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Determinants of domestic cat occurrence in forests in southeastern Norway

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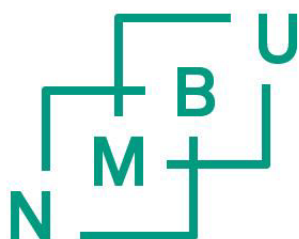
Master of science in Ecology

Preface

This study was carried out at the Faculty of Environmental Sciences and Natural Research Management (MINA) at the Norwegian University of Life Sciences. Writing this thesis has been a very educational and for the most part fun experience.

I would like to express my utmost gratitude to my supervisor Richard Bischof for always finding time to answer my questions, and for giving valuable feedback on the design, statistical analysis and writing of this thesis. I also want to thank all the people involved in the Scandcam project for lending me their data. A special thanks goes out to John Odden and Neri Horntvedt for valuable feedback on the study design and writing of this thesis, and to Neri for working hard to provide me with all the data I needed, without which this thesis would not have been possible.

I also want to thank my mother, father and brother for their interest in my project, and for giving feedback on my writing. Thanks to my classmates for making these two years fun, and a special thanks to Geneva Lish and Marianne Strand for providing constructive feedback on the writing of this thesis.



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Abstract

Domestic cats can pose a significant threat to local wildlife in urban and rural areas because of their high densities and proficiency as predators. However, few attempts have been made to quantify the impact of domestic cats on natural areas like forests, and even the extent to which cats use forests and areas further away from human influence remain uncertain.

I estimated cat occupancy at 411 forest locations in southeastern Norway from April 2018 to March 2021 using camera traps. I investigated how cat occupancy and detection probability was impacted by human infrastructure, habitat and the terrain. Subsequently, I used the best supported occupancy models to predict occupancy across forests in southeastern Norway.

Cat occupancy decreased strongly further away from houses, and cats if present were more likely to be detected closer to houses and forest edges. The best-supported models predicted that cats were present at 70% and 47% of forest sites 100 and 200m away from houses respectively, and cat presence only dropped below 10% more than 900m from residential houses. The model also predicted that cats were present in 12.5% (95% CI: 10-15%) of forests in southeastern Norway.

This study corroborates previous findings that cats are more likely to use natural areas near houses, but also show that cat activity may extend further away from houses into forests than previously thought. However, more information on cat abundance and hunting habits in forests is needed to assess the impacts cats have on forest fauna. This study represents the first population-level study on what determines where cats occur in a large forested area, while simultaneously accounting for habitat characteristics and imperfect detection.

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1. Introduction

Domestic cats prey on a wide range of fauna, making them a threat to wildlife in many places (Thomas et al., 2012; Van Heezik et al., 2010). They have played a role in 26% of all island extinctions (Doherty et al., 2016), and the estimates for how much wildlife they kill are staggering. In the United States alone, Loss et al. (2013) estimated that cats kill 1.3-4 billion birds, 6.3-22.3 billion mammals, 258-822 million reptiles and 95-299 million amphibians each year, making free-ranging cats the greatest source of human-related mortality for birds and small mammals in the US.

There are several reasons why domestic cats can have such a large impact on wildlife. Since humans provide food subsidies, cats are not regulated by the quantity of prey, allowing cats to persist at densities far higher than any natural predator, often around 200-450 cats pr. km² in urban areas (Baker et al., 2008; Sims et al., 2008; Thomas et al., 2012; Van Heezik et al., 2010). Cats also prey on a wide range of fauna (Hervías et al., 2014; Mori et al., 2019), and most free-ranging pet cats are active hunters (Seymour et al., 2020; Thomas et al., 2012; Van Heezik et al., 2010; Woods et al., 2003).

While several studies indicate domestic cats can have a negative impact on wildlife in urban areas (Thomas et al., 2012; Van Heezik et al., 2010), their impacts in natural areas are not well known, and few studies have focused on how cats impact forest fauna in particular. Forests often contain more vulnerable and native species, potentially making cats a greater conservation concern (Gillies & Clout, 2003; Herrera et al., 2022).

An important first step in determining how cats impact forest fauna is to discover how widespread domestic cats are in forests, and what determines where in forests they are found. Most studies indicate cats select against forests, and are mostly found near forest edges (Crooks, 2002; Gehrt et al., 2013; Kays & DeWan, 2004; Van Heezik et al., 2010), but some studies find cats show weak or no selection against forest habitat, and penetrate further into forests (López-Jara et al., 2021; Pirie et al., 2022; Thomas et al., 2014). Most pet cats also spend most of their time close to their house (Bischof et al., 2022; Kays et al., 2020; López-Jara et al., 2021). However, cat home ranges sizes are very variable, and some cats roam much

further away from their house and further into forests (Bischof et al., 2022; Kays et al., 2020; López-Jara et al., 2021; Pirie et al., 2022). Cats living close to natural areas may also have larger home ranges and hunt more (Pirie et al., 2022). Even if only a minority of cats roam extensively in forests, the impacts on wildlife could be significant due to the sheer number of pet cats in the world.

Few estimates exist on how widespread cats are in forests. Most studies on cat habitat use are telemetry studies that only track a small subset of the cat population. Since cat roaming and habitat preferences are highly variable, it is difficult to scale up inferences from individual cats in telemetry studies to provide population-level inferences on how widespread cats are in different habitats (Bischof et al., 2022). The few non-telemetry studies estimating cat abundance or occurrence in forests are often very local, small, and do not account for important characteristics of the environment, nor for the fact that cats can be present even if they are not detected (Crooks, 2002; Ferreira et al., 2011; Kays et al., 2015; Kays & DeWan, 2004; López-Jara et al., 2021).

In this study, I assessed whether cats were present at 411 camera trap sites in southeastern Norway over a three-year period while accounting for imperfect detection using occupancy modelling. I investigated how cat occupancy and detection was influenced by habitat characteristics like human population density and distance to nearest house and forest edge. I then used the best occupancy models to estimate the proportion of forested areas in southeastern Norway where cats were present.

The goal of this study was to answer (1) how likely cats are to be present at different distances from human residences in forests, (2) what other environmental variables influence cat occupancy in forests and (3) in what proportion of forests throughout southeastern Norway cats are present. I hypothesize that cats will be far more likely to occur close to houses and in areas with high human density, since several studies have found cats to spend most of their time within 50 or 100 meters of their house (Bischof et al., 2022; Kays et al., 2020). While I expect cats to be most influenced by the human factors above, I also expect cats to occur less in steep areas (Ferreira et al., 2011) and in areas with a higher proportion of forest in the landscape, since most studies indicate cats select against forests (Gehrt et al., 2013; Kays & DeWan, 2004; Van Heezik et al., 2010).

