Territoriality and movement dynamics of Scandinavian neighbouring wolf territories (*Canis lupus*)

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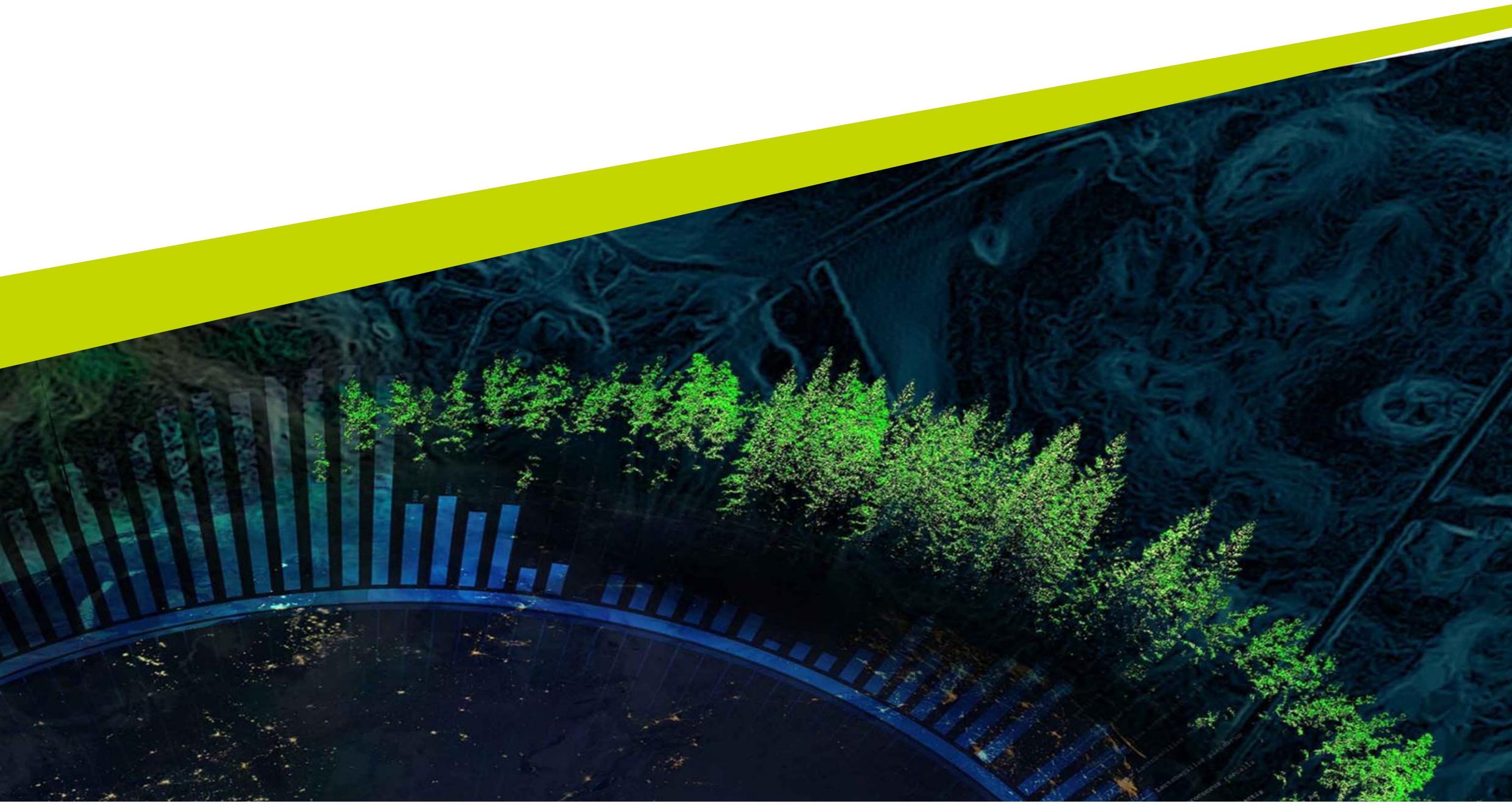

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Abstract

Territorial behaviour in wolves (*Canis lupus*) plays a central role in shaping social dynamics, resource access, and population structure. Although wolf packs are typically territorial, spatial overlap between neighbouring territories does occur. Understanding the drivers of these overlaps provides insight into wolf social organisation, resource competition, inter-pack conflict risk, and individual movement between packs, factors that collectively influence broader population dynamics.

This study investigates spatial overlap among neighbouring wolf territories in Scandinavia using GPS collar data, genetic relatedness, and spatial modelling. I applied Generalized Additive Models (GAMs) to model the size of spatial overlap (km²) between territorial pairs as a function of several covariates: (1) normalized difference in territory size, (2) dyadic social status (scent-marking pair vs. family group combinations), (3) genetic relatedness between alpha males and between alpha females, and (4) time since territory establishment. These covariates were selected based on ecological relevance and were derived from long-term monitoring data and pedigree records.

Spatial overlap was best predicted by territory size differences, dyadic social status, and female genetic relatedness. Overlap increased with greater disparity in territory size and was higher between scent-marking pairs compared to family groups. Female relatedness showed a non-linear effect; overlap increased with initial relatedness but declined beyond a threshold. Male relatedness had no notable effect.

Complementary Generalized Linear Mixed Models (GLMMs) were used to assess how wolves used different territorial zones (core, peripheral, overlap). These models revealed that wolves generally spent less time in overlap zones, with scent-marking pairs using these areas more than family groups. Additionally, territory age (defined as years since establishment) was negatively associated with overlap use, suggesting that older territories exhibit greater spatial stability and reduced inter-pack intrusion.

Together, these findings highlight the importance of social structure, territorial history, and genetic relationships in shaping spatial interactions among wolf packs. Understanding these drivers is essential for interpreting wolf space use in multi-use landscapes and has consequences for the management including monitoring of the population.

Keywords: wolves, Canis Lupus, territory, overlap, spatial analysis, movement analysis, territory usage, territoriality.

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Abbreviations

AIC	Akaike Information Criterion
dBBMM	Dynamic Brownian Bridge Movement Models
GAM	Generalized Additive Model
GCV	Generalized ross-Validation
GLMM	Generalized Linear Matrix
GPS	Global Positioning System
k-LoCoH	k-Nearest Neighbour Local Convex Hull
MCP	Minimum Convex Polygon
UD	Utilisation Distribution

1. Introduction

1.1 Social structure and territorial behaviour of wolves

Wolves (*Canis lupus*) are apex predators that exhibit complex social structures and strong territorial behaviours, both of which are crucial for their survival and reproductive success (Åkesson et al. 2022). A typical wolf pack consists of a breeding pair, their offspring, and occasionally unrelated subordinates (Mech, 1999). Recent research suggests that wolf packs function primarily as cohesive family units, with cooperative behaviours playing a more significant role in leadership than rigid dominance hierarchies (Kjørstad 2021; Nordli et al. 2023). The formation and maintenance of wolf packs are essential for hunting efficiency, reproduction, and protection against competing packs (Ausband 2024; Tallian et al. 2023).

Territoriality in wolves is primarily driven by the need to secure food resources and reduce intraspecific competition (Jedrzejewski et al. 2001; Schlägel et al. 2017). Packs defend their territories through scent-marking, vocalizations, and patrolling, which help minimize direct conflicts and the spread of diseases (Harrington & Mech 1983; Wehr et al. 2024). Territory size varies widely from 130 to 2,590 km² depending on prey density and ecological conditions (Kittle et al. 2015; Stępniak et al. 2020).

Comparative studies from other regions, such as Yellowstone National Park, provide important context for understanding territorial behaviour. In Yellowstone, high pack density and abundant elk (*Cervus canadensis*) lead to frequent territorial interactions and aggressive encounters, particularly during the breeding season (Cassidy et al. 2015; Stahler et al. 2019; Mech & Barber-Meyer 2017). These dynamics contrast with the more scattered distributionand lower density of territories observed in Scandinavia, as mainly resulting from a different management regime in Scandinavia (Mattisson et al. 2013; Benson & Patterson 2014).

1.2 Scandinavian wolf territories and ecological drivers

The Scandinavian wolf population has been closely monitored since 1978, offering valuable insights into territorial behaviour and the ecological factors influencing spatial dynamics (Wabakken et al. 2001; Gittleman 2019; Åkesson et al. 2022). Scandinavian wolves primarily hunt large herbivores, such as moose (*Alces alces*) and roe deer (*Capreolus capreolus*) mainly depending on their density and which also can influence territory size and hunting strategies (Sand et al. 2008; Sand et al. 2016).

Territory size in Scandinavian wolves varies regionally, primarily shaped by prey availability and landscape features. In northern regions, where roe deer are scarce and moose dominate as the main prey, wolves tend to maintain larger territories, often expanding seasonally during winter to follow prey movements (Mattisson et al. 2013; Sand et al. 2022). In contrast, southern Scandinavia supports higher densities of alternative ungulates, including roe deer, red deer, fallow deer, and wild boar, which allows wolves to occupy smaller, more compact territories (Mattisson et al. 2013; Åkesson et al. 2022). These spatial patterns reflect adaptive responses to prey distribution and energetic demands (Rich et al. 2012). While forest density, elevation, and seasonal prey shifts may influence the placement of territorial boundaries, they do not appear to limit overall territory size. Instead, the primary constraint on territory size is wolf density, as higher population pressure can lead to reduced territory sizes due to increased competition (Malcolm et al. 2020; Gebo et al. 2022).

While Yellowstone wolves often compete for prime prey areas in close proximity, Scandinavian wolves operate in more fragmented and human-influenced landscapes (Mech & Barber-Meyer 2017; Brandell et al. 2020). These differences raise questions about how ecological and anthropogenic pressures shape territorial overlap and pack interactions in low-density populations (Mattisson et al. 2013; Benson & Patterson 2014).

1.3 Territorial overlap and intraspecific competition

As highly territorial animals, wolves actively defend their territories against rival packs and dispersing individuals (Harrington & Mech 1983; MacNulty et al. 2009). While territoriality function to secure food resources and minimize direct competition, some territorial overlap does occur, particularly in areas with high prey density (Wehr et al. 2024). In Yellowstone, such overlap often results in aggressive encounters and even intraspecific mortality, especially during the breeding season (Cassidy et al. 2015; Brandell et al. 2020). In contrast, direct disputes in Scandinavia are less frequently recorded, raising questions about whether territorial conflicts occur less often or are simply harder to document due to lower predator/prey ratio and observational challenges.

Despite the risks associated with territorial disputes, intraspecific competition is not the primary driver of wolf mortality in Scandinavia. Instead, human-induced causes such as legal harvest and poaching that pose the greatest risks (Åkesson et al. 2022; Milleret et al. 2025). The Scandinavian wolf population has since the re-establishment of the population experienced significant losses due to illegal hunting, undermining conservation efforts (Liberg et al. 2011; Chapron et al. 2012; Liberg et al. 2020; Bischof et al. 2019).

Territorial boundaries also limit the spread of disease, as wolves generally avoid direct interactions with infected individuals from rival packs (Kittle et al. 2015; Kittle et al. 2017; Brandell et al. 2020). In addition to broad territorial patterns, finer-scale spatial behaviours can offer insight into the internal dynamics of pack life. These movement patterns may be shaped by ecological conditions as well as individual traits like social role, inbreeding status, or the age of the territory.

1.4 Knowledge gaps and study rationale

Although Scandinavian wolves have been extensively studied, key questions remain about how territorial overlap arises and what ecological or social factors drive it. Comparative studies suggest that territorial conflict is more visible in high-density populations like Yellowstone, but it is unclear whether similar dynamics exist in Scandinavia under different ecological pressures. Furthermore, the role of human disturbance, such as habitat fragmentation and hunting pressure, may alter pack stability and force dispersing wolves into overlapping territories (Lesmerises et al. 2012; McPhee et al. 2012; Tallian et al. 2019; Carricondo-Sanchez et al. 2020).

