Norwegian University
of Life Sciences

Master's Thesis 2024 60 ECTS
The Faculty of Environmental Sciences and Natural Resource Management

Eurasian Lynx Home Range Overlap: Influence of Migratory Prey, Seasonal Variation, and Social Dynamics

Ingrid Kleppe Normann
Ecology

Preface

The research presented in this thesis was conducted in the Faculty of Environmental Sciences and Natural Resource Management at The Norwegian University of Life Sciences. I would like to thank my main supervisor Ole-Gunnar Støen for his assistance. I also thank co-supervisor Neri Horntvedt Thorsen from Norwegian Institute for Nature Research for help throughout the entirety of the thesis and encouraging words. I would also like to express my gratitude to Scandlynx for data and John Odden for making this project happen.

I am grateful for my partner, family, and friends for their support throughout my education. Thinking about my grandfather Andor's time at NMBU sixty years ago brings me joy and motivation. His love for nature has been a big influence in my life since I was a kid, and it's something I still carry with me today.

Photo: A mother and her cub in Hallingdal. Borrowed with permission from wildlife photographer Thomas Mørch.

Table of contents

Abstract

This study investigates the spatial dynamics of Eurasian lynx in Norway, specifically addressing following primary research questions: how the overlap with other lynx is influenced by the size of their home ranges, the presence of migratory prey, social dynamics, and seasonal changes. By analyzing spatial data from 1995-2023, home ranges based on kernel density estimation were established and compared. Results show a significant negative correlation between home range size and overlap, suggesting that larger home ranges are associated with reduced overlap. There was no significant correlation between the presence of migratory prey and overlap, indicating that lynx might primarily rely on alternative food sources when reindeer migrate. Female-male overlap significantly differed from female-female overlap. This could stem from the fact that females have smaller home ranges and show less tolerance for intraspecific encounters, whereas increased overlap between female-male is anticipated due to males' larger home ranges and more frequent interactions during the mating season. Furthermore, seasonal analysis revealed higher overlap immediately prior to and during mating season, as well as gestation period and mid-winter, highlighting the relevance of reproductive cycles and weather effects on prey accumulation in driving spatial dynamics. Understanding how these factors influence spatial behavior can inform habitat management strategies aimed at maintaining suitable lynx habitats and mitigating potential conflicts with human activities.

Introduction

The study of home range size, migratory prey patterns, and seasonal variations in carnivores offers valuable insights into their behavior and ecological dynamics. A home range refers to the spatial area within which an animal typically conducts its daily activities, including foraging, mating, and sheltering. It is determined by a combination of factors such as habitat availability, resource distribution, and social interactions (Powell, 2000; Powell & Mitchell, 2012). Due to its extensive distribution throughout the northern Palearctic region (Koordinierte, 2004), the Eurasian lynx (*Lynx lyn*x Linnaeus, 1758) is an ideal species for studying individual and behavioral tactics of solitary carnivores across various environmental conditions (Sunde et al., 2000). Throughout its large spanning range, including a significant portion of the boreal forest across Eurasia (Koordinierte, 2004), the Eurasian lynx establishes territories, which are defined areas defended against intrusion by conspecifics (Noble, 1939). These territories serve to secure exclusive access to resources and breeding opportunities, often demarcated by scent or other signaling mechanisms (Noble, 1939; Stamps, 1994). Research on Scandinavian lynx over the past decade has revealed significant variations in territory size depending on geographic location. This variability in size is likely influenced by latitudinal variations in the abundance, predictability, and distribution of primary prey species, as well as differing management practices (Herfindal et al., 2005; Linnell et al., 2021). Home range sizes of lynx in Scandinavia are notably large, ranking among the biggest reported for any felid species (Linnell et al., 2021). The size of the observed home ranges in a study conducted across Sweden and Norway were among the largest reported for the species, with an average ranging from 600 to 1400 km^2 for resident males and 300 to 800 km^2 for resident females (Linnell et al., 2001). In southern Scandinavia, particularly in regions abundant with deer, female lynx may occupy territories as small as 2-300 km^2, while males may range over areas of 5-600 km^2 (Odden et al., 2013). In contrast, in Finnmark and Troms, female lynx may utilize territories exceeding 2,000 km^2, with males roaming across areas exceeding 4,000 km^2 (Odden et al., 2013).

Researchers have proposed three main hypotheses to elucidate the fundamental explanations behind dispersal and the different movement patterns between sexes (Zimmermann et al., 2005). These hypotheses comprise the competition for mates (Dobson, 1982), avoidance of inbreeding (Wolff, 1993a; Wolff, 1994) and competition for resources (Greenwood, 1983;

Greenwood, 1980). The determinants of carnivore spatial behavior include intrinsic traits such as sex, body weight, and feeding behavior, as well as extrinsic factors such as population density, prey abundance, and patterns of environmental productivity (Duncan et al., 2015; Kelt & Van Vuren, 2001; Nilsen et al., 2005).

Changes in the amount of food or prey that is available is often seen as a key reason why animals of the same species might have differing home range sizes and density (Carbone & Gittleman, 2002; Powell et al., 1997; Sandell, 1989). Studies have shown that the size of home range in lynx may be related to roe deer (*Capreolus capreolus*) density and environmental productivity (Herfindal et al., 2005) and/or lynx density (Aronsson et al., 2016; Pesenti & Zimmermann, 2013). Roe deer constituted a more significant portion of the diet during winter compared to summer, potentially due to their heightened visibility in winter months when congregating around feeding areas (Odden et al., 2006). In the northernmost population of lynx, the only prevalent large herbivore prey shaping its behavior is semi-domestic reindeer (*Rangifer tarandus*)(Linnell et al., 2021). The spring migration precedes calving in early May, with female reindeer seeking snow-free areas rich in food essential for calving (Eira, 2020). The autumn migration, extending from September to Christmas, is characterized by varying weather conditions and necessitates more extensive herding efforts, with migration distances ranging widely from tens to hundreds of kilometers (Eira, 2020). As research has found reindeer to compromise a large part of the lynx diet in northern Scandinavia (Pedersen et al., 1999), lynx may follow the movements of migrating reindeer, thereby overlapping with each other.

When undisturbed, lynx typically revisit a large prey carcass one to several times over the following days before eventually abandoning it, with an average consumption period of approximately 3 days for a roe deer, 2 days for a domestic reindeer or sheep, and few hours for smaller prey (Krofel et al., 2019; Odden et al., 2013). The revisiting of carcasses can lead to an animal staying in one area for extended periods, especially when there is an abundance of food available. This behavior can narrow their home ranges and may also influence their short-time spatial behavior. This may vary with sex and age, as female lynx with cubs tend to consume prey more rapidly during winter compared to solitary individuals (Odden et al., 2013). Research has shown that a predator's home range size may also be connected to their hunting behavior in addition to the prey distribution (Goszczyński, 1986). Female lynx with kittens were found to kill on average 1.5 times more deer than adult males, which may lead to an expansion of their home ranges to encompass more hunting grounds (Okarma et al., 1997). Female home ranges may also remain smaller as long as the prey abundance is sufficient (Sandell, 1989). Because of the lower population densities and seasonal migration patterns of prey in boreal regions, the behavioral tactics of lynx in these areas may differ from those in more resource-rich and stable environments (Sunde et al., 2000). This raises the question of how overlap might differ in areas characterized by stable prey abundance compared to those with migrating prey, while also considering variations in sex and age.

Solitary felid species typically do not form long-lasting family bonds and are expected to have limited interactions with related individuals over their lifetime, and the population structure is mainly based on territoriality (Sunquist & Sunquist, 2017). Hence, the social structure of solitary species, which is characterized by male-biased dispersal, may effectively facilitate the exclusion of related individuals, resulting in low levels of kinship within the population (Sunquist & Sunquist, 2017). Dispersal and philopatry patterns in wild carnivores are often linked to inbreeding avoidance mechanisms (Pusey & Wolf, 1996). Kinship plays an important role in determining overlap and home range size in other feline species, such as cougars (Laing & Lindzey, 1993), leopards (Bailey, 1993) and tigers (Smith, 1987), where females have been shown to reside near or even within their mothers home range (Schmidt et al., 1997). However, Schmidt et al. 2016 found evidence of male-biased dispersal and female philopatry in the lynx population, which resulted in higher average relatedness in females than in males. Philopatry refers to the tendency of an organism to remain in or return to its birthplace or a familiar area to breed or raise offspring. Nonetheless, there was no evidence of spatial family clusters, indicating that daughters may not regularly inherit portions of their mothers' home range (Schmidt et al., 2016). Information on the topic is however contrasting, as genetic evidence of female kin clusters has been found, meaning closely related females tend to cluster together geographically (Holmala et al., 2018). Thus, female reproductive success depends on various factors, primarily offspring survival, which is intricately linked to maternal investment and the provision of essential resources necessary for the offspring's well-being (Davies et al., 2012). As resources critical for survival become scarce, irregularly distributed, or slow to regenerate, females are known to establish exclusive territories encompassing these vital resources (Wolff, 1993b). Females with offspring, and generally in scarce areas, could possibly expand their home ranges, leading to increased overlap during these periods.