2. Methods

2.1. Study area

The study area extends across more than 80 000 km² in southeastern Norway, between 58.3 and 61.9 degrees latitude (Fig. 1). The area includes 70 municipalities spread across four counties: Innlandet, Vestfold and Telemark, Viken and Oslo. The climate is temperate, with quite large differences in temperature and daylength within seasons. The study area is partially covered by snow from December-March (some parts November-May), with more snow at higher latitudes and higher elevations.

More than half the study area is forested, and roughly 80% are production forests (Svensson, 2021). The most common forest type is boreal coniferous forests dominated by European spruce (*Picea abies*), Scotch pine (*Pinus sylvestris*) and birch (*Betula pubescens*) (Svensson, 2021). These forests are characterized by winters that are long, cold and dry, and short, warm and moist summers. Temperate deciduous forests are also found in the more southeastern low-elevation parts of the study area, with species like linden (*Tilia cordata*), maple (*Acer platanoides*), ash (*Fraxinus excelsior*), elm (*Ulmus glabra*) and common oak (*Quercus robur*) (Grindeland, 2020). In addition, mixed forests are common in the transition from temperate to boreal forests.

The average population density in the larger study area is 30 people pr km² (SSB, 2018), although the cameras were placed on local sites with a lower average population density than in the larger area of southeastern Norway. The larger study area contains a few relatively large cities like Oslo (~700 000 inhabitants), Drammen (~100 000 inhabitants) and Fredrikstad (~80 000 inhabitants) along with many smaller towns and more sparsely populated areas. Our study area is almost devoid of wilderness (i.e. areas more than five kilometres away from any human development intervention), even though the national average is 11% wilderness (Lundberg & Halleraker, 2021).

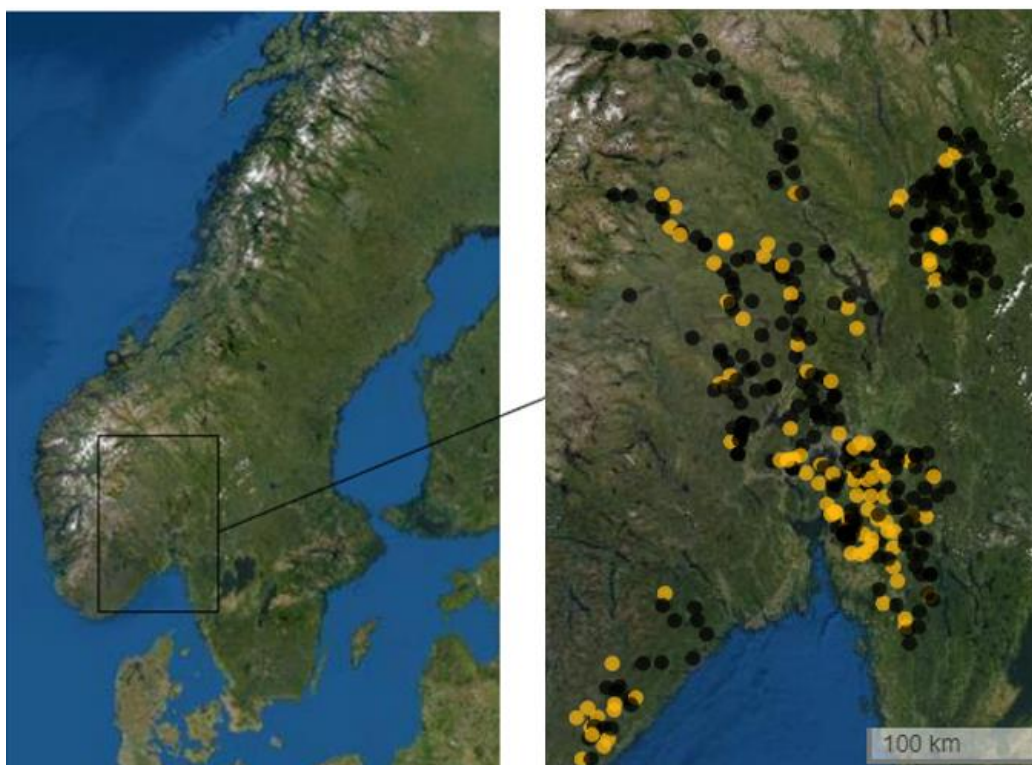


Figure 1. Study area in southeastern Norway showing camera traps where cats were observed (yellow) and not observed (black) for the study duration. Source: Google Maps.

2.2. Camera trapping

The camera trap data used in this study was collected by the Norwegian Institute for Nature Research (NINA) as part of the SCANDCAM project. The goal of SCANDCAM is to monitor Eurasian lynx (*Lynx lynx*) populations, so cameras were placed at locations to maximize the probability of detecting lynx. The cameras were mostly placed at features like cliffs, boulders, trails and forestry roads (roads used for timber harvest). Almost all cameras were placed in forests and attached to trees roughly 70 cm above ground (20 to 150cm depending on the terrain and snow depth in winter). The density of camera traps was approximately one camera trap per 50 km², and cameras were rarely placed closer than 2 km from another camera. Since cats have small home ranges (3.6 ± 5.6 ha) and seldom roam more than one kilometre from their home (Kays et al., 2020), we can assume almost all cats only visit one camera.

I only used cameras that took daily timelapse pictures in addition to motion-triggered images. This allowed me to distinguish when cameras were not active vs when cameras were active but no animals were detected. The cameras used were five Reconyx® camera models (<http://www.reconyx.com>, Holmen, WI, USA): HC500 HyperFire Semi-Covert IR, PC800 Hyperfire Professional Semi-Covert IR, PC900 HyperFire Professional Covert IR, HC600 HyperFire High Output Covert IR, and PC850 HyperFire Professional White Flash LED. I also used some Bushnell Trophy Cam Aggressor cameras. All models used a trigger speed of 0.2 seconds, and fired bursts of three images with no delay for trigger interval.

We used photos taken in the three year-period April 2018 - March 2021. All pictures were revised manually at least twice by different observers, to minimize the probability of false positives and false negatives caused by misidentifying species.



Figure 2. Camera trap photos of domestic cats from this study. Source: <https://viltkamera.nina.no/>

2.3. Environmental covariates

I collected several covariates that I hypothesized could impact occupancy and/or detection (Table 1-2). For occupancy I estimated human population density, distance to nearest house, terrain ruggedness index and forest proportion, and for detection the distance to nearest house, distance to nearest road, distance to nearest forest edge, and terrain ruggedness index. The detection covariates were selected because they could influence the abundance of cats at the site, and greater abundance of cats means cats are more likely to be detected if present. Since I assume cats are mostly bound to human settlements, I defined distance to forest edge as the distance from each camera to the nearest anthropogenic landscape or structure (distance to the nearest field, road or building), so as not to include the distance to lakes and bogs located inside of forests. Covariates were calculated using data from 50 x 50 m raster cells (250 x 250 m for population density) from various publicly available Norwegian map databases (Table 1-2). For more information on how the rawdata from these map databases were processed to create the covariates, see appendix table 1.