Understanding the causes and consequences of territorial overlap in Scandinavian wolves is essential for effective population management. Unlike Yellowstone wolves, which often engage in aggressive competition for space and prey, Scandinavian wolves may exhibit territorial overlap due to factors such as prey distribution, genetic relatedness (e.g., kinship), or territory inheritance mechanisms (Jędrzejewski et al. 2005; Bischof et al. 2019). These overlaps are particularly relevant for monitoring efforts, as they can complicate population counts and territory delineation (Rich et al. 2012; Åkesson et al. 2022). Accurate interpretation of spatial dynamics is therefore critical, not only for ecological understanding but also for ensuring reliable census data and informing conservation strategies that reflect the unique social and spatial structure of the Scandinavian wolf population (Rich et al. 2012; Åkesson et al. 2022).

2. Objectives

In this thesis, I aimed to quantify the area of overlap between neighbouring wolf territories and which factors influence the size of this overlap. Specifically, these factors included the normalized size difference between neighbouring territories (calculated as the absolute difference in territory size divided by the average of the two, which provides a standardized measure of how unequal the territories are in size), the social status of the wolf pack (scent-marking pair or family group), and the level of co-ancestry between the alpha individuals of each pack. My hypotheses were:

H1: Larger normalized size differences between neighbouring wolf territories may result in greater overlap, as such disparities can reflect unequal competitive abilities or differing resource needs, potentially influencing both the extent and directionality of territorial overlap.

H2: Family groups will have the smallest overlap when neighbouring other family groups, whereas scent-marking pairs will have the largest overlap when neighbouring with other scent-marking pairs.

H3: A higher genetic relatedness between two alpha individuals from neighbouring packs will correspond to increased territorial overlap, regardless of direct interactions between the wolves.

As a part of my alternative analysis, I wanted to investigate the proportion of time each wolf spent in the core, peripheral, and overlap area of its territory, and how the social status and inbreeding coefficient of the collared individual influenced this proportion. In the context of movement dynamics, the inbreeding coefficient may serve as a factor influencing individual dispersal tendencies, including the likelihood of occupying overlapping territories. Genetic factors such as limited dispersal potential could contribute to individual variation in movement patterns. I hypothesized that:

H4: Family groups (breeding adults and offspring) spend less time in overlap zones and more time in core zones where safety and stability in cases of a possible litter.

H5: Inbred adult territorial individuals may exhibit reduced physical fitness and cognitive ability, potentially limiting their hunting efficiency. As a result, they might be more likely to enter overlap areas looking for prey killed by the neighbouring pack.

H6: Wolves from older territories spend less time in overlap zones due to enhanced territorial stability and resource familiarity.

Lastly, I investigate the spatial and temporal proximity of individual wolves across multiple years, identifying cross-territorial interactions and assessing movement patterns between neighbouring individuals. The aim was to quantify the conditions under which wolves engage in close-range interactions outside their established territories. My hypotheses were:

H7: Wolves with larger territorial overlap will engage in more frequent interactions due to increased spatial proximity and shared resources.

H8: Closely related wolves, such as same-sex individuals (female-female or male-male) from neighbouring territories, may exhibit higher interaction rates, as genetic relatedness between individuals occupying adjacent areas can promote cooperative behaviours like territory defence, tolerance at shared boundaries, or resource sharing.

3. Method

3.1 Dataset

For this study, I used GPS location data collected from GPS-collared wolves in south-central Scandinavia between 2001 and 2022 (Figure 1). The data were gathered by the Scandinavian Wolf Research Project (SKANDULV), a long-standing collaborative initiative focused on monitoring and studying the wolf population in Sweden and Norway (Liberg et al. 2012). GPS collars, deployed by SKANDULV, recorded the wolves' locations at regular intervals ranging from a 1 minute to 248 days with a mean of 13 038 seconds (approximately 3,62 hours). All collaring procedures followed ethical guidelines and were conducted under the supervision of Swedish authorities, in accordance with legal frameworks and approved by relevant ethical review boards (Arnemo et al. 2007).

The resulting dataset included approximately 396,000 GPS points from 155 unique wolf individuals. For spatial and movement analyses, the data were imported and processed in R v4.3.3 (R Core Team 2025). The study applied a biologically relevant temporal framework, using "wolf years" that spanned from May 1st to April 30th of the following year, aligning with the species' reproductive cycle and seasonal behaviours.

To ensure consistency in territorial behaviour, the dataset was filtered to exclude subordinate pack members and long-distance dispersers. The final sample included only alpha individuals (i.e. scent-marking pairs or from family groups), resulting in 44 unique wolf IDs used for the analysis.

3.1.1 Study area

The study area covers the geographical range of wolves in south-central Scandinavia (Figure 1). This region is characterized by dense coniferous forests, mixed woodlands, and interspersed wetlands (Eriksson & Dalerum 2018; Roberge et al. 2024). The area experiences a temperate climate, with cold winters and mild summers. The landscape is a mix of intact natural areas and managed forests, with occasional human settlements and infrastructure such as roads and logging trails (Zimmermann et al. 2014; Ordiz et al. 2015).

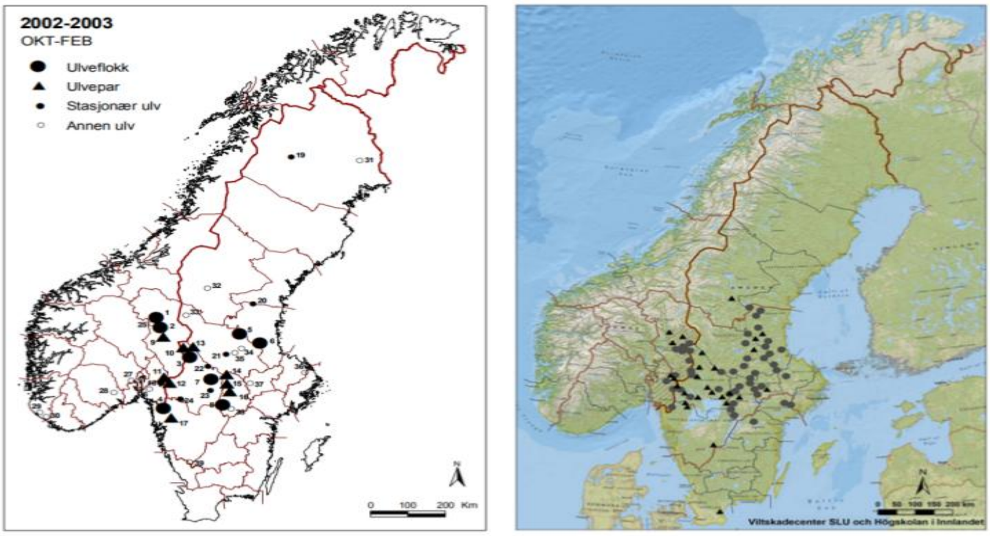

Figure 1. Figure 1. Study area showing wolf territory distribution in Sweden and Norway for year 2002-2003 (left map) and 2020-2021 (right map) (Source: Viltskadecenter SLU & Högskolan i Innlandet.

3.2 Territory and overlap estimation

3.2.1 Method selection

To identify neighbouring territories, I first had to estimate territory size and borders for each pack for each year. I decided to test three known home range estimators to determine which was best suited to my research questions, with particular attention to minimizing overestimation of territory size (Boyle 2021). These home range estimators were: minimum convex polygons (MCP), k-nearest neighbour local convex hull (k-LoCoH) and dynamic Brownian bridge movement models (dBBMM). I considered two or more territories as being neighbouring when the distance between borders was less or equal to 5 kilometres.

Minimum convex polygons (MCP)

The MCP method was applied to estimate the territory by creating the smallest convex polygon that encloses 100% of the recorded GPS locations of wolves from one territory annually (Calenge 2024). While this approach is widely used due to its simplicity and comparability across studies, it tends to overestimate territory size, especially when animals make occasional exploratory movements or outlier trips (Calenge 2024).

k-Nearest neighbour local convex hull (k-LoCoH)

The k-LoCoH method generates a set of convex hulls around each GPS location using the 50 nearest neighbors in the dataset (Getz et al. 2007; Calenge 2024). Compared to MCP, this method is more responsive to the shape and intensity of space use, allowing for more accurate exclusion of unused or rarely visited areas (Getz et al. 2007; Calenge 2024). It helps reduce overestimation of territory size while preserving ecological realism, although the choice of *k* can influence hull fragmentation and overall territory continuity (Getz et al. 2007; Calenge 2024).

Dynamic Brownian Bridge Movement Models (dBBMM).

To incorporate movement dynamics, dBBMM was applied. This model integrates movement paths, GPS error, and time intervals to generate a probabilistic utilization distribution, resulting in a more nuanced representation of space use (Kranstauber et al. 2024). The dBBMM is particularly effective at capturing core-use areas and movement corridors, avoiding overestimation by concentrating on areas wolves are likely to traverse (Kranstauber et al. 2024). However, it can be computationally intensive and sensitive to the frequency of GPS fixes (Kranstauber et al. 2024).

3.2.2 Territory estimation

After comparing the outputs of the three home range estimators in relation to my objective of minimizing territory size overestimation while accurately reflecting biologically relevant space use, I selected the dynamic Brownian bridge movement model (dBBMM) for further analysis to estimate wolf territory size and identify neighbouring packs. Compared to MCP and k-LoCoH, dBBMM provided a more realistic and biologically meaningful representation of space use by incorporating the movement paths, time intervals, and behavioural variance of wolves (Kranstauber 2019; Kranstauber et al. 2012). This allowed for a better distinction between areas of active use and infrequent excursions, helping to minimize overestimation of territory size (Kranstauber 2019; Kranstauber et al. 2012). The territories were generated using the brownian.bridge.dyn function (move package; Kranstauber et al. 2024) in R for each adult wolf and year. This was done with the key parameters: location error - 25, margin - 15, scale of granularity (dimSize) - 125, time step – 2, and boundary extension (ext) -1,2.

Territory boundaries were generally defined by the 99% Utilisation Distribution (UD) isopleth contours, which capture nearly all routine space use while excluding rare excursions (Kranstauber et al. 2016; Kranstauber et al. 2024). In years with sparse GPS data, the UD contour was adjusted downward to avoid overgeneralization while ensuring inclusion of all individuals.

The UD is a continuous probability surface of space use; the 50% core area represents the smallest area containing 50% of the UD i.e., the highest-use probability region (Kranstauber et al. 2016). Biologically, this core is expected to encompass intensively used sites such as resting locations, dens, rendezvous sites, and key feeding patches (Roffler & Gregovich 2018). The peripheral zone was defined as the remaining area within the 99% UD contour, excluding both the core and any overlap zones. Final territory sizes were calculated in square kilometres using the st_area function from the sf package (Pebesma & Bivard 2023).

3.2.3 Overlap estimation

Territory boundaries generated via dBBMM were inspected annually to identify spatial overlaps between neighbouring packs. Overlap areas were calculated using spatial intersection tools and expressed in square kilometres (Pebesma & Bivard 2023). To quantify asymmetry in territory size, I calculated the normalized territory size difference, defined as the absolute difference in territory size divided by the mean size of the two territories. This metric ranges from 0 (equal-sized territories) to 2 (one territory twice as large as the other), offering a standardized measure of spatial disparity.

To explore factors influencing spatial overlap, I constructed statistical models using overlap area (km²) as the primary response variable. The analysis included dyads of neighbouring territories, both overlapping and non-overlapping, defined as territories located within 5 kilometres of each other. Overlapping dyads shared physical territory, while non-overlapping dyads had an overlap area of 0 km². This approach allowed for a comprehensive assessment of spatial interactions across varying territorial configurations.

The start years 2001, 2007, 2014 and 2016 since were excluded from the analysis since they showed no overlap or neighbouring territories. Ultimately year 2021 and 2022 were also excluded due to problematic non directional spatial data resulting in using 16 different years all together.

