variable included in the best model in the analysis of capture habitat selection.

Variables	Estimate	SE	z	p
(Intercept)	0.27	0.45	0.60	0.55
Open firm ground	0.0055	0.0026	2.15	0.031

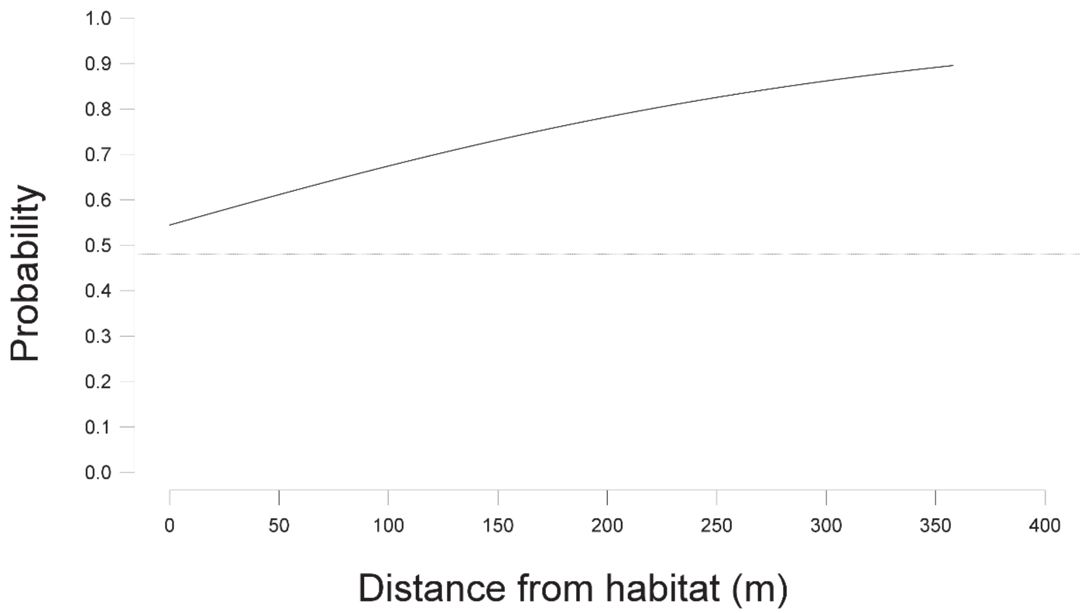

Figure 18. The probability of a plot being a prey capture GPS fix (1) rather than a random point (0) as a function of distance from open firm ground. The dotted line is the average probability of a plot being a prey capture GPS fix (0.48).

3.3 Activity

3.3.1 General activity

The best model (M_6) included all variables, including the 1st, 2nd, and 3rd harmonic components, their fundamental period (24 h), as well as sex (table 17), even though sex was non-significant (table 18). The predicted distance moved was highest at midnight (the 0-hour block) and lowest in the afternoon (the 17-hour block) (figure 19). The distance moved per hour block, as function of time of day, indicated a diel pattern, with a peak in activity around midnight. Sex was also included in the model, with the best model having a lower AICc value than the second best model (M_2) that did not include this variable. However, the order of the best ranked model in the analysis, together with the estimates from the best model, suggested that the time aspect was more important than gender (table 18).

Table 17. The eight models in the analysis of general activity distance moved per hour block (n = 877, cats = 11). K includes the random variable cat ID.

Model	K	AICc	ΔAICc
M_6	9	12697.3	0.00
M_3	8	12705.2	7.92
M_5	7	12712.2	14.95
M_2	6	12720.1	22.84
M_4	5	12733.7	36.43
M_1	4	12741.6	44.37
M_7	3	12791.0	93.74
M_0	2	12799.0	101.72

Table 18. Parameter estimates for variables in the best model in the analysis of distance (m) moved per hour block (n = 877, cats = 11). The estimate for sex is given for males relative to females.

Fixed effects	Estimate	SE	t	p
(Intercept)	764.36	42.51	17.98	<0.0001
I(cos(2 * pi * Hour/24))	92.19	17.59	5.24	<0.0001
I(sin(2 * pi * Hour/24))	54.38	17.80	3.05	0.0023
I(cos(2 * 2 * pi * Hour/24))	49.22	17.10	2.88	0.0041
I(sin(2 * 2 * pi * Hour/24))	13.62	17.65	0.77	0.44
I(cos(3 * 2 * pi * Hour/24))	4.40	17.00	0.26	0.80
I(sin(3 * 2 * pi * Hour/24))	-33.15	16.78	-1.98	0.049
Sex	22.80	53.34	0.43	0.67

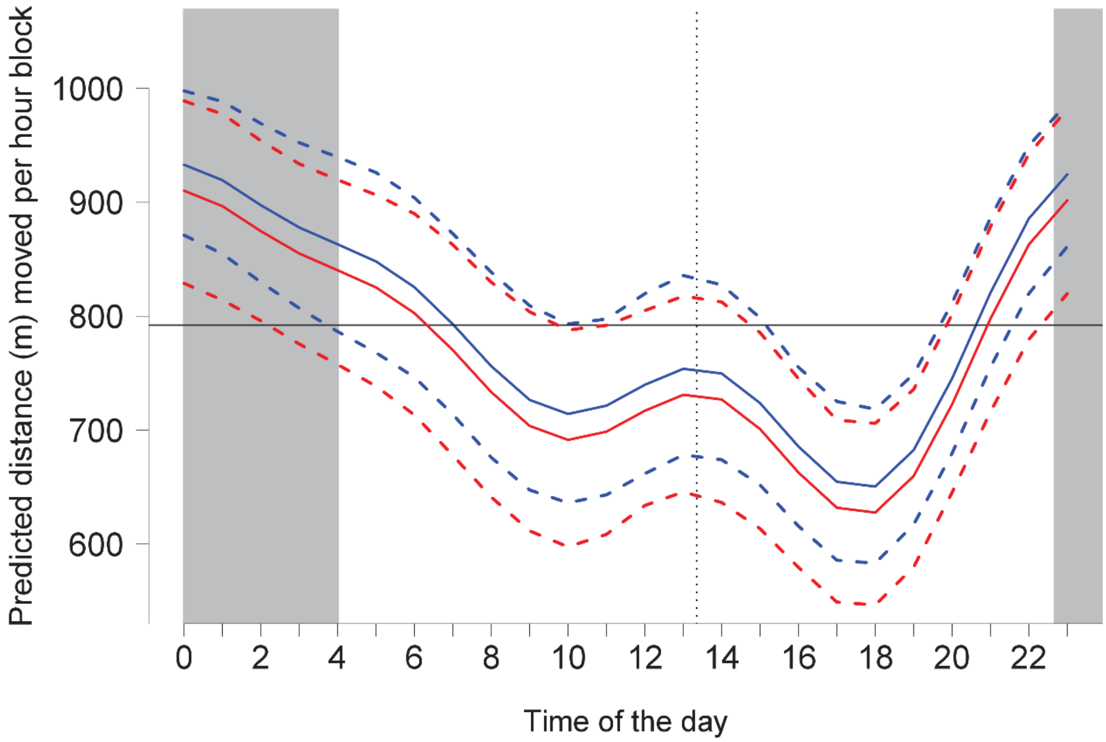

Figure 19. The best model from the analysis of predicted distance (m) moved per hour block as a function of the time of the day and sex, showing the modelled activity of the cat (fitted line in solid, and upper and lower 95% Cl in dashed line), for females (red) and males (blue). The horizontal black line represents the predicted average distance moved per hour block during a 24 period (MESOR). Grey area denotes the time after sunset (22.41 hours) and before sunrise (04.00 hours). The vertical dotted line represents solar noon (13.21 hours). Parameter estimates given in table 18 (n = 877, cats = 11).

