



Eurasian lynx movement patterns

- Do lynx return to specific locations, and what factors influence them?
-

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Swedish University of Agricultural Sciences, SLU

Faculty of Forest Sciences • Department of Ecology

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Eurasian lynx movement patterns – Do lynx return to specific locations, and what factors influence them?

Rörelsemönster hos lodjur – Har lodjur särskilda platser som de återvänder till och vilka faktorer leder dem dit?

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Keywords: Camera traps, cluster, Eurasian lynx, GPS, habitat selection, *Lynx lynx*, monitoring, movement pattern, Sweden

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Abstract

In recent years, large carnivores have recolonised human-dominated landscapes after near extinction. As their populations recover, efficient monitoring has become a crucial part of management. In Scandinavia, various techniques are used for the annual survey of Eurasian lynx (*Lynx lynx*). This study investigated whether female lynx revisit specific locations in their home range for extended periods, and what habitat factors characterise these locations. These results could improve camera trap placement for the yearly monitoring of lynx family groups. GPS locations from 17 female lynx in periods between 2008 and 2023 were used to identify long-term GPS location clusters. A total of 214 long-term clusters were identified, with a minimum of three positions within a 100-meter radius, exceeding 96 hours from first to last position. Generalised linear mixed models (GLMMs) were used to analyse the effects of proportion of total forest, human infrastructure and water and wetland, distance to large and small roads, the index value of terrain ruggedness and habitat suitability on the position, on the probability of a lynx cluster compared to random position and lynx single position, which were locations that were not included in a cluster. The habitat suitability index was higher at lynx clusters compared to lynx single positions. Terrain ruggedness and total forest had a positive effect on the probability of a lynx cluster in the highest-ranked models for both datasets: lynx cluster – lynx single positions, as well as in lynx cluster – random positions. In contrast, human infrastructure had a negative effect on lynx clusters compared to lynx single positions. The long-term clusters were likely selected for safety as the lynx prefer forested and rugged terrain for protection. By analysing long-term clusters, it is identified that the lynx returns to specific locations with safe habitats. Camera traps could be placed in similar habitats which could enhance camera trap placement, ultimately improving lynx monitoring in Scandinavia.

Keywords: Camera traps, cluster, Eurasian lynx, GPS, habitat selection, *Lynx lynx*, monitoring, movement pattern, Sweden

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1. Introduction

Large carnivores play a crucial role in regulating prey and mesopredators in the ecosystem through top-down control (Ripple et al. 2014). However, habitat loss and fragmentation, as well as human-wildlife conflicts and other threats, have resulted in a decline in carnivore population sizes and many species are considered threatened (Ripple et al. 2014; Wolf & Ripple et al. 2014; Morehouse et al. 2018; Romero-Muñoz et al. 2019; Davoli et al. 2022). In recent years, several large carnivore populations in Europe have started to recover, largely due to changes in legislation and management (Chapron et al. 2014). The return of large carnivores in human-dominated landscapes highlights the need for a deeper understanding of the species, their effects on human interests, and their role in the ecosystem (Davoli et al. 2022).

Monitoring large carnivores is crucial for management and conservation (Walters & Hilborn 1978; Smallwood & Fitzhugh et al. 1995). Several methods, such as snow tracking, scats sampling, Global Positioning System (GPS) collars, and camera traps, can be used to monitor large carnivores (Landa et al. 1998; Aronsson & Persson 2016; Garrote et al. 2021; Åkesson et al. 2022). The monitoring data is important for estimating population size and evaluating the population's management goals (Smallwood & Fitzhugh 1995; Aronsson & Persson 2016).

Tracking carnivores with GPS collars is a common method in wildlife research and has led to a better understanding of the behaviour of carnivores and their effect on prey (Merrill et al. 2010; Oliveira et al. 2022). By analysing the GPS data, clusters of locations can be identified as kill sites, which can be utilised to estimate the kill rate of a predator on a prey species (Merrill et al. 2010; Krofel et al. 2013; Oliveira et al. 2022). Cluster analysis also provides information about the habitat use during different activities, depending on factors such as time of day, season, sex or age (Merrill et al. 2010; Krofel et al. 2013; Podolski et al. 2013).

Camera traps are also frequently used in research to estimate species population size and distribution, as well as to identify individuals based on individual characteristics, such as fur patterns (Rovero & Zimmermann 2016; Hočevár et al. 2020; Fležar et al. 2023). In Scandinavia, camera traps have become an increasingly

common method for the yearly surveys of the Eurasian lynx (*Lynx lynx*), hereafter lynx, to estimate the number of females with kittens (Tovmo & Frank 2024). The most common method for the lynx survey is snow tracking, but since it requires suitable snow conditions, which are increasingly rare in southern Sweden, camera traps are now frequently used (Tovmo & Frank 2024). Effective lynx monitoring with camera traps requires an understanding of lynx movement patterns and landscape features to optimise camera trap placement (Hočevár et al. 2020; Fležar et al. 2023).

1.1 Habitat selection

Habitat selection is when an animal selects a specific habitat to inhabit (Partridge 1978; Johnsson 1980). Environmental factors affect habitat selection and whether the animals prefer a particular habitat (Beyer et al. 2010). Preference is often studied by comparing habitat use and availability and is used to describe the species' ecology (Johnsson 1980). Environmental factors, such as elevation and temperature, and behavioural factors such as finding food, territoriality, or mating affect species habitat and resource selection (Beyer et al. 2010). Species can also choose different resources, such as food, shelter, and habitat, depending on the spatial and temporal scale, meaning that there will be a variation in the selection of a resource depending on the landscape and the time of the day or season (Boyce 2006).

Large carnivores utilise different resources across both spatial and temporal scales. Resource and habitat selection occur on both small and large scales, for example, using areas inside the home range or choosing the home range in the landscape (Mayor et al. 2009; Oeser et al. 2023). Humans can affect the habitat selection for large carnivores on both small and large scale, for example, brown bears (*Ursus arctos*) have been shown to have smaller home ranges in more anthropogenic landscapes (Hertel et al. 2025), and they also adapt by being nocturnal and resting further from human settlements during the day (Kaczensky et al. 2006; Ordiz et al. 2011).

Environment, prey availability, season, human density, age and sex are some factors that affect where the lynx chooses to live and establish its home range (Oeser et al. 2023). Human landscape modification and high human activity have been shown to affect lynx behaviour (Schadt et al. 2002; Oeser et al. 2023). The lynx avoids areas with high human disturbance when establishing its home ranges (Oeser et al. 2023). The lynx can, however, choose to establish its home range in landscapes with high human disturbance if the area has relatively high forest

availability (Oeser et al. 2023). The forest serves as a refuge area and is essential for the lynx in landscapes with high human pressure (Oeser et al. 2023).

The lynx habitat selection also depends on the time of the day (Filla et al. 2017; Oeser et al. 2023). The lynx is crepuscular-nocturnal and rests during the daytime (Hočevár et al. 2021). During nighttime, specifically during evening and early morning, they are most active and typically hunt or revisit kill sites to feed on carcasses of larger prey, often over several consecutive days (Molinari-Jobin et al. 2007; Mattisson et al. 2011; Heurich et al. 2014; Krofel et al. 2019; Hočevár et al. 2021). The lynx selects more open habitats like meadows and clear-cuts during the night, where prey is more abundant and human activity is lower (Filla et al. 2017). Kill sites are often more open than feeding sites, meaning that the lynx drags the carcass to denser, more protected areas for feeding when visibility at the kill site is high (Podgórski et al. 2008).

The lynx has been described as a forest-dwelling species, and they select forest habitat since it provides cover and usually has low human activity (Podgórski et al. 2008; Rauset et al. 2013; Filla et al. 2017; Hemmingmoore et al. 2020; Hočevár et al. 2021; Oeser et al. 2023). Forest habitat is selected more during the day, offering safe resting sites (Oeser et al. 2023). During daytime, different types of dense forest habitats are often selected, such as young forest or clear-cuts with dense vegetation, fallen trees or root plates, that provide the lynx with sheltered daybeds (Filla et al. 2017).

Increased terrain ruggedness is also selected for during daytime and when human activity is high in the area (Rauset et al. 2013; Filla et al. 2017; Oeser et al. 2023). Rugged terrain with rocks and slopes provides a view of the surroundings and secure daybeds (Hočevár et al. 2021). Rugged terrain is also favoured due to low accessibility, reducing the presence of humans and predators as well as protection from harsh weather (Sunde et al. 1998; Falk 2009; Bouyer et al. 2015a; Belloti et al. 2018; Duřa & Krofel 2020; Hemmingmoore et al. 2020; Hočevár et al. 2021).

Previous habitat selection studies have also found that the lynx avoids areas with high densities of roads and humans (Basille et al. 2009; 2013; Bouyer et al. 2015a; Hemmingmoore et al. 2020). The lynx also keeps a distance from large roads (Basille et al. 2009; 2013; Hemmingmoore et al. 2020). The lynx avoids establishing their home ranges near areas of high human density and disturbance (Bouyer et al. 2015a; Hemmingmoore et al. 2020).

Sex and age also influence lynx habitat selection. The lynx mates in March, and the kittens are usually born in May or June (Nilsen et al. 2012; Mattisson et al. 2022).

The lynx females often use several den sites during the denning period (Krofel et al. 2013). Females restrict their movements to a smaller area in the vicinity of the den for six to nine weeks before moving further away to hunt (Kaczensky 1991 see Breitenmoser-Würsten et al. 2007; Krofel et al. 2013). The kittens start moving outside the dens and following the mother around August (Schmidt 1998; Krofel et al. 2013). The offspring leave their mother and start their natal dispersal at 10-11 months old (Samelius et al. 2011). Males usually disperse longer distances and have larger home ranges than females (Samelius et al. 2011). Females may even have overlapping home ranges with their mothers (Samelius et al. 2011).

2. Objectives

The aim of this study was to investigate movement patterns of the Scandinavian lynx population in south-central Sweden. The focus of the study was to investigate if female lynx has specific locations in their home range that they visit regularly and identify what type of habitat is available in these locations. The result can lead to further improvements in the lynx monitoring in Scandinavia by improving the use of camera traps.

The study investigated whether the index value of terrain ruggedness and habitat suitability, the proportion of habitat classes (total forest, human infrastructure, and water and wetland), and the distance to large and small roads influence lynx movement patterns and whether these variables affect lynx movement to specific locations.

In this study, I predict that the specific locations that the lynx visit regularly and return to over longer periods have a higher habitat suitability index than single lynx positions (Hemmingmoore et al. 2020). Thus, I predict that the specific locations will have a higher forest proportion, higher terrain ruggedness, and be further from large roads than lynx single positions and random positions (Basille et al. 2009; 2013; Rauset et al. 2013; Bouyer et al. 2015a; Filla et al. 2017; Hemmingmoore et al. 2020; Oeser et al. 2023).

3. Methods

3.1 Population and study area

The Eurasian lynx is a large carnivore with a broad distribution in Europe and Asia (Schmidt et al. 2011; von Arx 2020). In Europe, the lynx is found in 23 countries and is considered into 11 distinct subpopulations (Chapron et al. 2014). The lynx is the largest feline species in Europe and lives solitary, except for females with kittens (Nilsen et al. 2012; Bull et al. 2016). The species is territorial and has large home ranges (Linnell et al. 2001).

During the 19th and the beginning of the 20th century, the lynx population in Sweden and Norway was almost extinct due to severe hunting (Liberg 1977 see Andrén & Liberg 2008). The Scandinavian lynx population increased in the mid-20th century when the species became protected from hunting in Sweden (Andrén & Liberg 2008). The population was estimated in 2024 to be 296 family groups, corresponding to around 1738 individuals (Tovmo & Frank 2024). The Scandinavian population exhibits the lowest genetic diversity among Eurasian lynx subpopulations (Schmidt et al. 2011; Rueness et al. 2014; Lucena-Perez et al. 2021). Genetic loss is explained by the relative isolation from the broader continent (Schmidt et al. 2011; Rueness et al. 2014).