3.3 Covariates

To explain variation in territorial overlap, I compiled biologically meaningful covariates at both the individual territory level and the dyad-year level. These variables reflect ecological pressures, social structure, and genetic relationships that may influence how wolf packs interact spatially.

Each wolf territory was assigned an age value based on the first year of its establishment, as documented in Scandinavian wolf status reports (i.e., time since wolf territory establishment).The social status, territory age, and pack size of each territory were obtained from the Scandinavian wolf status reports (Svensson et al. 2019, 2021, 2015, 2017, 2022; Wabakken et al. 2004a, 2004b, 2005, 2011, 2010, 2009, 2007, 2008, 2013, 2012, 2018, 2020, 2022). Additionally, the inbreeding coefficient and relatedness between individuals were determined for all wolves included in this study, with data provided by SKANDULV.

3.3.1 Territory-Level Covariates

- **Territory age (terr_age):**
  Defined as the number of years since a territory was first established, based on Scandinavian wolf status reports. Older territories may reflect greater stability, strong'er territorial defence, and accumulated local knowledge, potentially reducing overlap with neighbours.
- **Social status (soc_stat):**
  Each territory was classified as either a family group (F), comprising breeding adults and offspring, or a territory-marking pair (T), a mated pair or individuals marking territory without confirmed offspring. Family groups may defend space more aggressively due to reproductive investment, while pairs may be more flexible or transitional.
- **Pack size (pack_size):**
  Estimated annually for each territory. Larger packs may require more resources and space, potentially leading to larger territories or increased territorial defence. Smaller packs may be more vulnerable to encroachment or more tolerant of overlap.
- **Territorial space use (location_type)**:
  GPS locations were classified into three zones based on each wolf's dBBMM Utilisation Distribution (UD), and the proportion of fixes in each zone was used as a proxy for time spent:
    - Core: 50% UD contour, representing the most intensively used area (e.g., resting, feeding, denning).
    - Peripheral: Remaining 99% UD contour, excluding core and overlap zones.
    - Overlap: Areas where a pack's 99% UD contour intersected with another pack's territory.

3.3.2 Dyadic Covariates

Dyadic data were compiled for each unique pair of neighbouring packs observed in the same calendar year. These covariates capture asymmetries between packs that may shape overlap outcomes:

- **Normalized territory size difference (norm_size_diff):**

A standardized measure of spatial disparity between two packs. Larger differences may reflect unequal competitive ability or resource needs, influencing overlap extent or directionality.

- **Pack size difference (pack_size_diff):**
  Absolute difference in the number of individuals per pack. Packs with more members may exert greater territorial pressure or be more resistant to encroachment.
- **Territory age difference (terr_age_diff):**
  Difference in years each pack has held its territory. Older packs may have stronger territorial claims, while newer packs may be more exploratory or subordinate.
- **Neighbour overlap difference (nr_overlap_diff):**
  Difference in the number of neighbouring packs each territory overlaps with. This may reflect local density, landscape fragmentation, or pack tolerance levels.
- **Dyadic social status (dyad_soc_stat):**
  Categorical variable representing pairwise combinations of social status:
  - F_F: Two family groups
  - F_T: One family group and one territorial pair
  - T_T: Two territorial pairs These combinations may influence the likelihood of overlap, with family groups potentially defending space more aggressively than pairs.
- **Genetic relatedness (Coancestry_M and Coancestry_F):**
  Coefficients of relatedness between individuals in neighbouring packs were obtained from SKANDULV (Ø. Flagstad). These values estimate the probability of shared ancestry and may influence tolerance or avoidance behaviours, especially in overlapping zones. Kin-related packs may exhibit reduced aggression and increased spatial tolerance (overlap).

3.4 Spatial and temporal proximity

To assess spatial and temporal proximity between wolves in different territories, I identified the closest recorded encounters between neighboring individuals. For each year, all unique wolf pairs were generated using expand_grid() in the dplyr package (Wickham et al. 2019), excluding duplicate combinations. Only pairs from different territories were retained to capture cross-territorial interactions. For each pair, GPS locations were temporally matched using the fuzzyjoin package (Robinson 2020) with a 30-minute tolerance, ensuring that locations were recorded close in time. Euclidean distances were then calculated between matched locations, and encounters were filtered to include only those within 5 km.

3.5 Statistical analyses

3.5.1 Statistical analysis - overlap

I investigated variation in spatial overlap between neighbouring wolf territories using Generalized Additive Models (GAMs) (mgcv package, Wood et al. 2016). This type of model is a flexible extension of linear models that use smooth functions to model non-linear relationships between a response variable and its covariates, making them particularly suitable for ecological data where predictor effects may not follow strict linear patterns.

I used territory overlap as the response variable and modelled it as a function of normalized territory size difference, dyadic social status (F-F, F-T, T-T), and genetic relatedness between the alpha females as well as between the males of each neighbouring pack. The GAMs were chosen to capture complex and potentially nonlinear effects of continuous predictors such as relatedness and territory size difference, without overfitting the data. Given the data characteristics, a Tweedie distribution (Tweedie 1.25) with a log link function (power 0.1) was selected to accommodate both continuous and zero-inflated responses, providing a robust and appropriate variance structure.

I used Akaike Information Criterion (AIC) to select the best model explaining variation in the size of the overlap between neighbouring territories.

3.6 Statistical analysis – territorial space use

To investigate how wolves use different parts of their territories, I applied generalized linear mixed models (GLMMs) using the glmmTMB package (Brooks et al. 2017). The response variable was the proportion of time spent in each zone (core, peripheral, overlap), modelled with a beta distribution, which is suitable for continuous proportions bounded between 0 and 1. Each model included Wolf_ID as a random effect to account for repeated measures and individual variation (Signer et al. 2019; Ruíz et al. 2023).

I began with a full model, which included all biologically relevant predictors and their interactions with zone type (location_type). This model tested whether the proportion of time spent in different zones varied depending on: Social status (family group vs. territorial pair), inbreeding coefficient, and territory. To evaluate model performance and parsimony, I compared the full model to three nested candidate models, each excluding one or more predictors. Model fit was assessed with AIC, where lower values indicate better support. The difference in AIC (ΔAIC) was calculated relative to the best-performing model.

4. Results

This study includes 23 individual territories established between 2002 and 2020 (Appendix 1.1). The minimum number of territories established in a single year was 2, observed in several years including 2002, 2003, 2005, 2006, 2008, 2013, 2015, and 2020 (Appendix 1.1). The highest number was recorded in 2010, with 8 territories established (Appendix 1.1). On average, approximately 3.44 territories were established per year across the 16-year period examined (Appendix 1.1). Territory sizes range widely, with core areas spanning from 1.6 km² to 389 km² and total territory areas from 69 km² to 3,768 km² (Appendix 1.1). Packs could consist of 2 to 12 individuals, with a mean of 4 wolves (Appendix 1.1). Using dBBMM, 32 overlapping and 5 neighbouring territories (i.e. not overlapping, but neighbouring closer than 5 kilometres) could be recorded (Appendix 1.2). Overlap areas range from 0.3 to 840 km², with a median of approximately 35 km² and average proportional overlap around 10% (Appendix 1.2)

4.1 Overlap analysis

The best model explaining variation in spatial overlap between neighbouring wolf territories was the one including the normalized territory size difference, the dyadic social status (F-F, F-T, T-T), and the co-ancestry coefficient between the alpha females of the neighbouring packs (AIC = 653.7098; Table 1; Appendix 2.1).

Table 1. Model selection results for candidate generalized additive models (GAMs) predicting overlap area (km²) between wolf territories in Scandinavia. Competing models vary in the set of predictors included and in the functional form of those predictors, with s(covariate, k = 5) indicating a smooth term with basis dimension k = 5, and I(covariate)^2 indicating the squared covariate. Models were ranked by Akaike Information Criterion (AIC), with ΔAIC representing the difference from the lowest AIC model. Columns show model name, formula, estimated degrees of freedom (df), AIC, and ΔAIC.

Model name	**Model formula**	**df**	**AIC**	**ΔAIC**
Full smooth model	Overlap area (km^2) ~ s(norm_size_diff, k=5) + dyad_soc_status + s(coancestry_F, k=5) + s(coancestry_M, k=5)	8,97	653,7098	0
Smooth model 1	Overlap area (km^2) ~ s(norm_size_diff, k=5) + dyad_soc_status + s(coancestry_F, k=5)	7,79	669,0191	15,3092
Smooth model 2	Overlap area (km^2) ~ s(norm_size_diff, k=5) + dyad_soc_status + s(coancestry_F, k=5) + coancestry_M	8,97	653,7099	1,0096E-05
Smooth model 3	Overlap area (km^2) ~ s(norm_size_diff, k=5) + dyad_soc_status + coancestry_F + coancestry_M	7,00	684,3434	30,6335

Smooth model 4	Overlap area (km^2) ~ s(norm_size_diff, k=5) + dyad_soc_status + I(coancestry_F)^2 + coancestry_M	7,00	684,3434	30,6335

The final model had an adjusted R^2 of 0.6, suggesting that all the selected predictors significantly contributed to the variation in territorial overlap (Table 2).

Table 2. Summary of the Full smooth model generalized additive model (GAM) predicting adjusted overlap area (km²) between wolf territories in Scandinavia. The model was fitted with a Tweedie distribution (p = 1.25) and a μ0.1 link function. Parametric coefficients are reported as estimates, standard errors, test statistics, and p-values for categorical predictors. Smooth terms are reported with their effective degrees of freedom (edf), reference degrees of freedom (ref.df), test statistics, and p-values. Model performance metrics include adjusted R² (R_sq_adj), deviance explained, generalized cross-validation score (GCV), scale estimate, and sample size (n).

Modell formula:	overlap_area_km2_adj ~ s(norm_size_diff, k = 5) + dyad_soc_status + s(Coancestry_M, k = 5) + s(Coancestry_F, k = 5) + s(terr_age_diff, k = 5)				
	Family: Tweedie (1.25)				
	Link function: mu^0.1				
Parametric coefficients	**term**	**estimate**	**std.error**	**statistic**	**p.value**
	(Intercept)	1,189339	0,099236	11,9849	**1,51E-12**
	dyad_soc_status F_T	0,380131	0,103002	3,690535	**0,000956**
	dyad_soc_status T_T	0,469899	0,118645	3,960544	**0,000466**
Approximate significance of smooth terms	**term**	**edf**	**ref.df**	**Statistic**	**p.value**
	s(norm_size_diff)	1,000001	1,000001	12,218	**0,001364**
	s(Coancestry_M)	1,000133	1,000266	2,69135	0,112043
	s(Coancestry_F)	2,970543	3,484063	4,221032	**0,009192**
	R_sq_adj	**Deviance_explained**	**GCV**	**Scale_est**	**n**
	0,6	70,6	33,936	22,146	36

The smooth term for female genetic relatedness (Coancestry_F) showed a positive relationship with overlap and was statistically significant (p = 0.0092), indicating a non-linear relationship between spatial overlap and female coancestry (Figure 2; Table 2). In contrast, male genetic relatedness (Coancestry_M) did not show statistical significance (p = 0.112); Table 2; Appendix 2.1).

Dyadic social status showed a strong effect ($p < 0.01$), with overlap being lowest for neighbouring family groups (F_F) and highest for neighbouring scent marking pairs (T_T) (Figure 4; Table 2). The normalized territory size difference also exhibited a significantly non-linear relationship with the spatial overlap ($p < 0.1$) (Figure 4; Table 2).

