



With neighbours like these

– What influences the size of Scandinavian wolf territories?

Jakob Ahlberg



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Abstract

The home-range of an animal and what factors influence its size and appearance is vital information when it comes to understanding and protecting a species. One of these factors can be intraspecific competition over resources, especially amongst territorial species like large carnivores. The intensity of this competition can vary depending on geography, resource abundance and population density

In this study over 20 years of telemetry-location data from wolves belonging to the Scandinavian population were used along with data on social and environmental factors to analyse variation in territory size, building on an already existing study published in 2013. The goal was to observe potential changes within the Scandinavian population and if it has grown to a point where intraspecific competition had become a significant factor in territory size variation.

I identified three factors that correlated with wolf territory size. Wolf territories increased in size with latitude, most likely due to different variables and processes that are correlated with latitude, such as decreasing landscape productivity and decreasing densities of agricultural fields and human density. Meanwhile, territories shrank in size as packs grew larger in numbers. Finally, territories grew smaller as the Scandinavian wolf population increased in size, possibly hinting at increased competition between packs over territory.

Keywords: Wolves, Home-range size, Intraspecific competition

Populärvetenskaplig sammanfattning

Ett djur rör sig inte på måfå genom landskapet, utan har ett område som det håller sig till. Det kallas för ett hemområde och hur det ser ut påverkas av flera faktorer, så som tillgång på föda, boplatser och chansen att föröka sig. När en del av eller hela hemområdet försvaras mot konkurrenter kallas området för ett territorium eller revir. Beteendet återfinns hos flera olika arter. En av dessa är gråvargen (*Canis lupus*).

Vargen är ett socialt och otroligt anpassningsbart rovdjur som återfinns över större delen av det norra halvklotet, från arktisk tundra till stekheta öknar. De lever i familjegrupper som kallas för flockar, vilka oftast består av ett föräldrapar och deras valpar. Varje flock har ett revir som de försvarar från andra vargar.

I den här studien har jag tittat på vad som påverkar storleken på vargrevir i Skandinavien. Den skandinaviska vargstammen är speciell, då mycket forskning har gjorts om den. Sen den praktiskt taget blev utrotad på 1970-talet så har populationen sakta men säkert vuxit, från en lyckad föryngring 1983 till runt 480 vargar år 2021. Många vargar har genom åren utrustats med vad i folkmun kallas för radiohalsband som låtit forskare följa dessa individer när de rört sig genom landskapet. Den här studien använde sådan radiohalsbandsdata för att först uppskatta revirstorlekar och sen räkna ut vilka faktorer som främst styr variationen i storlek mellan reviren. Studien är i sig baserad på en tidigare studie som kom ut 2013, men med utökade tidsramar från 1999 till 2021 och en delvis förändrad metod, samt ett större fokus på effekten av konkurrens mellan flockar.

Eftersom mycket potentiellt kan påverka storleken på vargrevir var det flera faktorer som behövde ingå i studien. Hur stor flocken var ett specifikt år, hur stor hela vargpopulationen var samtidigt, breddgraden reviret befann sig på och olika mänskliga faktorer är bara några exempel. I slutändan fann jag att tre faktorer spelade störst roll i att förklara skillnader i revirstorlek: revir blev större ju längre norrut de låg, mindre ju fler vargar som fanns i flocken och mindre ju större populationen var.

De här resultaten var mycket intressanta! Att revir blir större ju längre norrut man kommer är ett känt faktum, då väldigt många processer är invävda i breddgradsfaktorn, och var dessutom ett resultat som den tidigare studien fick. Att större flockar har mindre revir kan verka motsägelsefullt, men är väl dokumenterat från andra håll i världen. Sist men inte minst tyder effekten av den totala populationsstorleken på att en viss konkurrens om utrymme gör att reviren blir mindre, men samtidigt ser vi inte alls samma nivå av direkta konflikter mellan flockar som i t.ex. Nordamerika. Med varje studie som utförs ökar vår kunskap om en av den skandinaviska vildmarkens mest karismatiska och kontroversiella invånare. Mitt hopp är att den här studien ska kunna bidra till framtida forskning och förvaltningsbeslut rörande vargen!

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Abbreviations

To make it easier for the reader, you can make a list with common abbreviations in alphabetical order. Here you have a table you can use to make your list.

See example below:

SLU	Swedish University of Agricultural Sciences
SKANDULV	Scandinavian Wolf Research Project

1. Introduction

1.1. Home range

In the field of ecology and nature conservation one key trait of an animal species is the size of an individual's home range and what factors influence it.