In previous telemetry studies conducted in central Europe, it was discovered that male lynx utilize larger areas compared to females (Breitenmoser & Haller, 1993; Breitenmoser et al., 1993; Schmidt et al., 1997). The studies also found that male lynx travel longer distances per day (Breitenmoser & Haller, 1993; Breitenmoser et al., 1993; Schmidt et al., 1997), which is in line with theoretical predictions for solitary carnivores (Erlinge & Sandell, 1986; Sandell, 1989). As a polygamous species, lynx engage in mating behaviors that promote competition among males for access to females, potentially leading to a larger home range to accommodate mating opportunities beyond their usual territories (Odden et al., 2013). This competition may favor exceptionally competitive males, allowing them to mate with more females than those typically within their territorial range. Thus, home range overlap among lynx has been shown to depend mainly on the age and sex of the individuals involved, as the lynx typically avoids interaction with conspecifics, except for females with dependent kittens (Schmidt et al., 1997). Additionally, both male and female lynx maintain home ranges with significant inter-sexual overlap, but little intra-sexual overlap, suggesting intra-sexual resource defense through territoriality (Sunde et al., 2000). This pattern is also observed in related species such as the Iberian lynx *Lynx pardinus* (Ferreras et al., 1997), Canadian lynx *Lynx canadensis* (Poole, 1995), and bobcat *Lynx rufus* (Lovallo & Anderson, 1996). Considering the rare incidence of violent confrontations among lynx (Sunde et al., 2000), it is likely that these animals maintain their territory boundaries through mutual avoidance tactics.

The dispersal behavior observed in lynx across Scandinavia is believed to have evolved primarily as a mechanism to prevent inbreeding, rather than solely to minimize competition for resource (Odden et al., 2013). Density of females can therefore be expected to shape the home range size of males, in other words overlap between males and females may be increased during pre-mating and mating season, depending on lynx density. When solitary females occupy relatively small territories, compared to the areas defendable by males, males can enhance their reproductive success by monopolizing access to these females (Maher & Lott, 1995). To secure mating opportunities with the limited number of receptive females, males typically establish large territories that overlap the home ranges of multiple females (Ferguson et al., 2009; Maher

& Lott, 1995). In contrast, adult female lynx exhibit higher site fidelity than males, allowing them to become more familiar with their range and potentially improving their hunting success and reproductive success in a different way (Sandell, 1989). In this study I aim to investigate these patterns by analyzing the spatial behavior of VHF- and GPS-collared lynx in Norway, examining the effects of migratory prey, seasonal variation, and social dynamics on home range overlap.

Materials and methods

Study species

The life history and reproductive strategy of the lynx play a crucial role in shaping overlap and home range sizes. The lynx's mating season typically occurs in March, with peak heat observed between March 1st and April 1st, varying depending on the region within Scandinavia (Odden et al., 2013; Vogt et al., 2014). Ovulation may commence as early as mid-January, and potential mates may seek each other out during pre-estrus (Odden et al., 2013). Given the solitary nature of lynx and their sparse populations, engaging in pre-estrus activities likely serves to attract males for potential mating opportunities. The gestation period for lynx lasts around 70 days, with births typically occurring in the latter half of May or the early weeks of June (Mattisson et al., 2020; Painer et al., 2014). Family groups typically disperse after the next years heat, allowing the offspring to become independent (Samelius et al., 2012). The period when the cubs separate from their mother ranges from February to May, when they may roam considerable distances from their birthplace (Samelius et al., 2012). In general, male lynx tend to wander farther from their natal territory compared to females, while female lynx often establish themselves in proximity to their birthplace (Holmala et al., 2018).

Data collection and processing

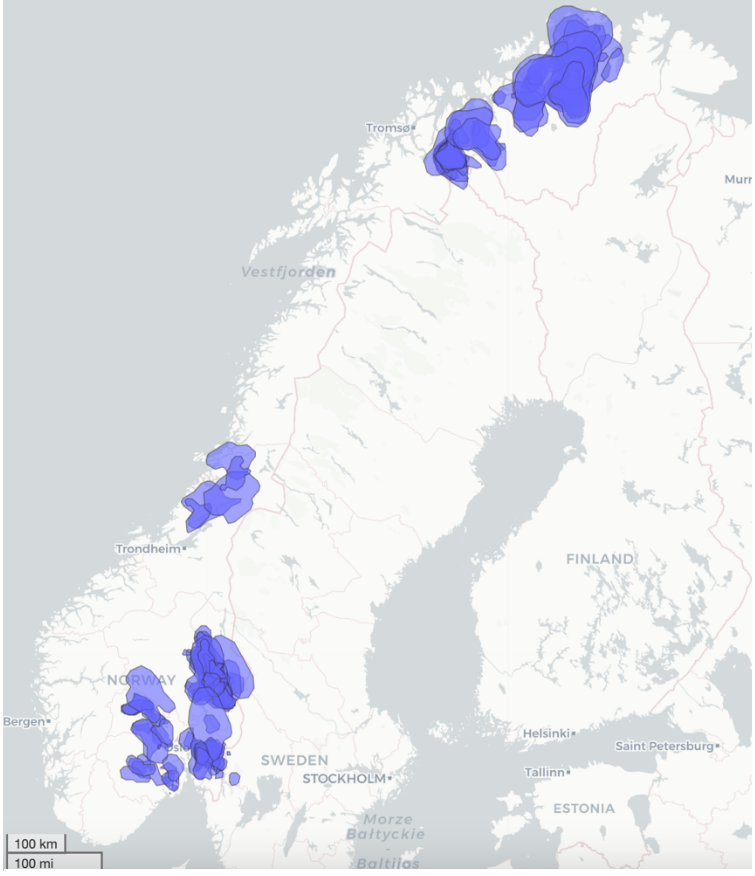

Figure 1: Map of Norway with yearly kernel density estimations (95%) of home ranges for unique lynx ID from overlapping lynx in the subsampled dataset. n = 137.

The data has been collected by the Scandinavian lynx project Scandlynx, from VHF and GPS-collared lynx in eight counties in Norway. Collaring of lynx has taken place in different time periods in the different counties, starting in Hedmark in 1995, until present time. Data used in this study ranges from 1995-2023. The original dataset contained 137 unique lynx, consisting of 13746 observations, of which 7866 were females and 5880 were males. After setting a minimum limit of 30 days observations within a year, data consisted of 85 lynx and 11729 observations (Figure 1). After extracting overlapping pairs, 74 unique lynx were left for the analyses of overlap. To investigate the effect of migrating prey, data from lynx in northern Norway was used, where the lynx's most important prey, semi-domestic reindeer, moves between summer and winter grazing. Data from 19 lynx were used in the investigation of those with migratory prey. The remaining 55 lynx, located south of Troms/Finnmark, were categorized as having no migratory prey.

Statistical analyses

Statistical analyses were conducted using R-studio (version 2022.12.0+353). To calculate home ranges and overlap, the kernel method, recommended by studies for the estimation of the utilization distribution (Worton, 1989; Worton, 1995), was employed. The default method for estimating the smoothing parameter, the ad hoc method, was used. home range was estimated using kernelUD from adehabitatHR with a 95% kernel area, a vector of percentage levels for home range size estimation. In this case, the isopleth refers to the contour or boundary line that encloses 95% of the probability density. Spatial relationships between lynx territories were then assessed by calculating pairwise overlap home range.

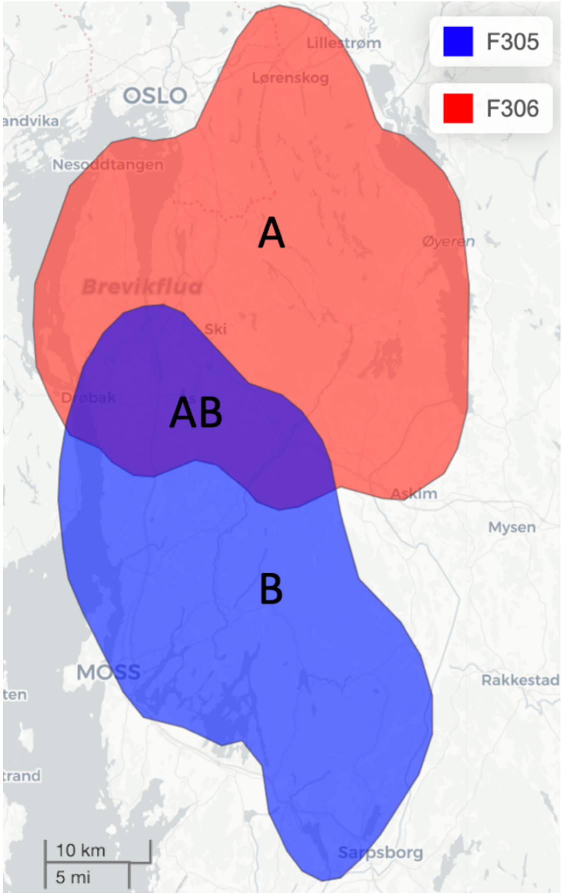

Figure 2: Visualization of home range and overlap estimation, where each overlapping pair has one area A or B representing kernel density home range estimation, and shared area AB. Here: F305 and F306.