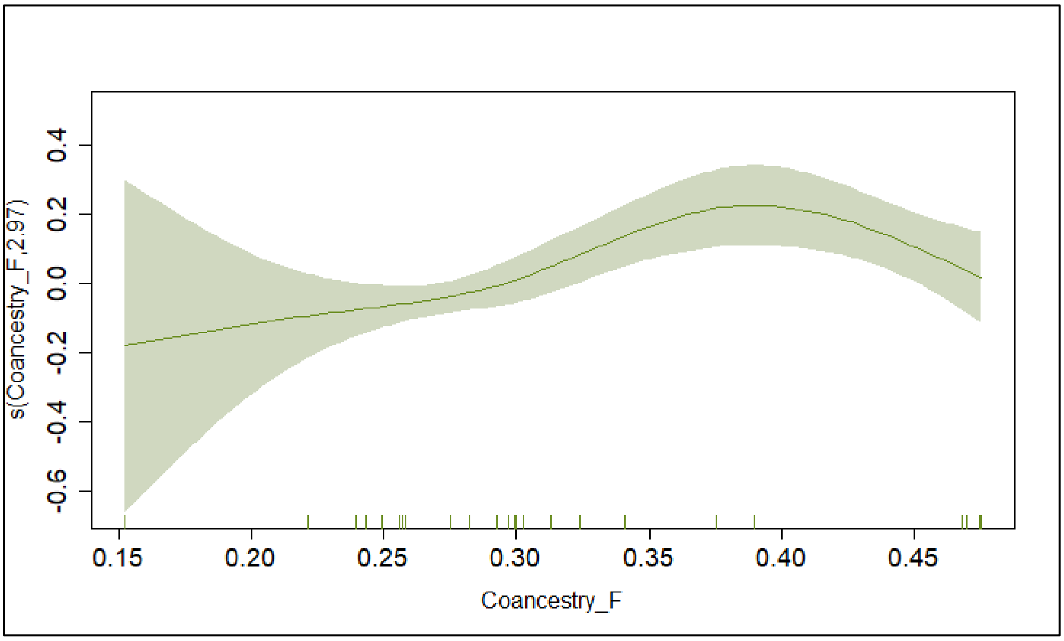

Figure 2. Partial effect plot showing how female genetic relatedness (Coancestry_F) influences adjusted territorial overlap (km²). The curve represents the predicted relationship, while the shaded green band indicates the 95% confidence interval, reflecting uncertainty around the prediction.

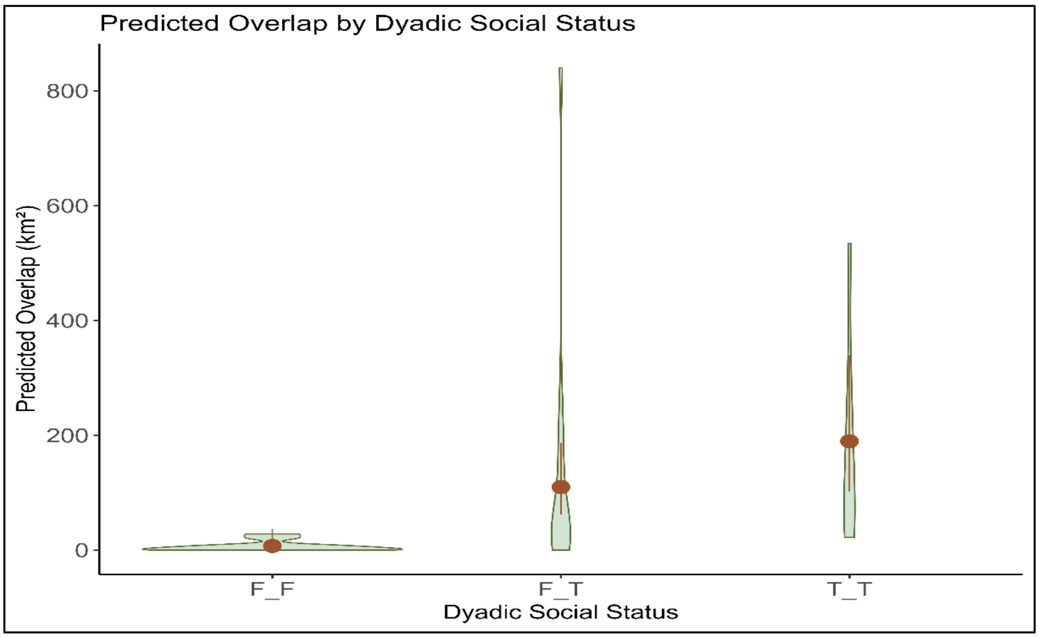

Figure 3. Predicted territorial overlap (km²) across dyadic social status categories. The x-axis shows three social pairing types: two family groups (F_F), one family group and one territorial pair (F_T), and two territorial pairs (T_T). The y-axis represents the model-predicted overlap area. The violin shapes display the distribution and spread of observed overlap values for each social pairing, while the red point-range markers indicate the predicted mean overlap with 95% confidence intervals. Together, these elements illustrate both the range of observed variation and the model's estimate of average overlap across social groupings.

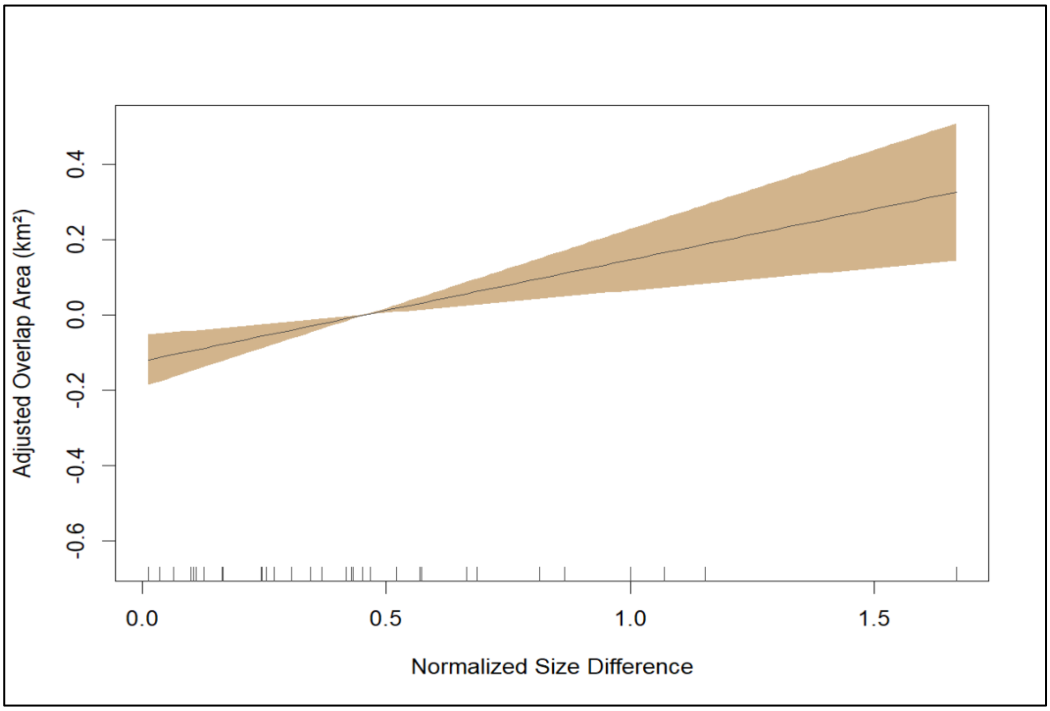

Figure 4. The relationship between norm_size_diff (x-axis) and its smooth function s(norm_size_diff, 1) (y-axis). The plot shows a positive relationship between the two variables. The shaded area represents the confidence interval.

4.2 Territorial space use

Among the tested models, the best-supported structure was the one including location type, social status (soc_stat), and territory age (terr_age), along with their interactions (Model 3: prop ~ location_type × soc_stat + location_type × terr_age + (1 | Wolf_ID)). This model offered a strong fit with relatively few parameters (AIC = -254.2; Table 3, Appendix 3.2), suggesting that both social structure and the duration of territory occupancy play key roles in shaping how wolves use different spatial zones.

Table 3. Model selection results for candidate generalized linear mixed models (GLMMs) predicting the proportion of time wolves spent in different territorial zones (core, peripheral, overlap). All models include a random intercept for individual wolf identity (Wolf_ID) to account for repeated measures. Fixed effects vary across models, with interaction terms specified using location_type × covariate to test whether zone-specific space use varies by social status (soc_stat), inbreeding coefficient, and territory age. Models were ranked by Akaike Information Criterion (AIC), with ΔAIC representing the difference from the lowest AIC model. Columns show model name, formula, estimated degrees of freedom (df), AIC, and ΔAIC.

Model name	Model formula	df	AIC	ΔAIC
Full model	prop ~ location_type × soc_stat+ location_type × inbreeding_coef + location_type × terr_age + (1 | Wolf_ID	14	-249,7252	4,4986
Model 1	prop ~ location_type × soc_stat + (1 | Wolf_ID)	8	-249,4370	4,7868
Model 2	prop ~ location_type × soc_stat+ location_type × inbreeding_coef + (1 | Wolf_ID)	11	-244,3697	9,8541
Model 3	prop ~ location_type × soc_stat + location_type × terr_age + (1 | Wolf_ID)	11	-254,2238	0

Notably, the interaction between location type and social status revealed zone-specific behavioural differences between family groups and territorial pairs, while the inclusion of territory age highlighted that long-established packs may exhibit more stable or concentrated space use. Although the full model included all predictors, adding inbreeding coefficient and its interactions, it did not substantially improve explanatory power (AIC = -249.73; Table 3, Appendix 3.1), indicating that genetic relatedness may be less influential than social and temporal factors in explaining territorial space use.

*Table 4. Summary of generalized linear mixed model (GLMM) results for Model 3, which examines the proportion of time wolves spent in different territorial zones (core, peripheral, overlap). The model includes fixed effects for location type, social status (soc_stat_1), and territory age (terr_age_1), along with their interactions, and a random intercept for Wolf_ID to account for repeated measures. The response variable was modeled using a beta distribution with a dispersion parameter of 2.69. With estimate effects size (estimate) standard error of the estimate (std. error), Z value - indicating how far a coefficient is from zero in standard deviations, Pr(>|z|) is the p-value associated with the Z statistic. Also included are AIC result, Bayesian information criterion (BIC, Log-likelihood (lokLik), 2*log(L) deviance and the residual degrees of freedom (df.resid).*

Model 3 formula: prop ~ location_type * soc_stat_1 + location_type * terr_age_1 + (1 | Wolf_ID)

Dispersion parameter for beta family: 2,69

Conditional model:	**Estimate**	**Std. Error**	**Z value**	**Pr(>|z|)**
(Intercept)	-0,546	0,199	-2,746	**0,006**
location_typePeripheral	0,291	0,279	1,042	0,297
location_typeOverlap	-1,122	0,303	-3,703	**0,000**
soc_statT	-0,449	0,206	-2,176	**0,030**
terr_age	0,026	0,017	1,577	0,115
location_typePeripheral:soc_statT	0,447	0,291	1,537	0,124
location_typeOverlap:soc_statT	1,082	0,312	3,467	**0,001**
location_typePeripheral:terr_age	0,003	0,023	0,147	0,883
location_typeOverlap:terr_age	-0,070	0,025	-2,736	**0,006**
AIC	**BIC**	**logLik**	**2*log(L)**	**df.resid**
-254,2	-213,3	138,1	-276,2	297

I found a significant effect of the interaction between social status and zone type, with territorial pairs spending more time than the two adults in family packs in overlap zones (p = 0,006) (Figure 5; Table 4).