Lynx prey upon several ungulate species. The main prey in most of Scandinavia is roe deer (*Capreolus capreolus*), except within the reindeer husbandry area, where the main prey is reindeer (*Rangifer tarandus*) (Odden et al. 2006; Mattisson et al. 2014; Andrén & Liberg 2015; Aronsson et al. 2016). When the main prey is unavailable, several species are preyed upon as alternative prey, and if ungulates are unavailable, smaller prey is usually consumed (Khorozyan & Heurich 2023).

This study was conducted on radio-collared lynx in south-central Sweden (Fig. 1). Intensively managed boreal forests with mainly Norway spruce (*Picea abies*) and Scots pine (*Pinus sylvestris*), mixed with deciduous tree species (*Betula pubescens*, *B. verrucosa* and *Populus tremula*) dominate the area (Statistics Sweden 2020; SLU Riksskogstaxeringen 2022; Andrén & Liberg 2024). The second major land cover

type is agricultural land, which becomes more prevalent toward the south (Statistics Sweden 2020; SLU Riksskogstaxeringen 2022). The agricultural land consists of cropland and grazing areas (Hemmingmoore et al. 2020).

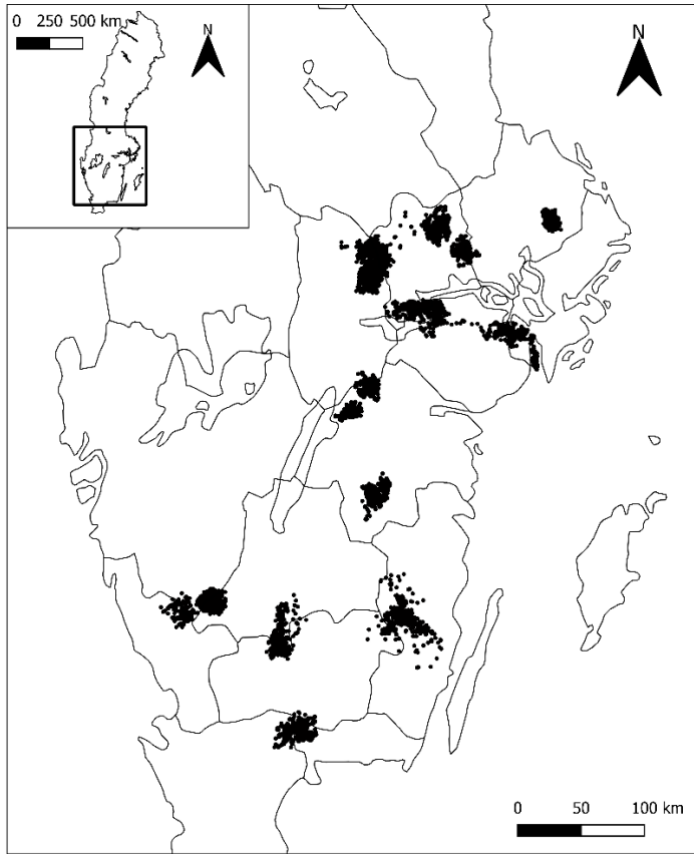


Figure 1. GPS locations ($n = 11687$) from 17 female lynx monitored between 2008-2023 in south-central Sweden.

3.2 Monitoring of the Scandinavian lynx population

In Scandinavia, the lynx population is monitored by counting the number of family groups, defined as females with kittens, from the first of October to the last of February each year (Linnell et al. 2007). The population size is then estimated based on the number of family groups calculated with extrapolation factors from four different areas of Scandinavia, which are based on the density of the main prey in the areas (Andrén et al. 2002; Gervasi et al. 2013; Tovmo & Frank 2024). The surveys are primarily conducted through snow tracking, where tracks of a female accompanied by one or several kittens are confirmed by field personnel from the County Administrative Boards in Sweden and the Norwegian Nature Inspectorate (SNO) in Norway (Tovmo & Frank 2024; Swedish Environmental Protection Agency & Rovdata 2024). The lynx monitoring is also supplemented with photos

from camera traps and direct observations or discoveries of dead kittens (Swedish Environmental Protection Agency & Rovdata 2024).

3.3 GPS data

In this study, GPS data from lynx were analysed to investigate movement patterns in different habitats and to identify specific locations that the lynx frequently visited by using cluster analysis. The study used 11687 GPS locations, from 17 GPS-collared female lynx during periods between 2008 and 2023 (Fig. 1). All procedures for capturing, handling and collaring the lynx were approved by the Swedish Animal Welfare Agency, see details from Andrén et al. (2006) and Arnemo & Evans (2017).

3.3.1 Cluster analysis

The specific locations that are visited regularly by the lynx are defined as smaller areas that the lynx return to several times during longer periods and other places are visited in between. To find the specific locations that the lynx frequently visited, lynx clusters were formed from the GPS data. The GPS data was processed and filtered using R 4.3.3 (R Core Team 2024). The cluster analysis was done in R using the GPSeqClus package (Clapp 2023). The package used different arguments for; search radius from cluster centroid, window days to search for new locations and minimum number of locations to build the clusters. A 100-meter search radius was selected in accordance with previous studies on cluster analysis (Mahoney & Young 2008; Mattisson et al. 2011; Svoboda et al. 2013; Tallian et al. 2023). The temporal window was set to 1080 days since the most extended dataset was almost three years long. The minimum number of locations was set to three locations. From the cluster analysis, a data frame was produced with the sequential clusters and their attributes, for example, cluster-ID, time of first and last location in the cluster, coordinates of the mean geometric centroid, number of locations, the duration from first to last location in the cluster and number of night locations.

The lynx clusters were further analysed in Q-GIS v. 3.34.0 (QGIS.org 2023). Also, lynx single positions, which are the GPS locations that were not included in a cluster, were added to Q-GIS. The home range of each lynx was defined by using all available GPS locations from its study period (Table 1) and producing one minimum convex polygon (MCP) per individual. Within each home range, random locations were added at a 1:1 ratio to the number of clusters per individual. These random locations served as controls to describe the available habitat types and enable the assessment of the lynx habitat selection.

Table 1. Animal ID, number of GPS locations, study period (start-end in month and year) and fix rate (mode) (interval of number of locations per day, with the most common fix rate in parentheses), defined as the interval between the first and last location per individual. The GPS locations were used to estimate home ranges and perform cluster analysis for each individual. The number of GPS locations ranged from 175 to 1788. GPS data from 17 collared lynx in Sweden during 2008-2023.

Animal ID	No. of GPS locations	Study period (start-end)	Fix rate (mode)
8173	482	Sep 2008 – Apr 2009	1-4 (3)
9183	424	Oct 2009 – Nov 2010	1-9 (1)
9186	264	Nov 2009 – May 2010	1-10 (1)
9187	400	Dec 2009 – Dec 2010	1-13 (1)
10192	699	Apr 2010 – Jan 2012	1-7 (1)
10200	175	Nov 2010 – Mar 2011	1-6 (1)
11202	549	Feb 2011 – May 2012	1-8 (1)
12209	519	Jan 2012 – Apr 2013	1-7 (1)
12210	1061	Feb 2012 – Jan 2015	1-7 (1)
12211	489	Feb 2012 – Mar 2013	1-7 (1)
12224	345	Nov 2012 – Apr 2013	1-7 (1)
14237	807	Mar 2014 – Feb 2016	1-7 (1)
14238	676	Apr 2014 – Nov 2015	1-7 (1)
18250	709	Mar 2018 – Jan 2019	1-24 (1)
20258	1142	Mar 2020 – Feb 2021	1-24 (3)
22265	1158	Feb 2022 – Mar 2023	1-24 (3)
22267	1788	Mar 2022 – Oct 2023	1-24 (3)

Lynx clusters were filtered to only include clusters where the duration from the first to the last location exceeded 96 hours since the focus was on analysing the clusters that the lynx had visited for a longer period. The time was decided to be able to avoid kill sites since studies show that lynx tend to visit kill sites of roe deer several nights in a row in order to feed on the carcass, with an average of three visits (Krofel et al. 2013; Tallian et al. 2023). Lynx spends an average of 32 hours on handling wild prey (Tallian et al. 2023).

The cluster data were also filtered based on the lynx reproduction season. In south-central Sweden, lynx kittens are born in May or June (Samelius et al. 2011; Mattisson et al. 2022). Lynx clusters that overlapped with the reproduction season were removed from the dataset since females return to the same den for several weeks to feed the kittens, which would be a cluster in the analysis (Kitchener 1991 see Bautros et al. 2007; Mattisson et al. 2010). Therefore, if both the cluster start and end date fell between 15 May and 31 July in the same year, the clusters were removed from the dataset.

3.4 Explanatory variables

The explanatory variables were processed using Q-GIS.

3.4.1 Habitat

The habitat data used in the study was the National Land Cover Database 2018 (NMD) in 10 x 10-meter raster grid cells from the Swedish Environmental Protection Agency (2019). The NMD included 25 landcover categories that were categorised into eight habitat classes (Appendix 1, Table S1). The four different forest habitats were also combined into a new habitat class, referred to as total forest, resulting in a total of nine habitat classes (Table 2). For each lynx cluster, lynx single position and random position, a 100-meter buffer was created in which the proportion of each habitat class was calculated from the total area of the buffer.

*Table 2. The nine habitat classes used for analysing lynx habitat selection. Habitat classes marked with * were combined into one habitat class, called total forest. For each lynx cluster, lynx single position and random position, the proportion of each habitat class was calculated from the 100-meter buffer around the position.*

Habitat class
Water and wetland
Agricultural land
Open areas, grasslands and meadows
Human infrastructure
Coniferous forest*
Mixed forest*
Deciduous forest*
Young forest*
Total forest

3.4.2 Road

Road data was used from Lantmäteriet Topografi 100 vector data (scale 1:100 000). The roads were categorised into large or small roads, where “Allmän väg” was considered large (paved) and “Enskild väg” was considered small (gravel). The shortest distance in meters to small and large roads was calculated for each lynx cluster, lynx single position and random position.

3.4.3 Terrain ruggedness

A 250 x 250-meter grid cell raster layer over Sweden and Norway with terrain ruggedness index ranging from 0 to 243.4 (European Environment Agency (EEA) and Riley et al. 1999) was used to derive terrain ruggedness values for each lynx cluster, lynx single position and random position. The values ranged from 0 to 17.1,

with a mean value of 0.9 in the lynx home ranges. The terrain ruggedness was calculated from the raster layer's cell value at the location of each cluster or position.

3.4.4 Habitat suitability

The habitat suitability data were obtained from Hemmingmoore et al. (2020) habitat suitability map. The map was a raster layer of south-central Sweden with pixel values on a 25 x 25-meter grid. It was based on models predicting the habitat selection of established lynx in central Sweden (Appendix 5, Table S1). The pixel values ranged from 0 to 1, where 0 means avoidance and 1 is selection, with a neutral selection of $1/6 = 0.167$. Habitat suitability values were extracted for each lynx cluster and lynx single position, but not for random positions since the map by Hemmingmoore et al. (2020) was based on lynx positions compared to random positions.

3.5 Statistical analysis

The statistical analyses were conducted using R. A correlation test on all explanatory variables was assessed using Spearman's rank-order correlation coefficient. Variables with a $r_s > 0.4$ were excluded from the same model. Four of the 13 variables were uncorrelated: total forest, human infrastructure, water and wetland, and terrain ruggedness (Appendix 2, Figures S1 and S2). The variable total forest was chosen instead of variables of other forest types or agricultural land due to the study's objectives, predicting a higher forest proportion to be found on lynx clusters than on positions. The human infrastructure variable was correlated with the variable small roads, but the variable large roads was also excluded from the same model since road data is included in the human infrastructure variable. The variables large roads and small roads were analysed in another model together with the variables total forest and terrain ruggedness. The habitat suitability variable was analysed as a single variable since it is derived from several other variables (Hemmingmoore et al. 2020, Appendix 5, Table S1).