3.3.2 Hunting activity

A total of 62 out of the recorded 877 hour blocks included an attack. In the analysis of factors affecting the probability of an attack per hour block as function of time of day, the best model was M_2 (tables 19, 20), including the 1st and 2nd harmonic components and their fundamental period (24-h). M_3 had lower AICc value but was a more complex model, including a 3rd harmonic component. Sex was not included in the best model. The probability of an attack peaked at hour block 1 (figure 20), close to the peak in general activity.

Table 19. The eight models in the analysis of probability of an attack occurring within an hour block (n = 877, cats = 11). K includes the random variable cat ID.

Model	k	AICc	ΔAICc
M_3	8	399.1	0.00
M_2	6	400.8	1.71
M_6	9	401.0	1.90
M_5	7	402.7	3.59
M_1	4	404.6	5.50
M_4	5	406.5	7.41
M_0	2	438.2	39.11
M_7	3	440.1	40.95

Table 20. Parameter estimates for variables in the best model in the analysis of hunting activity per hour block (n = 877, cats = 11).

Fixed effects	Estimate	SE	z	p
(Intercept)	-3.23	0.32	-10.21	<0.0001
I(cos(2 * pi * Hour/24))	0.92	0.26	3.48	0.00051
I(sin(2 * pi * Hour/24))	0.52	0.31	1.71	0.087
I(cos(2 * 2 * pi * Hour/24))	0.62	0.24	2.60	0.0094
I(sin(2 * 2 * pi * Hour/24))	0.28	0.25	1.10	0.27

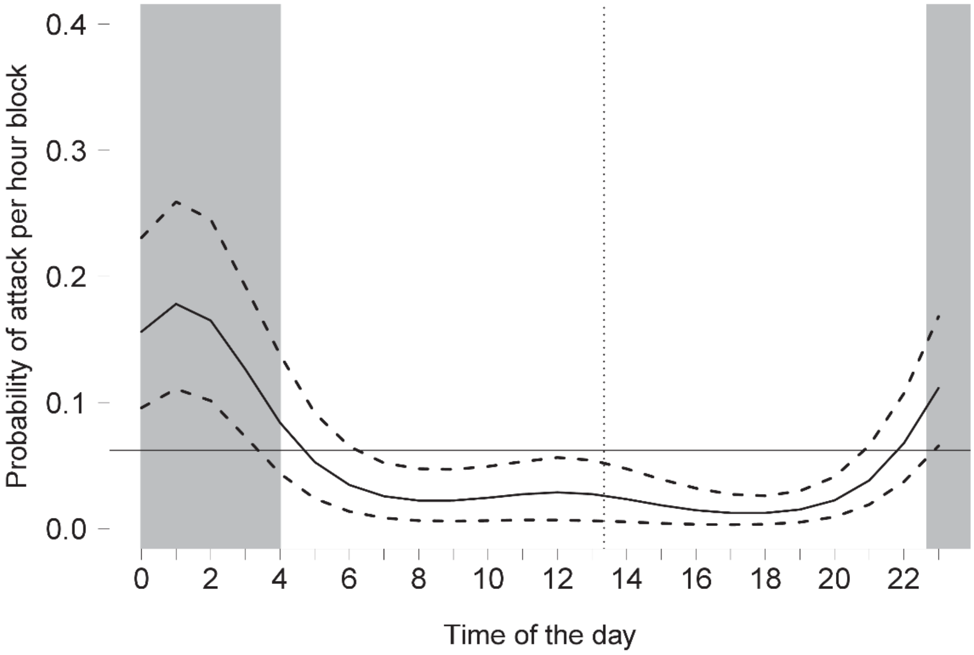

Figure 20. The best model of the probability of attack per hour block as a function of the time of the day, showing the modelled activity of the cat (fitted line in solid and upper and lower 95% Cl in dashed line). The horizontal black line represents the average probability of attack per hour block (MESOR). Grey area denotes the time after sunset (22.41 hour) and before sunrise (04.00 hour). The vertical dotted line represents solar noon (13.21 hour). Parameter estimates given in table 20 (n = 877, cats = 11).

3.3.3 Capture activity

A total of 21 out of the 877 hour block included a prey capture. In the analysis of factors affecting the probability of capture per hour block, as a function of the time of day, the best model was M_2 (table 21), which included 1st and 2nd harmonic components and their fundamental period (24-h) (table 22). The results were very similar to the results from the analysis of the probability of attacks. The probability of capture had a peak at hour block 1 (figure 21), the same as for hunting activity.

Table 21. The eight models in the analysis of probability of a prey capture occurring within an hour block (n = 877, cats = 11). K includes the random variable cat ID.

Model	k	AICc	ΔAICc
M_2	6	343.0	0.00
M_3	8	344.4	1.36
M_6	9	345.0	1.95
M_1	4	345.2	2.15
M_5	7	346.3	3.31
M_4	5	347.1	4.09
M_0	2	372.1	29.08
M_7	3	374.1	31.06

Table 22. Parameter estimates for variables in the best model in the analysis of capture activity per hour block (n = 877, cats = 11).

Fixed effects	Estimate	SE	z	p
(Intercept)	-3.55	0.39	9.034	<0.0001
I(cos(2 * pi * Hour/24))	0.89	0.29	3.048	0.0023
I(sin(2 * pi * Hour/24))	0.72	0.34	2.15	0.031
I(cos(2 * 2 * pi * Hour/24))	0.57	0.26	2.16	0.030
I(sin(2 * 2 * pi * Hour/24))	0.16	0.27	0.58	0.57

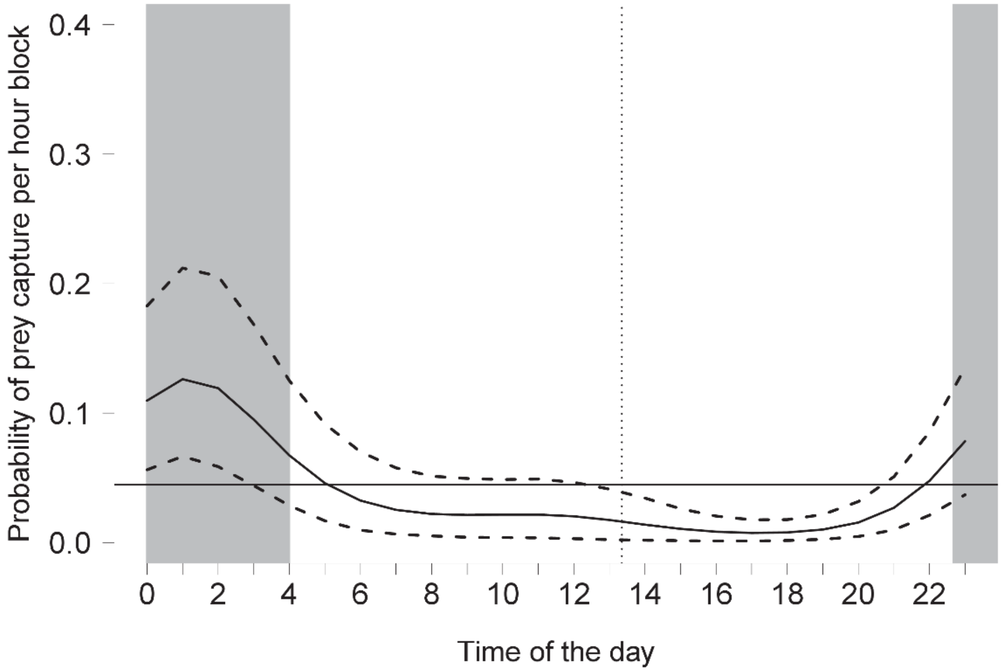

Figure 21. The best model of the probability of prey capture per hour block as a function of the time of the day, showing the modelled activity of the cat (fitted line in solid, and upper and lower 95% Cl in dashed line). The horizontal black line represents the average probability of capture per hour block (MESOR). Grey area denotes the time after sunset (22.41 hours) and before sunrise (04.00 hours). The vertical dotted line represents solar noon (13.21 hours). Parameter estimates given in table 22 (n = 877, cats = 11).