The home range concept is used to describe species- or population-specific spatial requirements, dispersal, seasonal variation in movement, and metapopulation dynamics (Goodenough & Hart, 2017).

The ecological concept of the home range, as described by William Henry Burt, 1943, is "...the area which an animal traverses while carrying out its normal activities of food gathering, mating and caring for young". The area an animal travels through during exploratory movements does not count as part of the home range. An animal may have several successive home ranges throughout its life, with nomadic species continuously changing home ranges throughout the year. Also, adolescent animals may travel for some time before settling into their first home range.

When it comes to what factors affect the size and shape of an animal's home range, it can vary greatly from species to species. Securing enough food is a high priority. Home ranges of the boreal woodland caribou (*Rangifer tarandus caribou*) covered both alpine tundra and mature fir forest in a study on the Gaspé peninsula (Mosnier *et al.* 2003). While the caribou preferred the alpine tundra due to the availability of ground lichen, the preferred forage, it utilized tree-lichen in the mature fir forest when snow conditions caused foraging to become more difficult on higher elevations (Mosnier *et al.* 2003). In the case of generalists like the red fox (*Vulpes vulpes*), home range size in Scandinavia was found to follow a productivity gradient based on latitude and elevation, with greatest importance placed on elevation and availability of agricultural areas. Foxes living at higher elevations and in areas dominated by boreal forests tended to have larger home ranges than those living at lower elevations, where agricultural land was more common (Walton *et al.* 2017).

For social species, the relationship between home-range size and group size can be complex. Larger groups require more resources to sustain themselves and are competitively more capable of defending a larger home-range, but the relationship is not always linear. Lionesses (*Panthera leo*) living on the dystrophic savannah of Zimbabwe were found to show a strong correlation between home range size and the number of adult individuals in a pride when the prides total biomass was ≤ 800 kg (roughly four adult lionesses), but for prides larger than this, the correlation was less clear (Loveridge, Valexi *et al.* 2009).

1.2. Territoriality

A home range is different from a territory, though the two concepts may overlap. A territory is an area within an animal's home range that it has exclusive or priority use of and will defend from others, mainly conspecifics. Defence can take the form of physical struggles, but more often than not it primarily consists of calls, scent marking or displays. Both single individuals, pairs and larger groups can take part in claiming a territory, depending on circumstance and the species in question (Boitani & Fuller, 2000).

Territoriality is a strategy that can vary across species and habitat. In certain species, such as chimpanzee (*Pan troglodytes*), only individuals of a certain sex display territorial behaviour (Mitani *et al.*, 2010), while in other species both sexes will actively participate in claiming and holding territories (Heinsohn, 1997) (Loveridge, Valexi *et al.* 2009). In some species, like the brown bear (*Ursus arctos*), the quality of the habitat and resource abundance is an important determinant of territorial behaviour. In a study it was found that across North America female brown bear had high overlap in home ranges in areas with low seasonality (high habitat quality) and high seasonality (low habitat quality), but very little overlap in areas of intermediary habitat quality (Mcloughlin, Ferguson & Messier, 2000). It seemed that there was a trade-off, where in areas with plentiful resources there was little benefit trying to defend a territory, whereas in areas with scarce resources home ranges had to be so large that the cost would be too high trying to defend it. However, in areas of intermediary habitat quality there was enough benefits gained from defending resources that the behaviour became viable (Mcloughlin, Ferguson & Messier, 2000).

Just like home-ranges territories may change in size and location over time. In a red fox population in an urban environment (Oxford) it was observed that territories either constantly or periodically shifted over the year, as one group abandoned a part of their territory another would move in to claim it. This was believed to be due to less stable social hierarchies caused by higher mortality rates and the constantly changing environment and resource availability that the city provided (Doncaster & Macdonald, 1991).

The benefits of territoriality are always weighed against the cost of defending it. Be it direct (fighting with conspecific competitors) or more indirect methods of advertising territorial ownership (scent markings, song, patrolling etc.) there is always a cost of energy and mortality risk (Begon, Townsend & Harper, 2006). Most territorial species employ a variety of different defence strategies. Scent-marking at communal latrines using faecal matter, urine, cheek and anal glands is a known behaviour among dwarf mongoose (Christensen *et al.* 2016). In African lions (*Panthera leo*) females use roars to gauge the strength of a rival group and to

scare off potential intruders. Unlike males, females appear to “weigh in” the odds of successfully winning an engagement with an intruding group and will generally only approach when they out-number their opponents. However, this also depends on environmental and population factors. Higher population density appears to increase the willingness of females to confront intruders, as competition is a lot fiercer for territory (Heinsohn, 1997). However, even though male lions might be more willing to approach intruders regardless of numbers, the success of male coalitions often hinge on larger numbers and age (Borrego *et al.* 2018). Amongst chimpanzees the number of males in a community is also key in its success against neighbouring communities (Wilson & Wrangham, 2003).