Overlap was determined by degree of kernel density area within another lynx' home range. The analyses compute the overlap between pairs of lynx in terms of their respective areas (Figure 2). Firstly, calculating the overlap of Lynx A with Lynx B (overlapA). This was achieved by determining the area of intersection (areaAB) between the home range of Lynx A and Lynx B. Then, the overlap area (areaAB) was divided by the home range of Lynx A (areaA) to derive the proportion of overlap for Lynx A (overlapA). The lynx have been included once as Lynx A and once as Lynx B, so that the final comparison represents both home ranges.

In the analysis of seasonal data, I used the proportion of positions within another lynx' home range instead of using the degree of overlap between home ranges. The home ranges of the seasonal analysis were calculated from yearly home range by using the proportion of overlap per month. This metric quantifies the proportion of Lynx A's observed locations that are situated within the home range of Lynx B.

The dataset underwent several preprocessing steps to ensure robust data preparation. Initially, a single position per day, specifically at midday, was extracted to enhance comparability across individuals. A new variable, yearID, was created by combining individual ID and lynx year to uniquely identify each year a lynx was followed with VHF or GPS to compare the home ranges over the same years. A minimum observation period of 30 days was set when calculating home range to ensure consistency of data and to standardize the analysis. For the seasonal analyses, an additional minimum of five observations per month was set. Centroid coordinates were determined to classify lynx as dependent or independent on migratory prey based on their residency in Troms/Finnmark. Migratory prey as a variable therefore represents the home ranges in areas where this type of prey is present.

Variables under consideration included sex (female-female, female-male and male-male), migrating prey, age, and the size of the home range. For the seasonal analysis, month number was also a variable. Given that female lynx typically have smaller home ranges than males, the focus on female-male overlap provided a clearer perspective on territorial interactions compared to male-female overlap, highlighting the proportion of the female's range overlapping with the larger male territories.

Model selection was conducted using Akaike Information Criterion corrected (AICc) to identify the best fitting model explaining the observed data variation (Hurvich & Tsai, 2008). The analysis utilized various packages, including plyr, dplyr, sf, adehabitatHR, ggplot2, glmmTMB, MuMIn, mapview, and mgcv. The statistical analysis employed Generalized Linear Mixed Models (GLMMs) and Generalized Additive Models (GAM) to test the significance of variables in explaining variation within the dataset. For monthly overlap, the decision to employ GAMs stemmed from the recognition of potentially non-linear relationships between the predictor variables and the response variable. Given the complex nature of monthly overlap data, GAMs provided a fitting framework to capture these non-linear patterns more effectively compared to traditional linear models. Generalized Linear Mixed Models (GLMMs) were applied using Template Model Builder (TMB) with beta regression from the package "glmmTMB". Beta family regression was chosen for both types of analyses because of its suitability for modeling continuous response variables that are bounded between 0 and 1. In many cases, such as proportions or percentages, data exhibit such bounded behavior. The logit link function, employed in both generalized linear mixed models (GLMMs) and generalized additive models (GAMs), is chosen for its ability to transform a probability into the log of the odds ratio. This odds ratio represents the ratio between the predicted probability of the positive outcome to the predicted probability of the negative outcome. Results were considered significant at $p<0.05$.

Results

Overlap analysis

Figure 3 illustrates the yearly home range calculated for individual unique lynx, divided into sex categories. The mean home range size for females was 1478 km^2, whereas the mean value for males was 2579 km^2. The best model for explaining variations in overlap based on AICc was M8: home range size and sex (A1). The second-best model was M11 (A2): home range size, migratory prey, and sex - performing almost equally well with an AICc that was only 0.41 higher. The two next models were M13: home range size, sex, and age (A3), M15: home range size, age, migratory prey, and sex (Table 2). All models that contained the variable home range size was amongst the top eight models (Table 1).

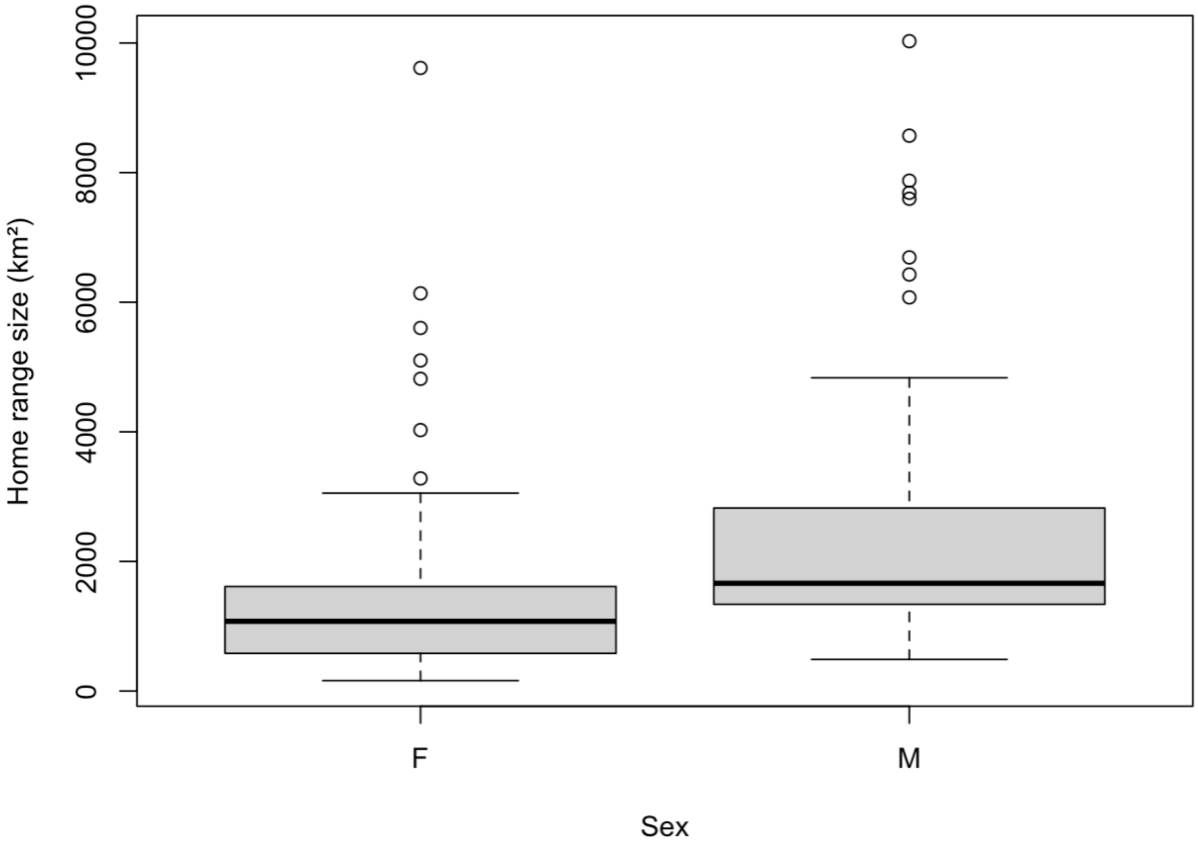

Figure 3: Home range size in km^2 calculated for unique lynx ID from the subsampled data, categorized by sex. The lower end of the box marks the 1st quartile, and the upper end indicates the 3rd quartile. The vertical line within each box represents the median value, and solitary dots represent outliers. Mean for females = 1478 km^2, males = 2579 km^2. n = 85.

Table 1: Akaike Information Criterion corrected (AICc) for the different models ranked highest to lowest value. HR = home range.

Model ranked	*df*	*AICc*	*ΔAICc*
M8: HR size, sex	5	-141.45	0
M11: HR size, migratory prey, sex	6	-141.04	0.40
M13: HR size, age, sex	6	-139.58	1.86

M15: HR size, age, migratory prey, sex	7	-139.13	2.31
M1: HR size	3	-135.22	6.22
M9: HR size, migratory prey	4	-134.84	6.60
M5: age, HR size	4	-133.33	8.12
M14: HR size, age, migratory prey	5	-132.92	8.52
M2: sex	5	-124.90	16.54
M6: age, sex	5	-107.06	34.38
M10: migratory prey, sex	5	-107.03	34.41
M12: age, migratory prey, sex	6	-105.05	36.39
M3: age	3	-98.34	43.10
M4: migratory prey	3	-98.23	43.21
M7: age, migratory prey	4	-96.39	45.05

Model M15 was selected as the preferred choice for predicting variables in the plots due to its alignment with trends and values observed in the other top-ranking models (Table A1, A2 and A3). Additionally, the inclusion of all variables within this model enhances its capacity to provide a dimensional understanding of the analyses.