I calculated detection and occupancy covariates at different landscape scales, using the covariate values at the site to reflect the probability of detecting cats if they are present and the covariate value within a 400m buffer of the camera as the probability the unit was occupied. For detection covariates, I used the covariate value in the 50 m x 50 m cell the camera was located in. For occupancy covariates I used the `exact_extract` function in the package `exactextractr` (Baston, 2020) to calculate the mean covariate value within a 400m radius buffer of each camera. Raster cells that were partially covered by the buffer were weighed against the proportion of the cell covered when calculating the mean value, to ensure the most representative estimates.

Table 1. Occupancy covariates used in the models. Occupancy covariates were calculated within a 400m radius buffer of each camera.

Variable	Description	Range: mean (min-max)	Source
Dist_house	Distance to nearest residential house (m)	883 (102-7200)	FKB-Bygning (Kartverket, 2017)
Pop_dens	Human population density (pr. km ²)	11.3 (0-767.8)	Befolkning på rutenett (SSB, 2018)
TRI	Terrain ruggedness index	7.8 (0.1-26.0)	DEM50 (Kartverket, 2018a)
Prop_forest	Forest proportion	0.84 (0.02-1)	Ar50 (NIBIO, 2016)

Table 2. Detection covariates used in the model. The covariate value was extracted from the 50 x 50 m raster cell the cameras were located in.

Variable	Description	Range: mean (min-max)	Source
Dist_house	Distance to nearest residential house (m)	881(50-7191)	FKB-Bygning (Kartverket, 2017)
TRI	Terrain ruggedness index	9.6(0-37.9)	DEM50 (Kartverket, 2018a)
Dist_road	Distance to nearest road (m)	411(0-3650)	FKB-Veg (Kartverket, 2018b)
Dist_forest_edge	Distance to nearest road, building or agricultural field (m).	129(0-707)	-Road: FKB-bygning (Kartverket, 2018b) -Building: FKB-bygning (Kartverket, 2017) -Fields: Ar50 (NIBIO, 2016)

2.4. Data analysis

All analyses were carried out in R version 4.1.1 (R Core Team, 2021). I used occupancy models for all the analyses. Occupancy models are used to model species occurrence while accounting for the fact that a species can be present without being detected (MacKenzie et al., 2002). Thus, occupancy models calculate both occupancy probability, ψ and detection probability, p . Occupancy is the proportion of sampling units occupied by a given species, while detection probability is the probability that a species will be detected in a given survey within a unit if the species is present (MacKenzie et al., 2002). By surveying units multiple times, occupancy models calculate the probability that the species is present by also including the probability the species is present without being detected. Both occupancy and detection probability can be modelled as a function of covariates. Occupancy models assume that the site is closed to changes in occupancy status between surveys, but not between seasons. How to define a sampling unit, season and survey in occupancy modelling is flexible and depends on the study objectives (MacKenzie et al., 2017).

I defined a season as a year, and each year was divided into 52 weekly surveys. To avoid any bias caused by differing surveying effort, I only included surveys where the cameras were active the whole week. I treated each camera-year combination as separate sites, thus “stacking” the yearly detection histories (see Fuller et al., 2016; Linden et al., 2017) to increase the sample size we can use to model the effect of habitat covariates.

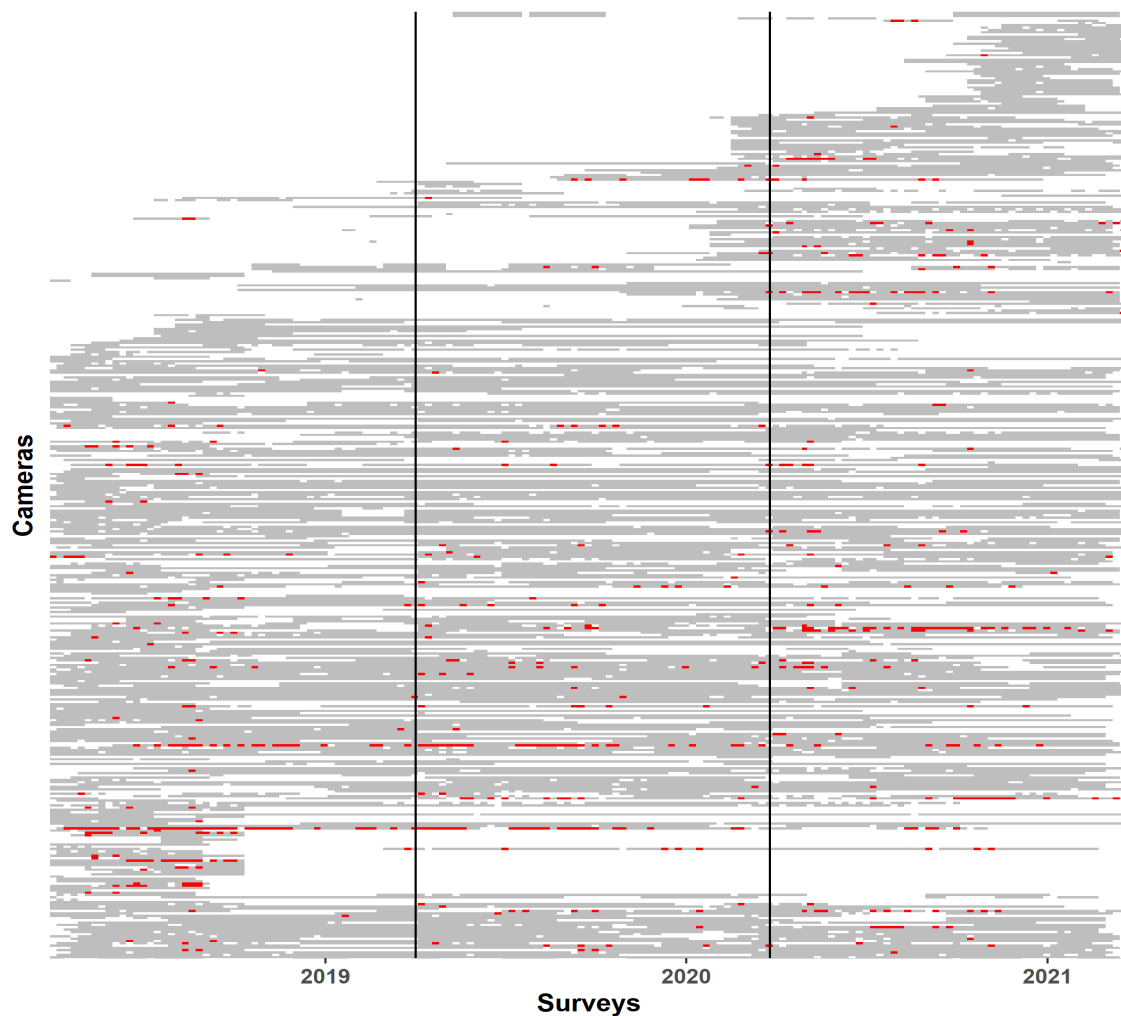


Figure 3. Overview of which weekly surveys the 411 study cameras were active in from April 2018 – March 2021. Red = camera active and cat detected, grey = camera active, white = camera inactive. The two vertical lines delineate where cameras were split into year-camera “sites” for the occupancy analysis.