1.3. The Grey Wolf (*Canis lupus*)

The grey wolf is the most widely distributed of all land mammals and one of the most adaptable. Found in all biomes of the northern hemisphere and capable of surviving in temperatures ranging from -56 to 50 °C, it is an apex predator which is capable of bringing down most large mammals found across its range, from bison to moose. Yet it is also capable of adapting to other food-sources, from smaller game to even occasionally fruit or berries (Mech & Boitani, 2003).

The basic social unit is the mated pair, with the larger unit containing the pairs offspring’s along with the occasional siblings (aunts and uncles) and unrelated wolves, though numerous variations have been documented (Mech & Boitani, 2003). Wolves are by nature highly territorial animals. Scent-marking with urine, faecal matter and scratching is a key method of advertising ownership of a territory, with increased frequency around the border of the territory. Howling is another complementary strategy to scent-marking, and while the behaviour has other functions apart from territorial defence, it does appear to play a part in signalling ownership of an area to other packs. Finally, direct confrontations occur in the form of territorial defence and excursions into neighbouring territories (Mech & Boitani, 2003). Here group size and composition are key to the success of a pack, with the presence of older individuals and prime-aged males correlating positively with success in aggressive interactions with other packs (Cassidy *et al.* 2015).

In populations with low human interference intraspecific violence is one of the main causes of mortality in wolves (Mech & Boitani, 2003), especially in more densely populated areas such as Yellowstone National Park where between 1998 and 2010 it was found that 37.4 % of all documented mortalities were caused by intraspecific violence (Cubaynes *et al.* 2014). However, this is markedly different in other populations. Out of 92 dead wolves found in Croatia between 1986 and 2001 only one was determined to have been killed by other wolves, compared to the 60 (65,2 %) shot and the 18 (19,6 %) killed in traffic (Huber *et al.* 2002).

The size of the home-range of a wolf pack is affected by several factors. In a large and fairly well-established population in Montana, USA, home-range size decreased with increased density of prey, density of other wolves and low-use roads. The same study found that larger packs tended to have smaller territories (Sells *et al.* 2021).



Figure 1. Eurasian grey wolves (*Canis lupus lupus*). Photo taken by Karin Andersson.

1.4. Wolves in Scandinavia

While historically the grey wolf has been constantly present in the Scandinavian peninsula since the end of the last ice age, it has suffered greatly from human persecution. By the 1960s the population was reduced to a few scattered individuals. Policy gradually changed, with bounties being removed by 1965 (Ekman, 2010) and the species later being classified as a protected species. In 1983 the first successful documented reproduction occurred in south-central Sweden (Wabakken *et al.* 2001) and in the following decades the population has gradually increased in Scandinavia so that by 2021 480 wolves in all of Scandinavia is the official number (Svensson *et al.* 2021).

Scandinavian wolves are noteworthy for a few different reasons. The population is an excellent example of a recolonization of a historical range by a species that has previously been extirpated from said area. It is intensively studied, particularly when it comes to genetics (Åkesson *et al.* 2016). It is also a highly inbred population due to low genetic diversity and few immigrants from the neighbouring Finnish-Russian population. In 2021 the average inbreeding coefficient amongst

Scandinavian pups was 0.23 (Åkesson & Svensson, 2021), which for reference means that their parents were roughly genetically related on the same level as full-siblings (Kardos *et al.* 2017). The problem is compounded with the fact that even the few immigrants that manage to successfully breed shows signs of inbreeding (Kardos *et al.* 2017).

Wolf mortality in Scandinavia is dominated by anthropogenic causes (hunting, poaching, road kills) similarly to other European populations (Huber *et al.* 2002, Lovari *et al.* 2007), with an overwhelming majority of Swedish wolves between 2001 and 2017 being estimated to have been killed either through legal or illegal hunting (Sand *et al.* 2020).

Mattisson *et al.* (2013) found that between 1999 and 2011 the main factors affecting home range size in the Scandinavian wolf population were latitude (territory size increased with latitude) and roe deer population density (territory size decreased with a higher density of roe deer). During this time the population grew from 74 to 295 individuals. The number of neighbouring packs did not appear to have an effect on territory size, neither did the population density of moose, the main prey of the Scandinavian population.