3.4 Predation rate

Attack frequency varied greatly between the cats (range 0-0.58 attacks/h), with a mean of 0.15 ± 0.052 attacks/h (table 23). Capture frequency varied in a similar way (range 0-0.36), with a mean of 0.10 ± 0.033 captures/h. The success rate varied greatly between cats (range 0.20-0.86), with a mean of 0.57 ± 0.11.

Table 23. Predation frequency, capture frequency, success rate, and total number of predation events for the study period, for each cat studied.

Cat ID	Number of attacks	Number of captures	Success rate	Attack frequency (number of attacks/h)	Capture frequency (number of captures/h)
A	15	9	0.60	0.25	0.15
B	0	0	-	0.00	0.00
C	23	17	0.74	0.28	0.20
D	42	26	0.62	0.58	0.36
E	5	1	0.20	0.04	0.01
F	12	8	0.67	0.11	0.07
G	16	10	0.63	0.29	0.18
H	3	2	0.67	0.06	0.04
I	7	6	0.86	0.12	0.10
J	4	3	0.75	0.04	0.03
K	3	1	0.33	0.04	0.01
Total	130	83	-	-	-

A total of 130 attacks (83 captures and 47 attempts), were recorded (table 24, appendix 7). Of the 83 captures, 67 were insects, making up the largest share of the total number. Of these, 20 were Lepidopterans, including two prey items of Sphingidae, six owlet moths (Noctuidae), and twelve moths (Heterocera). In addition to butterflies, one grasshopper (Caelifera) and one crane fly were identified. A total of 45 prey items were not possible to identify to any lower level than insect. Ten mammals were captured, one common shrew, three wood mice, four field voles, and two rodents only possible to identify to Muridae. Six avian prey situations were identified, of these one was a raid of a bird nest including two unidentified nestlings. The other five avian prey items were identified as one thrush (*Turdus*), two great tits, and two non-identified birds. The average capture rate for vertebrate and invertebrate prey was 0.023 ± 0.0073 and 0.082 ± 0.032, respectively.

Table 24. Recorded attacks, separated on recorded prey captured and recorded attempts.

Type	Number
Insects	67
Birds	6
Mammals	10
Attempts	47
Total	130

3.5 Home-brought prey

None of the prey items were presented for the owners. Ten prey items were moved after capture by seven of the eleven cats (table 25). The distance these items were moved ranged from 8 m to 286 m. All prey items caught in built-up land were dropped in the same habitat. Two prey items were moved from another habitat (agricultural land and road) to built-up land. Some of the prey items were brought fairly close to home (figure 22). By viewing the video recordings, several prey items were observed dropped in locations with cover, such as under cars, under trampoline and in shrubs (table 25).

Table 25. Prey items moved after capture, with cat ID and the prey group (I = insect, B = bird, and M = mammal). D_1 is distance the prey item was moved, D_2 is distance from the capture location to the cat's home, D_3 is distance from the drop site to the cat's home, and D_4 is distance the prey item was moved relative to the cat's home (negative value indicating movement away from home). $Habitat_1$ is habitat in which the prey item was captured, and $habitat_2$ is habitat in which the prey was dropped.

Cat ID	Prey group	D_1 (m)	D_2 (m)	D_3 (m)	D_4 (m)	$Habitat_1$	$Habitat_2$	Physical structure of drop location
G	B	7.5	3.2	1.2	2.0	Built-up land	Built-up land	Close to wall
I	M	41.0	90.9	115.7	-24.8	Road	Coniferous forest	Unknown
J	M	32.9	37.7	10.0	27.7	Built-up land	Built-up land	Unknown
I	M	44.5	36.3	0.0	36.3	Coniferous forest	Home	Close to wall
H	M	285.6	262.7	8.5	254.2	Agricultural	Built-up	Under trampoline
C	I	36.9	31.4	24.9	6.5	Built-up land	Built-up	Close to wall
F	B	31.3	38.2	6.5	31.7	Built-up land	Built-up land	Under car
A	M	31.3	399.5	370.7	28.8	Open firm ground	Open firm ground	In shrub
I	M	16.5	11.7	18.1	-6.4	Agricultural	Built-up land	Under trampoline
A	B	118.9	79.1	151.2	-72.1	Road	Built-up land	In shrub

Only one insect (Sphingidae) out of the 67 captured was moved (table 26). In contrast, three of six avian prey items were moved. Of ten mammalian prey items, six were moved. The direction the prey items were moved differed, and some were moved away from home (table 26, figures 22, 23). Mammalian prey were on average brought closer to home, while avian prey were on average moved further away from home than the capture site.

Table 26. Average distance prey items in each prey group were moved, including and excluding prey items that were not moved, respectively. In addition, average distance prey items were moved relative to home for each prey group.

Prey group	Number of prey items moved	Total number of prey items	Range moved	Average distance moved (m) per prey item if moved	Average distance moved (m) per prey item	Average distance moved (m) per prey item relative to home if moved
Insects	1	67	0-36.9	36.9	0.6	6.5
Birds	3	6	0-118.9	52.6 ± 33.9	26.8 ± 19.2	-12.8 ± 30.9
Mammals	6	10	0-285.6	75.3 ± 42.2	45.2 ± 27.3	52.6 ± 41.5

Figure 22. Maps showing the moved prey items, direction indicated by arrow, for cat C, F, H, I, and J. Filled squares represents capture locations, open squares are drop locations, and triangles represents attempts.

Figure 23. Maps showing the moved prey items, direction indicated by arrow, for cat A and J. Filled squares represent capture locations, open squares are drop locations, and triangles represents attempts.. For legend, see figure 22.

The probability of a prey item being moved was affected by whether the prey type was a bird or an insect, with a significantly less probability that the cat moved insect prey (table 27). No difference was observed for avian and mammalian prey. A significant difference was also found between mammals and insects, with the probability that the cat moved a prey being significantly higher for mammals (table 28).

Table 27. Parameter estimates for variables in the analysis of the probability of prey item being moved as a function of prey type (n = 83, cats = 11). The estimates are given relative to bird.

Fixed effects	Estimate	SE	z	p
(Intercept)	-0.05	1.18	-0.04	0.97
Insect	-5.19	2.02	-2.57	0.010
Mammal	0.43	1.30	0.33	0.74

Table 28. Parameter estimates for variables in the analysis of the probability of prey item being moved as a function of prey type (n = 83, cats = 11). The estimates are given relative to mammal.

Fixed effects	Estimate	SE	z	p
(Intercept)	0.38	1.08	0.35	0.72
Bird	-0.43	1.30	-0.33	0.74
Insect	-0.62	1.91	-0.29	0.0033

4. Discussion

4.1 Home range

The calculated home range sizes in this study were relative small, with an average of 5.4 ha 99 % MCP home ranges. The recorded home ranges for the domestic cat home ranges have varied greatly between study areas, and ranges from 0.27 ha (99 % MCP) in Jerusalem, Israel, to 170 ha (95 % MCP) in Victoria, Australia have been observed for feral cats (Turner & Bateson 2000). Home ranges may also vary greatly between cats in the same area (Barratt 1997). House cats living in residential areas generally tend to have smaller home range sizes than other domestic cats (Das 1993; Barratt 1997). A study including house cats in Canberra, Australia, calculated a mean of 2.34 ha 95 % MCP home ranges, while a mean of 112 ha 99 % home range was observed in Illinois, USA (Turner & Bateson 2000). Home range size has been found to be negatively affected by cat density, as well as food abundance (Turner & Bateson 2000). I did not measure food abundance, but all cats were fed regularly. There exist no data on cat density for my study area, but with c. 767 000 cats in Norway (FEDIAF, The Pet Food Industry 2014) and a population of c. 5 million people, an estimate of 3000 cats in the Ås would be reasonable, considering that Ås municipality has 19 000 inhabitants. My study exclusively included house cats that were regularly fed and living in a residential area likely to have relatively high cat-density, thus, my results of small home ranges is in accordance with Turner & Bateson (2000).