General linear mixed models (GLMMs) were fitted with a binomial distribution using the R-package glmmTMB (Brooks et al. 2017). Lynx ID was included as a random factor in the model. The dredge function from the MuMIn package (Bartón 2023) was used to produce the best-fitting models based on the Akaike Information Criterion corrected for small sample size (AICc). AICc was used to account for the small dataset and avoid overfitting. The dredge function was used to be able to analyse the large number of variables for both datasets. However, the road variables, distance to large roads and small roads, were only analysed together with

the most important environmental variables, total forest and terrain ruggedness, producing one model for each dataset. The variable human infrastructure was correlated with distance to small roads and was also derived from similar road data, therefore it was excluded from these models.

Two datasets were included in the analysis. In both, the response variable was binary, coded as 1 for lynx clusters and 0 for lynx single positions or random positions. The first dataset, containing lynx clusters and lynx single positions, comprised 7447 samples, of which 214 were lynx clusters. The second dataset, consisting of lynx clusters and random positions, comprised 999 samples, including 214 lynx clusters. Because of the filtering of the lynx clusters, the number of clusters and random positions was no longer balanced at a 1:1 ratio. Due to the unequal number of lynx clusters, lynx single positions and random positions in the datasets, a baseline selection probability of the data was calculated as a reference value for comparison with the predicted probability of a position being classified as a cluster in the graphs. This value was derived as the arithmetic mean of the ratio of lynx clusters to the total sample across all individuals.

4. Results

The lynx GPS locations resulted into 214 clusters. Lynx visited a large proportion of the clusters during nighttime, and a smaller proportion of the clusters was visited only during daytime or both day- and nighttime (Appendix 4, Fig. S1). The duration of the lynx clusters, from first to last position, had a large interval, where some clusters were revisited after one to two years (Appendix 4, Fig. S2). An overview of the explanatory variables used in the analysis for the lynx clusters, lynx single positions and random positions is presented in Table 3.

Table 3. Summary statistics (minimum, mean, standard deviation and maximum values) for the explanatory variables total forest, human infrastructure, water and wetland, terrain ruggedness, habitat suitability, large roads and small roads, for the three different datasets: lynx clusters, lynx single positions and random positions. Clusters and single positions are based on GPS data from collared lynx in Sweden during 2008-2023.

Dataset		Total forest	Human infrastructure	Water & wetland	Terrain ruggedness	Habitat suitability	Large roads	Small roads
Lynx cluster	Minimum	0	0	0	0	0.03	27.59	0.65
	Mean	0.79	0.02	0.04	1.27	0.21	1179.13	190.58
	SD	0.25	0.04	0.12	1.20	0.10	917.05	141.76
	Maximum	1.00	0.18	1.00	9.92	0.73	4061.97	745.53
Lynx single positions	Minimum	0	0	0	0	0.02	0.05	0.02
	Mean	0.75	0.04	0.05	1.10	0.19	1088.88	170.82
	SD	0.27	0.05	0.14	0.87	0.08	887.87	145.38
	Maximum	1.00	0.99	1.00	9.05	0.93	5949.66	1056.93
Random positions	Minimum	0	0	0	0	-	1.10	0.75
	Mean	0.70	0.03	0.11	0.95	-	1039.17	221.53
	SD	0.36	0.05	0.26	0.83	-	912.46	244.15
	Maximum	1.00	0.47	1.00	10.27	-	6081.66	3068.28

4.1 Lynx cluster - lynx single positions

The result of the analysis of the dataset lynx clusters compared to lynx single positions, where the lynx clusters are 1, and lynx single positions are 0, in the binary logistic regression models. The baseline selection probability for the dataset was 0.026, calculated as the arithmetic mean of the ratio of lynx clusters to the total sample for all individuals.

4.1.1 Habitat suitability

The distribution curves of habitat suitability for the 7233 lynx single positions and the 214 lynx clusters are shown in Figure 2.

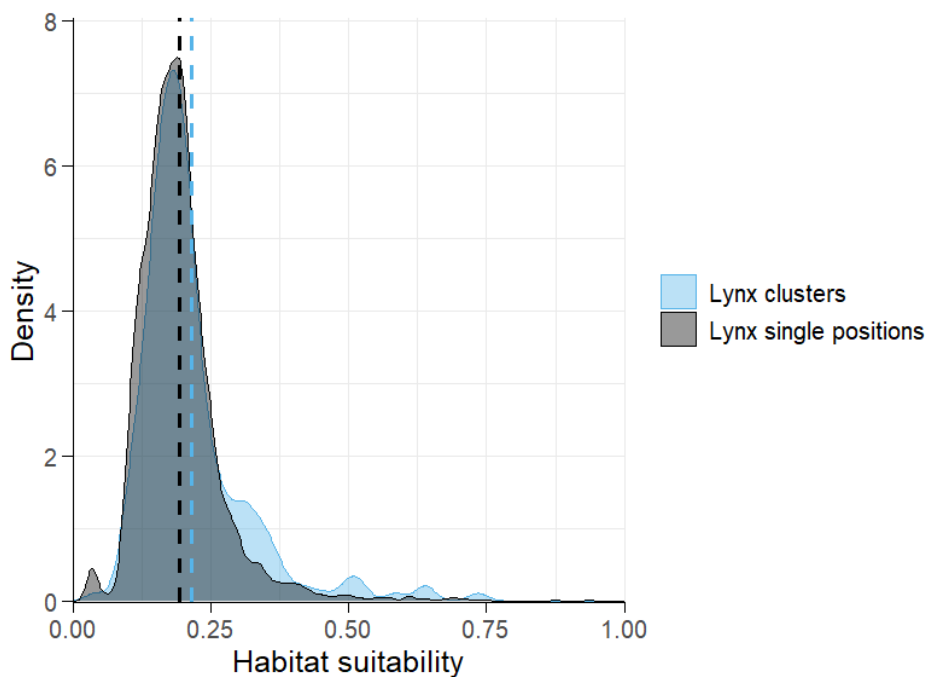


Figure 2. Density of lynx clusters ($n=214$), and lynx single positions ($n=7233$), across the habitat suitability, with values between 0 and 1. The blue dashed line represents the mean value of lynx clusters (0.21), and the black dashed line represents the mean value of lynx single positions (0.19). Clusters and single positions are based on GPS data from collared lynx in Sweden during 2008-2023, using Hemmingmoore et al. (2020) habitat suitability map with a neutral selection of $1/6 = 0.167$.

The density reflects how concentrated the clusters and positions are at specific habitat suitability values. The density is scaled relative to the total area under each curve, with the area representing 100% of the clusters or positions. Both clusters and positions showed higher density at habitat suitability values between 0.1 and 0.3, indicating that the values were around the neutral selection (Fig. 2). However, the density of clusters was higher at habitat suitability values >0.25 compared to lynx single positions. The lynx clusters had a mean habitat suitability value of 0.21,

while lynx single positions had a mean value of 0.19, both exceeding the neutral selection value (Table 3 and Fig. 2).

The habitat suitability had a strong positive impact on lynx clusters compared to the lynx single positions. The logistic regression shows that increasing habitat suitability increases the probability of a location being a cluster (estimate = 3.92, 95% CI: 2.49, 5.36, $p < 0.0001$; Table 4 and Fig. 3).

Table 4. A logistic regression model with habitat suitability as the explanatory variable and the response variable; 0 = lynx single positions, 1 = lynx cluster. Conditional model parameter estimates (Estimate), standard errors (SE), 95% confidence intervals (CI), Z values, and P values for the explanatory variable. Clusters and single positions are based on GPS data from collared lynx in Sweden during 2008-2023.

Explanatory variable	Estimate	SE	95% CI	Z value	P value
Intercept	-3.72	0.16	-4.04, -3.40	22.83	<0.0001
Habitat suitability	3.92	0.73	2.49, 5.36	5.36	<0.0001

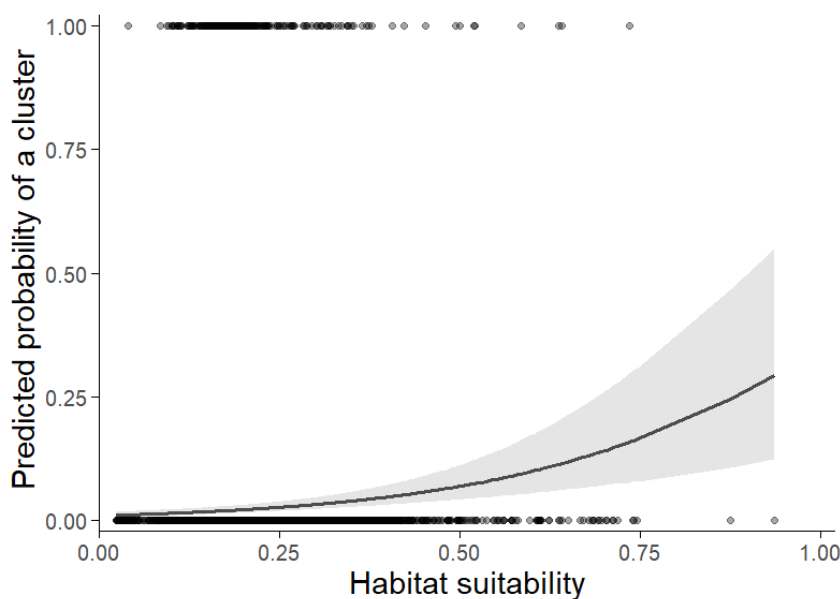


Figure 3. The predicted probability of a lynx cluster as a function of habitat suitability. The line represents the probability and the shaded area the 95% confidence interval. The points display the habitat suitability values for the lynx single positions = 0, and the lynx clusters = 1. Clusters and single positions are based on GPS data from collared lynx in Sweden during 2008-2023.

4.1.2 Environmental variables

The dataset comparing lynx clusters to lynx single positions identified five models with $\Delta AICc < 4$, including two models with $\Delta AICc < 2$, from a total of 16 candidate models (Table 7). Terrain ruggedness consistently showed a strong positive effect

on the probability of a lynx cluster across all five models (p value < 0.001). Total forest was included in three models, human infrastructure in four models, and water and wetland in two models (Tables 7 and 8).

In the highest-ranked model, terrain ruggedness, total forest and human infrastructure were included, with terrain ruggedness and total forest showing positive effects on the probability of a cluster, and human infrastructure demonstrating a negative effect (Table 8). The combined effects of the variables in the highest-ranked model are presented in separate figures, with two variables shown in each figure. The third variable is kept constant at its mean value (Fig. 4 and Appendix 3, Figures S1-S5).

The second highest-ranked model included all four variables, though total forest and water and wetland had non-significant effects, while terrain ruggedness retained a positive effect and human infrastructure a negative effect (Table 8). In the third highest-ranked model, terrain ruggedness again showed a positive effect and human infrastructure a negative effect. In the fourth highest-ranked model, terrain ruggedness and total forest showed a positive effect. In the fifth highest-ranked model, terrain ruggedness had a positive effect and human infrastructure had a negative effect, while water and wetland showed a non-significant negative effect (Table 8).