The presence of Scandinavian wolves has allowed researchers to study how the return of an apex predator affects an ecosystem that is managed by humans. Unlike the more classic example of wolves returning to Yellowstone National Park, most of the area where Scandinavian wolves are found today consists of intensively managed forests. The populations of the preferred prey animals, moose (*Alces alces*) and roe deer (*Capreolus capreolus*) (Sand *et al.* 2008), are managed via hunting and this triggers conflict with humans (Jonzén *et al.* 2013).

1.5. Aim of the study and hypothesis

This study is based on the 2013 work by Mattisson *et al.* It extended the time period with new data to 2020/2021 and changed the method slightly to make it more streamlined and accessible for future studies.

The focus was also slightly shifted from generally analysing what factors affects the home-range size of Scandinavian grey wolves (*Canis lupus lupus*) to test the hypothesis that home-range size is now being affected by population density, leading to intraspecific competition.

2. Materials and methods

2.1. Study area



Figure 2. A typical landscape from the study area. Photo taken by Jakob Ahlberg

The study area was situated in south-central Scandinavia, across the border between Sweden and Norway (59°–62° N, 11°–19° E). Most of the area is covered by intensely managed boreal coniferous forest (Jansson & Antonson, 2011) with the main tree species being Scots pine (*Pinus sylvestris*) and Norway spruce (*Picea abies*) (Naturvårdsverket, 2011), with the proportion of agricultural land increasing towards the lowlands in the southeast (Jordbruksverket, 2020). To the northwest, the land is more mountainous. Due to the dominance of forestry in the region there is an extensive network of forest gravel roads (Naturvårdsverket, 2011). Mean population density for humans in Scandinavia is currently around 25.5/km² in Sweden (SCB, 2021) and 15/km² in Norway (Worldometer, 2021) though it is usually much lower within wolf territories. The climate is maritime and the region falls within the boreal zone, and in the southern-most parts in the boreonemoral zone (Naturvårdsverket, 2011).

The main prey species are moose (*Alces alces*) and roe deer (*Capreolus capreolus*), both of which are found in all the study territories, with regional variations in population size (Sand *et al.* 2005, 2008 & 2016). Other ungulates include red deer (*Cervus elaphus*), fallow deer (*Dama dama*), wild boar (*Sus scrofa*) and wild reindeer (*Rangifer tarandus*), though these have so far been found to be much less important prey species in Scandinavia.

2.2. Study animals and data collection

The animals used in this study have all been monitored as part of the ongoing Scandinavian Wolf Research Project, also called SKANDULV (<https://www.slu.se/institutioner/ekologi/forskning/teman1/rovdjur-och-vilt/skandulv/>). Wolves were tracked and darted from helicopter according to veterinary procedures that are continuously revised and updated (Arnemo & Evans, 2017). After immobilization each wolf was outfitted with either a very high frequency (VHF) radio collar (Telonics model 500, Mesa, AZ) or a global position system (GPS) collar (GPS-Simplex TVP Positioning, Lindesberg, Sweden or Tellus GPS-Plus VECTRONIC Aerospace GmbH, Berlin, Germany) (Mattisson *et al.* 2013, Carricondo-Sanchez *et al.* 2020). The capture methods were approved by the Swedish Animal Welfare Agency and the Norwegian Experimental Animal Ethics committee. For the VHF collars data was collected at least once a week, either from the ground or using a fixed-wing airplane. GPS-collars were programmed to take a position 2-6 times in each 24-hour cycle, with intense study periods having 1 position per half-hour (Sand *et al.* 2005). Only adult, scent-marking animals were used in this study with the size of each pack being estimated based on repeated snow tracking of individual packs as being a part of the yearly count of the Scandinavian wolf population. This national survey carried out both in Norway and Sweden includes snow-tracking and gathering of faecal DNA-samples during a 5-month period each winter, as well as visiting den sites to confirm reproduction in spring (Svensson *et al.* 2021). The average pack size for the study was 4.7 wolves.

2.3. Home-range estimations

The method used for estimating home-range size was similar to the study by Mattisson *et al.* (2013), with some differences. Work was primarily done in R 4.03. To estimate annual home-range size I used the requirement of minimum 5 positions per month for at least 9 out of 12 months-period (Mattisson *et al.* 2013). A total of 46 packs, spanning from 1999 to 2021, were selected for fulfilling these criteria. The annual data set for each pack consisted of either one or both of the adult resident, scent-marking individuals, depending on what data was available. When both adults of the original pair had been replaced by new individuals, we considered it to be a new pack, sometimes using the same name but changing the suffix number (For example Juvberget 1, 2 and 3). A small pre-study concluded that there was no significant difference in the estimated home-range size between males and females, therefore all data was combined with no regards to the individual.