The cats' home range sizes were best explained by the variable age, with home range size declining with age. To my knowledge, the effect of age on home range size of the domestic cat has not been studied. However, Kendal & Lay (2008) found that cat activity declined with increasing age. In addition, cats older than 12 years had increased probability of experiencing cognitive dysfunctions, including dementia, and subsequently may have reduced their home range size (Pan et al. 2013). Three of the eleven cats in my study were old cats (13, 14, and 15 years), and these were among the cats with the smallest home ranges. In studies of hunting behavior in domestic cats, age only accounted for a small proportion of the difference in number of home-brought prey items between individuals (Churcher & Lawton 1987). It is likely that hunting activity relates to general activity, and further to home range size. This suggests that the home range size declines with decreasing activity, as age increase. However, whether the home range size would decline in a steady manner, or would drop when the cats reached a certain stage in the aging process, is unsure. In my study, only one cat between seven and 13 years was included, and a larger sample size of medium-aged cats is required to answer this question.

I found no effect of sex on total home range size. A trend was found for sex on home range size per bout per cat, with males having larger home ranges. Studies on domestic cats' home range sizes have often focused on variation between the sexes. Most studies have found that males typically have larger home range sizes than females (Langham & Porter 1991; Turner & Bateson 2000). Male cats have been observed to often roam larger distances to locate fertile females, while females tend to concentrate their roaming on smaller areas to secure access to food (Turner & Bateson 2000). Males' home range sizes have found to be up to ten times larger home ranges than females (Turner & Bateson 2000). Yet, other studies have failed to find any effect of age on home range size (Page et al. 1992; Horn et al. 2011). My findings fail, as Horn et al. (2011), to find a significant effect of sex on home range size, but one should not make strong conclusions considering the small sample size for females (4).

Overlapping home ranges were observed between males, and between males and females. No particular overlapping between female home ranges was recorded. Overlap between domestic cats' home ranges have been found to differ between females and males (Turner & Bateson 2000), with overlap occurring between sexes and between males, but female home ranges not tending to overlap (Barratt 1997). My results are in accordance with what Turner & Bateson (2000) and Barratt (1997) found, yet I only observed a weak pattern of differences between males and females. All the cats in my study were neutered, which is known to cause the biological differences between males and females to fade (Turner & Bateson 2000). Thus, the lack of significant difference in home range size, and only a weak observational difference in overlapping, between males and females, were probably an underestimation of the natural pattern.

I found no effect, of neither body mass or whether the owner had installed cat flap, on home range size. It may be reasonable to assume that house cats that can move between indoors and outdoors as they please are more active, by having the opportunity to spend time outside when they like to. However, whether or not the cat owner had installed a cat flap had no effect on home range size in my study. To my knowledge, no study have included the effect of cat flap on home range sizes of the domestic cat. In my study, only three owners had cat flap installed, and the small sample size may be the cause for the lack of effect.

4.2 Habitat selection analyses

4.2.1 Habitat selection

The probability of a plot being a cat GPS fix rather than a random plot increased with distance to coniferous forest. For deciduous and mixed forest, the opposite was observed. To my knowledge, no study has addressed habitat selection of domestic cats regarding forest type. A study in mid-Europe found that wild cats spent much more time in forested areas than what would be expected by random choice (Klar et al. 2008). Marks & Duncan (2009) found that feral cats were more likely to visit camera traps in forest interior than camera traps in more open landscape and edge-habitat, as did Oehler & Litvaitis (1996) and Crooks & Soulé (1999). For American marten (*Martes americana*) in Maine, USA, vertical and horizontal structures were more important habitat components in forest land than tree age and plant species composition, while there was no effect of coniferous versus deciduous forest type (Chapin et al. 1997). In my study area, coniferous forests were primarily forest plantations, while the small patches of deciduous and mixed forest were primarily edge areas between human-altered landscape types. Consequently, the structure components were quite different in coniferous forest, which probably offered less heterogeneous structure and cover, than the two other forest types. Deciduous and mixed forest have a higher diversity of avian and mammalian species than coniferous forest (Willson & Comet 1996; Niedziałkowska et al. 2010), and offer more potential prey for the cats. The different uses of forest types were not observed in my predation habitat analyses, and I did not record any attacks in deciduous or mixed forest. Thus, the observed preference for deciduous and mixed forest may as well be due to their edge-area ratio, suggesting that cats prefer to spend time in locations with cover, as that they prefer the habitats based upon prey abundance.

The cats in my study preferred agricultural land, with decreasing probability of a plot being a cat GPS fix rather than a random plot with distance from this habitat. Warner (1985) found that domestic cats showed disproportionally low use of cultivated and agricultural land (Warner 1985). Doherty (2015) found that agricultural land and grasslands were avoided by feral cats. Not all cats in my study lived close to agricultural land, but those that did, utilized this habitat. However, the cats usually moved along the edge of agricultural lands. My results were in contrast with Warner (1985). However, most agricultural lands in my study area were, for a large extent of the study period, covered with wheat, barley and tall grass, which may have contributed with cover. In addition, video recordings showed that cats often moved along the edges, and did not use the interior areas. This was also reflected in the shapes of the home ranges.

I found that the probability of a plot being a cat GPS fix increased rapidly with the distance from home, up to 200 m. After 200 m from home, the effect of distance faded, which indicate that cats going on excursions move in a decisive manner toward preferred areas, and do not linger in close proximity to home. Leyhausen (1979) and Schär & Txchanz (1982) found that cats tended to travel more or less directly to their preferred hunting grounds when leaving their household. Turner & Bateson (2000) supported this, stating that when the cat departed for a hunt, it moved along roads or paths without many stops, to an area that differed from the surroundings, and then started to search for prey. My study was in accordance with this. However, the home habitat is not perfectly suited for this type of analysis. Because all indoor observations are removed, the cat only obtain a 0 m distance to home due to the error margin of the GPS device, or that the cat is located below the eaves of the roof, below the terrace or a similar structure included in the home polygon. Consequently, the result observed in my study may be due to the unbalance caused by the nature of the test.

The probability of a plot being a cat GPS fix rather than a random point decreased with distance from building structure, most steeply the first 200 m. Cats were observed to move alongside buildings when moving to new locations. Many of the GPS fixes were located inside building structures. This was a result of the GPS device not being fully accurate, recording some of the plots inside building structures, however, this indicates that the cats moved very close to the outside of the walls. To my knowledge, no study has examined the house cat's preference for staying close to building structures, but it is suggested that building structures are habitat components that may act as shelter, as well as decreasing direct visibility (Doherty et al. 2015). Barratt (1997) found that available cover, such as fences, bushes, and tall grass, primarily determined cats' choice of routes during day. It is likely that houses do this as well. In addition, properties in the study area often consist of flowerbeds, bushes and similar structures close to the buildings. This may make it preferable for cats moving between hunting grounds, as it offers more cover than roadsides and open firm ground. Calhoon (1989) found that feral cats used abandoned buildings to seek shelter from rainfalls, and it is likely that building structures offer shelter from rain and wind. Cats avoided home in this study, but preferred to stay close to building structures, which indicates that food or contact with cat owners did not induce this preference.

Cats seemed to avoid water, with the probability of a plot being a GPS fix increasing with distance to water. To my knowledge, no studies have included water in habitat selection analysis in the domestic cat. There was very little water in close proximity to the cats' households. Because none of the cats in this study sought out areas with water, the results suggest that they had no preference for this habitat. However, because of little amount of water bodies available, it is not possible to assess whether cats intentionally avoided water.