Table 2: Summary of Generalized Linear Mixed Model (GLMM) of M15 examining overlap of home ranges, based on AICc from Table 1. HR = home range. n = 470.

Variable	*Estimate*	*Std. Error*	*z-value*	*p-value*
Intercept	-0.65	0.13	-4.99	5.83e-07 ***
HR size	-0.31	0.05	-5.72	1.03e-08 ***
Age	-7.62e-04	1.91e-03	-0.39	0.69
Migratory prey	0.18	0.14	1.27	0.20
F-M	0.27	0.11	2.37	0.01 *
M-M	-0.09	0.15	-0.63	0.52

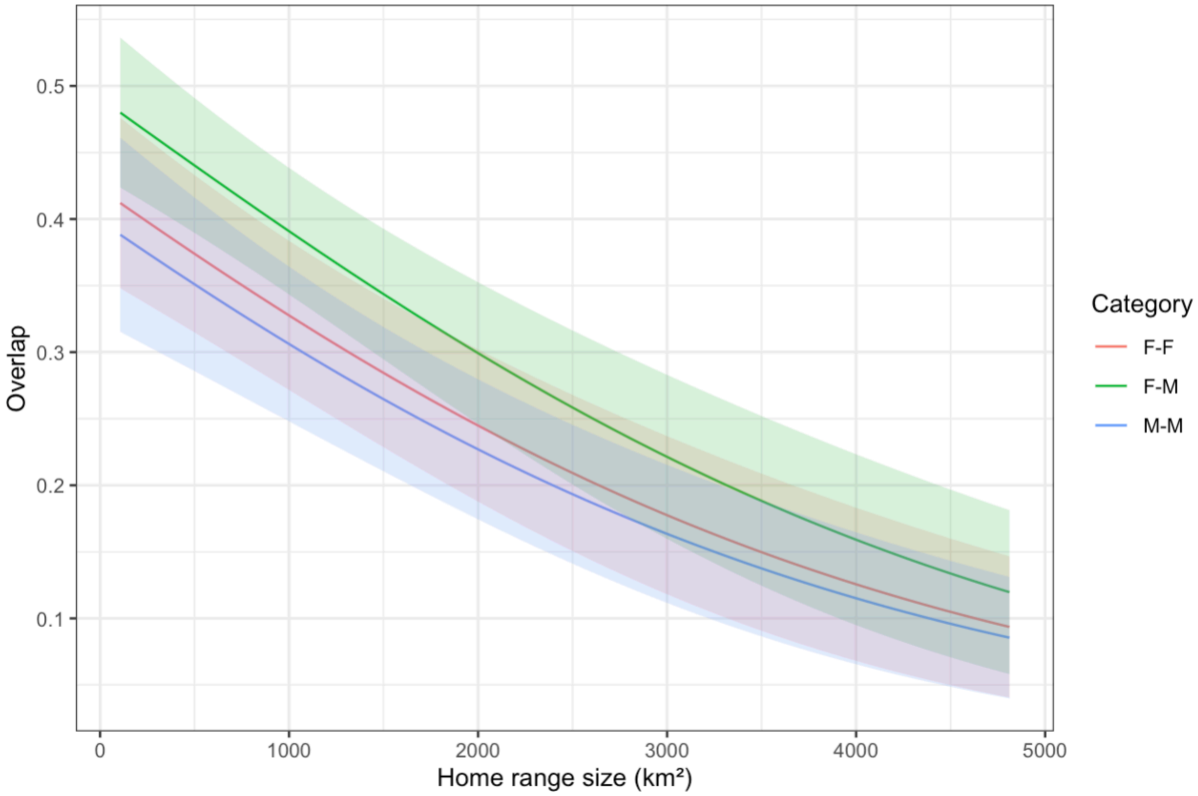

Figure 4: Generalized Linear Mixed Model (GLMM) of overlap and home range size in km² from data predicted from model M15. 95% confidence interval is marked in color corresponding to each category. n = 470.

The home range size was included in all the models that were among the top performing models, indicating a clear trend: as home range size increased, overlap decreased significantly across all sex categories (Figure 4, Table 2).

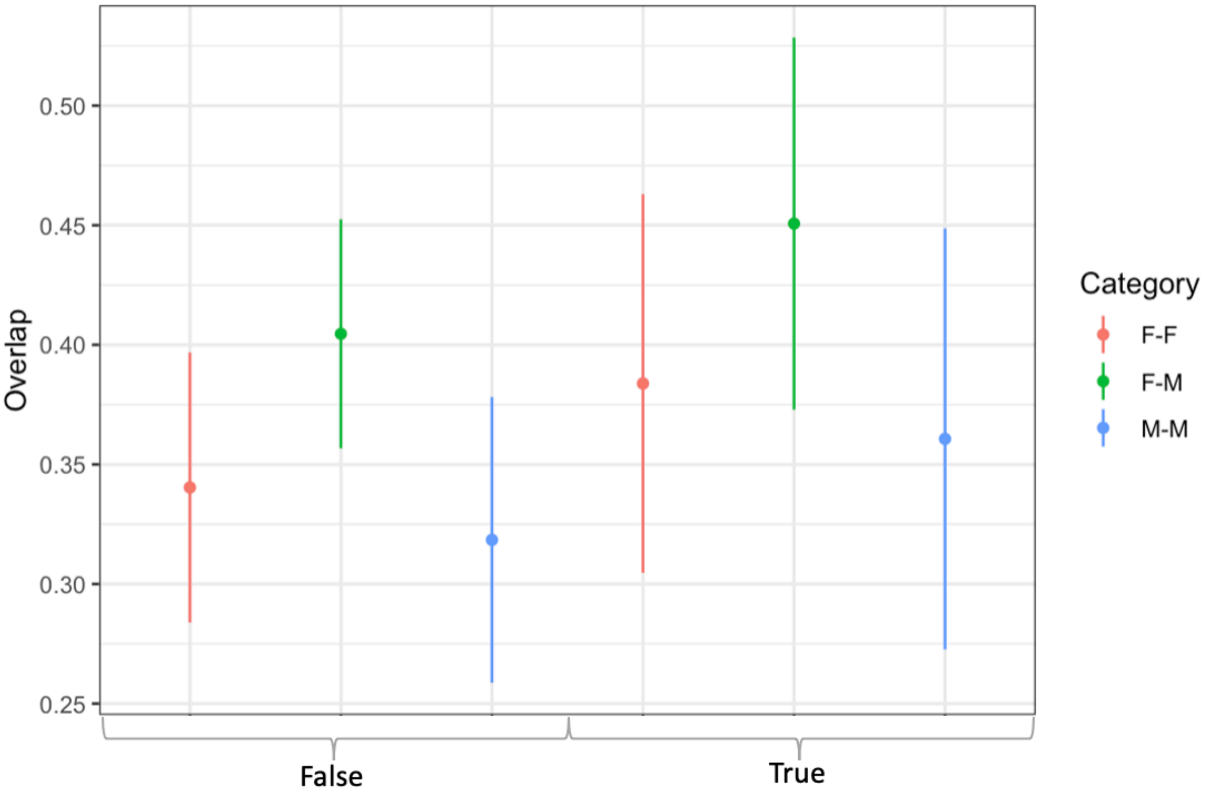

Figure 5: Overlap in relation to no presence (false) and presence (true) of migratory prey plotted from M15 for the sex categories. Lines represent 95% confidence intervals, circles represent the mean for each category. n FALSE = 55 lynx, 408 observations, n TRUE = 19 lynx, 62 observations.

The presence of migratory prey was not statistically significant in relation to overlap. Moreover, it's noteworthy that the dataset of lynx in areas with migratory prey included a relatively limited sample size, encompassing only 19 lynx. Therefore, the somewhat higher overlap in areas with migratory prey are inconclusive (Figure 5).