The data was organized so that each annual pack data began on the 1st of May or the closest appropriate date, which according to the biological yearly cycle of wolves is the time of birth (Mech & Boitani, 2003). The annual data set ended on the 30th of April the next year. The data was also reduced to the 2 positions per day

and pack that were the closest to 00:00 and 12:00 (GMT+1) when more was available.

Three different home range estimators were used: 100% minimum convex polygon (MCP)(Mohr & Stumpf, 1966), fixed kernel (95%)(Seaman & Powell, 1996) and 95% time local convex hull (t-LoCoH)(<https://tlocoh.r-forge.r-project.org/>) with k-value set to 24. t-LoCoH is built upon the LoCoH method but adds analytical methods for data sets that have time values as part of them, with specific tailoring towards data gathered from GPS-tracking. As part of the home range estimation an MCP-polygon was generated for each annual pack data-set and was used for obtaining other environmental data linked to the specific territory.

2.4. Number of neighbours and other wolf data

To estimate the number of neighbouring packs for each study pack, two methods were used. If two study packs were so close that the MCP-polygons generated by the home range estimations overlapped, they were counted as neighbours. For the uncollared packs, yearly centre-points estimated from tracks and DNA during wolf monitoring were buffered with increasing radius (20, 30 and 40 km). Using the ArcGIS tool Intersect overlap with other packs was then calculated for each study pack.

The size of the yearly total Scandinavian wolf population was received from the yearly report published by NINA, INN and SLU. Generally, population size is given as an upper and a lower value for the population – with the values used in this study being the exact mean.

2.5. Road and building density

Roads were divided into two categories: main roads and forest roads (Zimmermann *et al.* 2022).

ArcGIS was used to estimate the mean density of these man-made features in each territory. MCP-polygons were transformed into raster and then zonal statistics were used to calculate the mean density for each territory.

2.6. Prey density

For this study both of the grey wolf's main prey in Scandinavia (moose and roe deer) were at first taken into consideration as factors that could influence the size of the territory. However, based on the results (Mattisson *et al.* 2013) showing only the importance of roe deer density and on the difficulty obtaining complete data on moose population density, it was decided to only include roe deer data. Roe deer bag statistics provided by hunters were used as an index of local population density as have previously shown to give a reliable estimate (Mattisson *et al.* 2013). Bag statistics represented the number of roe deer shot per hectare of specific hunting

units in Sweden while in Norway bag statistics are reported based on municipalities. To get a number for each pack ArcGIS was used to superimpose pack territory-polygons over a map of Sweden's hunting units and on Norway's municipalities. As territories rarely follow human administrative divisions, I used harvest data from the hunting unit that had $>X\%$ area within the specific territory. The bag statistics from this division/municipality was then used as a proxy for the roe deer density within the territory.

2.7. Statistical analysis

All statistical analyses were conducted using the R version 4.03.

Data was first visualized using histogram and abline plots. 6 outliers were removed, either due to extreme size (ex. Koppang 2004, where the pair consisted of a father and his daughter, and the two started to move independently of each other after pup loss in late summer, MCP area 4344,29 km²) or due to some other strangeness in the data, ex. Osdalen 2010, where the collared male was defeated and driven out by another male and later both the new male and the female were shot (Wabakken *et al.* 2011). 6 packs were selected where data was available from both of the breeding pair, home range was calculated for all 12 individuals and then a paired t-test was run and showed that there was no pattern of females having smaller home ranges compared to males.

I used linear regression models with territory size (100% MCP) as response variable, and the predictors described above. To correct for repeated measurements of the same wolf pair in multiple years, I weighted the observations by the inverse of the number of years per pack. In this way, the 21 pack-years where the pack was only monitored for one year, had the highest weight (weight = 1). Packs monitored over two years had weight 0.5 (n = 10 pack-years), over three years 0.33 (n = 8), while the 7 pack-years of packs monitored for four years contributed the least (weight = 0.25) to the linear regression model. We used the weight as a substitute of including wolf pair as a random factor in a mixed model framework. The latter was not possible, because there were too few repeated observations (mostly one year) per wolf pair.

Then the collinearity between predictors was estimated using Pearson correlation coefficient, and visualized with the command `ggcorrplot()`. Predictor variables with Pearson's $r > 0.6$ were not included in the same models. To determine which of the correlated predictors performed best in explaining variation in territory size, we included them intermittently in a full model and used AICc model selection to find the best predictor. We ran models both with unscaled and scaled predictors and used `sjPlot` to visualize the estimates of the scaled predictors, and the model predictions using the unscaled predictors and then `MuMIn` to compare the models to one-another.