4.2.2 Predation habitat selection

The probability of a plot being an attack or a prey capture GPS fix, rather than a random plot, increased with distance to open firm ground. A study from South Africa found that leopards (*Panthera pardus*) preferred to hunt in habitats with medium cover (Balme et al. 2007), possibly because denser habitats reduced prey detectability. Lozano et.al (2003) found that feral cats preferred to hunt in open habitats, and used more dense habitats as shelter. Doherty (2015) observed that domestic cats' hunting frequency was lower in dense habitats, as detectability was decreased. Cats may prefer more open areas that differ from the surroundings, such as recently harvested fields, new forest clearing or mown pastures, in which the lack of cover facilitate detectability of prey (Turner & Bateson 2000). Domestic cats rely on the same sensory systems as other felids; acoustic and visual cues (Turner & Bateson 2000), which are challenged in very dense habitats.

Simultaneously, as other felids, the domestic cat exercises hunting strategies which require crypticity for success (Kleiman & Eisenberg 1973).The Eurasian lynx (*Lynx lynx*) preferred habitat edges when hunting (Sunde et al. 2000), where roe deer (*Capreolus capreolus*) is known to be abundant (Tufto et al. 1996). Domestic cats may in a similar way prefer to spend time in the edges of habitats due to larger prey availability and possibly increased hunting success, as edge habitats may provide a trade-off between cover and visual detection of prey (Leopold 1987). Feral cats in Albany, USA, was found to capture 80 % of their prey either in gardens or in the first 10 m of forest (Kays & DeWan 2004). Many of the attacks in my study were observed close to habitat edges, in accordance with the findings of Leopold (1987) and Kays & Wan (2004). Many of the prey items in my study were captured in build-up land, which included both open grounds and cover. My results thus suggest that the cats preferred to hunt in habitats with some extent of cover, avoiding open habitats unfavorable for hunting. The lack of a positive effect of any habitat in the tests based on predation events is likely due to the small sample size. A study including more predation events is needed to better understand a cat's preference of hunting grounds.

No habitat type was included in both the best model for habitat selection and the best models for predation habitat selection. The lack of correlation between where the cat spent most of its time and were it hunted may be due to the differences in the sample sizes of the tests. The habitat selection analysis was based on a large dataset, while the hunting and capture habitat selection analyses consisted of few data points.

4.3 Activity

4.3.1 General activity

I found that cats moved longer distances than average between sunset and sunrise, suggesting a nocturnal diel pattern. Guggisberg (1975) and Turner & Bateson (2000) have suggested that domestic cats tend to be the most active during night, like their assumed ancestor, the African wildcat *(Felis silvestris libyca*). Barratt (1997) recorded larger nocturnal than diurnal home ranges. Feral cats have been observed to move over larger areas during night (Langham & Porter 1991). Other studies in feral cats have observed highest activity at sunrise and sunset (Jones & Coman 1982), with lowest activity during midday (Konecny 1987), suggesting a crepuscular diel pattern. My study is in accordance with the majority of studies on diel activity pattern in the domestic cat (Turner & Bateson 2000), suggesting a nocturnal pattern. Prey availability have been observed to affect diel pattern (Turner & Bateson 2000), which it also may have done in my study, considering the correlation between general and activity predation activity. Barratt (1997) found that the cat's choice of routes during day was primarily determined by available cover, such as fences, bushes, and tall grass, while movement during the night was mainly influenced by the location of favored hunting sites. These findings indicate that cats seek cover to a greater extent during the day. However, it may also suggest that cats hunt differently during the day, as avian prey are more accessible and favored, and require a less mobile hunting strategy. Anyway, both explanations would lead to reduced movement speed, and thus lower general activity.

Sex was included in the best model explaining general activity, with higher activity for males than females, yet this had a non-significant effect. Males are thought to be more active and move further than females (Turner & Bateson 2000), as indicated in the larger home ranges. However, in my study, no significant effect of sex was recorded in neither general activity nor home range size, which suggests that females move as much as males.

4.3.2 Predation activity

Hunting and capture activity showed a similar diel pattern as general activity, with a peak during the darkest hours. Hunting activity is likely to be correlated with general activity, because the more time the cat spend roaming, the more likely it is to detect prey items (Turner & Bateson 2000). The domestic cat may also hunt during daytime. Nowadays, as an adaption of living close to diurnal humans, the domestic cat is showing a shift towards a more diurnal activity pattern, resulting in more attacks during daytime (Turner & Bateson 2000). George (1974) and Barratt (1997) found that domestic cats captured 50 % of their prey during daytime; mainly birds in the morning, reptiles in the afternoon and mammals in the evening. I did not examine prey choice as a function of time of the day due to the low sample size, but, as Turner & Bateson (2000) argued, I found that birds were caught in the morning.

I found that both mammals and insects were usually caught during nighttime. Few attacks were recorded during daytime, suggesting that avian prey were not much hunted. This resulted in highest recorded hunting activity during the darkest hours, showing very similar diel pattern as general activity. Consequently, my results suggest that cats both hunt and move the most during nighttime, and may be a result of prey availability, as both mammals and insect, the most frequently captured prey groups, were much more hunted during nighttime than daytime.

4.4 Predation rate

The recorded capture rate in my study was on average 0.10 ± 0.033 per hour block. Studies examining stomachs of shot feral cats found that 20-40 % of the examined cats had recently captured prey (Turner & Bateson 2000). House cats are successful hunters (Braastad 2012), yet they often have lower hunting frequencies than other domestic cats (Turner & Bateson 2000). Studies of hunting behavior in the domestic cat have often been conducted by recording home-brought prey (Churcher & Lawton 1987; Turner & Bateson 2000; Woods et al. 2003). Through a 5-month period, Woods et al. (2003) recorded an average of 16.6 prey captures per cat, based on home-brought prey. Churcher & Lawton (1987) and Barratt (1997) recorded 14 and 10 home-brought prey items on average for 12 months, respectively. To my knowledge, few studies have calculated number of prey captured per hour roaming, because little data on time spent roaming have been recorded. It is not possible to compare the capture rate recorded in my study to studies that have not recorded the time cats spent roaming.

The only study, to my knowledge, that have mounted cameras on domestic cats is Loyd et al. (2013), which did so in northeastern Georgia, USA. They found that only 30 % of a total of 55 house cats made prey captures. They recorded 36 captures during a total of 2090 h video recording, giving a capture rate of 0.017, which is lower than in my study. However, 31 prey items of these 36 were vertebrates, with reptiles making up the largest share (14). Consequently, they observed a capture rate of vertebrate prey was 0.015. In my study, capture rate for vertebrate prey was 0.023. Thus, the discrepancy in capture rate between my study and Loyd et al. (2013) is mainly due to the larger amount of insect prey in my study. When considering only vertebrate prey, my study was in accordance with Loyd et al. (2013), both suggesting that the domestic cat's capture rate is generally low.

The predation success in my study was high, with a mean of 0.57 ± 0.11. Studies that have observed hunting cats, found that the number of required attacks to capture a prey item on average ranged from 3 to 5 per captured prey, depending on prey group, with lowest success rate for rodents and rabbits (Turner & Bateson 2000). The discrepancy between previous studies and my study is likely to mainly be due to the use of different study methods.

4.5 Home-brought prey

Given the total number of mammalian prey (10) and avian prey (6), and that none of these were presented to the owner, it is possible to state that at most one in seventeen prey could have been presented (6 %). Recording prey brought to the owner have until recently been the only used method to assess domestic cat's capture frequency (Turner & Bateson 2000). Thus, the capture frequency of cats may have been grossly underestimated. Loyd et al. (2013) was the first to mount cameras on cats in order to examine capture rate in domestic cats. Loyd et al. (2013) found that less than a quarter of the cats' captures were brought back to the household. The proportion of returned prey may, among other factors, depend on the cats' reproduction state, as female cats with kittens tend to bring more prey back to the household (Turner & Bateson 2000). Meister (1986) found that cats with kittens brought back far more prey than those without. Another factor the type of prey the cats capture. In my study, insects was the most frequently captured prey group. However, only one insect was brought home. Consequently, it is likely that studies estimating capture rate based on home-brought prey underestimate the number of insect prey, which may make up a large proportion of the total number of captured prey by domestic cats, based on my study.