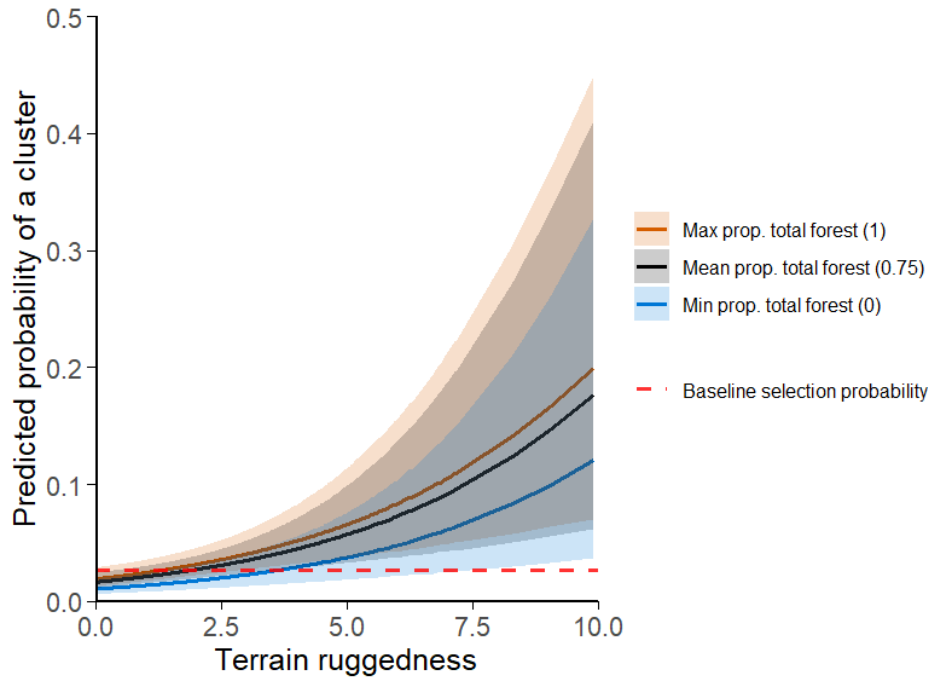


Figure 4. Predicted probability of a lynx cluster occurrence as a function of terrain ruggedness (x-axis, with values from 0 - 9.9; note that most values are below 2.5), conditioned on the proportion of total forest. The three lines represent different levels of total forest proportion (maximum = 1, mean = 0.75, minimum = 0), while the shaded areas indicate the 95% confidence intervals. The red dashed line represents the baseline selection probability (0.026). The third variable in the model (human infrastructure) is kept constant at its mean value. The figure illustrates the highest-ranked model with the response variable; 0 = lynx single positions, 1 = lynx clusters. Clusters and single positions are based on GPS data from collared lynx in Sweden during 2008-2023.

4.1.3 Roads

The road variables, distance to large and small roads, had a non-significant positive effect on the probability of a cluster. However, total forest and terrain ruggedness had a positive effect (Table 5).

Table 5. A logistic regression model with the response variable; 0 = lynx single positions, 1 = lynx cluster. Conditional model parameter estimates (Estimate), standard errors (SE), 95% confidence intervals (CI), Z values, and P values for each explanatory variable. Explanatory variables are in bold when p value < 0.05. Clusters are based on GPS data from collared lynx in Sweden during 2008-2023.

Explanatory variable	Estimate	SE	95% CI	Z value	P value
Intercept	-4.75	0.32	-5.39, -4.12	-14.76	<0.0001
Large roads	0.00008	0.00008	-0.00008, 0.0002	1.00	0.32
Small roads	0.0004	0.0005	-0.0005, 0.001	0.88	0.38
Total forest	0.69	0.29	0.12, 1.26	2.36	0.02
Terrain ruggedness	0.26	0.07	0.12, 0.39	3.80	0.0002

4.2 Lynx cluster - random positions

The result of the analysis of the dataset lynx clusters compared to random positions, where the lynx clusters are 1, and random positions are 0, in the binary logistic regression models. The baseline selection probability for the dataset was 0.184, calculated as the arithmetic mean of the ratio of lynx clusters to the total sample for all individuals.

4.2.1 Terrain ruggedness

The distribution of terrain ruggedness for the 785 random positions and the 214 lynx clusters is shown in Figure 5. The density of the clusters and positions was higher in areas with low terrain ruggedness values (0 - 2.5), with lower density in areas with higher terrain ruggedness values (>2.5). However, the density of lynx clusters was higher than random positions at a higher index of terrain ruggedness. The lynx clusters had a mean terrain ruggedness value of 1.27, whereas the random positions had a mean terrain ruggedness value of 0.95 (Table 3 and Fig. 5).

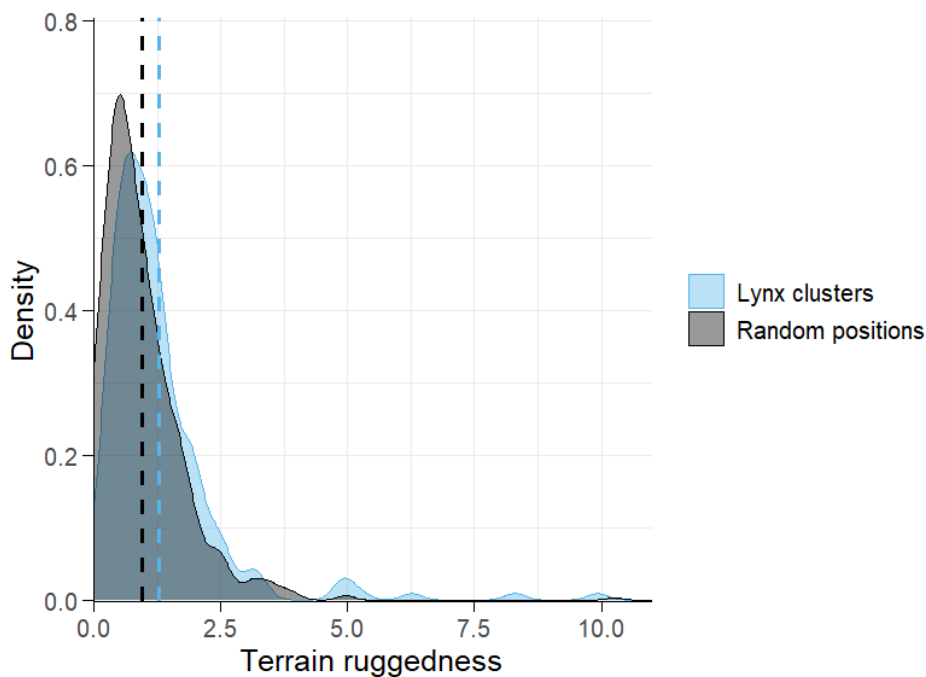


Figure 5. Density of randomly distributed positions ($n=785$) in the lynx home range, and lynx clusters ($n=214$), across the terrain ruggedness values. The terrain ruggedness ranged from 0 - 9.9 for the lynx clusters and 0 - 10.3 for the random positions. The blue dashed line represents the mean value of lynx clusters (1.27), and the black dashed line represents the mean value of random positions (0.95). Clusters are based on GPS data from collared lynx in Sweden during 2008-2023.

4.2.2 Environmental variables

The dataset comparing lynx clusters to random positions identified four models with $\Delta\text{AICc} < 4$, including three models with $\Delta\text{AICc} < 2$, from a total of 16 models (Table 7). Terrain ruggedness consistently showed a strong positive effect on the probability of a lynx cluster across all four models (p value < 0.001). Total forest also exhibited a positive effect in all models. Water and wetland, as well as human infrastructure, were included in two models each (Tables 7 and 8).

Water and wetland had a non-significant negative effect in the highest- and third-ranked models. Similarly, human infrastructure was included in the third- and fourth-ranked models, also with non-significant negative effects (Table 8). The combined effect of the two variables in the second highest-ranked model is presented in two different figures (Fig. 6 and 7).

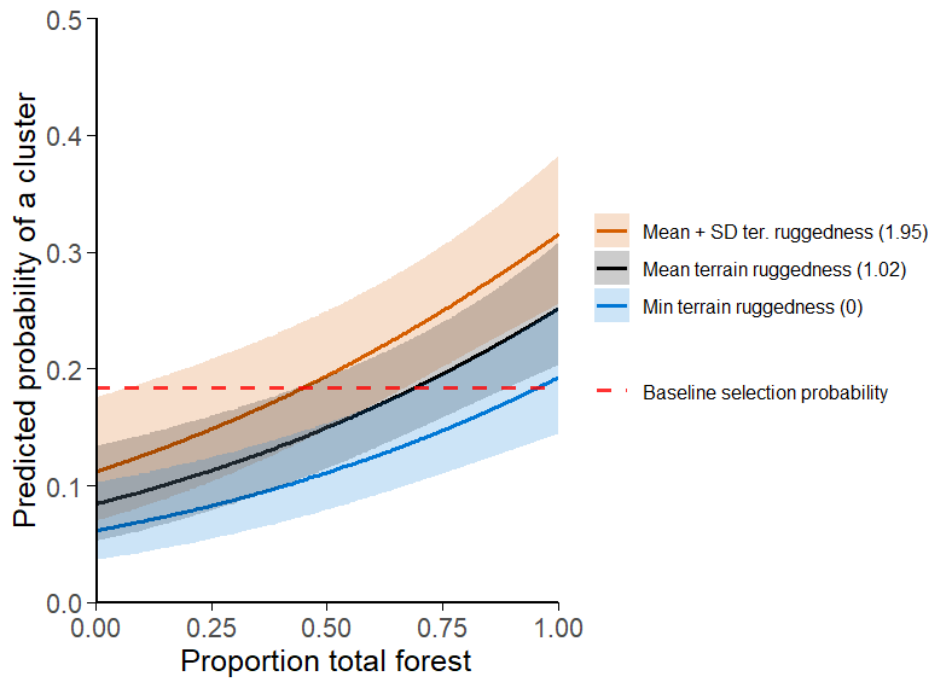


Figure 6. Predicted probability of a lynx cluster occurrence as a function of proportion total forest (x-axis, with values from 0 - 1), conditioned on terrain ruggedness. The three lines represent different levels of terrain ruggedness (mean + 1 SD = 1.95, mean = 1.0, minimum = 0), while the shaded areas indicate the 95% confidence intervals. The red dashed line represents the baseline selection probability (0.184). The figure illustrates the second highest-ranked model with the response variable; 0 = random positions, 1 = lynx clusters. Clusters are based on GPS data from collared lynx in Sweden during 2008-2023.

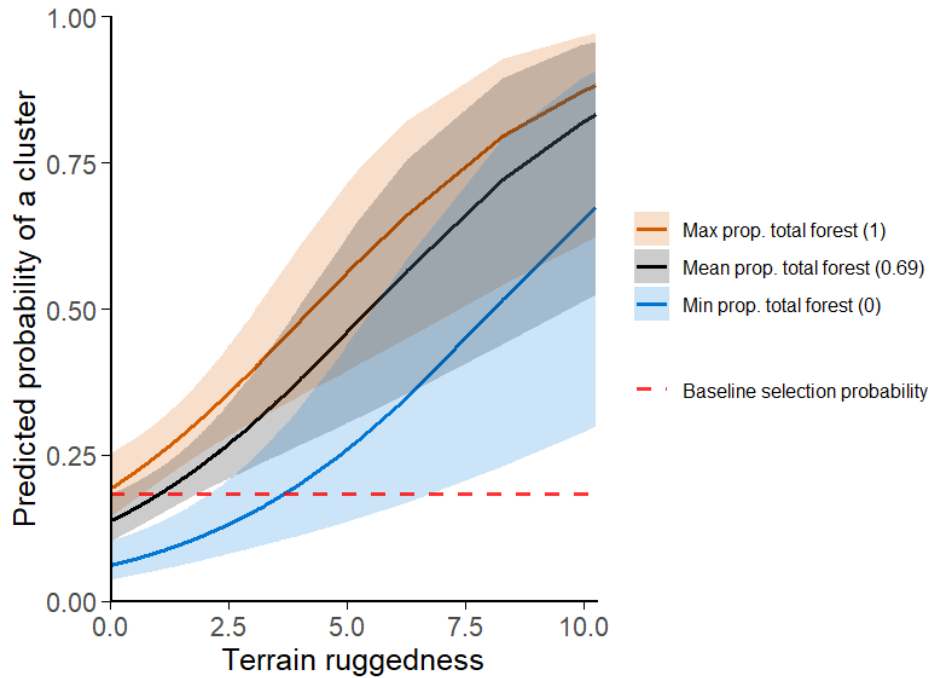


Figure 7. Predicted probability of a lynx cluster occurrence as a function of terrain ruggedness (x-axis, with values from 0 - 10.3; note that most values are below 2.5 (Fig. 5), conditioned on the proportion of total forest. The three lines represent different levels of total forest proportion (maximum = 1, mean = 0.69, minimum = 0), while the shaded areas indicate the 95% confidence intervals. The red dashed line represents the baseline selection probability (0.184). The figure illustrates the second highest-ranked model with the response variable; 0 = random positions, 1 = lynx clusters. Clusters are based on GPS data from collared lynx in Sweden during 2008-2023.