3. Results

A great variation in territory size was observed, with territories covering as little as 237 km² (Riala 2009) to almost 10 times as large, 2046 km² (Fulufjället 2016). The minimum convex polygon method (MCP) consistently produced larger territories than time local convex hull (T-LoCoH), though greater variation was observed between MCP and fixed kernel (95%), with a trend towards larger projections from kernel when the overall size of the territory increased (see figure 3).

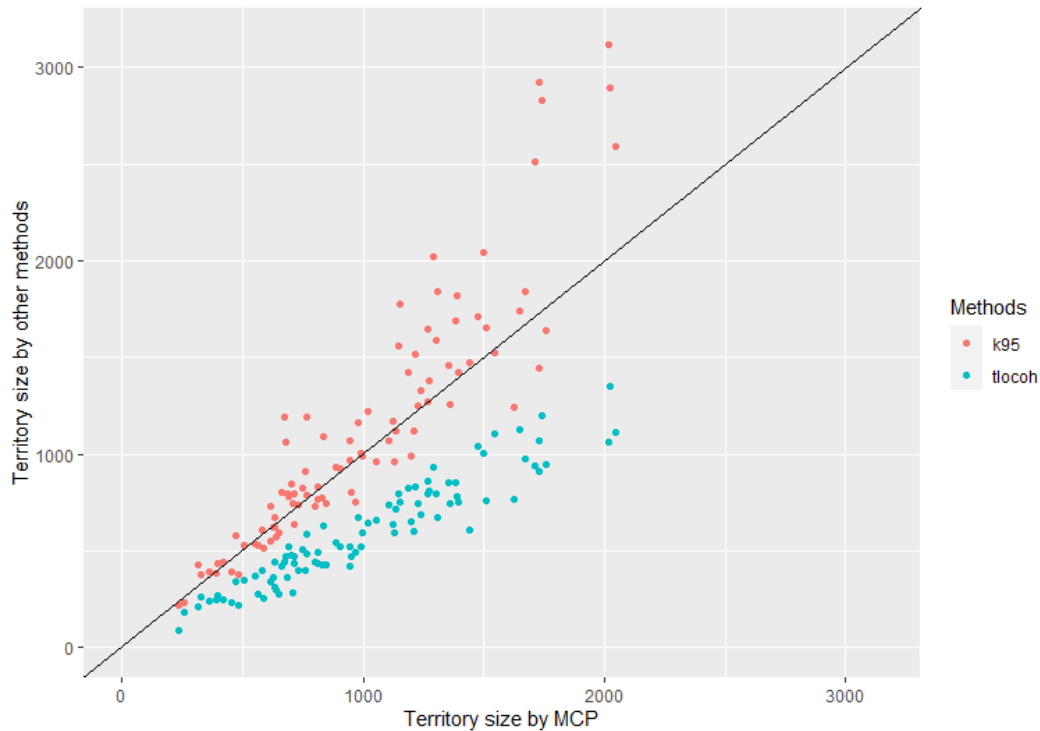


Figure 3. Territory size calculated through kernel 95% and T-LoCoH in relation to territory size calculated through MCP.

Using Pearson’s correlation coefficient, it was found that total population, the number of neighbouring packs, and year were strongly correlated (appendix 1 for graph). When running several models total population was the predictor that gave the best AIC-value, so only that variable was used in the remaining analysis.

Similarly, latitude was correlated with building density, forest road density, main road density and roe deer density, but when running different models only latitude came out as statistically significant ($P\text{-value} \leq 0.05$). However, the best model (best AIC-value) used both latitude and forest road density, so both variables was used in the final model selection.

Backward selection included three models and the NULL model, using the predictors pack size, total population size, latitude and forest road density (Table 1). The best model was the one using pack size, total population and latitude.

Table 1. Comparing models using different predictors to explain variation in territory size: Pack size (Pack), total population size (Pop.), latitude (Lat.) and forest road density (FRD. Non-scaled values.

Model name	K	AIC _c	ΔAIC _c
Pack + Pop. + Lat.	5	2250.6	0.00
Pack + Lat.	4	2251.5	0.90
Pack + Pop. + Lat. + FRD	6	2251.7	1.12
NULL	2	2266.4	15.80

Out of these three predictors, both pack size and latitude were found to be statistically significant (P-value ≤ 0.05 , see table 2, figure 4), while total population was not. Despite the inclusion of this predictor the model gave a positive response in the model selection. As with the previous study, latitude has remained as a key predictor, while pack size became more important whereas roe deer was not important (Mattisson *et al.* 2013).

Table 2. Summary of the effects of each predictor for the final model.