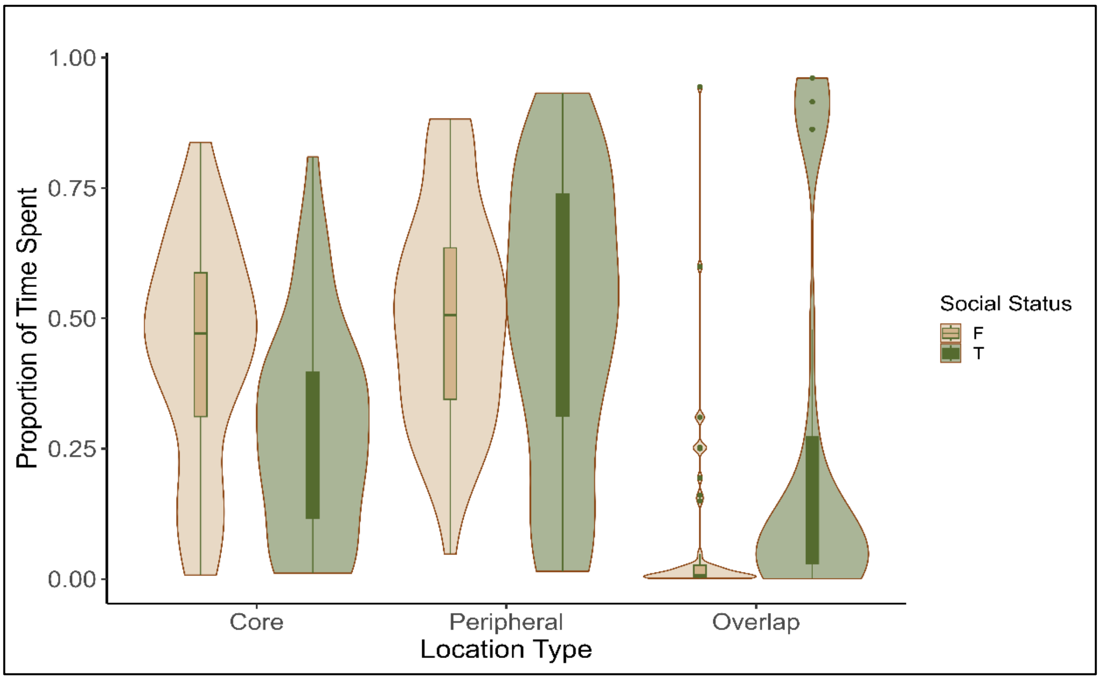

Figure 5. Proportion of time spent in location type core (left), peripheral (middle) and overlap (right) by social statuses family groups (F, beige) and territorial pairs (T, green). The box plot inside the violin plot shows the median (bold line), interquartile range (box edges), data spread (whiskers), and outliers (dots beyond the whiskers), helping to summarize the distribution of time spent in different location types.

The model indicates that wolves in general spend significantly less time within overlap zones ($p < 0.001$, Table 4; Figure 5), while peripheral zones show no strong effect ($p = 0.297$, Table 4). Additionally, social status influence's location use, with scent-marking pairs (T) spending significantly more of their time in overlap zones compared to the adults in family groups ($p = 0{,}001$, Table 4; Figure 5). Territory age has a negative effect on overlap zone usage, suggesting that older territories lead to less time spent in these areas ($p = 0.0062$, Table 4; Figure 6).

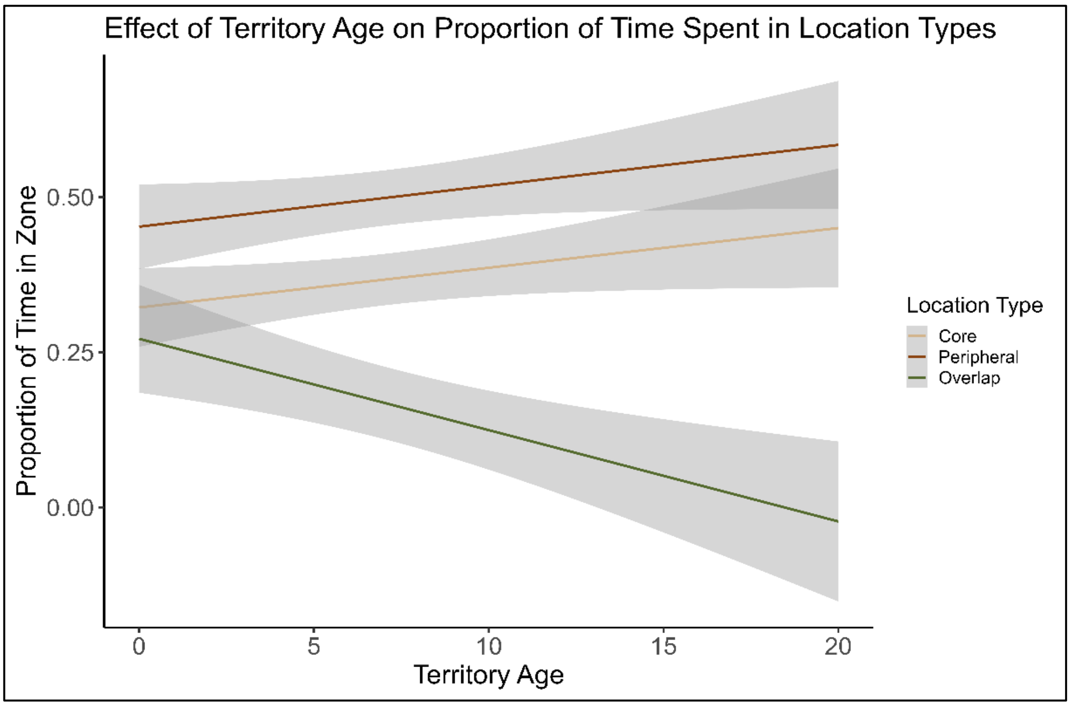

Figure 6. Illustration of how age of a territory affects the proportion of time spent in different location types: core (beige line), peripheral (brown line), and overlap (green line). Time spent in overlap zones decreases with higher territory age. The shaded areas around each line indicate the confidence intervals.

4.3 Spatial and temporal proximity results

The proximity calculations revealed that all observed encounters occurred at distances greater than 300 meters, with the majority exceeding 1 km (Appendix 4). The closest simultaneous encounter recorded in the dataset involved wolf M0109 and wolf M0402 in 2003/2004, with a distance of approximately 366meters, recorded at the same time (Table 5; Appendix 4). 103 encounters below 5 km could be recorded with varying spatial and temporal differences (Table 5).

Table 5. This table presents descriptive statistics for wolf encounters occurring within 5 km, summarizing both spatial and temporal proximity. It includes key measures such as minimum, maximum, mean, median, quartiles, and standard deviation for the distance between wolves (in meters) and the time difference between their movements (in hours).

Min distance	**q1 distance**	**Median distance**	**Mean distance**	**q3 distance**	**Max distance**	**Sd distance**
366,742	1850,154	2769,238	2984,927	4236,256	4996,614	1344,725
Min time_diff	**q1 time_diff**	**Median time_diff**	**Mean time_diff**	**q3 time_diff**	**Max time_diff**	**Sd time_diff**
0	0	0,016	0,093	0,25	0,266	0,117

5. Discussion

5.1 Differences in overlap

The results of this study show that wolf territory sizes, core areas, and overlap zones are far from static; instead, they fluctuate significantly over time (Appendix 1). For territories that could be estimated across multiple years, both the territorial boundaries and core areas exhibited notable changes, highlighting the dynamic nature of wolf space use (Kittle et al. 2015).

This pattern aligns with previous findings in wolf ecology. Kochetov (2023) documented similar trends in the Russian Central Forest State Nature Reserve (CFNR), demonstrating that wolves adjust their territorial and core boundaries in response to several factors, including local habitat conditions and prey availability. Previous studies show that wolf territories in Scandinavia did not change size based on pack numbers but rather on resource availability (Mattisson et al. 2013). Studies by Kittle et al. (2015) and Lake et al. (2015) provide strong evidence that habitats with low prey density force wolves to expand their territories to cover larger hunting areas, whereas in regions with high prey abundance, wolves can maintain smaller territories while still securing sufficient food for the pack.

Mech (1994) incorporates the concept of "buffer zones" as neutral spaces between core pack areas and territorial borders, which may help reduce direct confrontations. In larger Scandinavian wolf territories, these buffer zones could play a more prominent role in preventing immediate conflicts, whereas in Yellowstone, the denser population with smaller territories might lead to higher encounter rates and more frequent territorial disputes (Cubaynes et al. 2014; Cassidy et al. 2015).

The variability observed in overlap areas in this study (Table 5; Appendix 1) likely reflects a combination of environmental, ecological, and social influences. While factors like prey availability, seasonal conditions, and landscape features are known to shape spatial behaviour (e.g., Kittle et al. 2015, 2017; Kochetkov 2023; Lake et al. 2015; Sand et al. 2022), they may only partially explain the observed variation. Integrating genetic and demographic factors allows for a more complete understanding of how wolves adapt their space use and interact with neighbouring packs (Jędrzejewski et al. 2005).

5.1.1 What factors influence the overlap?

This study identified several predictors of variation in the size of territorial overlap between wolf packs. Overall, overlap zones were used infrequently compared to core and peripheral areas (Table 4; Figure 5). Overlap size increased with female relatedness up to moderate levels, after which the effect plateaued. Specific combinations of pack social status and differences in the age of neighbouring territories also influenced the extent of overlap. These findings suggest that kinship, social structure, and territorial history all contribute to how wolves negotiate shared space

Genetic Relatedness and Overlap

The effect of female genetic relatedness suggests that shared genetic ties among the adult females in neighbouring territories contribute to greater territorial overlap. The relationship was non-linear, with overlap size increasing at low to moderate relatedness and then plateauing at higher relatedness values. This suggests that moderate kinship may promote tolerance in shared border areas, but very close genetic ties do not necessarily lead to further increases in overlap. Social cohesion among female relatives may facilitate cooperation or reduce territorial conflicts (Hamilton 1963; Messier 1985; Randall et al. 2007; Pacheco et al. 2024). In contrast, male genetic relatedness (Coancestry_M, $p = 0.112$; Table 2; Appendix 2.2) did not show a statistically significant effect, suggesting that male-male interactions may not shape territorial overlap in the same way as for females (Table 2).

The role of genetic ties in territorial overlap raises interesting questions regarding kin-selection mechanisms in wolves. One potential explanation for the observed higher territorial overlap among genetically related females is kin-based tolerance. Pacheco et al. (2024) found that female offspring tend to remain in their natal territory rather than disperse, often pairing with an unrelated immigrant male to reduce inbreeding while maintaining strong genetic ties within the pack (Liberg et al. 2005; Milleret et al. 2019). This female philopatry results in greater genetic relatedness within territories, potentially influencing space-sharing behaviours and territorial overlap. Similarly, Lehman et al. (1992) demonstrated that female wolves exhibit short-range dispersal, reinforcing genetic ties among territorial individuals.

Relatedness between females may promote social cohesion and spatial tolerance, potentially allowing closely related females from neighbouring packs to maintain overlapping territorial areas with reduced conflict. This is consistent with findings in other canids, such as Ethiopian wolves, where female-biased dispersal has been linked to kin structuring and cooperative dynamics that enhance local stability (Randall et al. 2007). Although inter-pack cooperation is unlikely, the presence of kin across adjacent territories may reflect kin-selected tolerance, helping explain patterns of increased overlap observed among related dyads in this study (Hamilton 1963).

In contrast to females, male wolves typically disperse over longer distances to establish new territories (Lehman et al. 1992; Wabakken et al. 2015). This wide-ranging dispersal reduces the likelihood of neighbouring territorial males being closely related, resulting in generally low coancestry values among adjacent male dyads. While this may help explain the limited explanatory power of male coancestry in predicting territorial overlap, it is also important to consider whether the variation in male coancestry was comparable to that observed among females. If variation was similarly high, the low predictive value may reflect biological patterns rather than a lack of statistical resolution. This interpretation aligns with findings in other canids, such as Ethiopian wolves (Randall et al. 2007), where male space use appears more influenced by access to mates and establishment opportunities than by proximity to kin (Storch et al. 2024).