4.2.3 Roads

The road variables, distance to large and small roads, did not have a significant effect on the probability of a cluster, where large roads had a weak positive effect while small roads had a weak negative effect. However, total forest and terrain ruggedness had a positive effect (Table 6).

Table 6. A logistic regression model with the response variable; 0 = random points, 1 = lynx cluster. Conditional model parameter estimates (Estimate), standard errors (SE), 95% confidence intervals (CI), Z values, and P values for each explanatory variable. Explanatory variables are in bold when p value < 0.05 . Clusters are based on GPS data from collared lynx in Sweden during 2008-2023.

Explanatory variable	Estimate	SE	95% CI	Z value	P value
Intercept	-2.76	0.33	-3.40, -2.12	-8.47	<0.0001
Large roads	0.0002	0.0001	-0.00003, 0.0004	1.69	0.09
Small roads	-0.0005	0.0005	-0.001, 0.0004	-1.13	0.26
Total forest	1.18	0.28	0.62, 1.74	4.14	<0.0001
Terrain ruggedness	0.35	0.09	0.18, 0.52	3.99	<0.0001

Table 7. Generalised linear mixed models assessing the effects of total forest, human infrastructure, water and wetland, and terrain ruggedness, on the predicted probability of a lynx cluster compared to lynx single positions or random positions of collared lynx in Sweden during 2008-2023. For all models, degrees of freedom (df), differences in AICc relative to the highest-ranked model ($\Delta AICc$), AICc weight and log-likelihood (LogLik) are presented.

Dataset	Model No.	Intercept	Total forest	Human inf.	Water and wetland	Terrain rugg.	df	$\Delta AICc$	LogLik	AICc weight
Lynx cluster - lynx single positions	1	-	+	-	NA	+	5	0	-942.56	0.47
	2	-	+	-	-	+	6	1.96	-942.54	0.18
	3	-	NA	-	NA	+	4	2.38	-944.75	0.14
	4	-	+	NA	NA	+	4	2.66	-944.89	0.12
	5	-	NA	-	-	+	5	3.20	-944.17	0.09
Lynx cluster - random positions	1	-	+	NA	-	+	5	0	-495.82	0.37
	2	-	+	NA	NA	+	4	0.42	-497.04	0.30
	3	-	+	-	-	+	6	1.08	-495.35	0.21
	4	-	+	-	NA	+	5	2.12	-496.88	0.13

Table 8. Conditional model parameter estimates (Estimate), standard errors (SE), 95% confidence intervals (CI), Z values, and P values for each explanatory variable from the models with $\Delta AICc < 4$ (Table 7). Explanatory variables are in bold when p value < 0.05 . Analyses were conducted on two datasets of collared lynx in Sweden from 2008-2023.

Dataset	Model no.	Explanatory variable	Estimate	SE	95% CI	Z value	P value
Lynx cluster - lynx single positions	1	Intercept	-4.41	0.32	-5.04, -3.78	13.69	<0.0001
		Total forest	0.59	0.29	0.02, 1.17	2.03	0.04
		Human infrastructure	-3.61	1.78	-7.10, -0.13	2.03	0.04
		Terrain ruggedness	0.26	0.07	0.12, 0.39	3.78	0.0002
	2	Intercept	-4.37	0.35	-5.06, -3.68	12.41	<0.0001
		Total forest	0.56	0.32	-0.07, 1.20	1.75	0.08
		Human infrastructure	-3.70	1.82	-7.27, -0.13	2.03	0.04
		Terrain ruggedness	0.26	0.07	0.12, 0.39	3.78	0.0002
		Water and wetland	-0.15	0.68	-1.47, 1.18	0.22	0.83
	3	Intercept	-3.91	0.20	-4.31, -3.52	19.42	<0.0001
		Human infrastructure	-4.43	1.73	-7.82, -1.04	2.56	0.01
		Terrain ruggedness	0.26	0.07	0.13, 0.39	3.82	0.0001
	4	Intercept	-4.65	0.31	-5.26, -4.05	15.03	<0.0001
		Total forest	0.76	0.29	0.20, 1.33	2.63	0.008
		Terrain ruggedness	0.26	0.07	0.13, 0.39	3.81	0.0001
	5	Intercept	-3.88	0.20	-4.28, -3.49	19.16	<0.0001
		Human infrastructure	-4.64	1.75	-8.06, -1.21	2.66	0.008
		Terrain ruggedness	0.26	0.07	0.13, 0.39	3.83	0.0001
		Water and wetland	-0.63	0.62	-1.84, 0.57	1.03	0.30
Lynx cluster - random positions	1	Intercept	-2.47	0.32	-3.10, -1.85	7.76	<0.0001
		Total forest	1.06	0.31	0.45, 1.67	3.40	0.0007
		Terrain ruggedness	0.33	0.09	0.16, 0.49	3.82	0.0001
		Water and wetland	-0.92	0.62	-2.15, 0.30	1.48	0.14
	2	Intercept	-2.73	0.28	-3.28, -2.17	9.65	<0.0001
		Total forest	1.29	0.28	0.74, 1.84	4.61	<0.0001
		Terrain ruggedness	0.34	0.08	0.17, 0.50	3.98	<0.0001
	3	Intercept	-2.34	0.34	-3.01, -1.67	6.84	<0.0001
		Total forest	0.96	0.32	0.32, 1.59	2.96	0.003
		Human infrastructure	-1.91	2.01	-5.85, 2.02	0.95	0.34
		Terrain ruggedness	0.33	0.08	0.16, 0.50	3.89	0.0001
		Water and wetland	-1.05	0.64	-2.30, 0.20	1.65	0.10
	4	Intercept	-2.67	0.30	-3.25, -2.09	9.03	<0.0001
		Total forest	1.26	0.29	0.69, 1.82	4.38	<0.0001
		Human infrastructure	-1.10	1.96	-4.94, 2.73	0.56	0.57
		Terrain ruggedness	0.34	0.08	0.17, 0.51	4.02	<0.0001

5. Discussion

This thesis analysed two different datasets, lynx clusters compared to lynx single positions and lynx clusters compared to random positions. Overall, similar results were found for both datasets where the explanatory variables terrain ruggedness and total forest were included in the highest-ranked model. The variable human infrastructure had a significant effect only in the dataset comparing lynx clusters to lynx single positions.

5.1 High proportion of forest at the lynx clusters

As predicted, total forest had a positive effect on the probability of a lynx cluster in all models, with only one model showing a weak effect. Previous studies indicate that lynx selects different habitats depending on activity and time of day (Oeser et al. 2023). Forest habitat is important for lynx since it provides a safe environment from human disturbance and serves as a refuge area (Oeser et al. 2023). The lynx rests primarily during the day and selects forest habitats for cover and safe resting spots (Filla et al. 2017; Oeser et al. 2023).

Lynx clusters had a higher proportion of forest than lynx single positions and random positions, suggesting that the lynx clusters function as refuge areas. The lynx clusters are used for extended periods and are sporadically revisited several times. This result suggests that clusters are used as daybed sites, explaining the high proportion of forest. However, since many lynx clusters were visited at night, they also have a purpose other than daybeds.

The lynx is primarily a crepuscular-nocturnal species, with peak activity at twilight (Heurich et al. 2014; Krofel et al. 2019; Hočevár et al. 2021). The peak corresponds to the activity of roe deer, which are also crepuscular and the main prey for lynx in southern Sweden (Krop-Benesch et al. 2012; Samelius et al. 2013; Heurich et al. 2014). Thereby, the lynx is likely inactive between hunting and feeding events during some periods of the night, which could explain their use of clusters with a high proportion of forests for resting. Previous studies indicate that the lynx selects more open habitats such as meadows and clear-cuts during nighttime, likely

because of higher prey availability (Filla et al. 2017). Given this, lynx cluster locations are probably not primarily selected due to high hunting availability.

5.2 Terrain ruggedness has a strong impact on lynx

Terrain ruggedness was one of the key explanatory variables in this study. Consistent with the prediction, terrain ruggedness showed a positive effect on the probability of a cluster across all models in both datasets. Rugged terrain provides lynx protection, similar to forest habitats (Oeser et al. 2023). Previous studies have shown that lynx use rugged terrain more frequently during the day and in areas with higher human pressure (Filla et al. 2017; Oeser et al. 2023). Increased terrain ruggedness offers protection from human disturbance and provides secure resting sites (Bouyer et al. 2015a; Filla et al. 2017; Hočevár et al. 2021). The lynx clusters identified in this study may therefore function as safe resting sites, particularly when used during the daytime.

A study on lynx in Norway found differences in habitat selection between males and females for resting sites (Bouyer et al. 2015a). Females preferred rugged terrain at high elevations, along with medium roe deer density and high forest cover, while males selected lower elevations with lower roe deer density (Bouyer et al. 2015a). Additionally, lynx selected rugged terrain across all activities, including resting sites, kill sites and movement, regardless of the level of human habitat modification (Bouyer et al. 2015a). Although that study did not focus on clusters that get revisited over longer periods, its findings suggest that terrain ruggedness is an important habitat for lynx regardless of activity, which aligns with its strong explanatory power in this study.

The distribution of terrain ruggedness values for the lynx clusters in this study showed that a substantial part of the clusters was in areas with relatively low ruggedness. This indicates that terrain ruggedness alone does not determine lynx habitat selection. The analysis also showed that a low proportion of human infrastructure or a high proportion of total forest, together with terrain ruggedness values above two, increased the probability of a lynx cluster. This suggests that these variables interact and shape lynx habitat selection.

5.3 Human infrastructure and roads are avoided

In contrast to the predictions, distance to large and small roads did not affect the probability of a cluster. However, human infrastructure had a negative effect when comparing lynx clusters to lynx single positions as predicted, but only a weak

negative effect when comparing lynx clusters to random positions. Previous studies have demonstrated that road density and road size impact the lynx movement patterns. Lynx tends to avoid areas with high road density and maintain distance from large roads (Basille et al. 2009; 2013; Hemmingmoore et al. 2020). In contrast, small roads are frequently used by lynx for travel and scent-marking (Krofel et al. 2017; Hemmingmoore et al. 2020). The effect of human modification on habitat selection suggests that lynx often select areas with moderate levels of human modification, as these areas typically have low human density and include agricultural land near forests, providing favourable hunting conditions (Basille et al. 2009; Bouyer et al. 2015a; 2015b; Hemmingmoore et al. 2020).

However, the results of this study indicate that a lower proportion of human infrastructure was associated with a higher probability of lynx clusters. Notably, lynx clusters were more likely to occur in areas with a higher proportion of human infrastructure when terrain ruggedness values were also high. This suggests that rugged terrain may serve as a refuge, allowing lynx to persist in human-modified landscapes, which other studies also have suggested (Bouyer et al. 2015a; Oeser et al. 2023).

5.4 Habitat suitability as a strong predictor of clusters

As expected, habitat suitability had a strong positive effect on lynx clusters compared to lynx single positions, indicating that higher habitat suitability increases the probability of a location being a cluster. This result was expected, as the habitat suitability map was based on important environmental variables, including human population density, roads, terrain ruggedness index, prey density and land cover (Hemmingmoore et al. 2020). These variables have been shown to influence lynx habitat selection in previous studies (Hemmingmoore et al. 2020), as well as in this study, since significant results were found for terrain ruggedness, forest and human infrastructure.

5.5 Strengths and weaknesses of the study

This study utilised a dataset of 11687 GPS locations from 17 individuals, which provided sufficient data to identify several relevant results. The dataset spanned a long period, from 2008 to 2023, including data from different time periods and home ranges which covered a large area of Sweden. This strengthens the reliability of the study and reflects the natural behaviour of the lynx population in Sweden. However, a more extensive dataset could have been achieved with a larger sample size, both in terms of individuals and GPS locations. An improvement of the study

would be ensuring a standardised number of GPS locations per day and consistent time intervals between locations across all individuals. This would allow for more precise filtering of clusters, reducing unwanted clusters by adding criteria, such as the number of locations, night locations per cluster and number of revisits, instead of only relying on duration at the cluster. This could result in more accurate results, for instance, by making it easier to exclude clusters that are likely kill sites.