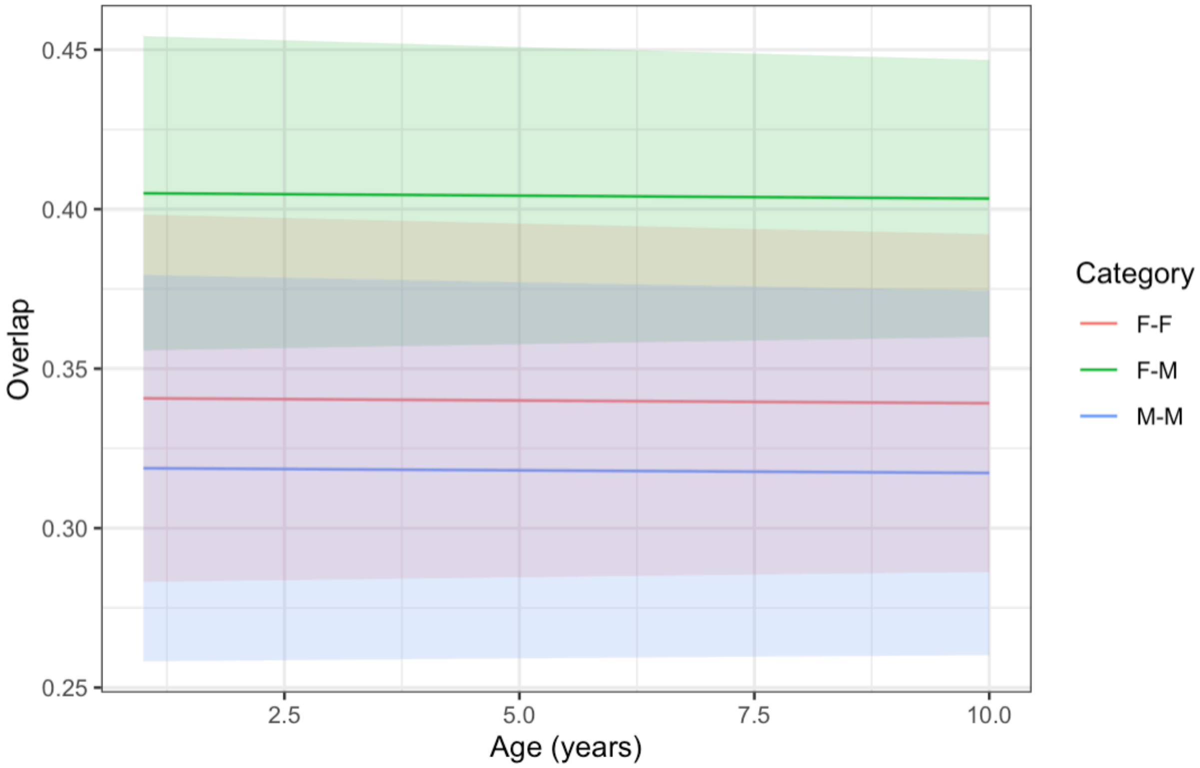

Figure 6: Overlap and age from model M15. 95% confidence intervals are marked in color corresponding to each category. n = 470.

Age did not correlate with overlap. This observation is further visualized by the linear relationship depicted in Figure 6. Figure A1 shows the density distribution of age groups, ranging from 2-127 months with a mean age of 3.5 years.

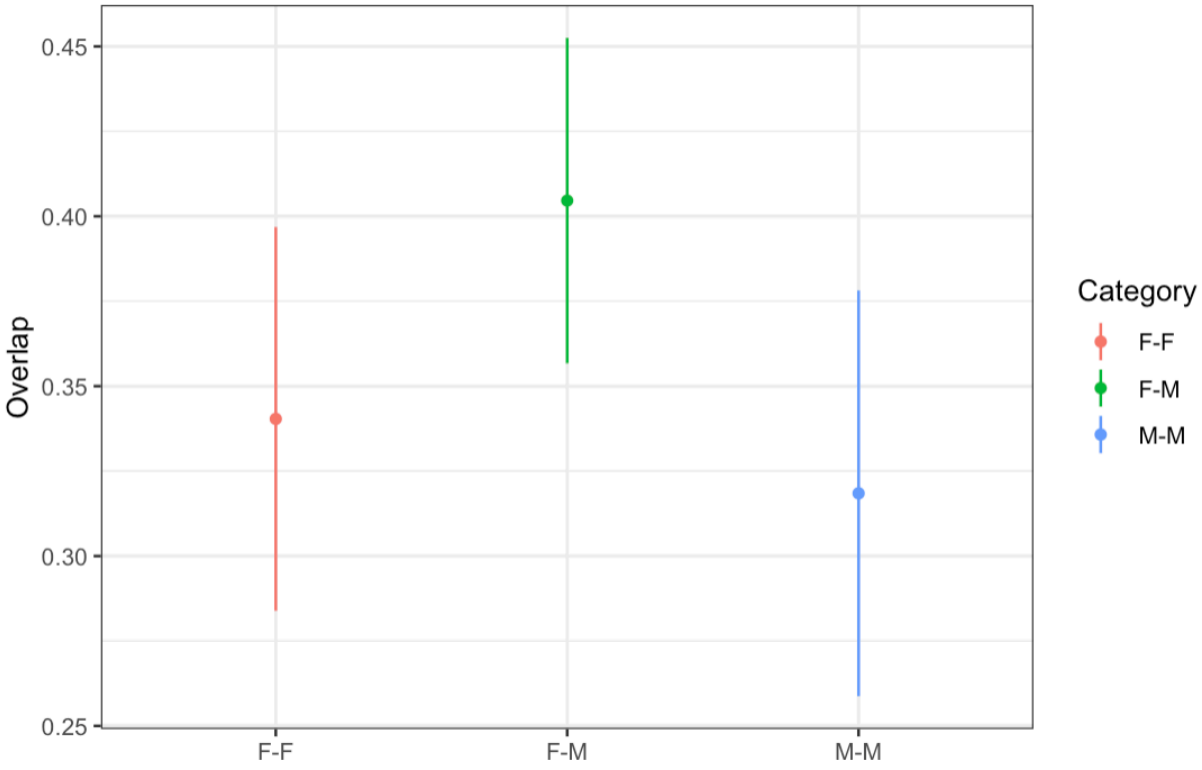

Figure 7: Overlap based on model M15 for the sex categories. Lines represent 95% confidence intervals, circles represent the mean for each category. n = 470.

Figure 7 illustrates the overlap and proportion of overlap when examining the sex categories. Specifically, the overlap was significantly higher for female-male compared to female-female. There was no significant difference between female-female overlap and male-male overlap, although mean overlap was smaller for males than females (Figure 7).

Seasonal shifts in overlap dynamics

Female-male overlap was found to be significantly higher than female-female overlap when looking at monthly proportion of overlap (Table 3a, Table 3b, Figure 8). Female-male was the only category with a significant smooth parameter, indicating that this was the only category where the overlap significantly differed throughout the year (Table 3b).

Table 3a: Proportional overlap of different months for the parametric values of the Generalized Additive Model (GAM). n = 2862.

Variable	*Estimate*	*Std. Error*	*z-value*	*p-value*
Intercept	0.03	0.07	0.38	0.69
F-M	0.42	0.09	4.56	5.01e-06 ***
M-M	0.23	0.13	1.78	0.07.

Table 3b: Proportional overlap between different months for smooth terms in the Generalized Additive Model (GAM). Smooth terms are used to model potentially nonlinear relationships between the response variable and continuous predictors. n = 2862.

Variable	*edf*	*Ref.df*	*Chi.sq*	*p-value*
Month:F-F	0.01	7	0.01	0.45
Month:F-M	1.28	7	14.48	5.78e-04 ***
Month:M-M	1.42	7	1.88	0.12