Even though no prey item were presented for the owner in my study, mammalian prey items were, on average, moved and dropped closer to home than the capture location. Some prey items were dropped fairly close to households. By viewing video recordings, prey items were observed to be dropped under cars, trampolines, and in shrubs. To my knowledge, no study has examined where prey items that are not brought home are being dropped. Cats may carry captured prey to more central areas of their home range in order to keep it for themselves. By dropping prey under solid structures, such as cars and trampolines, they may reduce the risk of theft by others, for example corvids (Corvidae).

4.6 Data bias

Domestic cats are a diverse group, and include house cats, farm cats, and feral cats. I studied the house cat, which makes up c. 60 % of all domestic cats in Norway (Eriksen, 2014). Other breeds are likely to show slightly different behavior. In addition, cats that depend less on households in terms of food and shelter, such as farm cats and feral cats, have been shown behavior that differ greatly from behavior observed in house cats (Barratt1997; Turner & Bateson 2000). Horn et al. (2011) found that house cats and feral cats differed in home range sizes, habitat selection and activity patterns, suggesting that my findings on house cats cannot be extrapolated to feral cats.

My study period lasted for less than two months, covering early summer. Domestic cats have been found to adjust their diel pattern according to seasonal changes and weather (Langham & Porter 1991; Alterio & Moller 1997). The cats are less active during autumn and winter, and have lower capture rate during winter than the rest of the year (Jones & Coman 1982; Churcher & Lawton 1987). The cats' home ranges also vary between seasons, with largest cats having largest home ranges during summer, and smallest home ranges during winter (Goszczynski et al. 2009). Southern Norway experiences great seasonal changes. Prey availability would very likely fluctuate during the year, especially the availability of insects, which made up the main share of the prey captured in my study. Passerine birds reproduced during my study period, which likely increased the availability of avian prey. Consequently, my results cannot be extrapolated to other periods of the year.

Cats are social animals, exerting different levels of social dominance between individuals (Turner & Bateson 2000). I did not study social connections, nor were other cats in the area accounted for. The presence of other cats have been found to affect a cat's habitat use and home range size (Turner & Bateson 2000). In addition, dominant individuals exclude subordinated ones from preferred habitats and thus decrease their predation success (Corbett 1979). Cats may also adjust their activity in time to avoid encounters with other cats (Turner & Bateson 2000).

The cats included in my study seemed to habituate to the collars, but a study examining the potentially altered activity in cats with different collar weights may be of interest, in order to assess if the study setup records the cats' natural behavior. When viewing the video recordings, identifying captures of avian and mammalian prey were easy, and were unlikely to remain undetected. Predation events that included insects, on the other hand, tended to be more cryptic, so it is possible that some captures and attempts including insects have gone undetected.

5. Conclusion

The most important findings in my study was that the house cat's general capture rate was low. No prey was brought back to the households, which suggests that estimating hunting activity from home-brought prey is likely to give an underestimation of the actual capture rate. General activity and predation activity were correlated, and both showed a nocturnal pattern of behavior. To understand the domestic cat's influence on wildlife, studies that include a larger dataset covering seasonal variations, including weather parameters, will be of interest. In addition, including edge habitat in habitat selection analyses would possibly shed light on the question of whether cats prefer edges rather than the interior of habitats.

My study method is low-cost and easy to manage, and possesses great potential to increase the knowledge of the ecology of the domestic cat. This study only included house cats living in a residential area. Farm cats and feral cats are likely to behave differently, also when it comes to home range sizes, habitat selection and predation frequency (Turner & Bateson 2000). A possible development of this study would be to mount cameras and GPS devices on farm cats. It should be manageable, considering that many such cats return home frequently (Barratt 1997).

Only lethal effects were included in this study. Even though few bird captures were recorded, it is possible that the cats exhibited stationary hunting strategies without making any attempts. This behavior may cause stress in bird populations, and be especially stressful for birds during the nesting period. To fully understand the impact of domestic cats on bird populations, this effect has to be taken into account in future studies.

6. References

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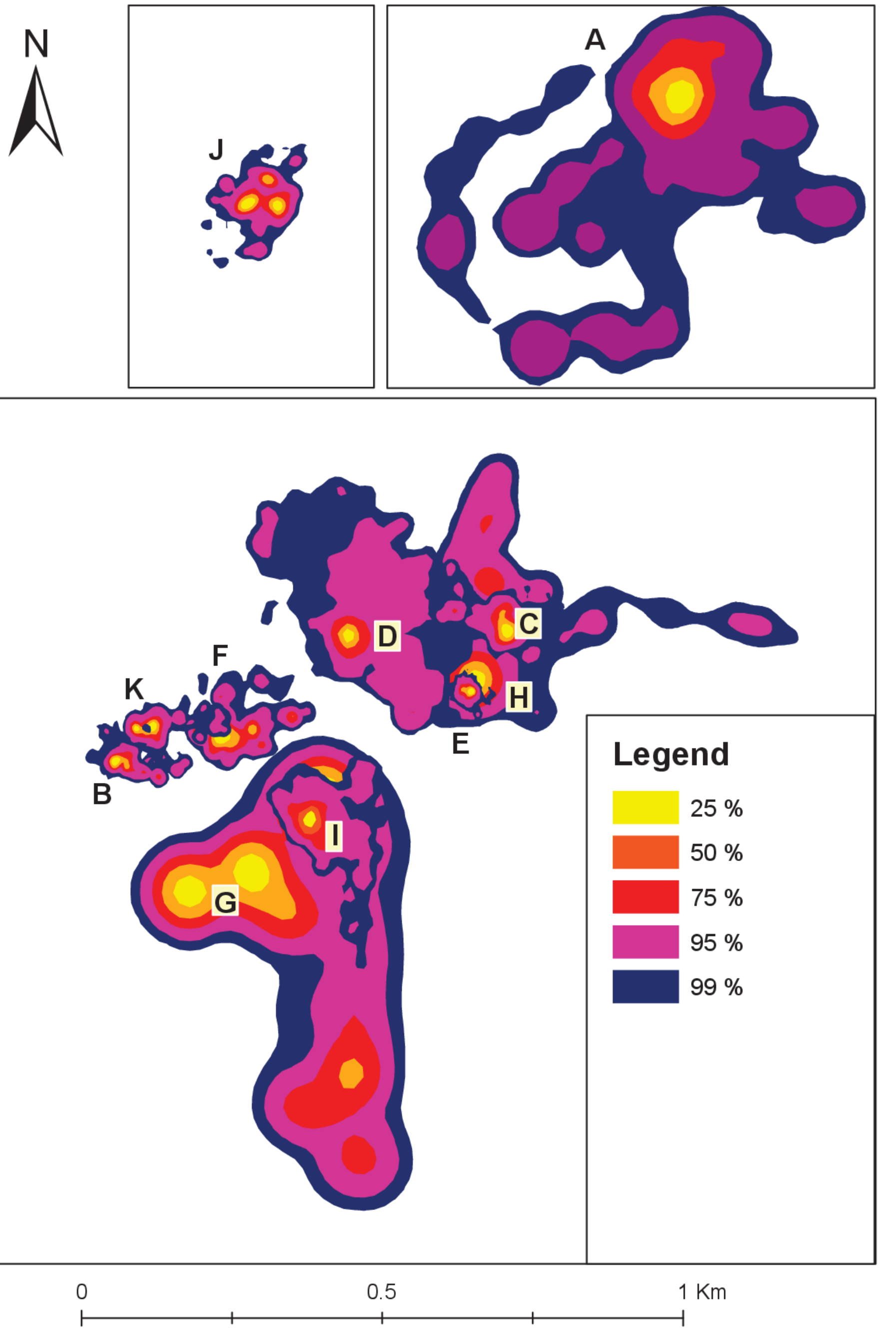
7. Appendix:



Appendix 1. The 25, 50, 75, 95, and 99 % total kernel home ranges for each cat. The spatial positions of the home ranges and home of cat A and cat J are shown in figure 1.