I calculated Pearson correlation coefficient between all covariates. Since all covariates were weakly correlated with each other ($r < 0.5$), I did not exclude any variables. I log-transformed all the distance variables (distance to nearest house-, forest edge- and road), since I assumed the distance effect would be stronger at short distances. All the covariates were then standardized.

I used the occu function in unmarked (Fiske & Chandler, 2011) to create the single season occupancy models of MacKenzie et al. (2002) for all the occupancy models. As a preliminary

analysis, I determined at which landscape scale the occupancy covariates were most important for predicting cat occupancy. I fitted occupancy models with occupancy covariates calculated at three landscape scales; within 100, 200 and 400 m buffers around each camera. For each landscape scale I fitted all possible combinations of my detection and occupancy covariates, resulting in 205 models for each occupancy scale. I then compared the combined model weights of models belonging to each occupancy scale using AIC with the AICcmodavg package (Mazerolle & Mazerolle, 2017). Since the model weights showed that covariates at the 400m scale best predicted cat occupancy, I ran all subsequent analyses using the 400m scale.

I then determined how the covariates impacted occupancy and detection probability by fitting all combinations of detection and occupancy models, and comparing them using Akaike Information Criterion (AICc). Since I had several candidates for best model, I model-averaged the best fitting occupancy models ($\Delta AICc \leq 2$) using the model.avg function in the MuMIn package (Barton, 2022). I also combined the AICc weights for all the models each covariate appeared in, giving the probability that each covariate is part of the best model (Burnham & Anderson, 2002).

We used the model averaged occupancy covariate estimates (Table 4) to predict occupancy probability in all forests in our study area. We only predicted occupancy probability for cells with >60% forest coverage, and for cells that were inside the data range of all our occupancy covariates (Table 1). Almost all the forest cells (96%) were inside the covariate data range. We also resampled the 50 x 50 m ar50 forest raster (NIBIO, 2016) to a resolution of 700 x 700 m so the raster cells would have roughly the same area as the 400m radius buffers we defined as the occupancy unit. We were left with almost 50 000 km² of forest to make predictions on. We then calculated and mapped the average occupancy probability across all the forest cells.

To calculate the confidence interval for the proportion of forests occupied, I simulated the values of the intercept and occupancy coefficients 100 000 times by drawing random normally distributed values using the model-averaged estimate and standard error for each occupancy covariate and the intercept. I applied these simulated coefficient values to the covariate values associated with each forest cell and averaged these values to get 100 000 mean occupancy

estimates. I then found the 2.5% and 97.5% quantiles for the 100 000 mean occupancy estimates to get the 95% CI estimate for proportion of forests occupied by cats.

3. Results

The camera traps were active for a total of 203 735 days over the three-year study period from April 2018 – March 2021 at 941 sites, where one site is a year-camera trap combination (mean = 217, SD = 123 active trapping days per site, Fig. 3). There were 411 unique active camera trap locations.

3.1. Covariates influencing cat occupancy and detection

The best cat occupancy model included distance to forest edge, distance to house, distance to road and TRI as detection covariates, and the distance to house for occupancy (Table 3). However, other potential best models ($AICc < 2$) also included the terrain ruggedness index and forest proportion as occupancy covariates, while maintaining the same detection covariates. All the top occupancy models contained TRI and the distance to house, forest edge and road as detection covariates.

Table 3. Top models of cat occupancy models evaluated by $AICc$. Covariate descriptions are found in Tables 1-2.

<i>Detection covariates</i>	<i>Occupancy covariates</i>	<i>Df</i>	<i>Log likelihood</i>	<i>AICc</i>	$\Delta AICc$	<i>AICc weights</i>
dist_forest_edge + dist_house + dist_road + TRI	dist_house	7	-1981.26	3976.5	0.00	0.26
dist_forest_edge + dist_house + dist_road + TRI	dist_house + TRI	8	-1980.45	3976.9	0.39	0.22

dist_forest_edge + dist_house + dist_road + TRI	dist_house + prop_forest + TRI	9	-1979.97	3977.9	1.43	0.13
dist_forest_edge + dist_house + dist_road + TRI	dist_house + prop_forest	8	-1981.13	3978.3	1.75	0.11
dist_forest_edge + dist_house + dist_road + TRI	dist_house + pop_dens	8	-1981.26	3978.5	2.01	0.10
dist_forest_edge + dist_house + dist_road + TRI	dist_house + pop_dens + TRI	9	-1980.45	3978.9	2.39	0.08
dist_forest_edge + dist_house + dist_road + TRI	dist_house + pop_dens + prop_forest + TRI	10	-1979.97	3979.9	3.43	0.05
dist_forest_edge + dist_house + dist_road + TRI	dist_house + pop_dens + prop_forest	9	-1981.13	3980.3	3.75	0.04
dist_forest_edge + dist_house + dist_road	dist_house	6	-1986.14	3984.3	7.76	0.01

Table 4. Occupancy and covariate estimates for the model-averaged highest ranking cat occupancy models ($\Delta AIC_c \leq 2$).

Covariate	Estimate	Std. Error	z.value	Pr(z)
Occupancy				
Int	-1.546	0.1473	10.4969	<.001
dist_house	-1.2316	0.1615	7.6271	<.001
TRI	0.1804	0.1355	1.3317	0.183
prop_forest	-0.0758	0.1017	0.7448	0.456
Detection				
Int	-2.9677	0.0858	34.5974	<.001
dist_forest_edge	-0.6233	0.0605	10.2993	<.001
dist_house	-0.6642	0.0675	9.8379	<.001
dist_road	0.2608	0.0598	4.3634	<.001
TRI	-0.199	0.0646	3.0818	0.002

All detection covariates were statistically significant ($p \leq 0.002$), while only distance to house significantly influenced occupancy ($p < 0.001$) (Table 4). Distance to house had a 6.8 times higher effect on occupancy than the second most influential occupancy variable (TRI). Cat occupancy strongly decreased further away from houses (Fig. 4). Occupancy was predicted at 70% and 48% when the mean distance from a house in a 400m buffer radius were 100 and 200m respectively, and only dipped below 10% more than 900m from the nearest house. The furthest away from houses we detected cats was 1532 meters. Occupancy also increased slightly in steeper terrain, and decreased slightly at more forested sites, but not significantly (Table 4).