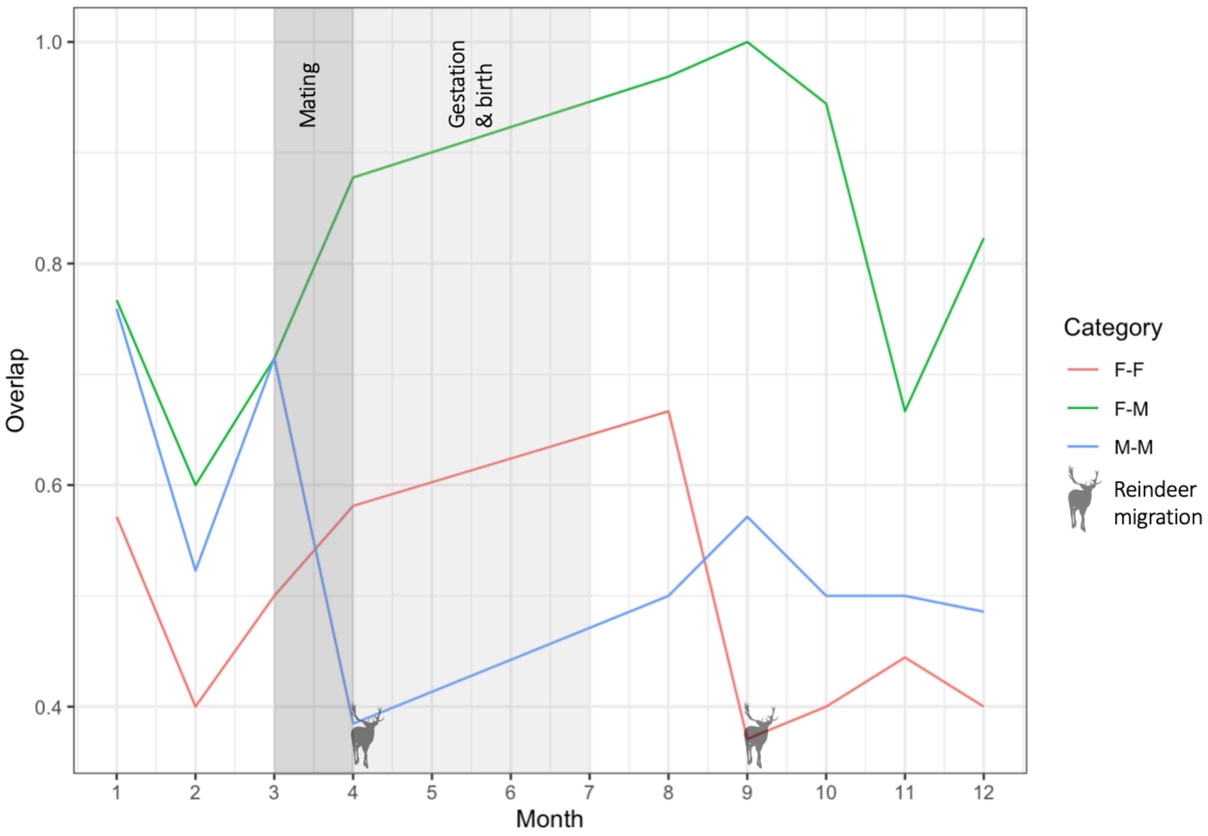

Figure 8: Overlap in the raw data throughout the months for the different sex categories. Peak mating season, March, is marked in dark grey. Gestation period, and later birth, is marked in light grey. Reindeer migration periods are marked with a symbol. These are estimates and may vary in onset and duration. n = 2862, mean observation number per month = 80.

Illustrated in figure 8, male-male overlap increased during winter and mating period, before decreasing during summer. Female-female overlap was higher during winter and gestation period. Female-male overlap increased before the mating period, and until October, before dropping and increasing again from November to January.

Discussion

Size of home range

The analysis revealed a significant negative correlation between home range size and overlap, meaning that as home range size increases, overlap among individuals decreases, indicating a mechanism for reducing competition and maintaining spatial segregation. This observed negative correlation between decreasing overlap as home range size increases supports the hypothesis that larger territories may lead to reduced overlap, as individuals have access to more resources within their exclusive ranges (Herfindal et al., 2005). This territorial behavior is crucial for minimizing conflicts over limited resources such as food, shelter, and mating opportunities (Herfindal et al., 2005; Linnell et al., 2021). The relationship between home range size and overlap underscores the importance of distribution of resources and availability in shaping lynx spatial ecology. Larger territories may confer reproductive advantages, allowing individuals to secure mating opportunities and successfully raise offspring (Maher & Lott, 1995; Sandell, 1989).

An important consideration when analyzing overlap between lynx pairs is the presence of unmarked lynx that may also overlap with the studied individuals, potentially impacting the estimation of overlapping home ranges. This means that the observed overlap between the studied lynx may not solely reflect their direct interactions but could also be influenced by the presence and movements of unmarked individuals within the same area.

Migratory prey

The data analysis yielded insignificant results regarding overlap and the presence of migratory prey. Other studies have found lynx to keep a stable home range in relation to migrating prey, coinciding with these findings (Danell et al., 2006; Walton et al., 2017). There could be several reasons for lynx not to follow migrating prey, thereby not increasing overlap with each other. One important reason may be the potential loss of territory (Hoem et al., 2007). In addition, lack of knowledge of available resources in new areas could result in reduced fitness due to resource fluctuations (Eide et al., 2004; Janmaat et al., 2009; Van Moorter et al., 2009). Mothers, especially their offspring, may also be increasingly exposed to predators in an unknown area (Persson et al., 2003). Implementing enforced long-distance reindeer migration could serve as a mitigating strategy to reduce reindeer losses, as lynx face these trade-offs (Walton et al., 2017).

Danell et. al. (2006) found that as the density of Eurasian lynx remains relatively consistent across seasons, while the density of semi-domesticated reindeer fluctuates, it is anticipated that regions with a stable lynx population will have greater access to other sources of food. Therefore, alternative prey such as mountain hare, ptarmigan and willow grouse may shape their spatial movement in reindeer winter and summer areas (Danell et al., 2006). Lynx which had access to reindeer all year had a better probability of reproducing versus those without access to reindeer during winter (Walton et al., 2017). Prey abundance may therefore be more important when considering the complex interplay between sex-specific behaviors, environmental factors, and territorial dynamics in lynx populations.

It is essential to acknowledge potential limitations, such as small sample size of lynx in certain regions, which may impact the robustness of the observed patterns (Figure 5). Investigating the influence of environmental variables, such as habitat characteristics, hereunder quality, and more detailed prey availability, on home range size and overlap could provide further valuable insights.

Inter- and intra-sexual overlap dynamics and age effects

The extent of overlap observed between female lynx was lower compared to the overlap between females and males. Similarly, interactions between male lynx showed a lower level of overlap compared to female-male, and female-female overlap. Occasional overlapping of areas may occur if individuals avoid each other at different times. This pattern indicates a dynamic interaction process near the boundaries of home ranges, possibly involving intraspecific communication through visual cues or scent marking rather than direct contact (López-Bao et al., 2014). This may contribute to the observed low overlap between males, in addition to their larger home ranges. Sandell's (1989) predictions suggest that female home range size should closely track prey density, while male home range size is expected to increase more rapidly due to shifts in mating behavior. Sandell's theory proposes that as prey density decreases and female density subsequently declines, males may shift from a territorial mating strategy to a roaming one. This change in behavior allows males to maximize their reproductive success by covering larger areas in search of receptive females. The observed larger overlap for female-male compared to female-female could therefore be explained by male roaming behavior related to mating, as observed in the increased overlap around March, where males enter the females home range. Female lynx may also tolerate this overlap due to their polygamous mating system where males are known to establish home ranges overlapping females home ranges for access to partners during mating season (Mattisson et al., 2013).

While Schmidt et al. (2016) observed male-biased dispersal and female philopatry within the lynx population, leading to higher average relatedness among females compared to males, they did not detect spatial family clusters. This suggests that offspring may not consistently inherit segments of their mothers' home ranges. This finding aligns with the insignificance of age regarding overlap, as familial relationships may not strongly influence home range overlap among lynx, although sex was not considered in combination with age in this study. Furthermore, it is plausible that young individuals may exhibit spatial behaviors influenced by their mothers the first year. Consequently, it could be argued that young animals that have not established permanent home ranges should have been excluded from the analysis.

Seasonal variation

Female-male overlap remained consistently high throughout the year, with notable increases in February/March. Males seek out females during this period, leading to a larger overlap (Sandell, 1989). Male-male overlap showed a seasonal trend with higher levels observed during winter months and breeding period. This fluctuation in male-male overlap could be influenced by factors such as changes in prey availability and in relation to mating behaviors, as studies have found males to overlap more, thereby getting into conflict more frequently during this period (Elbroch & Quigley, 2017; Emlen & Oring, 1977; Mattisson et al., 2013).

The greater aggregation of prey during winter months may result in higher overlap among lynx as they compete for resources, potentially influencing their spatial distribution and interaction patterns, as home range sizes of lynx show a tendency to increase with declining prey densities (Elbroch & Quigley, 2017; Schmidt, 2008). The breeding period and the presence of offspring could play a significant role in shaping seasonal overlap patterns. Female lynx may prioritize specific areas for denning and raising their young, leading to increased overlap with males during certain periods (Davies et al., 2012). Thus, as kittens grow older, females expand hunting areas, which may explain the observed increased overlap among females shortly after birthing.

Conclusion

As home range size increased, overlap among individuals decreased, meaning larger home ranges facilitated less overlap between lynx. This indicates a mechanism for reducing competition and maintaining spatial segregation. Notably, female-male home range overlap was significantly larger compared to female-female home range overlap. These findings reflect the complex dynamics of inter- and intra-sexual territorial interactions, influenced by factors such as mating strategies and resource distribution. Migratory prey did not influence overlap between lynx, suggesting they rely on other sources of food in these areas. Seasonal shifts in overlap dynamics further highlight the fluctuation of lynx spatial behavior: female-male overlap was high during mating period until early fall, indicating potential shifts in territorial behavior during reproductive cycles and change in prey abundance. Male-male overlap showed higher levels during winter months, possibly influenced by changes in prey availability, as well as mating season where they may encounter other males in the same females' territories. Protecting and preserving habitats that can support large territories is essential for maintaining healthy lynx populations and minimizing human-wildlife conflicts (Herfindal et al., 2005; Linnell et al., 2001). Moreover, it is important to prioritize the consideration of sex-specific strategies, habitat size, and quality when developing protected areas and management plans for carnivore species.