Appendix 2. Correlation matrix for the fixed variables included in the analysis of log-transformed home range size as fundtion of sex, age, body mass, and cat flap. Values are given as correlation coefficient r. Values more extreme than ± 0.50 are marked in red. The estimate for sex is given for males relative to females. The estimate for cat flap is given for yes (having cat flap) relative to no (not having cat flap).

		(1)	(2)	(3)
(1)	Cat flap			
(2)	Sex	-0.23		
(3)	Body mass	0.22	-0.65	
(4)	Age	-0.097	-0.0021	0.36

Appendix 3. Correlation matrix for the fixed variables included in the analysis of distance to habitat. Values are given as correlation coefficient r. Values more extreme than ± 0.50 are marked in red.

	(1)	(2)	(3)	(4)	(5)	(6)	(7)	(8)	(9)
(1) Agricultural land									
(2) Built-up land	0.22								
(3) Building structure	0.17	-0.50							
(4) Coniferous forest	0.25	-0.24	0.12						
(5) Deciduous forest	0.21	0.29	-0.43	0.32					
(6) Home	0.06	-0.51	-0.14	0.13	-0.08				
(7) Mixed forest	0.11	-0.37	0.07	0.25	0.11	0.19			
(8) Open firm ground	-0.72	-0.30	-0.32	-0.07	-0.02	0.12	0.07		
(9) Road	0.02	0.05	-0.08	0.02	0.15	-0.08	-0.16	0.03	
(10) Water	0.10	0.02	0.07	-0.20	-0.34	0.29	-0.20	-0.42	-0.06

Appendix 4. The proportion of observations recorded within and outside the habitats included in the best model in the habitat selection analysis (n = 119187)

Habitats	Number of observations within habitat	Number of observations outside habitat
Coniferous forest	4664 (3.9 %)	114523
Deciduous forest	284 (0.2 %)	118903
Mixed forest	0 (0.0 %)	119187
Water	177 (0.2 %)	119010
Agricultural land	8233 (6.9 %)	110954
Building structure	37874 (31.8 %)	81313
Home	22004 (18.5 %)	97183

Appendix 5. Correlation matrix for the fixed variables included in the hunting habitat selection analysis. Values are given as correlation coefficient r. Values more extreme than ± 0.50 are marked in red.

	(1)	(2)	(3)	(4)	(5)	(6)	(7)	(8)	(9)
(1) Agricultural land									
(2) Built-up land	0.19								
(3) Building structure	0.22	0.01							
(4) Coniferous forest	-0.10	0.07	-0.02						
(5) Deciduous forest	-0.09	-0.10	-0.08	0.10					
(6) Home	-0.16	-0.54	-0.39	-0.01	-0.08				
(7) Mixed forest	0.28	-0.01	-0.15	0.29	-0.15	-0.24			
(8) Open firm ground	-0.38	-0.21	-0.22	0.12	0.12	0.18	-0.02		
(9) Road	0.15	-0.01	0.04	-0.15	-0.03	-0.03	-0.18	-0.05	
(10) Water	-0.15	-0.16	-0.01	-0.01	-0.31	0.25	-0.38	-0.10	0.18

Appendix 6. Correlation matrix for the fixed variables included in the capture habitat selection analysis. Values are given as correlation coefficient r. Values more extreme than ± 0.50 are marked in red.

	(1)	(2)	(3)	(4)	(5)	(6)	(7)	(8)	(9)
(1) Agricultural land									
(2) Built-up land	0.23								
(3) Building structure	0.18	-0.01							
(4) Coniferous forest	-0.06	-0.06	0.02						
(5) Deciduous forest	0.11	-0.09	-0.10	0.17					
(6) Home	-0.15	-0.38	-0.52	-0.00	-0.24				
(7) Mixed forest	0.29	-0.17	-0.02	-0.12	0.27	-0.21			
(8) Open firm ground	-0.40	-0.22	-0.22	0.16	0.15	0.16	0.03		
(9) Road	0.15	-0.03	-0.01	-0.18	-0.00	-0.05	-0.15	-0.06	
(10) Water	-0.18	-0.01	-0.24	0.24	0.24	0.28	-0.32	-0.11	0.16

Appendix 7. Recorded attacks during the study period, June-July 2015.

Number	Cat ID	Date	Time	Handling time	Prey item	Prey group	Habitat
1	C	08 June	3:38:18	0:15:01	Sorex araneus	Mammal	Built-up land
2	F	10 June	0:28:39	0:00:08	Insect	Insect	Built-up land
3	F	10 June	3:50:19	0:11:00	Heterocera	Insect	Built-up land
4	G	11 June	2:00:58	0:00:27	Insect	Insect	Built-up land
5	G	11 June	2:17:42	0:03:52	Bird	Bird	Built-up land
6	G	11 June	3:15:12	0:00:17	Insect	Insect	Built-up land
7	G	11 June	3:16:53	0:00:38	Insect	Insect	Built-up land
8	G	11 June	3:17:43	0:00:11	Attempt	Attempt	Built-up land
9	G	11 June	3:17:56	0:00:04	Attempt	Attempt	Built-up land
10	I	12 June	1:08:30	0:02:28	Muridae	Mammal	Road
11	I	12 June	1:55:49	0:00:31	Heterocera	Insect	Open firm ground
12	C	18 June	22:15:18	0:00:08	Attempt	Attempt	Road
13	C	19 June	6:46:20	0:00:11	Caelifera	Insect	Open firm ground
14	C	19 June	8:22:23	0:00:17	Insect	Insect	Open firm ground
15	C	19 June	13:01:01	0:00:27	Insect	Insect	Open firm ground
16	C	19 June	16:13:36	0:00:20	Attempt	Attempt	Open firm ground
17	C	19 June	16:33:44	0:01:22	Nest with nestling	Bird	Open firm ground
18	J	19 June	23:49:07	0:01:27	Apodemus sylvaticus	Mammal	Open firm ground
19	J	20 June	0:06:10	0:00:15	Heterocera	Insect	Open firm ground
20	K	20 June	5:32:09	0:00:09	Insect	Insect	Open firm ground
21	G	20 June	23:27:41	0:00:57	Muridae	Mammal	Open firm ground
22	G	20 June	23:31:38	0:06:14	Bird	Bird	Coniferous forest
23	I	22 June	0:06:55	0:00:16	Attempt	Attempt	Coniferous forest
24	I	22 June	0:13:00	0:00:16	Insect	Insect	Built-up land
25	I	22 June	2:17:11	0:12:39	Apodemus sylvaticus	Mammal	Coniferous forest
26	D	22 June	23:50:23	0:00:18	Insect	Insect	Coniferous forest
27	D	22 June	23:55:15	0:00:31	Insect	Insect	Built-up land
28	D	23 June	23:05:01	0:00:08	Attempt	Attempt	Built-up land
29	D	23 June	23:56:17	0:00:35	Attempt	Attempt	Road
30	D	23 June	23:59:24	0:00:06	Attempt	Attempt	Built-up land
31	D	24 June	0:07:52	0:00:01	Attempt	Attempt	Built-up land
32	H	24 June	2:03:34	0:00:25	Insect	Insect	Built-up land
33	H	24 June	2:46:28	0:00:04	Attempt	Attempt	Built-up land
34	H	24 June	4:20:39	0:19:49	Apodemus sylvaticus	Mammal	Open firm ground
35	F	27 June	0:31:10	0:00:13	Insect	Insect	Agricultural land
36	F	27 June	0:50:41	0:00:04	Attempt	Attempt	Built-up land
37	K	29 June	1:09:55	0:00:03	Attempt	Attempt	Built-up land
38	D	28 June	23:07:09	0:00:08	Insect	Insect	Built-up land
39	D	28 June	23:51:20	0:00:20	Heterocera	Insect	Built-up land
40	D	29 June	2:08:38	0:00:15	Insect	Insect	Built-up land
41	A	29 June	9:49:55	0:00:16	Insect	Insect	Built-up land
42	G	29 June	23:29:14	0:01:02	Microtus agrestis	Mammal	Coniferous forest
43	G	30 June	0:44:54	0:00:23	Heterocera	Insect	Coniferous forest
44	G	30 June	1:01:16	0:00:16	Attempt	Attempt	Coniferous forest