Social Structure and Spatial Behaviour

Social status appears to be a major determinant of overlap area, as scent marking pairs (T_T) exhibit significantly higher overlap values compared to family groups (F_F) (Figure 3). This pattern may reflect increased spatial tolerance or overlapping movement routes among scent marking pairs, possibly driven by resource competition or differing territorial behaviour (Werba et al. 2021). Corresponding with this, we also see that the results also reveal a significant interaction effect between social status and zone type, indicating that territorial pairs spend considerably more time in overlap zones compared to family packs (Figure 5; Table 4).

The lower overlap values observed in family groups may indicate stronger territorial defence strategies, where established packs maintain stricter boundaries to protect their resources and offspring (Schlägel et al. 2017). In contrast, territorial pairs may navigate overlap zones more frequently, possibly due to greater flexibility in space use compared to larger packs (Messier 1985; Jedrzejewski et al. 2001). This aligns with previous research suggesting that smaller social units often demonstrate more fluid territorial boundaries compared to larger, more established family groups (Messier 1985; Cassidy et al. 2015).

The usage of overlap zones may also be influenced by prey availability (Petroelje et al. 2019). If prey is larger, more difficult to hunt, or scarce within a territorial pair’s domain, they may be compelled to move into neighbouring territories where prey is more accessible (Wehr et al. 2024). Seasonal variations in prey migration patterns further impact spatial usage, as wolves adjust their movements to optimize hunting success (McPhee et al. 2012; Kuijper et al. 2014; Wehr et al. 2024).

Family groups tend to spend more time in core areas during the pup-rearing season, as parents must balance territorial defence with pup care (Messier 1985; Mech & Harper 2002; Schlägel et al. 2017). Studies on wolf denning phenology and reproductive success indicate that territorial behaviour shifts significantly based on reproductive cycles, with increased defensive behaviours, such as scent marking, vocalizations, and active deterrence of intruders, observed when pups are present (Jedrzejewski et al. 2001; Schlägel et al. 2017; Mech & Harper 2002). This could result in reduced territorial scouting during this period which may restrict neighbouring packs to utilize overlapping zones more frequently (Schlägel et al. 2017).

Territory Age and Overlap Dynamics

The negative effect of territory age on overlap usage suggests that older territories experience reduced time spent in overlap zones. One plausible explanation is that as territories age, territorial boundaries become more stable, reducing the likelihood of inter-pack interactions in contested areas.

This could be due to long-term territorial establishment, where wolves reinforce clear spatial divisions over time, minimizing the need for frequent territorial shifts. However, this finding also raises further questions: Do older territories maintain a stronger sense of territorial exclusivity, or is the decrease in overlap a byproduct of established movement patterns within the core areas? Exploring how long-standing territories affect movement flexibility could yield additional insights into long-term space use behaviour in wolves.

Stahler et al. (2019) conducted a long-term research in Yellowstone National Park and found that packs with long-established territories often maintain consistent core areas over time, while recently disrupted packs show more fluid or shifting boundaries. These stable territories were typically associated with lower rates of inter-pack conflict and turnover.

In contrast, younger territories, especially those formed after dispersal or pack turnover, often show more overlap with neighbouring packs, likely due to ongoing competition for space and less established scent-marking or social boundaries (Stahler et al. 2019). This is particularly evident in high-density regions like Yellowstone’s northern range, where newer packs frequently experience more territorial disputes and higher mortality (Stahler et al. 2019).

So, while not a universal rule, territory age can influence spatial stability, with older territories often reflecting more entrenched social and ecological boundaries.

5.1.2 Proximity

The dataset used in this analysis presents some limitations that affect the ability to draw definitive conclusions about wolf interactions (Benson & Patterson 2014). One major constraint is the variation in GPS tracking duration. While some wolves were monitored for an entire year, others were tracked for only a few months. This inconsistency reduces the comparability of movement patterns across individuals and years, potentially leading to missed interactions (Merrill & Mech 2003).

Additionally, the frequency of GPS fixes varied considerably, ranging from a 1 minute to 248 days with a mean of 13 038 seconds (approximately 3,62 hours). This irregularity increases the likelihood that potential encounters occurred between recorded locations but were not captured due to gaps in tracking. As a result, many close-range interactions may have gone undetected, making definitive conclusions about direct encounters inconclusive (Merrill & Mech 2003).

Despite these limitations, the findings suggest that while wolves may inhabit overlapping territories, direct close-range interactions were rarely recorded within the dataset. The observed proximity indicates that some individuals may have been in the same vicinity at certain times, potentially engaging in territorial navigation, scent marking, or indirect interaction. However, without higher-resolution tracking data, it remains uncertain whether these instances involved actual encounters (Merrill & Mech 2003; Benson & Patterson 2014).

The low incidence of recorded wolf-to-wolf proximity aligns with the rare occurrences of wolf-on-wolf killings in Scandinavia, where intra-species aggression typically arises in territorial disputes. While direct encounters appear to be infrequent based on available data, a total of 9 cases of which two had GPS collars, has been reported (Svensson et al. 2019, 2021, 2015, 2017, 2022; Wabakken et al. 2004a, 2004b, 2005, 2011, 2010, 2009, 2007, 2008, 2013, 2012, 2018, 2020, 2022). A higher-frequency GPS sampling method could strengthen future analyses of territorial conflicts and social interactions among wolves, providing a more detailed understanding of their spatial dynamics (Merrill & Mech 2003; Benson & Patterson 2014; Werba et al. 2021). This reinforces the assumption that although wolves may share overlapping territories, recorded instances of close-range interactions remain scarce within the current dataset.

5.2 Weaknesses in this study

Interpreting the findings of this thesis requires careful consideration of the dataset's limitations. The GPS data, spanning from 2002 to 2022 included 152 unique wolf IDs, however, inconsistencies in timing schedules between individuals, along with technical faults in several collars, led to data irregularities. Some collars recorded only a limited number of locations, while others exhibited extreme locational shifts, sometimes several kilometres apart within short time intervals. Due to these inconsistencies, substantial filtering and processing were necessary to ensure a strong and reliable dataset for analysis.

Recognizing these challenges, multiple steps were taken to identify the most suitable approach for estimating territories. Various techniques were tested on both adult and juvenile wolves to determine which individuals could be included without excessively skewing the data (Boyle 2021). While k-LoCoH showed promise, it required individual territory estimations, which proved impractical given the dataset constraints (Getz et al. 2007; Winner et al. 2018). Additionally, processing time in R was a significant limitation, each k-LoCoH computation took approximately 45 minutes per territory, making it unsustainable within the time constraints of this thesis.

Given these factors, the dBBMM was ultimately selected as the most appropriate method. The dBBMM provided satisfactory results, balancing reliability with the available timeframe, while ensuring a robust estimation of wolf territories despite the known limitations in the dataset (Kranstauber 2019; Kranstauber et al. 2012).

Due to spatial and temporal inconsistencies, several adult wolves were excluded from the dataset, leading to the removal of certain territories and potential overlaps. While this refinement ensured that only the most reliable data was used, it also meant that some territorial interactions might not have been captured in this study. A more comprehensive investigation, leveraging improved methodologies and an extended timeframe, could potentially yield additional insights into territorial boundaries and overlap patterns (Fieberg & Kochanny 2005; Winner et al. 2018). However, this does not suggest that the current results are either weaker or stronger; rather, they reflect a dataset that is more solid and confident, ensuring that conclusions are based on the most robust and accurate information available at the time of analysis (Boyle 2021).

5.3 Ethics, sustainability and conservation

This study contributes to a more nuanced understanding of how wolves use space in relation to social structure, genetic relatedness, and territorial history. By identifying factors that influence territorial overlap, such as the role of social status, kinship, and territory age, these findings can inform more targeted and ethical management strategies (Storch et al. 2024). For example, recognizing that territorial pairs may exhibit higher spatial overlap than family groups suggests that certain social configurations may be more prone to conflict or instability (Werba et al. 2021). This knowledge can help wildlife managers anticipate areas of potential tension between packs and improve monitoring accuracy by clarifying where territorial boundaries may blur. In turn, this can reduce the likelihood of miscounting packs or individuals and help avoid unnecessary lethal control measures by promoting coexistence through proactive spatial planning (Liberg et al. 2011; Cassidy & McIntyre 2016; Liberg et al. 2020; Werba et al. 2021).

From a sustainability perspective, insights into how wolves negotiate space and respond to ecological pressures, including resource availability, landscape features, or human disturbance, can guide the design of protected areas and wildlife corridors (Droghini & Boutin 2018; Sunde et al. 2021; Miltz et al. 2024).

Ecological effects of wolves, such as trophic cascades, are highly context-dependent in anthropogenic landscapes, where human activities may blunt or redirect predator-prey dynamics (Ausilio et al. 2021). Incorporating this understanding into spatial analysis strengthens conservation planning and acknowledges the complexity of human wildlife coexistence (Ausilio et al. 2021; Miltz et al. 2024). Ensuring that territories are large enough and ecologically viable to support stable pack structures reduces the risk of fragmentation, dispersal failure, and genetic bottlenecks, which are key concerns for long-term population viability (Jędrzejewski et al. 2005; Droghini & Boutin 2018). This is particularly relevant to the present study, which investigates spatial overlap and territory dynamics among Scandinavian wolves. Overlapping territories, unstable social structures, or reduced space availability may signal increased competition or dispersal pressure, potentially undermining genetic diversity and pack cohesion (Jędrzejewski et al. 2005; Droghini & Boutin 2018). By identifying spatial patterns linked to social and ecological factors, this research contributes to more informed management strategies aimed at maintaining viable territories and promoting population stability.

Importantly, these findings also have direct relevance to the ongoing human-wolf conflict in Scandinavia (Liberg et al. 2011: Liberg et al. 2020). In regions where wolves share space with rural communities, livestock, and hunting interests, understanding the drivers of territorial stability and movement is essential (Lesmerises et al. 2012; Sunde et al. 2021; Sunde et al. 2024). The more we understand about how wolf territories are shaped by social dynamics, ecological conditions, and landscape features, the better equipped we are to predict and manage their spatial behaviour (Karlsson et al. 2007; Cassidy & McIntyre 2016; Sells et al. 2021). Stabilizing wolf territories through informed conservation planning could reduce the frequency of dispersal events and territorial shifts that bring wolves into closer contact with human activities (Karlsson et al. 2007; Sunde et al. 2024). By maintaining ecologically viable and socially stable territories, wolves are less likely to abandon or shift their ranges in search of mates, prey, or space movements that often lead them into human-dominated areas where conflict risk is higher (Sand et al. 2022; Ditmer et al. 2023). In turn, this may help lower the risk of livestock depredation, reduce fear or frustration among local residents, and foster greater tolerance for wolves on the landscape (Karlsson et al. 2007).

Moreover, this research supports the use of monitoring methods, such as GPS tracking and spatial modelling, which align with ethical standards for wildlife research. While challenges remain, including limited collaring coverage and the difficulty of observing behavioural interactions, this study demonstrates how robust ecological inferences can still be drawn from available data, minimizing the need for intrusive methods.

Finally, by contributing to the scientific understanding of wolf behaviour, this work supports more informed public discourse. In regions like Scandinavia, where wolves can inhabit human-dominated landscapes, fostering coexistence requires not only ecological knowledge but also societal trust (Lesmerises et al. 2012; Chakrabarti et al. 2023: Sunde et al. 2024). Transparent, evidence-based research helps bridge the gap between conservation goals and public concerns, promoting policies that are both scientifically sound and socially acceptable (Chakrabarti et al. 2023).

5.4 Implications and further research

Further behavioural analysis within territorial overlap zones could offer valuable insights into inter-pack dynamics, including aggression, avoidance, and potential cooperation (Sells et al. 2021). However, synchronizing GPS data across individuals is challenging due to limited collaring coverage, introducing sampling bias and limiting behavioural interpretation (Fieberg & Kochanny 2005). Unlike studies in Yellowstone that combine GPS with visual observations (Kittle et al. 2015), such multi-modal approaches are less feasible in Scandinavia due to dense forests and logistical constraints.