References

Aronsson, M., Low, M., López-Bao, J. V., Persson, J., Odden, J., Linnell, J. D. & Andrén, H. (2016). Intensity of space use reveals conditional sex-specific effects of prey and conspecific density on home range size. *Ecology and evolution*, 6 (9): 2957-2967.

Bailey, T. N. (1993). The African leopard. In *The African leopard*: Columbia University Press.

Breitenmoser, U. & Haller, H. (1993). Patterns of predation by reintroduced European lynx in the Swiss Alps. *The journal of wildlife management*: 135-144.

Breitenmoser, U., Kavczensky, P., Dötterer, M., Breitenmoser-Würsten, C., Capt, S., Bernhart, F. & Liberek, M. (1993). Spatial organization and recruitment of lynx (Lynx lynx) in a re-introduced population in the Swiss Jura Mountains. *Journal of Zoology*, 231 (3): 449-464.

Carbone, C. & Gittleman, J. L. (2002). A common rule for the scaling of carnivore density. *Science*, 295 (5563): 2273-2276.

Danell, A. C., Andrén, H., Segerström, P. & Franzén, R. (2006). Space use by Eurasian lynx in relation to reindeer migration. *Canadian Journal of Zoology*, 84 (4): 546-555.

Davies, N. B., Krebs, J. R. & West, S. A. (2012). *An introduction to behavioural ecology*: John Wiley & Sons.

Dobson, F. S. (1982). Competition for mates and predominant juvenile male dispersal in mammals. *Animal behaviour*, 30 (4): 1183-1192.

Duncan, C., Nilsen, E. B., Linnell, J. D. & Pettorelli, N. (2015). Life-history attributes and resource dynamics determine intraspecific home-range sizes in Carnivora. *Remote Sensing in Ecology and Conservation*, 1 (1): 39-50.

Eide, N. E., Jepsen, J. U. & Prestrud, P. (2004). Spatial organization of reproductive Arctic foxes Alopex lagopus: responses to changes in spatial and temporal availability of prey. *Journal of Animal Ecology*, 73 (6): 1056-1068.

Eira, I. M. G. (2020). *Flytting av og med rein*: NDLA. Available at: https://ndla.no/article/10224.

Elbroch, L. M. & Quigley, H. (2017). Social interactions in a solitary carnivore. *Current Zoology*, 63 (4): 357-362.

Emlen, S. T. & Oring, L. W. (1977). Ecology, sexual selection, and the evolution of mating systems. *Science*, 197 (4300): 215-223.

Erlinge, S. & Sandell, M. (1986). Seasonal changes in the social organization of male stoats, Mustela erminea: an effect of shifts between two decisive resources. *Oikos*: 57-62.

Ferguson, A. W., Currit, N. A. & Weckerly, F. W. (2009). Isometric scaling in home-range size of male and female bobcats (Lynx rufus). *Canadian Journal of Zoology*, 87 (11): 1052-1060.

Ferreras, P., Beltrán, J. F., Aldama, J. J. & Delibes, M. (1997). Spatial organization and land tenure system of the endangered Iberian lynx (Lynx pardinus). *Journal of Zoology*, 243 (1): 163-189.

Goszczyński, J. (1986). Locomotor activity of terrestrial predators and its consequences. *Acta Theriologica*, 31 (6): 79-95.

Greenwood, P. (1983). Mating systems and the evolutionary consequences of dispersal. *The ecology of animal movement*: 116-131.

Greenwood, P. J. (1980). Mating systems, philopatry and dispersal in birds and mammals. *Animal behaviour*, 28 (4): 1140-1162.

Herfindal, I., Linnell, J. D., Odden, J., Nilsen, E. B. & Andersen, R. (2005). Prey density, environmental productivity and home-range size in the Eurasian lynx (Lynx lynx). *Journal of Zoology*, 265 (1): 63-71.

Hoem, S. A., Melis, C., Linnell, J. D. & Andersen, R. (2007). Fighting behaviour in territorial male roe deer Capreolus capreolus: the effects of antler size and residence. *European Journal of Wildlife Research*, 53: 1-8.

Holmala, K., Herrero, A., Kopatz, A., Schregel, J., Eiken, H. G. & Hagen, S. B. (2018). Genetic evidence of female kin clusters in a continuous population of a solitary carnivore, the Eurasian lynx. *Ecology and evolution*, 8 (22): 10964-10975.

Hurvich, C. & Tsai, C.-L. (2008). A corrected Akaike Information Criterion for vector autoregressive model selection. *Journal of Time Series Analysis*, 14: 271-279. doi: 10.1111/j.1467-9892.1993.tb00144.x.

Janmaat, K. R., Olupot, W., Chancellor, R. L., Arlet, M. E. & Waser, P. M. (2009). Long-term site fidelity and individual home range shifts in Lophocebus albigena. *International Journal of Primatology*, 30: 443-466.

Kelt, D. A. & Van Vuren, D. H. (2001). The ecology and macroecology of mammalian home range area. *The American Naturalist*, 157 (6): 637-645.

Koordinierte, K. (2004). Status and conservation of the Eurasian lynx (Lynx lynx) in Europe in 2001. *Kora*, 19: 1-319.

Krofel, M., Skrbinšek, T. & Mohorović, M. (2019). Using video surveillance to monitor feeding behaviour and kleptoparasitism at Eurasian lynx kill sites. *Folia Zoologica*, 68 (4): 274-284.

Laing, S. P. & Lindzey, F. G. (1993). Patterns of replacement of resident cougars in southern Utah. *Journal of Mammalogy*, 74 (4): 1056-1058.

Linnell, J. D., Andersen, R., Kvam, T., Andren, H., Liberg, O., Odden, J. & Moa, P. (2001). Home range size and choice of management strategy for lynx in Scandinavia. *Environmental management*, 27: 869-879.

Linnell, J. D., Mattisson, J. & Odden, J. (2021). Extreme home range sizes among Eurasian lynx at the northern edge of their biogeographic range. *Ecology and Evolution*, 11 (10): 5001-5009.

López-Bao, J. V., Rodríguez, A., Delibes, M., Fedriani, J. M., Calzada, J., Ferreras, P. & Palomares, F. (2014). Revisiting food-based models of territoriality in solitary predators. *Journal of Animal Ecology*, 83 (4): 934-942.

Lovallo, M. J. & Anderson, E. M. (1996). Bobcat (Lynx rufus) home range size and habitat use in northwest Wisconsin. *American Midland Naturalist*: 241-252.

Maher, C. R. & Lott, D. F. (1995). Definitions of territoriality used in the study of variation in vertebrate spacing systems. *Animal behaviour*, 49 (6): 1581-1597.

Mattisson, J., Segerström, P., Persson, J., Aronsson, M., Rauset, G. R., Samelius, G. & Andrén, H. (2013). Lethal male-male interactions in Eurasian lynx. *Mammalian Biology*, 78: 304-308.

Mattisson, J., Odden, J., Linnell, J. D., Painer, J., Persson, J. & Andrén, H. (2020). Parturition dates in wild Eurasian lynx: evidence of a second oestrus? *Mammalian Biology*, 100 (5): 549-552.

Nilsen, E. B., Herfindal, I. & Linnell, J. D. (2005). Can intra-specific variation in carnivore home-range size be explained using remote-sensing estimates of environmental productivity? *Ecoscience*, 12 (1): 68-75.

Noble, G. K. (1939). The role of dominance in the social life of birds. *The Auk*: 263-273.

Odden, J., Linnell, J. D. & Andersen, R. (2006). Diet of Eurasian lynx, Lynx lynx, in the boreal forest of southeastern Norway: the relative importance of livestock and hares at low roe deer density. *European journal of wildlife research*, 52: 237-244.

Odden, J., Linnell, J., Solberg, H., Lurås, E., Lundby, R., Parmann, S., Bakka, D. & Brainerd, S. (2013). *Jakt på gaupe i Norge*.

Okarma, H., Jedrzejewski, W., Schmidt, K., KowALCZYK, R. & Jedrzejewska, B. (1997). Predation of Eurasian lynx on roe deer and red deer in Bialowieza Primeral Forest, Poland. *Acta theriologica*, 42 (2): 203-224.

Painer, J., Jewgenow, K., Dehnhard, M., Arnemo, J. M., Linnell, J. D., Odden, J., Hildebrandt, T. B. & Goeritz, F. (2014). Physiologically persistent corpora lutea in Eurasian Lynx (Lynx lynx)–Longitudinal ultrasound and endocrine examinations intra-vitam. *PloS one*, 9 (3): e90469.