45	G	30 June	1:15:16	0:00:06	Attempt	Attempt	Agricultural land
46	G	30 June	1:17:08	0:00:03	Attempt	Attempt	Coniferous forest
47	G	30 June	1:48:02	0:00:05	Attempt	Attempt	Coniferous forest
48	G	30 June	2:07:51	0:00:14	Insect	Insect	Coniferous forest
49	G	30 June	14:36:12	0:01:40	Microtus agrestis	Mammal	Coniferous forest
50	E	30 June	23:56:24	0:00:41	Noctuidae	Insect	Built-up land
51	C	30 June	21:24:40	0:00:34	Noctuidae	Insect	Road
52	C	30 June	22:28:22	0:00:13	Insect	Insect	Built-up land
53	C	30 June	23:14:53	0:00:13	Insect	Insect	Built-up land
54	C	30 June	23:22:35	0:00:10	Noctuidae	Insect	Built-up land
55	C	30 June	23:44:22	0:00:06	Attempt	Attempt	Built-up land
56	C	01 July	0:05:12	0:00:11	Attempt	Attempt	Built-up land
57	C	01 July	0:05:56	0:00:38	Insect	Insect	Built-up land
58	C	01 July	0:15:50	0:00:19	Attempt	Attempt	Built-up land
59	C	01 July	0:16:15	0:04:24	Sphingida	Insect	Built-up land
60	C	01 July	3:07:48	0:00:14	Insect	Insect	Built-up land
61	F	01 July	23:41:48	0:00:12	Insect	Insect	Built-up land
62	F	02 July	3:39:53	0:00:10	Attempts	Attempt	Built-up land
63	F	02 July	5:19:27	0:07:31	Parus major	Bird	Built-up land
64	D	02 July	23:26:28	0:00:35	Heterocera	Insect	Built-up land
65	D	02 July	23:28:43	0:00:22	Insect	Insect	Built-up land
66	D	02 July	23:34:51	0:00:23	Heterocera	Insect	Built-up land
67	D	02 July	23:40:09	0:00:12	Attempt	Attempt	Built-up land
68	D	02 July	23:40:32	0:00:11	Insect	Insect	Built-up land
69	D	02 July	23:44:08	0:00:18	Insect	Insect	Built-up land
70	D	02 July	23:47:36	0:00:15	Heterocera	Insect	Built-up land
71	D	02 July	23:51:17	0:00:11	Insect	Insect	Built-up land
72	D	02 July	23:51:34	0:00:05	Attempt	Attempt	Built-up land
73	D	02 July	23:52:48	0:00:16	Attempt	Attempt	Built-up land
74	D	02 July	23:53:29	0:00:14	Heterocera	Insect	Built-up land
75	D	02 July	23:54:22	0:00:10	Attempt	Attempt	Built-up land
76	D	02 July	23:55:07	0:02:37	Heterocera	Insect	Built-up land
77	D	02 July	23:58:39	0:00:31	Insect	Insect	Built-up land
78	D	03 July	0:00:28	0:00:07	Attempt	Attempt	Built-up land
79	D	03 July	0:00:54	0:00:10	Attempt	Attempt	Built-up land
80	D	03 July	0:02:46	0:00:10	Attempt	Attempt	Built-up land
81	D	03 July	0:03:17	0:00:13	Tupelidae	Insect	Built-up land
82	D	03 July	0:04:06	0:00:28	Insect	Insect	Built-up land
83	D	03 July	0:05:11	0:00:21	Insect	Insect	Built-up land
84	D	03 July	0:07:48	0:00:14	Heterocera	Insect	Built-up land
85	D	03 July	0:09:53	0:00:05	Attempt	Attempt	Built-up land
86	D	03 July	0:10:02	0:00:08	Attempt	Attempt	Built-up land
87	D	03 July	0:14:04	0:00:12	Insect	Insect	Built-up land
88	D	03 July	0:16:03	0:00:06	Attempt	Attempt	Built-up land
89	D	03 July	0:17:16	0:00:17	Insect	Insect	Built-up land
90	D	03 July	0:17:53	0:00:08	Attempt	Attempt	Built-up land

91	D	03 July	0:19:20	0:00:09	Insect	Insect	Built-up land
92	D	03 July	0:23:00	0:00:10	Insect	Insect	Built-up land
93	D	03 July	0:23:17	0:00:09	Insect	Insect	Built-up land
94	D	03 July	0:25:03	0:00:28	Heterocera	Insect	Built-up land
95	D	03 July	0:55:23	0:00:07	Attempt	Attempt	Built-up land
96	D	03 July	1:56:01	0:00:26	Sphingidae	Insect	Built-up land
97	K	04 July	14:19:40	0:00:13	Attempt	Attempt	Built-up land
98	A	03 July	23:04:37	0:00:03	Attempt	Attempt	Built-up land
99	A	03 July	23:24:25	0:00:09	Insect	Insect	Open firm ground
100	A	03 July	23:35:09	0:05:05	Microtus agrestis	Mammal	Open firm ground
101	A	03 July	23:44:04	0:00:15	Insect	Insect	Open firm ground
102	A	03 July	23:44:40	0:00:20	Insect	Insect	Open firm ground
103	A	03 July	23:45:35	0:00:15	Attempt	Attempt	Open firm ground
104	A	03 July	23:47:08	0:00:10	Attempt	Attempt	Open firm ground
105	A	03 July	23:48:09	0:00:09	Attempt	Attempt	Open firm ground
106	A	03 July	23:49:06	0:00:17	Insect	Insect	Built-up land
107	A	04 July	1:36:00	0:00:12	Attempt	Attempt	Agricultural land
108	I	04 July	21:59:37	0:08:51	Markmus	Mammal	Coniferous forest
109	I	05 July	0:03:05	0:00:21	Noctuidae	Insect	Built-up land
110	E	06 July	23:05:22	0:00:15	Attempt	Attempt	Built-up land
111	E	06 July	23:10:19	0:00:12	Attempt	Attempt	Built-up land
112	A	10 July	22:50:16	0:09:17	Parus major	Bird	Road
113	F	10 July	23:28:57	0:00:06	Attempt	Attempt	Built-up land
114	F	10 July	23:31:09	0:00:10	Insect	Insect	Built-up land
115	F	10 July	23:31:48	0:00:07	Insect	Insect	Built-up land
116	F	11 July	0:19:57	0:00:14	Insect	Insect	Built-up land
117	F	11 July	0:21:25	0:00:06	Attempt	Attempt	Built-up land
118	C	12 July	0:10:20	0:00:23	Insect	Insect	Built-up land
119	C	12 July	0:10:49	0:00:14	Insect	Insect	Built-up land
120	C	12 July	0:20:05	0:00:06	Attempt	Attempt	Built-up land
121	C	12 July	3:01:02	0:00:20	Insect	Insect	Built-up land
122	C	12 July	4:06:30	0:00:07	Insect	Insect	Built-up land
123	C	12 July	6:04:26	0:00:21	Insect	Insect	Built-up land
124	E	12 July	0:50:44	0:00:11	Attempt	Attempt	Built-up land
125	E	12 July	3:41:50	0:00:08	Attempt	Attempt	Built-up land
126	A	13 July	10:04:04	0:05:18	Turdidae	Bird	Built-up land
127	A	13 July	16:38:51	0:00:05	Attempt	Attempt	Built-up land
128	A	13 July	18:43:16	0:00:25	Insect	Insect	Built-up land
129	J	19 July	23:25:40	0:00:07	Attempt	Attempt	Built-up land
130	J	19 July	23:54:35	0:00:31	Insect	Insect	Built-up land

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