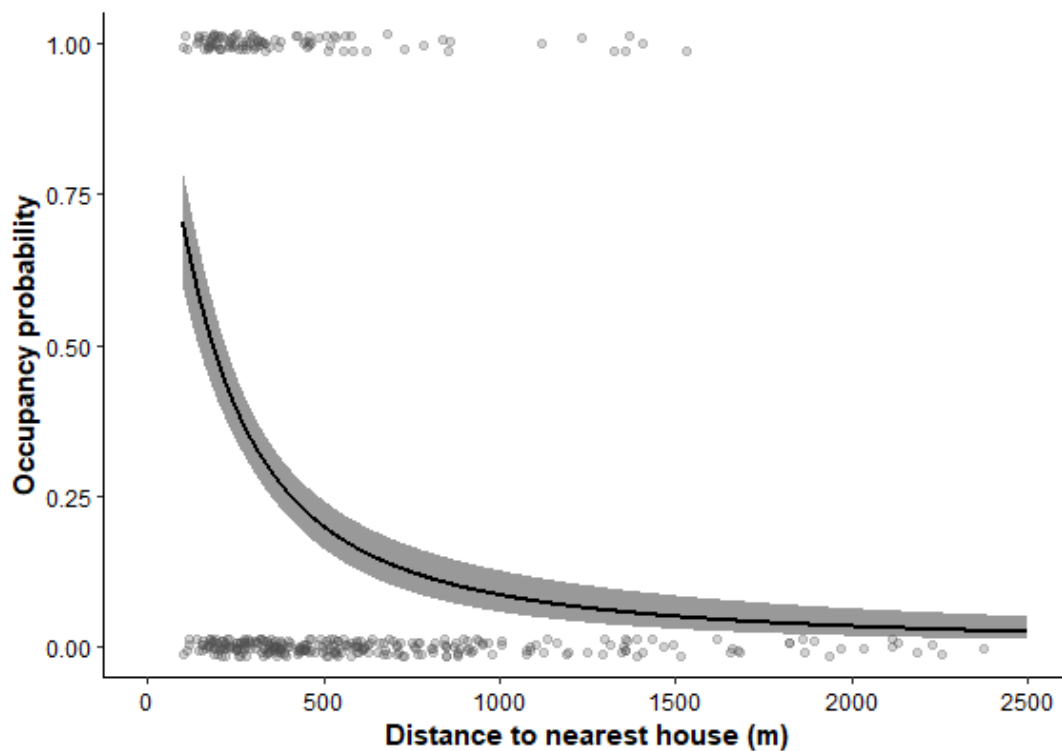


Figure 4. Predicted cat occupancy at different distances to nearest house in meters. All other variables were held constant at their mean values. The points show the camera sites where cats were observed (top) and not observed (bottom).

Predicted detection probability declined steeply when distance to house and distance to forest edge increased (Fig. 5a-b). Detection probability was 20% at the forest edge, but declined to 3% and 1.7% 50 and 200m from the forest edge respectively. Detection probability was 20% and 9% 50 and 200m away from the nearest house. Detection probability also decreased closer to roads and in more steep terrain (Fig. 5c-d).

For occupancy covariates, the probability that each covariate was part of the best occupancy model was 100% for distance to house, but for TRI, proportion of forest and population density this probability was low (Table 5). For all detection covariates, the probability they were part of the best model was close to 100%.

Table 5. Probability that each covariate is retained in the top occupancy model, as measured by AICc model weights.

Covariate	Detection	Occupancy
Dist_house	1	1
TRI	0.98	0.47
Prop_forest	-	0.33
Pop_dens	-	0.26
Dist_road	1	-
Dist_forest_edge	1	-

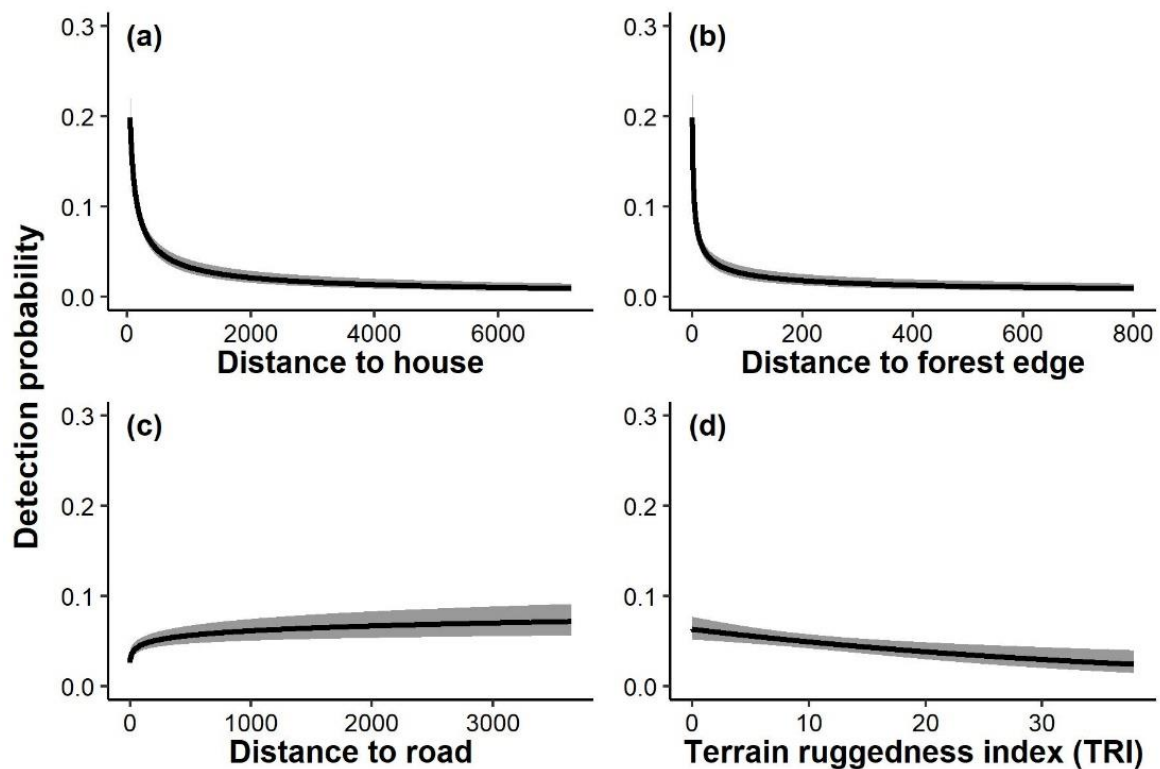


Figure 5. Predicted probability of detecting cats in a given survey week if they are present at the site for all detection covariates. (a) distance to nearest house (m), (b) distance to nearest forest edge (m), (c) distance to nearest road (m) and (d) terrain ruggedness index. All other covariates were held constant at their mean values when predicting.