The fix rate of the GPS locations may also have influenced the results. Factors such as rugged terrain or dense tree cover, as well as animal behaviour, can affect the accuracy of the locations and the number of successful fixes (Mattisson et al. 2010). Consequently, some GPS locations may have lower accuracy, potentially leading to wrong habitat classification in the analysis.

In this study, total forest was used as an explanatory variable instead of the different forest types. Previous research suggests that lynx select different forest types depending on the time of day, such as dense young forest during the day (Filla et al. 2017). However, since the GPS data in this study were collected over multiple years while habitat data were based on a single year, inconsistencies in forest age, structure or even the habitat classification may have occurred. Using total forest as a category for all forest classes may have reduced the risk of misclassification, as no field validation of habitat types was conducted. Nevertheless, a more detailed analysis with all specific forest types, as well as the other habitat classes that were removed due to correlation, could have provided deeper insights into habitat structure at the cluster locations. Future studies should consider these limitations, as variation in land cover classification can impact the result. Additionally, differences in the spatial resolution of the layers should be considered, as it can affect the accuracy of the results.

The study performed multiple statistical analyses, with explanatory variables carefully selected based on their biological relevance and the risk of correlation. Spearman's rank-order correlation coefficient was applied, with a threshold of a $r_s > 0.4$ for excluding correlated variables from the same model. This approach resulted in fewer variables in the analysis. Using a higher threshold would have allowed more variables, which could have resulted in a more detailed habitat analysis, although with a greater risk of strong correlations. However, the low threshold used in the analysis minimised the risk of correlation issues and increased the reliability of the results and can therefore be regarded as a strength of the study.

The dredge function was used in this study to be able to analyse the large number of variables for both datasets. There is a risk of overfitting when identifying the best-fitting models by combing the variables, as some combinations may lack

biological relevance. The top-ranked models are most statistically significant, and caution must be taken when interpreting the results. Nonetheless, the variables appear to be relevant in a habitat study since similar results have been reported in previous studies (Bouyer et al. 2015a; Oeser et al. 2023). Moreover, the variables showed consistent effects across the datasets, which further supports their biological relevance. The study may, therefore, contribute valuable insights into lynx habitat selection and their revisits to specific locations.

Despite certain limitations, the study produced well-supported results. The variables terrain ruggedness and total forest were significant in all four analyses, indicating the reliability of the results and methodology. Human infrastructure was also a strong predictor in one of the models. Similar results have been found in other studies, such as Hemmingmoore et al. (2020), suggesting that these variables are important factors in lynx habitat selection. Additionally, long-term clusters of lynx have not previously been analysed in Scandinavia, making this study an important contribution to improving the knowledge of the species and its monitoring.

5.6 Cluster analysis to improve monitoring

This study aimed to identify areas within the lynx home range that are regularly visited but are not kill sites and to assess the habitat characteristics of these locations to improve monitoring efforts. The monitoring could be improved by strategically placing camera traps in habitats similar to lynx clusters. This study found that high forest proportion, high terrain ruggedness, and low human infrastructure were the primary habitats for finding the frequently visited locations. Consequently, camera traps are likely more successful at capturing lynx if placed in areas with these habitats. Terrain ruggedness and forest distribution maps could assist in selecting optimal camera trap locations.

Similarly, habitat suitability maps could also serve as valuable tools for predicting lynx cluster locations and optimising the placement of camera traps for monitoring. By identifying areas with a high probability of lynx presence, these maps could improve the efficiency of monitoring efforts, particularly in regions of Sweden where snow cover may not be sufficient for the traditional snow-tracking survey method.

This study focused on female lynx that were GPS-collared in previous years. As a result, habitat conditions at the lynx clusters may have changed or may no longer be inhabited. However, using GPS collars on lynx females and installing cameras at frequently visited clusters could help determine reproductive status, which is crucial for the yearly surveys. Additionally, cluster analysis could reveal if two

females are visiting the same cluster, potentially indicating a shift in the home range and a new individual inhabiting the home range. This could suggest that the area has high-quality habitats.

A previous study examined the effectiveness of different camera trap placements for estimating the population density of lynx (Fležar et al. 2023). The study found that scent-marking sites, such as prominent rocks or objects, were more effective locations for camera traps than roads or other locations that are typically not normal marking sites (Fležar et al. 2023). This suggests that camera trap placement could be more optimised by selecting areas with habitats found at the lynx clusters and also includes a typical scent-marking feature.

5.7 Future implications and studies

As a large carnivore, the lynx has a great function in the ecosystem (Ritchie et al. 2012; Ripple et al. 2014). However, the presence of large carnivores can also cause problems, such as human-wildlife conflicts (Nyhus 2016; Khorozyan & Heurich 2023). In Sweden, lynx predation can negatively impact human interests, including reindeer husbandry in the north, sheep farming in the south, and the hunting of deer and other prey species (Andrén et al. 2006; Khorozyan & Heurich 2023). Further research on lynx behaviour and ecology is an essential part of improving management strategies and acceptance of this large carnivore in the landscape (Hunziker et al. 1998; Røskft et al. 2003; Liukkonen et al. 2009).

This study contributes to a better understanding of lynx habitat selection, which in turn is important for the monitoring of the species. Population monitoring is an important part of lynx management since an estimate of the population size and decision on the hunting quota is conducted using the yearly surveys (Swedish Environmental Protection Agency 2016; Tovmo & Frank 2024). New strategies and technologies are studied for lynx monitoring, for example, improving camera traps or using DNA sampling from scats and tracks (Hellström et al. 2019; Hočevár et al. 2020; Odden et al. 2022; Da Barba et al. 2024). New methods are necessary due to the poor snow conditions that are becoming more frequent because of climate change, which reduces the use of snow-tracking (Moen 2008; Odden et al. 2022).

Future studies on lynx habitat selection could provide deeper insights into how different individuals use the landscape. This study focused on adult female lynx, but previous research has shown that resident and dispersing individuals differ in their habitat use (Hemmingmoore et al. 2020). Consequently, the results of this study may not be fully representative of dispersing young females. Other behavioural factors, as well as sex and age, can influence habitat selection

(Bunnefeld et al. 2006; Bouyer et al. 2015a; Aronsson et al. 2016; Hemmingmoore et al. 2020).

For monitoring, adult females are of particular importance since the estimated population size is based on females with kittens every winter (Tovmo & Frank 2024). However, the behaviour of dispersers is also important to study, as they may occupy different habitats, including areas with more human activities. While Hemmingmoore et al. (2020) found that dispersers and resident individuals use similar habitats, dispersers also exploit more suboptimal habitats. Therefore, future studies should distinguish dispersers and resident individuals to ensure that the suboptimal habitats that are used by the dispersers are not overlooked in a habitat study (Hemmingmoore et al. 2020). Future studies could also investigate the effects of lynx territorial behaviour on long-term clusters. Their territorial behaviour might influence the placement of the clusters in their home range.

6. Conclusion

This study demonstrates that lynx repeatedly revisit specific locations within their home range over extended periods. Important habitat factors had a significant effect on lynx clusters, with results indicating a preference for high proportion of forest, high terrain ruggedness, high habitat suitability index, and low human infrastructure. This suggests that lynx selects safe environments. Identifying these frequently visited locations can improve camera trap placement for the yearly surveys and help improve the monitoring of lynx in Scandinavia.

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Popular science summary

Large carnivores, like the Eurasian lynx have recovered in population size after facing near extinction. With increasing numbers of individuals, effective monitoring methods are essential for management. In Sweden, lynx are monitored using techniques such as snow tracking and camera traps. The aim of this study was to investigate if female lynx return to specific locations in their home range for longer periods, and what types of habitats these locations have. With these results further improvements of the use of camera traps during the annual surveys could be possible, since a more efficient placement of camera traps in suitable habitats could increase encounters of lynx.

The study used GPS locations from 17 female lynx with collars in periods between 2008 and 2023 in a cluster analysis that identified long-term GPS location clusters. A total of 214 long-term clusters were identified, each containing at least three positions within a 100-meter radius and spanning more than 96 hours from the first to the last position to avoid potential kill sites. Statistical models were used to analyse the habitat variables: total forest, human infrastructure, water and wetland, terrain ruggedness, distance to large and small roads, and habitat suitability index on the probability of a lynx cluster compared to random position and lynx single position, which were locations that were not included in a cluster.

Higher habitat suitability was found at the lynx clusters compared to lynx single positions. High terrain ruggedness and a higher proportion of total forest were also more common at the lynx clusters compared to lynx single positions and random positions. The lynx clusters also had a lower proportion of human infrastructure compared to the lynx single positions. No effect of the variables distance to large and small roads or water and wetland was found. The findings suggest that lynx selects these locations for safety as forest and rugged terrain provide protection, especially in areas with high human activity. For the annual monitoring, camera traps could be used in similar habitats as the lynx clusters. This could lead to a more successful use of the camera traps and improve lynx monitoring in Sweden.

Acknowledgements

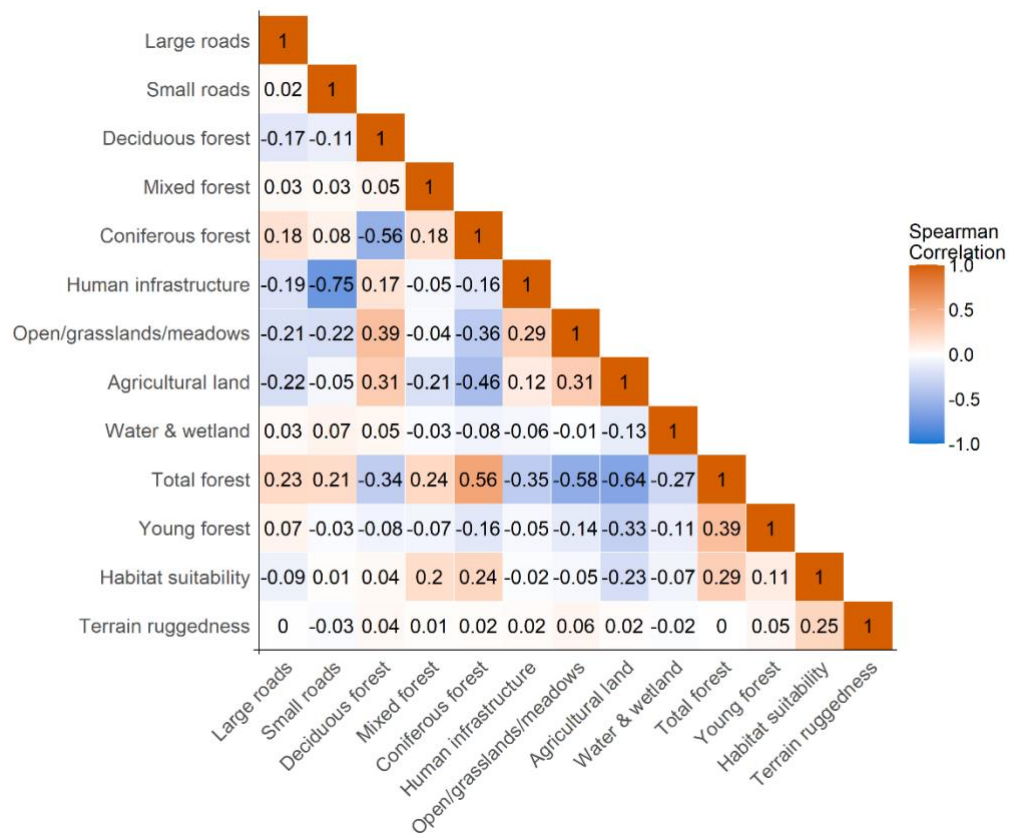
I would like to thank my supervisor Henrik Andrén for the opportunity to write this thesis. I am grateful to have worked with you at Grimsö and I appreciate all your help and support throughout this study. I also want to thank my co-supervisor Örjan Johansson for your help and for giving me the opportunity to see lynx and lynx clusters in real life. A special thank you to my friends in the bunker, especially to my two girls who have been by my side during all this time, so much support and a lot of giggles. Lastly, a big thank you to my family and friends for always encouraging me and cheering me on. Thank you!