Pedersen, V. A., Linnell, J. D., Andersen, R., Andrén, H., Lindén, M. & Segerström, P. (1999). Winter lynx Lynx lynx predation on semi-domestic reindeer Rangifer tarandus in northern Sweden. *Wildlife biology*, 5 (4): 203-211.

Persson, J., Willebrand, T., Landa, A., Andersen, R. & Segerström, P. (2003). The role of intraspecific predation in the survival of juvenile wolverines Gulo gulo. *Wildlife Biology*, 9 (1): 21-28.

Pesenti, E. & Zimmermann, F. (2013). Density estimations of the Eurasian lynx (Lynx lynx) in the Swiss Alps. *Journal of Mammalogy*, 94 (1): 73-81.

Poole, K. G. (1995). Spatial organization of a lynx population. *Canadian Journal of Zoology*, 73 (4): 632-641.

Powell, R. A., Zimmerman, J. W. & Seaman, D. E. (1997). *Ecology and behaviour of North American black bears: home ranges, habitat, and social organization*, vol. 4: Springer Science & Business Media.

Powell, R. A. (2000). Animal home ranges and territories and home range estimators. *Research techniques in animal ecology: controversies and consequences*, 442: 65-110.

Powell, R. A. & Mitchell, M. S. (2012). What is a home range? *Journal of mammalogy*, 93 (4): 948-958.

Pusey, A. & Wolf, M. (1996). Inbreeding avoidance in animals. *Trends in ecology & evolution*, 11 (5): 201-206.

Samelius, G., Andrén, H., Liberg, O., Linnell, J., Odden, J., Ahlqvist, P., Segerström, P. & Sköld, K. (2012). Spatial and temporal variation in natal dispersal by E urasian lynx in S candinavia. *Journal of Zoology*, 286 (2): 120-130.

Sandell, M. (1989). The mating tactics and spacing patterns of solitary carnivores. *Carnivore behavior, ecology, and evolution*: 164-182.

Schmidt, K., Jedrzejewski, W. & Okarma, H. (1997). Spatial organization and social relations in the Eurasian lynx population in Bialowieza Primeval Forest, Poland. *Acta theriologica*, 42 (3): 289-312.

Schmidt, K. (2008). Behavioural and spatial adaptation of the Eurasian lynx to a decline in prey availability. *Acta Theriologica*, 53: 1-16.

Schmidt, K., Davoli, F., Kowalczyk, R. & Randi, E. (2016). Does kinship affect spatial organization in a small and isolated population of a solitary felid: The Eurasian lynx? *Integrative Zoology*, 11 (5): 334-349.

Smith, J. (1987). Female land tenure system in tigers. *Tigers of the world*: 97-109.

Stamps, J. (1994). Territorial behavior: testing the assumptions. *Advances in the Study of Behavior*, 23 (173): 232.

Sunde, P., Kvam, T., Moa, P., Negard, A. & Overskaug, K. (2000). Space use by Eurasian lynxes Lynx lynx in central Norway. *Acta Theriologica*, 45 (4): 507-524.

Sunquist, M. & Sunquist, F. (2017). *Wild cats of the world*: University of chicago press.

Van Moorter, B., Visscher, D., Benhamou, S., Börger, L., Boyce, M. S. & Gaillard, J. M. (2009). Memory keeps you at home: a mechanistic model for home range emergence. *Oikos*, 118 (5): 641-652.

Vogt, K., Zimmermann, F., Kölliker, M. & Breitenmoser, U. (2014). Scent-marking behaviour and social dynamics in a wild population of Eurasian lynx Lynx lynx. *Behavioural processes*, 106: 98-106.

Walton, Z., Mattisson, J., Linnell, J. D., Stien, A. & Odden, J. (2017). The cost of migratory prey: seasonal changes in semi-domestic reindeer distribution influences breeding success of Eurasian lynx in northern Norway. *Oikos*, 126 (5): 642-650.

Wolff, J. O. (1993a). What is the role of adults in mammalian juvenile dispersal? *Oikos*: 173-176.

Wolff, J. O. (1993b). Why are female small mammals territorial? *Oikos*: 364-370.

Wolff, J. O. (1994). More on juvenile dispersal in mammals. *Oikos*: 349-352.

Worton, B. J. (1989). Kernel methods for estimating the utilization distribution in home-range studies. *Ecology*, 70 (1): 164-168.

Worton, B. J. (1995). Using Monte Carlo simulation to evaluate kernel-based home range estimators. *The Journal of wildlife management*: 794-800.

Zimmermann, F., Breitenmoser-Würsten, C. & Breitenmoser, U. (2005). Natal dispersal of Eurasian lynx (Lynx lynx) in Switzerland. *Journal of Zoology*, 267 (4): 381-395. doi: https://doi.org/10.1017/S0952836905007545.

Appendix

Table A1: Summary of GLMM of best ranked model M8 examining overlap of home range, based on AICc. n = 470.

Variable	*Estimate*	*Std. Error*	*z-value*	*p-value*
Intercept	-0.65	0.09	-6.80	9.83e-12 ***
Area	-0.30	0.05	-5.59	2.23e-08 ***
F-M	0.26	0.11	2.30	0.02 *
M-M	-0.11	0.15	-0.75	0.45

Table A2: Summary of GLMM of M11 examining overlap of home range, based on AICc. n = 470.

Variable	*Estimate*	*Std. Error*	*z-value*	*p-value*
Intercept	-0.69	0.10	-6.89	5.29e-12 ***
Area	-0.31	0.05	-5.71	1.10e-08 ***
Migratory prey	0.18	0.14	1.28	0.19
F-M	0.27	0.11	2.39	0.01 *
M-M	-0.09	0.15	-0.59	0.54

Table A3: Summary of GLMM of M13 examining overlap of home range, based on AICc. n = 470.

Variable	*Estimate*	*Std. Error*	*z-value*	*p-value*
Intercept	-0.62	0.12	-4.82	1.38e-06 ***

Area	-0.30	0.05	-5.60	2.04e-08 ***
Age	-8.25e-04	1.91e-03	-0.43	0.66
F-M	0.26	0.11	2.27	0.02 *
M-M	-0.12	0.15	-0.78	0.43

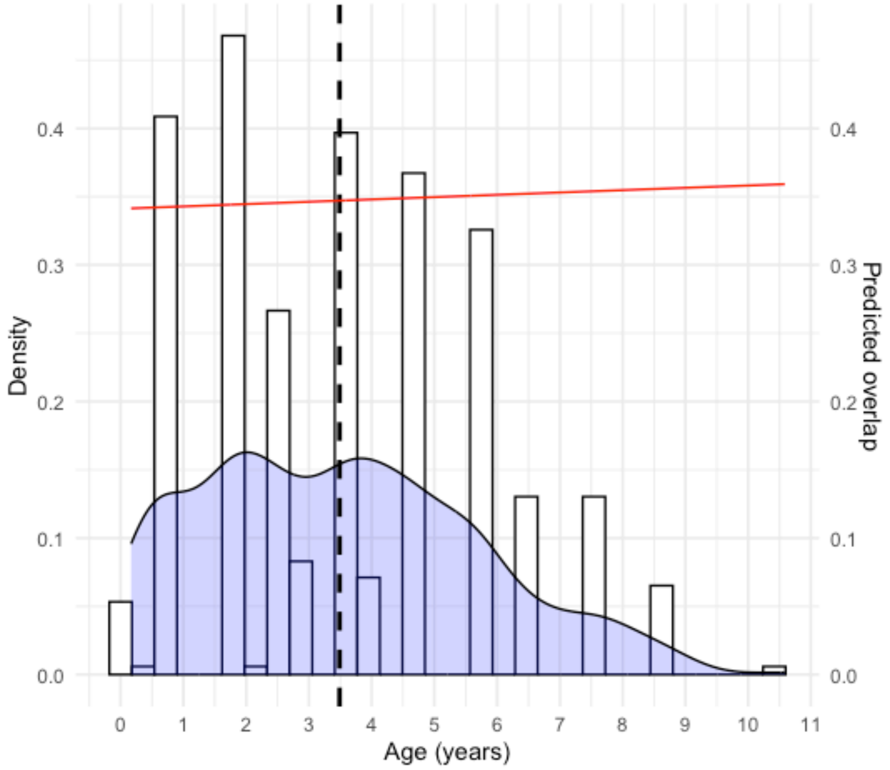

Figure A1: Age in years and density, density of age categories (marked in blue) and predicted overlap from GLM on right Y-axis. Age ranged from 2-127 months. Mean age (stippled line) = 42 months/3.5 years. n = 470.

Norges miljø- og biovitenskapelige universitet
Noregs miljø- og biovitskapelege universitet
Norwegian University of Life Sciences

Postboks 5003
NO-1432 Ås
Norway