3.2. Occupancy in forests in southeastern Norway

My model predicted that 12% (CI: 9-15%) of all forests in southeastern Norway are occupied by cats (Fig. 6). Most forest cells had a very low occupancy probability, as 46% had occupancy probability of less than five percent, while 64% had an occupancy probability of 10 percent or less. Only 2.5% of the forest area had an occupancy probability greater than 50%, and the highest predicted occupancy was 71%.

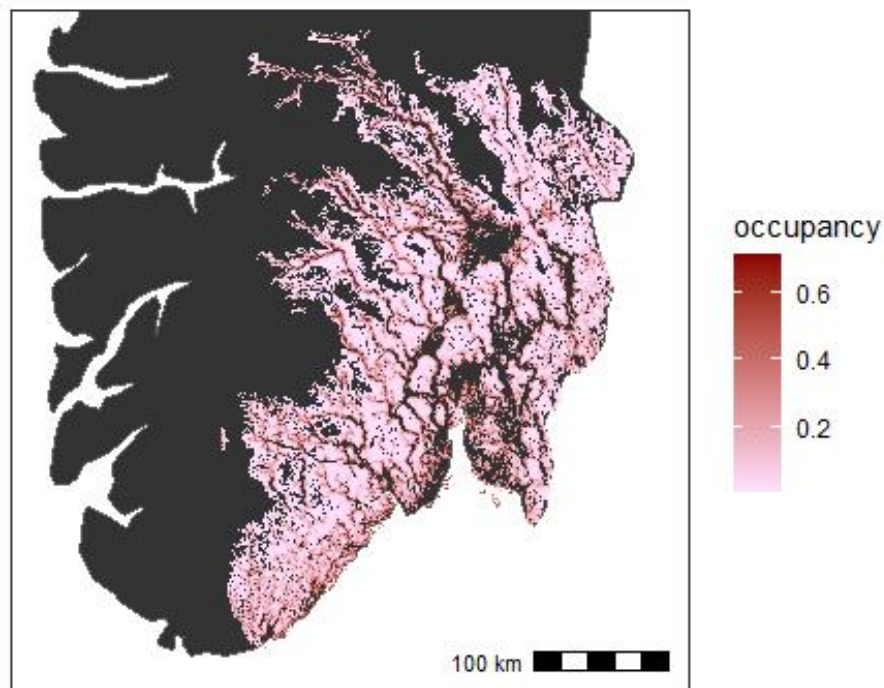


Figure 6. Predicted occupancy across all forest areas in southeastern Norway. Black areas were not included in the predictions, either because they were not primarily (>60%) forested, or because they were outside of the study area.

4. Discussion

4.1. How far do cats go from houses?

Distance to the nearest house was the strongest determinant of where cats were present in forests. Cats were more likely to be present closer to houses, but my model still predicted higher cat presence further away from houses than what we expected. Cats were predicted to occupy 70% of sites 100m from the nearest house, and occupancy only dipped below 10% more than 900 meters away from houses. Cats were also detected at more than 10% of cameras between 500-1000 and 1000-2000 meters from the nearest house over their whole activity period (Table A2). Other studies show pet cats spend most of their time within 50 or 100m from their house, and rarely roam further than a few hundred meters (Bischof et al., 2022; Hervías et al., 2014; Kays et al., 2020; López-Jara et al., 2021). At the same time, these studies uncover large variation in roaming, with some cats occasionally roaming much further. The maximum linear distance individual cats roamed from their house was 108-2534m (mean 739m) for López-Jara et al. (2021) and 48-3384m (mean 354m) for Bischof et al. (2022). My study seems to indicate that the occasional far-roaming cat other studies have recorded can translate into cats occurring at a significant number of sites far away from houses.

However, it is difficult to compare my estimates on how far away from houses cats roam with estimates from telemetry studies. Telemetry studies measure how far into forests individual cats go, but not the probability of encountering cats at a given distance from houses like this study. Most telemetry studies also only track a small number of cats for a few days or weeks. Thus, their estimates of the maximum distance cats roam are likely sometimes underestimated (López-Jara et al., 2021). Furthermore, most telemetry studies do not track enough cats to get representative estimates on how likely cats are to roam far, since cat home ranges are so variable (Hebblewhite & Haydon, 2010). In addition, telemetry studies have examined how far cats venture from houses regardless of habitat, while this study looks at how far away from houses cats are found while being inside forests. Since forests are likely not preferred cat habitat (Kays & DeWan, 2004; Van Heezik et al., 2010), we might have found cats to be even more common further away from houses if we had placed the cameras in more favourable cat habitats. López-Jara et al. (2021) found evidence supporting this assumption, as cats living more than 200m away from forests rarely entered the forest, even though they

roamed much further than 200m on average (average maximum distance travelled from house was 738 meters). Several studies indicate that while cats can penetrate more than 200 meters into forests, they are most common less than 50 meters into the forest (Kays & DeWan, 2004; Pirie et al., 2022). Thus, the probability of finding cats at different distances to houses inside forests likely depends on how far into forests the cameras were placed. Both previous telemetry studies and this study may underestimate how far away from houses cats go, as a result of short tracking duration of cats and cameras being placed inside forests respectively.

4.2. Importance of other occupancy and detection covariates

While distance to house strongly influenced cat occupancy, human population density had a weak non-significant impact on cat occupancy. Thus, I found no proof for my prediction that densely populated areas would have more cats, making cats occurring in local forest fragments more likely. The reason I found no support for my prediction could be that human population density likely is not a great predictor of the number of free-roaming pet cats, and more cats may not always make forest penetration more likely. In sparsely populated rural areas, households own more cats and a larger proportion of cats have outdoor access than in more densely populated urban areas (Lepczyk et al., 2004). While urban areas still have much higher cat densities on average (Baker et al., 2008; Lepczyk et al., 2004; Sims et al., 2008; Warner, 1985), the difference is smaller than what is expected from comparing human population density.

Perhaps more importantly, several studies have found that cats roam more at low cat and human densities. A meta-analysis by Hall, C. M. et al. (2016) found that rural pet cats had 14.4 times larger home ranges than urban pet cats, and a large recent study tracking 878 cats found rural cats had 1.6 times larger home ranges (Kays et al., 2020). Smaller cat home ranges have also been directly linked to higher housing densities (Hall, Catherine M et al., 2016; López-Jara et al., 2021) and higher cat densities (Van Heezik et al., 2010). There could be several reasons why cats roam more at lower densities. Sparsely populated areas often have fewer barriers to cat movements like trafficked roads (Barratt, 1997). Furthermore, cats may restrict each other's roaming at high densities through territoriality, but while feral cats are considered territorial (Genovesi et al., 1995; Hall et al., 2000), the extent to which pet cats are territorial

remains uncertain (Thomas et al., 2014). If greater home ranges at low cat densities is caused by territoriality, the commonly suggested cat mitigation measure of reducing the outdoor access of cats might not have the intended effect of reducing cat penetration into natural areas. If only some cat owners reduce outdoor access, the remaining outdoor cats may increase their roaming as a response (Thomas et al., 2014). Thus, the cats' pressure on more distant natural areas might not be reduced, although cat densities and their subsequent predation pressure close to cat households would likely decrease (Bischof et al., 2022). Discovering why cats apparently have smaller home ranges at higher human and cat population densities can thus have important implications for managing the impact of domestic cats. When considering the higher ratio of free-ranging cats to people and the larger cat home ranges in low population density areas, my finding that human population density did not influence cat occupancy is less surprising.