Predictor	Estimate	Error	P-value
(Intercept)	-1.227e+06	3.455e+05	0.0006
Latitude	2.258e+04	5.766e+03	0.0044
Total population	-5.310e+01	3.039e+01	0.0840
Pack size	-4.741e+03	1.623e+03	0.0002

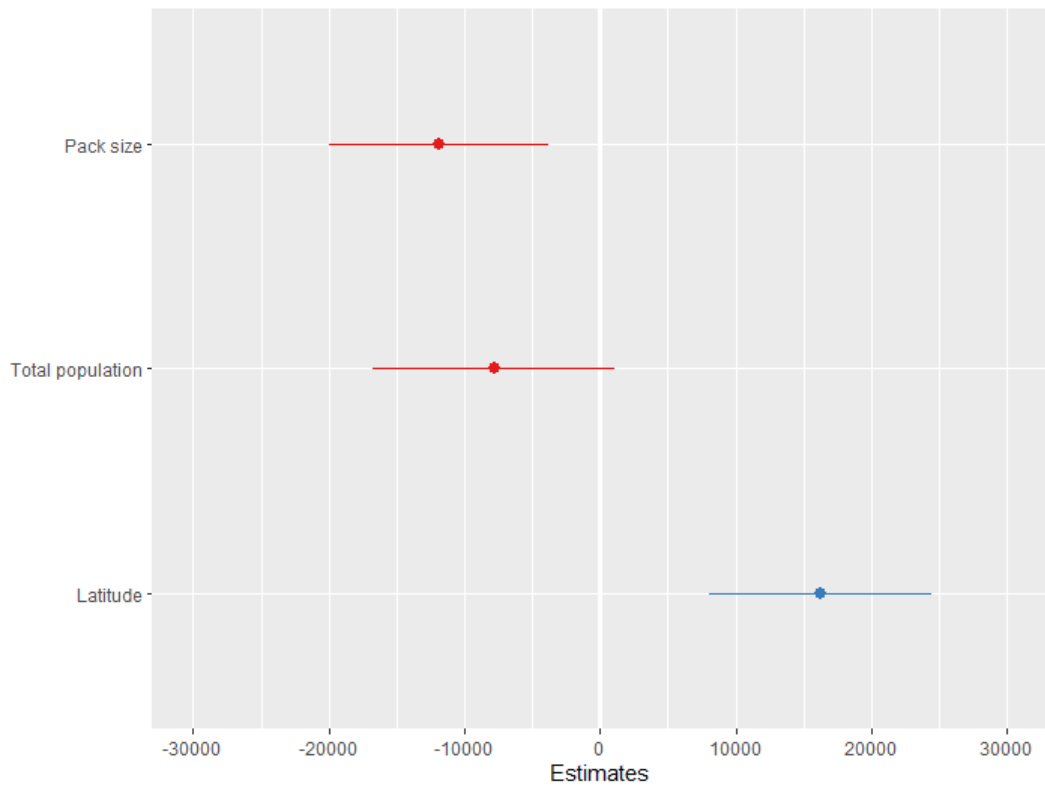


Figure 4. Regression plot for the predictors of the final model. Scaled for ease of reading.