Future research should explore how social structure, such as dominance, reproductive status, or pack composition, influences overlap behaviour (Bryce et al. 2022; Werba et al. 2021; Wikenros et al. 2021). Understanding these dynamics could improve ecological models and inform conservation strategies, especially in anticipating responses to pack disruptions or population pressures.

Topographical features like mountains and rivers often shape territory boundaries, acting as natural barriers that reduce conflict and support territory fidelity (Karlsson et al. 2007; Sells et al. 2021). Habitat structure should therefore be considered a key variable in models of territory formation and persistence (McPhee et al. 2012; Kauffman et al. 2007).

Ecological context, including sympatric predators and human disturbance, also modulates space use. For example, increased disturbance may lead to greater perimeter defence or retreat into core areas (Lesmerises et al. 2012; Milleret et al. 2018; Fowler et al. 2022).

Temporal variation in tracking data limits detection of fine-scale shifts in territory use. Since wolf territories are dynamic, overlap may be temporal rather than spatial, reflecting seasonal changes or passive succession rather than direct conflict (Demma & Mech 2011).

Finally, resource distribution and environmental conditions, such as prey availability, winter severity, and climate-driven habitat changes, likely contribute to variation in territory size and overlap (Kuijper et al. 2014; Droghini & Boutin 2018; Bryce et al. 2022). A deeper understanding of these drivers is essential for decoding how wolves navigate competition and coexistence, and for guiding conservation planning in human-dominated landscapes (Karlsson et al. 2007; Sells et al. 2021; Storch et al. 2024; Chakrabarti et al. 2023).

6. Conclusion

This study highlights the complex interplay between social structure, territorial dynamics, and spatial behaviour in shaping patterns of territorial overlap among wolves. Social status emerged as a key determinant of both the extent of overlap and the time wolves spent within shared areas, suggesting that the nature of social relationships between neighbouring packs plays a central role in mediating spatial tolerance. Notably, territorial pairs exhibited greater overlap than family groups, indicating that certain social configurations may be more flexible or less territorial in their spatial boundaries.

Contrary to expectations, pack size did not significantly influence overlap, whereas differences in territory size did. Larger disparities in territory size were associated with increased overlap, implying that spatial asymmetry may create opportunities or pressures for encroachment, particularly when one territory is substantially smaller or more constrained.

Furthermore, the results point to the potential influence of philopatric behaviour and kin-based selection in promoting tolerance between neighbouring groups. Overlap was more pronounced among related individuals, supporting the idea that genetic relatedness may reduce territorial aggression and facilitate coexistence through kin-selected strategies.

Together, these findings underscore the importance of considering both social and ecological factors when interpreting spatial behaviour in wolves. A deeper understanding of these dynamics can inform conservation strategies aimed at maintaining stable pack structures, minimizing conflict, and supporting long-term population viability in human-dominated landscapes.

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Popular science summary

Wolves are known for their strong territorial behaviour, but what happens when neighbouring packs come close to each other? In this study, we explored how social relationships, territory size, and family ties influence how much space wolves share, and how they use that space.

Using GPS collars and genetic data from wolves in Scandinavia, we found that social status plays a big role in how much neighbouring packs overlap. Pairs of wolves that scent mark and defend their territory, known as territorial pairs, were more likely to share space with other neighbouring packs compared to larger family groups. Interestingly, packs with very different territory sizes also tended to overlap more, possibly because smaller territories push wolves closer to their neighbours.

We also discovered that female wolves within different territories who are closely related were more likely to tolerate overlapping territories. This suggests that family bonds may reduce conflict between neighbouring packs. Male relatedness, on the other hand, did not seem to matter as much.

When we looked at how wolves used these overlapping areas, we found that they generally avoided spending much time there. However, territorial pairs spent more time in shared zones than family groups did. The longer a pack had held its territory, the less time it spent in overlap areas, suggesting that older territories are more stable and better defended.

Finally, we looked at how close wolves from different territories got to each other. Most encounters happened at distances greater than 1 kilometre, and only one case showed wolves being within 400 meters of each other at the same time. So even when territories overlap, wolves seem to avoid direct contact.

These findings help us better understand how wolves manage space and avoid conflict. This knowledge is important not just for science, but also for conservation. The more we know about how wolves move and interact, the better we can design strategies to reduce conflict with humans and support healthy, stable wolf populations in Scandinavia.

7. Appendix 1

Appendix 1.1 Summary of all estimated territories areas (territory area km^2) ranging form start year 2002 to 2020. Including name of territory (territory), territory core area (Core area km^2), territory age, pack size, social status (F – family group, T – territory marking pair) and number of overlaps (Nr overlaps).

Start year	Territory	Core area km2	Territory area km2	Territory age	Pack size	Social status	Nr overlaps
2002	Bograngen	14,20	703,35	3	2	T	2
2002	Nyskoga	388,99	2620,15	3	6	F	1
2003	Gråfjell	138,40	1514,82	3	7	F	2
2003	Koppang	195,77	1683,15	5	2	T	1
2004	Gråfjell	85,98	1141,91	4	7	F	2
2004	Juvberget	95,41	1385,52	1	2	T	2
2004	Koppang	186,19	3767,77	6	2	T	2
2004	Rotna	205,06	1238,73	1	2	T	1
2005	Gräsmark	14,67	756,67	1	5	F	1
2005	Rotna	2,67	68,53	2	9	F	1
2006	Juvberget	232,77	1588,08	3	2	T	1
2006	Kynna	54,10	529,45	3	7	F	2
2008	Kloten	67,65	692,35	9	5	F	1
2008	Uttersberg	88,88	527,16	5	5	F	1
2009	Färna	82,75	705,94	0	2	T	2
2009	Galven	54,50	1085,47	2	7	F	1
2009	Hedbyn	31,05	621,74	0	2	T	3
2009	Kloten	17,75	847,13	10	6	F	2
2009	Tenskog	31,82	636,87	3	2	T	1
2009	Uttersberg	74,37	1001,05	6	2	T	2
2010	Färna	116,83	883,76	1	4	F	1
2010	Hedbyn	201,52	1807,66	1	2	T	2
2010	Homna	134,15	2373,28	1	2	T	2
2010	Juvberget	101,92	983,81	7	2	T	2
2010	Kloten	45,14	1141,92	11	7	F	2
2010	Kynna	37,04	948,37	7	9	F	1
2010	Rotna	52,30	833,95	7	5	F	1
2010	Tenskog	275,47	1551,44	4	2	T	2
2011	Homna	255,71	1621,50	2	2	T	2
2011	Juvberget	143,64	1184,52	8	2	T	3
2011	Rotna	52,09	924,93	8	7	F	2
2011	Siljansringen	210,06	1269,77	7	3	F	2
2011	Tenskog	156,39	1612,29	5	7	F	1
2012	Juvberget	52,28	912,21	9	2	T	1
2012	Kukumäki	200,56	1449,31	0	2	T	1
2012	Rotna	140,21	825,47	9	3	F	1

2012	Siljansringen	170,74	1430,90	8	4	F	1
2013	Kukumäki	222,40	1058,29	1	3	F	1
2013	Siljansringen	226,80	1640,81	9	2	T	1
2015	Julussa	126,99	1010,35	13	10	F	1
2015	Slettås	28,82	425,46	6	8	F	1
2017	Juvberget	5,26	373,84	14	7	F	4
2017	Letjenna	31,68	398,58	5	6	F	1
2017	Osdalen	292,41	914,73	12	12	F	3
2017	Slettås	67,87	671,24	8	7	F	3
2017	Varåa	1,62	74,55	8	2	T	2
2018	Bograngen	10,14	358,51	19	2	T	2
2018	Juvberget	103,78	905,34	15	4	F	4
2018	Letjenna	75,73	689,31	6	8	F	2
2018	Varåa	43,37	453,57	9	2	F	1
2019	Bograngen	155,76	1378,52	20	3	T	2
2019	Juvberget	97,82	765,25	16	2	T	4
2019	Varåa	20,03	495,03	10	6	F	1
2020	Juvberget	72,81	593,73	17	4	F	4
2020	Skärsjön	32,47	408,83	0	2	T	4

Appendix 1.2. Summary of all estimated territories areas ranging from start year 2002 to 2020, listing the names of two neighbouring territories, their respective total area in square kilometres, and the size of their spatial overlap.

Start year	**Territory 1**	**Territory 2**	**Area territory 1 (km^2)**	**Area territory 2 (km^2)**	**Overlap area (km^2)**
2002	Bograngen	Nyskoga	703,35	2620,15	56,96
2003	Gråfjell	Koppang	1514,82	1683,15	323,24
2004	Gråfjell	Koppang	1141,91	3767,77	840,21
2004	Juvberget	Rotna	1385,52	1238,73	37,4
2005	Gräsmark	Rotna	756,67	68,53	28,23
2006	Juvberget	Kynna	1588,08	529,45	194,64
2008	Kloten	Uttersberg	692,35	527,16	3,6
2009	Färna	Hedbyn	705,94	621,74	22,25
2009	Färna	Uttersberg	705,94	1001,05	163,71
2009	Galven	Tenskog	1085,47	636,87	1,63
2009	Hedbyn	Kloten	621,74	847,13	12,88
2009	Hedbyn	Uttersberg	621,74	1001,05	534,61
2009	Kloten	Uttersberg	847,13	1001,05	41,83
2010	Färna	Hedbyn	883,76	1807,66	148,84
2010	Kloten	Färna	1141,92	883,76	0
2010	Hedbyn	Kloten	1807,66	1141,92	286,59
2010	Homna	Tenskog	2373,28	1551,44	287,9

2010	Juvberget	Kynna	983,81	948,37	162,98
2010	Juvberget	Rotna	983,81	833,95	31,22
2011	Homna	Siljansringen	1621,5	1269,77	57,56
2011	Juvberget	Rotna	1184,52	924,93	44,62
2011	Tenskog	Siljansringen	1612,29	1269,77	0
2012	Juvberget	Rotna	912,21	825,47	0,31
2012	Kukumäki	Siljansringen	1449,31	1430,9	11,15
2013	Kukumäki	Siljansringen	1058,29	1640,81	34,79
2015	Julussa	Slettås	1010,35	425,46	0
2017	Juvberget	Letjenna	373,84	398,58	0,29
2017	Juvberget	Slettås	373,84	671,24	7,83
2017	Varåa	Juvberget	74,55	373,84	0
2017	Osdalen	Slettås	914,73	671,24	4,38
2017	Varåa	Slettås	74,55	671,24	0
2018	Bograngen	Juvberget	358,51	905,34	54,44
2018	Juvberget	Letjenna	905,34	689,31	8,2
2018	Juvberget	Varåa	905,34	453,57	21,27
2019	Bograngen	Juvberget	1378,52	765,25	138,97
2019	Juvberget	Varåa	765,25	495,03	48,23
2020	Juvberget	Skärsjön	593,73	408,83	9,15

8. Appendix 2

Appendix 2.1 Modell summary of all models: Model Semi to model semi5. Bold green indicates statistically significant values. s (covariate, k=5) - applied nonlinear smoothing on the covariate with a basis dimension (k) of 5. I(covariate)2 - the covariate is explicitly squared. With estimate effects size (estimate) standard error of the estimate (std. error) test statistics (statistics), and p-value for the parametric coefficients. For the smoothed terms there is: effective degrees of freedom (efd), reference degree of freedom (ref.df), test statistics and p-value. Also included are adjusted R2 (R_sq_adj), deviance explained, generalized cross-validation score (GCV), scale estimate (scale_est) and the sample size (n)