The steepness and proportion of forest in the landscape also had a weak, not significant effect on cat occupancy. I expected to see a strong selection against sites with a higher forest proportion in the landscape (Gehrt et al., 2013; Kays & DeWan, 2004; Van Heezik et al., 2010), and a preference for less steep sites (Ferreira et al., 2011). However, not all studies find cats select strongly against forests, as Thomas et al. (2014) found pet cats selected for green habitats. Unfortunately, Thomas et al. (2014) did not distinguish between forest and grassland, so it is possible cats only selected for grassland. Feral cats in New Zealand have also been found to select for forest habitat (Harper, 2007). Thus, my findings demonstrate that we need more research to determine how cats select for or against forests and the landscape steepness. These findings also demonstrate that human factors like distance to house is likely much more important for the space use of cats than other habitat characteristics, which is consistent with most other studies on cats (i.a. Kays et al., 2020; López-Jara et al., 2021).

At sites occupied by cats, the model predicted that cats are detected 20% of all weeks at the forest edge, but the detection probability decreased very rapidly to just 3.4% 50 meters into the forest. The difference in detection probability is likely due to cats being more abundant closer to the forest edge, since there is no reason to believe it is easier to detect the same number of cats on camera closer to the forest edge. Other studies have also found that cats are far more abundant in the first 50 meters of the edge. Kays and DeWan (2004) detected cats at half the scent stations <50m from forest edge, but only at 5% of scent stations >50m

from edge. However, they still observed cats more than 200m into forest fragments. Pirie et al. (2022) found that the average maximum penetration distance into heathland or forests was 69 meters, with some cats penetrating more than 300 meters into these natural areas. Thus, my study corroborates previous studies showing that cats are likely to be much more prevalent in forest edges.

4.3. How widespread are cats in forests in Southern Norway?

This study predicted that cats occur in between 9 and 15% of forests in southeastern Norway. Kays et al. (2015) examined occupancy of cats in 32 mostly forested North American protected areas using camera traps, and found cats in half the areas. However, cats were very uncommon, and were detected 100 times less than in small urban forests in the same region. They found that cats occupied 27% of urban forests and only 1.6% of protected areas. This result might coincide well with my 9-15% estimate, since forests in southeastern Norway on average falls somewhere in between the human influence of urban forests and protected areas. However, Kays et al. (2015) disclose limited information on the habitat of the protected areas, and how far away from houses and edges the cameras were placed, so it is difficult to compare how similar our study areas are in terms of factors relevant for cat roaming. This study is the first to my knowledge to sample enough sites across almost the entire range of relevant variables to allow for predicting cat occurrence across a vast (50 000 km²) area of forest. Population-level studies on cat space use are necessary as a complement to telemetry studies, since the roaming behaviour of cats is so variable, making the ecological practice of scaling inferences from a limited number of cats to the population level difficult.

After learning that cats are found in a significant portion of forests in southeastern Norway, it becomes important to parse out how vulnerable these forests are to cat predation. The vulnerability is likely not uniform across different types of forests. In the study area, temperate deciduous forests might be more vulnerable to cat intrusion due to higher species diversity and higher bird densities. In particular, these forests have several bush- and ground-feeding birds that could be vulnerable to cat predation (Suding & Solheim, 2022). Boreal forests can be less vulnerable due to their lower species diversity- and prevalence of bush- and ground-feeding birds. Small mammals constitute an even greater proportion of cat kills (Seymour et

al., 2020; Tschanz et al., 2011; Woods et al., 2003), and while rodent control might be seen as a benefit of cats in some urban and rural areas, it would not be in forests. By predating rodents, cats could compete for food with predators like hawks and owls (George, 1974). More knowledge on the prevalence and threat status of species that could be predated by cats is necessary to get a better picture of how vulnerable Norwegian forests are to cat intrusion.

Unfortunately, my estimates on how common cats are in forests can be difficult to generalize, due to the high diversity of forests and their local conditions that can impact cats space use. In Europe alone there are 42 different forest habitats according to IUCN, spread across several biogeographical regions, each with their own fauna, vegetation and climate (Biurrun et al., 2016). Some forests can have properties that make them more attractive to cats, like abundant prey, mild climate and few predators. For instance, some studies suggest predators like coyotes can create a landscape of fear for cats, limiting their roaming in natural areas (Crooks & Soulé, 1999; Gehrt et al., 2013; Kays et al., 2015). Forests with abundant cat predators may thus have less cat penetration. However, not all studies find cats avoiding predators (Kays et al., 2020), and many studies claim cats avoid predators based only on cats preferring more developed and less natural habitats (Gehrt et al., 2013; Kays et al., 2015), which could also be explained by differences in habitat preference. The uncertainty surrounding the influence on predators on cat space use demonstrates how we know too little about many of the factors impacting cat roaming in natural areas like forests, making it difficult to state how my results can be generalized to other forest areas.

However, we can be more confident in how other factors influence cat roaming in different forests. This study corroborates previous findings that clearly demonstrates we can expect more cats in forest areas with a greater human presence and more fragmented forests. In addition, cats are likely more common in forests in areas with more feral cats. Feral cats have larger home ranges (Horn et al., 2011), and likely use more forest habitats. A review of 27 studies on the habitat use of unowned and feral cats found they used a wide range of forest types (Doherty et al., 2015), and feral cats on Stewart Island in New Zealand actively selected for broadleaf forest habitats (Harper, 2007). Thus, while feral cats are still mostly attached to human settlements they are likely to roam further away from houses and into forests. While there are no good estimates on how many feral cats there are in Norway (Heggøy &

Shimmings, 2018), they are probably much less abundant than in places like the United States, Australia and Canada where their impacts on wildlife is larger than that of pet cats (Blancher, 2013; Legge et al., 2017; Loss et al., 2013). Since this study area is relatively sparsely populated and probably has few feral cats, forests in other parts of the world could face a greater threat from cats on average.