Appendix 1

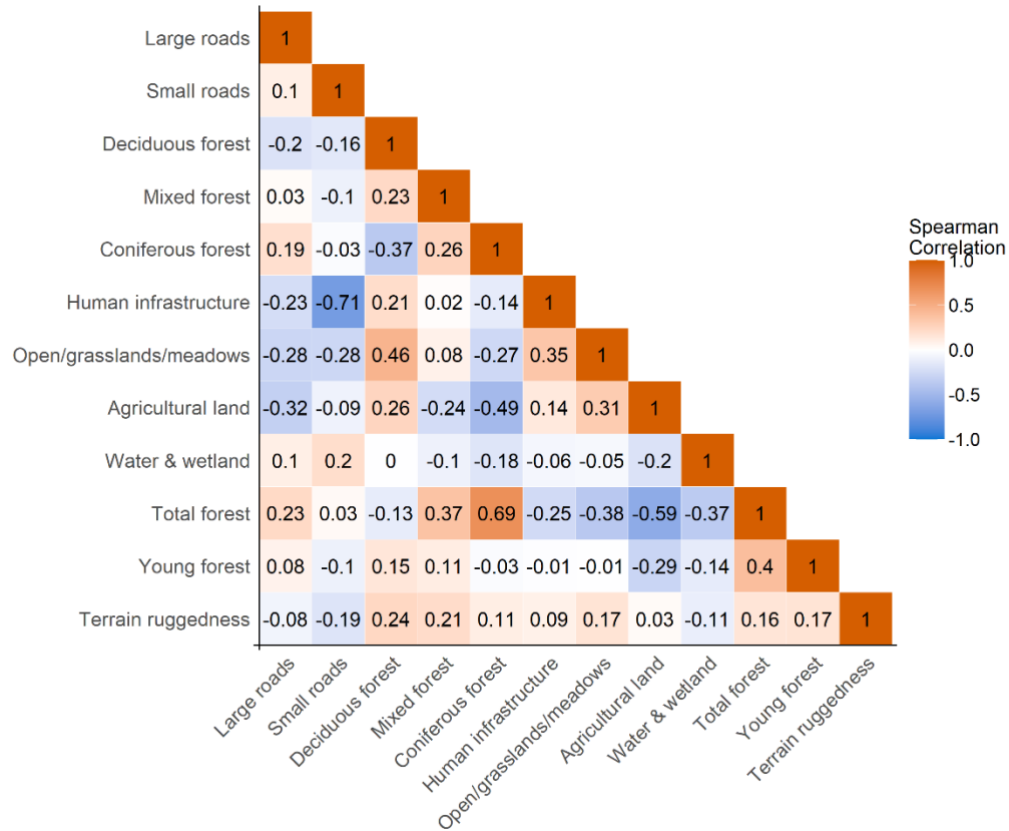
Appendix 1, Table S1. Classification of habitats based on land cover classes from the National Land Cover Database (NMD) (Swedish Environmental Protection Agency 2019).

NMD Value	Land cover class (NMD)	Habitat class
2	Open wetland	Water and wetland
3	Arable land	Agricultural land
41	Non-vegetated other open land	Open areas, grasslands and meadows
42	Vegetated other open land	Open areas, grasslands and meadows
51	Artificial surfaces, building	Human infrastructure
52	Artificial surfaces, not building or road/railway	Human infrastructure
53	Artificial surfaces, road/railway	Human infrastructure
61	Inland water	Water and wetland
62	Marine water	Water and wetland
111	Pine forest not on wetland	Coniferous forest
112	Spruce forest not on wetland	Coniferous forest
113	Mixed coniferous not on wetland	Coniferous forest
114	Mixed forest not on wetland	Mixed forest
115	Deciduous forest not on wetland	Deciduous forest
116	Deciduous hardwood forest not on wetland	Deciduous forest
117	Deciduous forest with deciduous hardwood forest not on wetland	Deciduous forest
118	Temporarily non-forest not on wetland	Young forest
121	Pine forest on wetland	Coniferous forest
122	Spruce forest on wetland	Coniferous forest
123	Mixed coniferous on wetland	Coniferous forest
124	Mixed forest on wetland	Mixed forest
125	Deciduous forest on wetland	Deciduous forest
126	Deciduous hardwood forest on wetland	Deciduous forest
127	Deciduous forest with deciduous hardwood forest on wetland	Deciduous forest
128	Temporarily non-forest on wetland	Young forest

Appendix 2

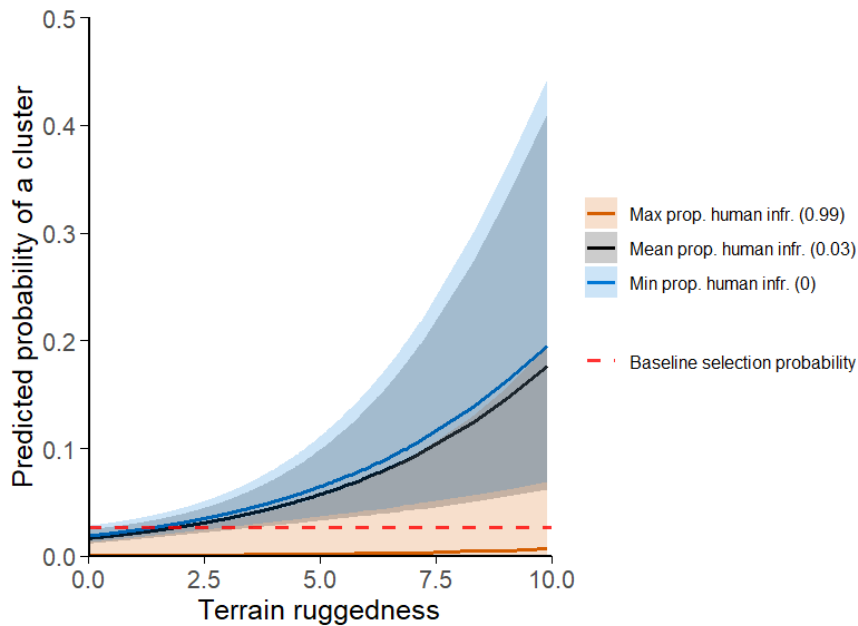


Appendix 2, Figure S1. Spearman's rank-order correlation coefficient of the explanatory variables from the dataset lynx cluster – lynx single positions.

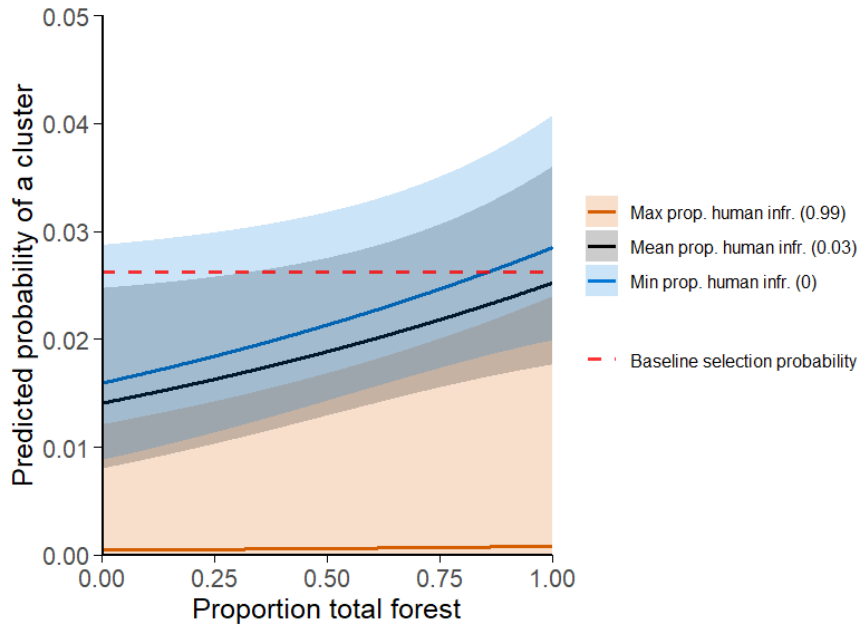


Appendix 2, Figure S2. Spearman's rank-order correlation coefficient of the explanatory variables from the dataset lynx cluster – random positions.

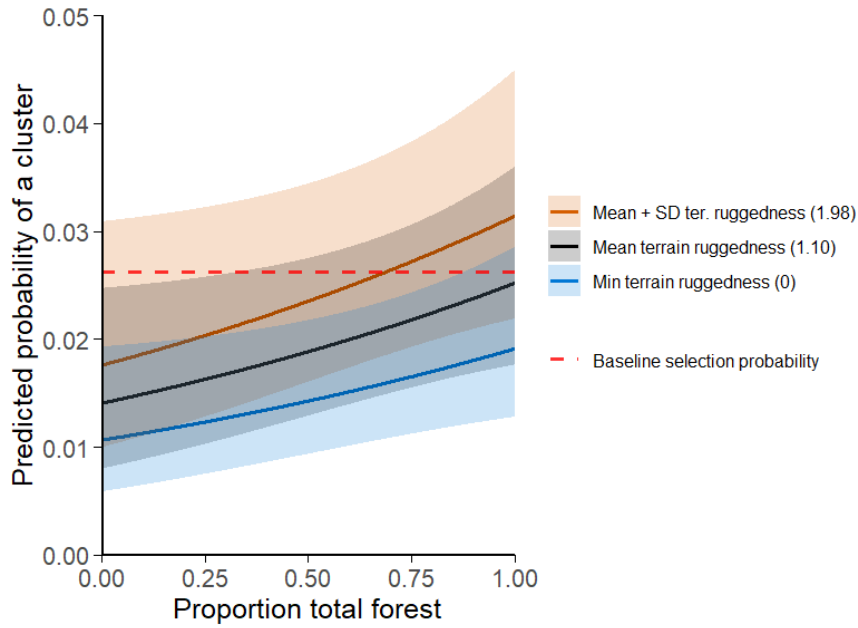
Appendix 3



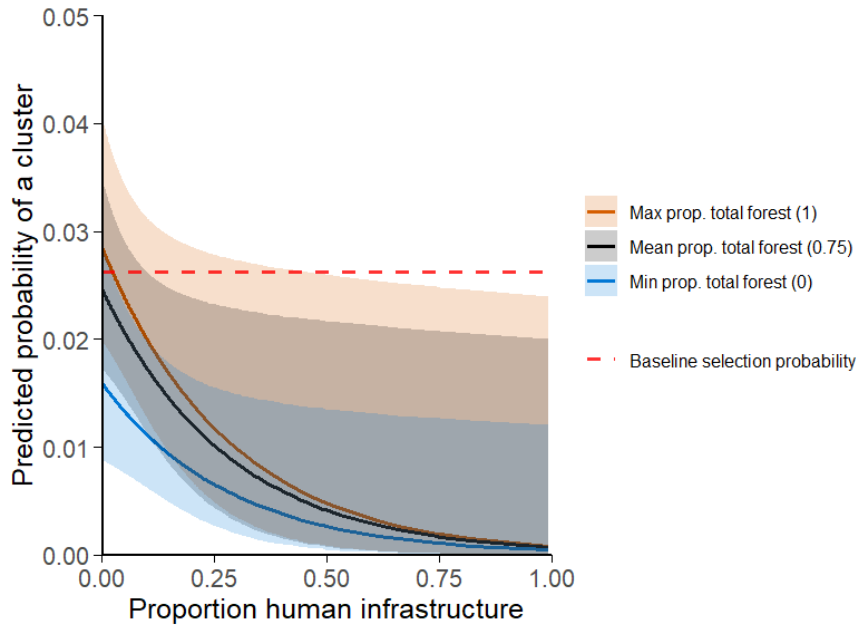
Appendix 3, Figure S1. Predicted probability of a lynx cluster occurrence as a function of terrain ruggedness (x-axis, with values from 0 - 9.9; note that most values are below 2.5), conditioned on the proportion of human infrastructure. The three lines represent different levels of human infrastructure proportion (maximum = 0.99, mean = 0.03, minimum = 0), while the shaded areas indicate the 95% confidence intervals. The red dashed line represents the baseline selection probability (0.026). The third variable in the model (total forest) is kept constant at its mean value. The figure illustrates the highest-ranked model with the response variable; 0 = lynx single positions, 1 = lynx clusters. Clusters and single positions are based on GPS data from collared lynx in Sweden during 2008-2023.