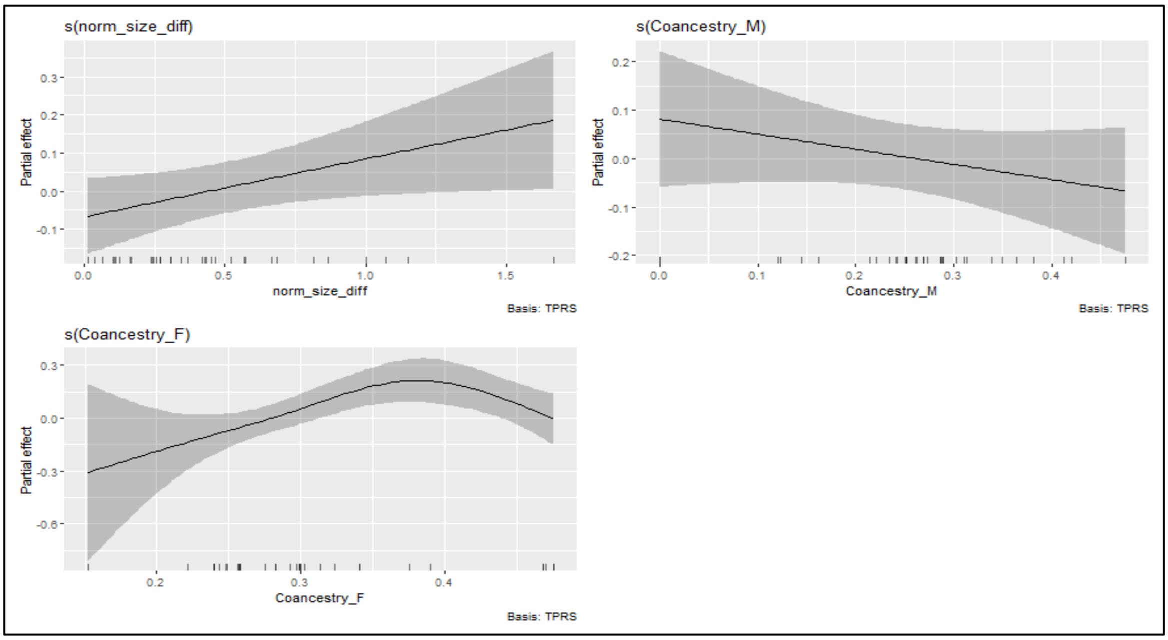
GAM Model Semi		**Name: Semi**		**Family: Tweedie (1.25)**		**Link function: mu^0.1**
	Formula: overlap_area_km2_adj ~ s(norm_size_diff, k = 5) + dyad_soc_status + s(Coancestry_M, k = 5) + s(Coancestry_F, k = 5)					
	Parametric coefficients		Estimate	STD error	t.value	Pr(>|t|)
		Intercept	1.1893	0,0992	11.985	**1.51e-12**
		dyad_soc_statusF_T	0.38013	0.10300	3.691	**0.000956**
		dyad_soc_statusT_T	0.46990	0.11864	3.961	**0.000466**
	Smooth terms		edf	ref.df	F	P-value
		s(norm_size_diff)	1	1	12.765	**0.00130**
		s(Coancestry_M)	1	1	2.691	0.11204
		s(Coancestry_F)	2.971	3.484	4.221	**0.00919**
		R-sq.(adj)	Deviance explained	GCV	Scale est.	n
		0.6	70.6%	33.936	22.146	36
GAM Model Semi 2		Name: Semi 2		Family: Tweedie (1.25)		Link function: mu^0.1
	Formula: overlap_area_km2_adj ~ s(norm_size_diff, k = 5) + dyad_soc_status + s(Coancestry_F, k = 5)					
	Parametric coefficients		Estimate	STD error	t.value	Pr(>|t|)
		Intercept	1.1952	0.1062	11.251	**3.89e-12**
		dyad_soc_statusF_T	0.3859	0.1103	3.497	**0.00152**
		dyad_soc_statusT_T	0.4535	0.1259	3.603	**0.00115**
	Smooth terms		edf	ref.df	F	P-value
		s(norm_size_diff)	1	1	9.989	**0.00381**
		s(Coancestry_F)	2.795	3.324	3.043	**0.03473**
		R-sq.(adj)	Deviance explained	GCV	Scale est.	n
		0.0583	67.7%	34.275	26.154	36

GAM Model Semi 3		**Name: Semi 3**		**Family: Tweedie (1.25)**		**Link function: mu^0.1**
	Formula: overlap_area_km2_adj ~ s(norm_size_diff, k = 5) + dyad_soc_status + Coancestry_M + s(Coancestry_F, k = 5)					
	Parametric coefficient		Estimate	STD error	t.value	Pr(>|t|)
		Intercept	1.2909	0.1147	11.257	**6.53e-12**
		dyad_soc_statusF_T	0.3801	0.1030	3.691	**0.000956**
		dyad_soc_statusT_T	0.46990	0.11864	3.961	**0.000466**
		Coancestry_M	-0.3887	0.2369	1.641	0.111999
	Smooth terms		edf	ref.df	F	P-value
		s(norm_size_diff)	1.000	1.000	12.765	**0.00130**
		s(Coancestry_F)	2.971	3.484	4.221	**0.00919**
		R-sq.(adj)	Deviance explained	GCV	Scale est.	n
		0.6	70.6%	33.936	22.146	36

GAM Model Semi 4		Name: Semi 4		Family: Tweedie (1.25)		Link function: mu^0.1
	Formula overlap_area_km2_adj ~ s(norm_size_diff, k = 5) + dyad_soc_status + Coancestry_M + Coancestry_F					
	Parametric coefficient		Estimate	STD error	t.value	Pr(>|t|)
		Intercept	0.9979	0.1590	6.276	**6.47e-07**
		dyad_soc_statusF_T	0.4391	0.1134	3.873	**0.00054**
		dyad_soc_statusT_T	0.5722	0.1270	4.506	**9.36e-05**
		Coancestry_M	-0.2406	0.2457	-0.979	0.33531
		Coancestry_F	0.6801	0.3544	1.919	0.06456
	Smooth terms		edf	ref.df	F	P-value
		s(norm_size_diff)	1.000	1.000	23.41	**3.71e-05**
		R-sq.(adj)	Deviance explained	GCV	Scale est.	n
		0.381	58.9%	41.395	28.7	36

GAM Model Semi 5						
		Name: Semi 5		**Family: Tweedie (1.25)**		**Link function: mu^0.1**
	Formula: overlap_area_km2_adj ~ s(norm_size_diff, k = 5) + dyad_soc_status + Coancestry_M + I(Coancestry_F)^2					
	Parametric coefficient		Estimate	STD error	t.value	Pr(>|t|)
		Intercept	0.9979	0.1590	6.276	**6.47e-07**
		dyad_soc_statusF_T	0.4391	0.1134	3.873	**0.00054**
		dyad_soc_statusT_T	0.5722	0.1270	4.506	**9.36e-05**
		Coancestry_M	-0.2406	0.2457	-0.979	0.33531
		I(Coancestry_F)	0.6801	0.3544	1.919	0.06456
	Smooth terms		edf	ref.df	F	P-value
		s(norm_size_diff)	1.000	1.000	23.41	**3.71e-05**
		R-sq.(adj)	Deviance explained	GCV	Scale est.	n
		0.381	58.9%	41.395	28.7	36

Appendix 2.2. Partial effects from the final GAM model illustrating how key predictors influence spatial overlap between neighboring wolf territories. Top left: Overlap increases with greater normalized territory size difference (norm_size_diff), suggesting that spatial asymmetry may promote shared use. Top right: Male coancestry (Coancestry_M) shows no significant effect, with a flat curve and wide confidence intervals. Bottom: Female coancestry (Coancestry_F) has a significant positive effect, indicating that related alpha females are more likely to tolerate spatial overlap. Shaded areas represent 95% confidence intervals.



9. Appendix 3

Appendix 3. Percentage model summary. Model 1- Interaction between location type and social status. Model 2 - Interaction between location type and inbreeding coefficient and social status. Model 3 - Interaction between location type and territory age and social status. Full model - Interaction between location type and social status, inbreeding coefficient and territory age. With estimate effects size (estimate) standard error of the estimate (std. error) test statistics (statistics), and p-value for the parametric coefficients. Bold green values indicate statistical significance.

	term	estimate	std.error	statistic	p.value
Model 1	(Intercept)	-0,309	0,133	-2,335	**0,020**
	location_typeOverlap	-1,735	0,209	-8,306	**0,000**
	location_typePeripheral	0,318	0,187	1,699	0,089
	soc_statT	-0,547	0,198	-2,763	**0,006**
	location_typeOverlap:soc_stat	1,328	0,301	4,415	**0,000**
	location_typePeripheral:soc_statT	0,429	0,278	1,542	0,123
Model 2	(Intercept)	-0,296	0,259	-1,141	0,254
	location_typeOverlap	-1,970	0,416	-4,736	**0,000**
	location_typePeripheral	0,432	0,372	1,162	0,245
	soc_statT	-0,550	0,200	-2,749	**0,006**
	inbreeding_coef	-0,054	0,876	-0,062	0,951
	location_typeOverlap:soc_statT	1,373	0,306	4,484	**0,000**
	location_typePeripheral:soc_statT	0,419	0,280	1,495	0,135
	location_typeOverlap:inbreeding_coef	0,878	1,362	0,644	0,519
	location_typePeripheral:inbreeding_coef	-0,449	1,264	-0,355	0,722
Model 3	(Intercept)	-0,546	0,199	-2,746	**0,006**
	location_typePeripheral	0,291	0,279	1,042	0,297
	location_typeOverlap	-1,122	0,303	-3,703	**0,000**
	soc_statT	-0,449	0,206	-2,176	**0,030**
	terr_age	0,026	0,017	1,577	0,115
	location_typePeripheral:soc_statT	0,447	0,291	1,537	0,124
	location_typeOverlap:soc_statT	1,082	0,312	3,467	**0,001**
	location_typePeripheral:terr_age	0,003	0,023	0,147	0,883
	location_typeOverlap:terr_age	-0,070	0,025	-2,736	**0,006**
Full Model	(Intercept)	-0,546	0,199	-2,746	**0,006**
	location_typePeriphera	0,291	0,279	1,042	0,297
	location_typeOverlap	-1,122	0,303	-3,703	**0,000**
	soc_stat_	-0,449	0,206	-2,176	**0,030**
	terr_age	0,026	0,017	1,577	0,115
	location_typePeripheral:soc_statT	0,447	0,291	1,537	0,124

location_typeOverlap:soc_statT	1,082	0,312	3,467	**0,001**
location_typePeripheral:terr_age	0,003	0,023	0,147	0,883
location_typeOverlap:terr_age	-0,070	0,025	-2,736	**0,006**

10. Appendix 4

Appendix 4. Result of the top 20 closest encounters in the spatial and temporal proximity analysis. Wolf ID X and Y representing wolves from each territory witch a shared overlap.

Wolf ID X	Wolf ID Y	Distance (m)	Time difference (h)	Start year
M0109	M0402	366,74	0,00	2003
M0110	M0402	397,73	0,00	2003
M0110	M0402	443,33	0,00	2003
M0109	M0402	818,26	0,23	2004
M0110	M0402	847,98	0,00	2003
M0109	M0402	887,20	0,27	2004
M0109	M0402	911,78	0,02	2004
M0109	M0402	1102,13	0,00	2003
M0110	M0402	1102,13	0,00	2003
M0109	M0402	1179,68	0,25	2004
M0109	M0402	1204,35	0,00	2004
M0110	M0402	1230,64	0,02	2003
M0109	M0402	1340,52	0,00	2004
M0109	M0402	1402,63	0,25	2004
M0607	M0610	1455,97	0,02	2005
M0110	M0402	1458,16	0,02	2003
M0607	M0611	1462,55	0,02	2005
M0110	M0402	1510,84	0,00	2003
M0109	M0402	1532,24	0,00	2003
M0109	M0402	1718,58	0,25	2004
M0110	M0402	1799,48	0,00	2003

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