4.4. Implications for management

This study demonstrates the importance of reducing fragmentation and residential houses close to forests in order to reduce the probability of cats occurring there. Several studies have advocated for creating no-building buffer zones around vulnerable habitats to mitigate cat impacts, often suggesting buffers of 300-400 meters (Lilith et al., 2008; Metsers et al., 2010; Thomas et al., 2014). This study indicates that creating a cat-less outer perimeter in settlements or fully resident-free buffer zones around forests can greatly reduce the probability of cats entering the forest, but buffers would need to be unpractically wide (>1000m) to make the probability of cats being present minimal. Still, considering no building buffers for example when establishing protected areas with vulnerable fauna could greatly reduce the impact of cats (Hanmer et al., 2017). Fortunately, this study indicates cat abundance drops of very rapidly further into forests, to the point where cats might not be much of a conservation issue more than 50 meters from the forest edge. Thus, avoiding fragmentation might be the best way to reduce the prevalence of domestic cats in forests. In cases where cat ownership close to vulnerable areas cannot be avoided, measures like keeping cats indoors all the time or at night when they roam the most (Barratt, 1997; Meek, 2003; Metsers et al., 2010; Thomas et al., 2014) might greatly reduce the impact on wildlife (Woods et al., 2003).

4.5. Determining the impact of cats in forests

This study is likely the first to assess where cats occur across a large forested area while also accounting for environmental variables important for cats and imperfect detection, but this is

only the first step to assessing the impact cats have on forest fauna. The impact also depends on how abundant cats are, and on their hunting habits in forests. Cat abundance could be calculated relatively easily with spatial capture/recapture using camera traps since most cats are individually recognizable. However, determining how much and what cats hunt in forest can be more challenging. Studies have often examined prey returns to determine how much and what species cats kill (i.a. Baker et al., 2008; Mori et al., 2019), but this method has flaws. Since most cats will not live exclusively in forests, GPS collars or video recorders would be needed to assess if prey returns were killed in forests. Measuring prey returns also does not account for prey eaten or left behind, and studies on video monitored cats show cats only returning 18% (Seymour et al., 2020) or 23% (Crowley et al., 2019) of prey killed. Cats might also be biased in the proportion of different species and taxa they return (Seymour et al., 2020). It is hard to say if the proportion of killed prey that is returned is representative for regions with different climate, habitat and prey species, and getting reliable estimates of cat predation rates from video recordings might be too time consuming for many research projects. The difficulty in obtaining reliable predation estimates from forests makes it difficult to assess the impact cats have on forest fauna.

Even if we could establish how abundant cats are in forests, which species they kill and how much they hunt on average, it would be difficult to determine how big a threat cats pose to the fauna without also having more knowledge on population sizes of local prey species. Van Heezik et al. (2010) compared bird population sizes with cat predation rates in the city of Dunedin, and found that some bird species were unlikely to persist long term without nearby areas acting as sinks, but no studies have researched whether the predation pressure from cats is sustainable in forests where cat densities would be lower. Another question is if cats kill prey that would have perished anyways (compensatory mortality) or if cat predation comes in addition to other causes of mortality (additive mortality). Studies on cat predation have reached different conclusions with some arguing that cat predation could be more compensatory (Baker et al., 2008) while others think predation is more additive (Van Heezik et al., 2010). Predation by cats can also have several indirect impacts, such as creating a landscape of fear for prey species that reduces reproductive success (Beckerman et al., 2007; Bonnington et al., 2013). Such sublethal effects of predation can sometimes have a larger impact than the predation itself, but are hard to quantify (Cresswell, 2008; Cresswell, 2011).

While we can assume that sublethal effects of predation are smaller in forests due to lower cat densities, they could still be important, especially close to forest edges. Both how resilient forest fauna is to cat predation, whether cat predation is additive or compensatory and the extent of sublethal effects of cat predation warrant further investigation, and must be better understood in order to grasp the overall impacts of cat predation in forests.

Accurately quantifying the full extent of cats' impact on forests is likely impossible. There are too many ways cats can impact forest fauna, and many of them are hard to investigate. In addition, differences in local conditions between forests can make it hard to generalize results from studies in one forest area. However, many forests still share a lot of similarities in how they are likely perceived by cats, allowing some broad generalizations so that studies in one forest still provide some valuable insight for other forest. By finding that cats occur at a significant portion of forest sites and relatively far from houses, this study demonstrates that the impacts of cats on forest fauna could be a conservation problem that warrants more research.

5. Conclusion

The goal of this study was to find the proportion of forest habitat in southeastern Norway occupied by domestic cats, and how cat occupancy and detection probability was impacted by certain habitat characteristics like the proximity to houses. I found cats were most common close to houses, while population density, proportion of forests and steepness of the terrain had a negligible effect on where cats occur in forests. My model predicted that cats are present in 9-15% of forests in southeastern Norway. My results suggest cats may use forests more, and extend their activity further away from houses into forests than previously thought. However, we need more knowledge on cat abundance and hunting habits in forests to know the extent of their threat to forest fauna, and in order to mitigate their impacts.

6. References

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7. Appendix

Appendix table 1. Detailed description of how covariates were processed from raw data. The original data was collected from 50 x 50m rasters for all covariates except population density (250 x 250m).

Covariate	Data processing
Distance to house	Data collected from FKB-Bygning (Kartverket, 2017). FKB-Bygning was converted to 50 x 50m raster cells with either value 1 (at least one building in cell) or 0 (no buildings in cell) using GRASS. Only full-time homes ("byggningskode" lower than 160) were defined as a building. Then the euclidian distance in meters to the closest cell with buildings was calculated using the execGRASS function in the rgrass7 package (Bivand, 2022).
Distance to road	Data extracted from FKB-veg50 (NIBIO, 2016). Cells were transformed to either 1's (at least one road in cell) or 0's (no roads in cell) using GRASS. The euclidian distance in meters to the closest cell with roads was calculated using the execGRASS function in the rgrass7 package (Bivand, 2022).
Terrain ruggedness index (TRI)	Digital terrain model (DTM) data was extracted from DTM50 (Kartverket, 2018a). I used the terrain function in the raster package (Hijmans, 2022) to convert from DTM to TRI.
Distance to forest edge	Distance to forest was calculated as the lowest value of three distance rasters for each cell; distance to nearest road- building and field. Distance to building was created using the same rawdata as distance to house, but with all building codes instead of only full-time homes. Data on fields was calculated from ar50 (NIBIO, 2016), by defining fields as area type 20. The euclidian distance in meters to the closest cell with roads was calculated using the execGRASS function in the rgrass7 package (Bivand, 2022).

Forest proportion	Data on area use was extracted from AR50 (NIBIO, 2016). I defined all cells with area type 30 as forests.
Population density	Data on human population density was collected from SSB (2018), and NA-values were transformed to 0's.

Appendix table 2. Percentage of cameras with cat detections at different distances from the nearest house.

Distance to nearest house (m)	Cats detected (%)	Total number of cameras
50-100	41,7	24
100-200	41,0	44
200-500	34,0	145
500-1000	13,9	101
1000-2000	15,7	51
2000-4000	0	37
4000-8000	0	9



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