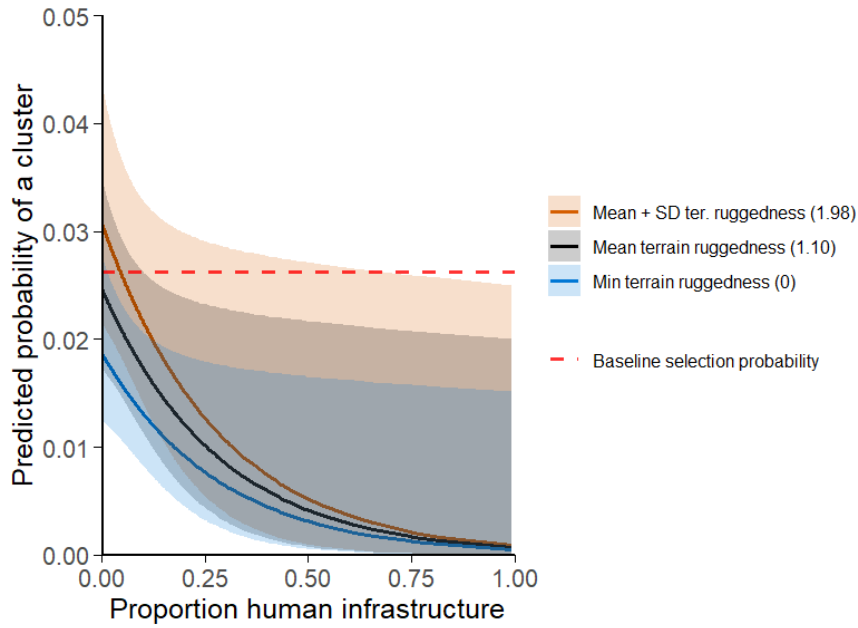
Appendix 3, Figure S2. Predicted probability of a lynx cluster occurrence as a function of proportion total forest (x-axis, with values from 0 - 1), conditioned on the proportion of human infrastructure. The three lines represent different levels of human infrastructure proportion (maximum = 0.99, mean = 0.03, minimum = 0), while the shaded areas indicate the 95% confidence intervals. The red dashed line represents the baseline selection probability (0.026). The third variable in the model (terrain ruggedness) is kept constant at its mean value. The figure illustrates the highest-ranked model with the response variable; 0 = lynx single positions, 1 = lynx clusters. Clusters and single positions are based on GPS data from collared lynx in Sweden during 2008-2023.



Appendix 3, Figure S3. Predicted probability of a lynx cluster occurrence as a function of proportion total forest (x-axis, with values from 0 - 1), conditioned on terrain ruggedness. The three lines represent different levels of terrain ruggedness (mean + 1 SD = 1.98, mean = 1.1, minimum = 0), while the shaded areas indicate the 95% confidence intervals. The red dashed line represents the baseline selection probability (0.026). The third variable in the model (human infrastructure) is kept constant at its mean value. The figure illustrates the highest-ranked model with the response variable; 0 = lynx single positions, 1 = lynx clusters. Clusters and single positions are based on GPS data from collared lynx in Sweden during 2008-2023.

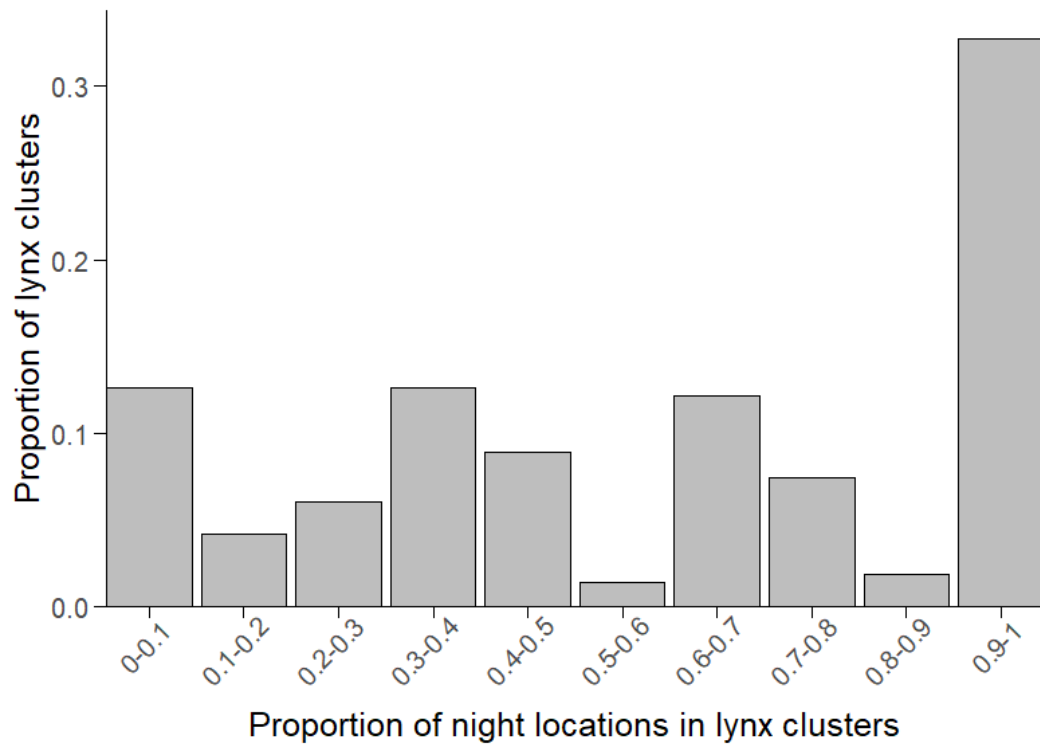


Appendix 3, Figure S4. Predicted probability of a lynx cluster occurrence as a function of proportion human infrastructure (x-axis, with values from 0 - 1), conditioned on the proportion of total forest. The three lines represent different levels of total forest proportion (maximum = 1, mean = 0.75, minimum = 0), while the shaded areas indicate the 95% confidence intervals. The red dashed line represents the baseline selection probability (0.026). The third variable in the model (terrain ruggedness) is kept constant at its mean value. The figure illustrates the highest-ranked model with the response variable; 0 = lynx single positions, 1 = lynx clusters. Clusters and single positions are based on GPS data from collared lynx in Sweden during 2008-2023.

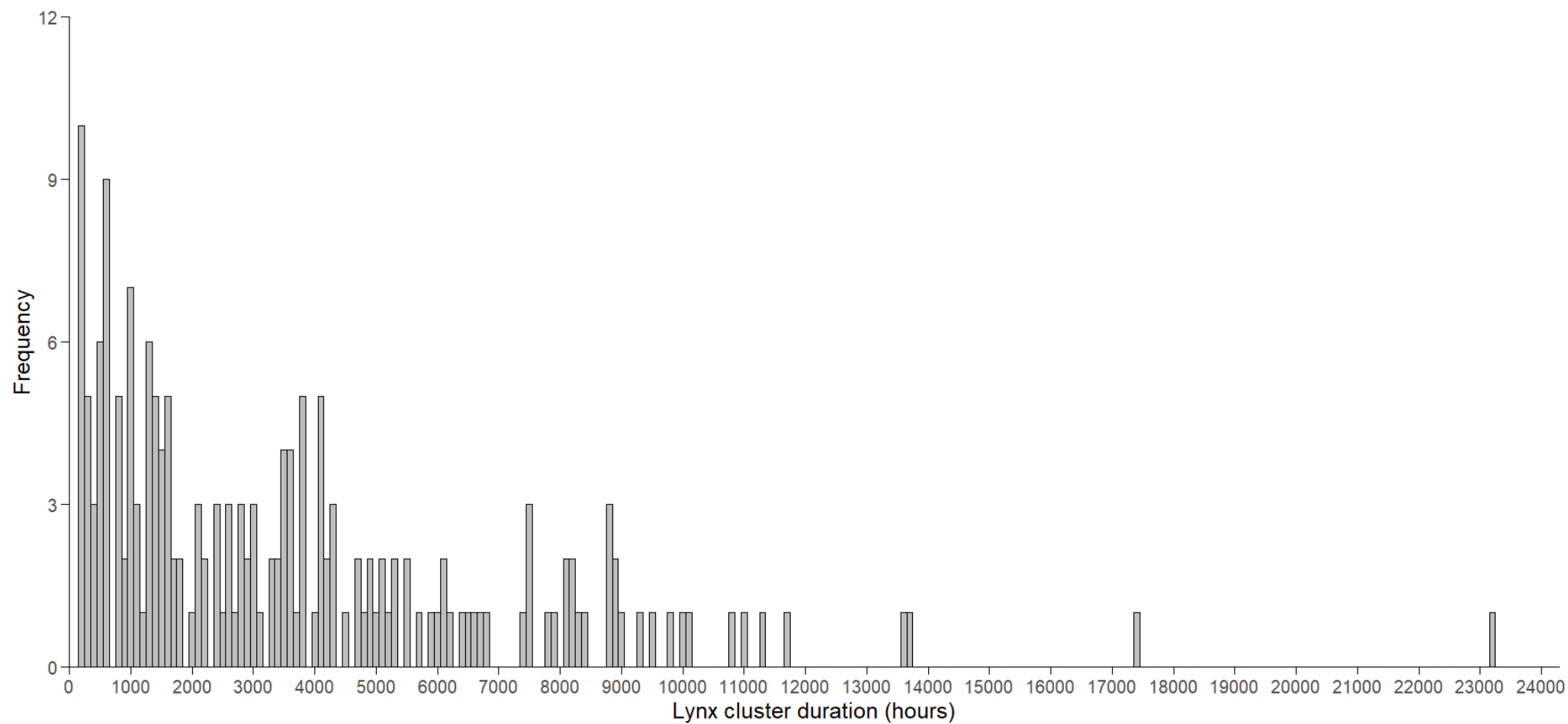


Appendix 3, Figure S5. Predicted probability of a lynx cluster occurrence as a function of proportion human infrastructure (x-axis, with values from 0 - 1), conditioned on terrain ruggedness. The three lines represent different levels of terrain ruggedness (mean + 1 SD = 1.98, mean = 1.10, minimum = 0), while the shaded areas indicate the 95% confidence intervals. The red dashed line represents the baseline selection probability (0.026). The third variable in the model (total forest) is kept constant at its mean value. The figure illustrates the highest-ranked model with the response variable; 0 = lynx single positions, 1 = lynx clusters. Clusters and single positions are based on GPS data from collared lynx in Sweden during 2008-2023.

Appendix 4



Appendix 4, Figure S1. Proportion of 214 lynx clusters in intervals by the proportion of night locations in lynx clusters, from 0 - 1 in intervals of 0.1. The proportion of night locations in lynx clusters is calculated by the number of night locations divided by the total number of locations per cluster. Night locations are classified by sunrise and sunset times. Clusters are based on GPS data from collared lynx in Sweden during 2008-2023.



Appendix 4, Figure S2. Frequency of lynx cluster duration in 100-hour intervals. Cluster duration was between 102 and 23163 h for the 214 lynx clusters, which corresponds to the time between the first and the last cluster location. Clusters are based on GPS data from collared lynx in Sweden during 2008-2023.

Appendix 5

*Appendix 5, Table S1. Predictors used in the habitat suitability map from Hemmingmoore et al. (2020). Categorical variables are marked with *.*

Predictors
Coniferous Forest (Intercept)*
Deciduous Forest*
Young Forest and Thicket*
Mixed Forest*
Grassland*
Semi-Natural*
Bare Ground, Rock*
Agricultural Land*
Human Infrastructure*
Bog and Water*
Altitude
Distance to Forest Edge
Log Human Population Density
Distance to Large Road
Distance to Small Road
Terrain Ruggedness Index
Roe Deer Hunting Bag

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