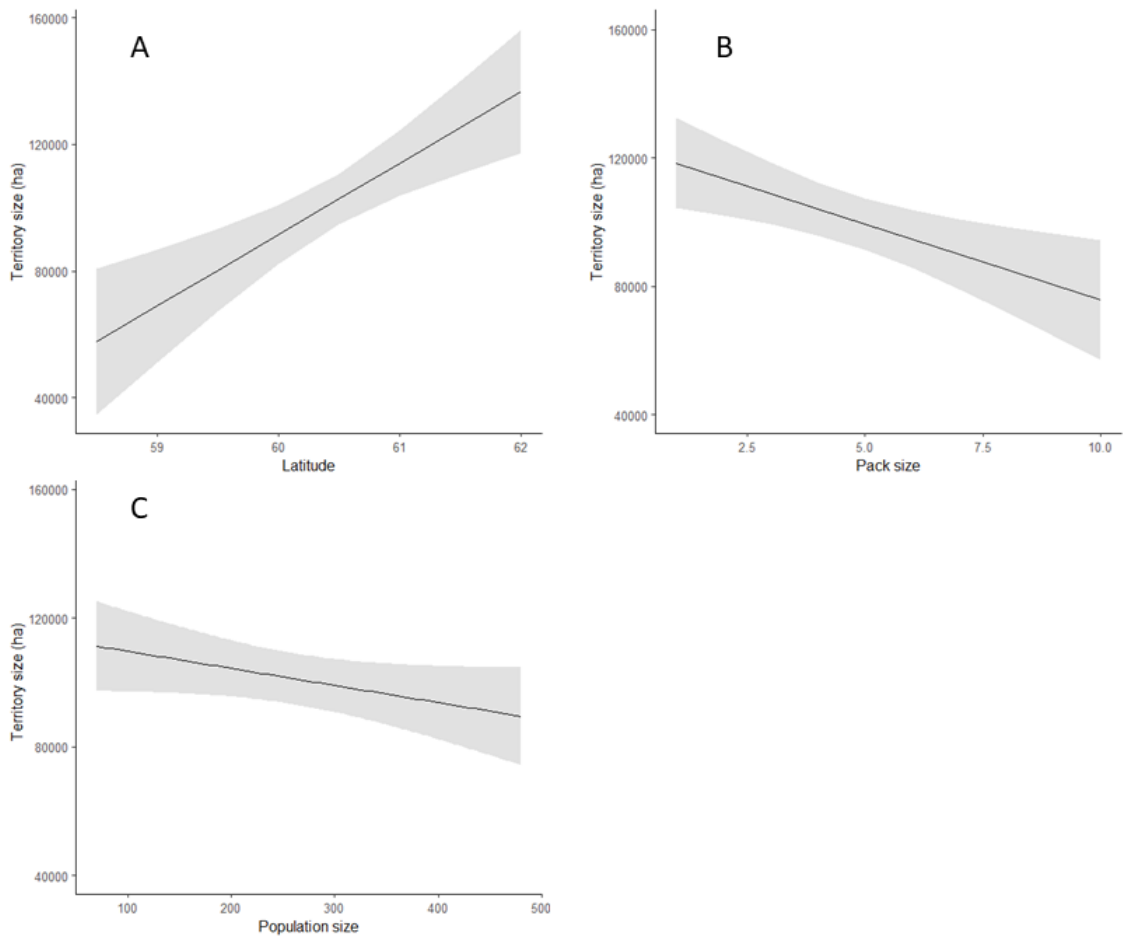


Figure 5. Prediction plots for the three predictors in the final model: Latitude (A), Pack size (B) and Population size (C).

4. Discussion

This project set out to test the hypothesis that increased intraspecific competition has caused wolf pack territories to shrink in size over the last decade in Scandinavia. While there seem to be a certain negative effect on territory size as the population has increased, statistically it was not as important as pack size and latitude.

Pack size was found to be statistically significant with a negative correlation with territory size. This is interesting, as pack size has previously been found to have a negative effect on territory size in studies from Montana (Rich *et al.* 2012, Sells *et al.* 2021), and it has also been proposed that newly established packs must often claim far larger territories than what they might require, so that the area they control can support the future litters of pups (Mech & Boitani, 2003). Our results show that territory size mostly decreased with an increase in pack size, which is different from how lionesses of the dystrophic savannah of Zimbabwe function (Loveridge, Valexi *et al.* 2009). The studies from Montana on wolves propose that larger packs have an advantage in securing better areas with higher density of prey, thus reducing the need for a larger territory (Sells *et al.* 2021). This is supported by another study from Yellowstone (Cassidy *et al.* 2015), where pack size was noted as a key factor in determining if a pack would successfully displace a bordering pack or not. It was also noted that larger packs can make up for higher energy needs by killing prey at a higher rate. In Scandinavia it has been noted previously that higher roe deer density was correlated with smaller territories (Mattisson *et al.* 2013), however in our study roe deer density was not a statistically significant predictor and there was no clear correlation between pack size and roe deer density (see appendix I).

The correlation between latitude and territory size has been attested to previously (Mech & Boitani, 2003, Mattisson *et al.* 2013). It has been suggested that this is due to a decrease in general ecosystem productivity and prey biomass, though this was found not to be necessarily true in the case of the Mattisson *et al.* (2013) study. In my study I found that latitude was correlated with all three anthropogenic predictors (forest road density, main road density, building density) as well as with roe deer density (see appendix I for figure). Given this it is probable that latitude works as a simplified variable for all these different changes that goes on along the north-south gradient, meaning that while ecosystem productivity and prey biomass certainly could play a part in the effect we observe, there may be several additional processes included in this simple relationship.

Roe deer density, which was along with latitude one of the strongest factors affecting territory size in the previous study (Mattisson *et al.* 2013), was found not to be statistically significant in my study. In that study it was suggested that roe deer density, latitude and changes in the landscape were interconnected with how

they influenced territory size. In this study it seems like this is still the case, but that roe deer density has become less significant as a separate factor in the past 10 years. Possibly, this study contained too few observations of moderate or high roe deer density to emerge as an important predictor variable.

When it comes to the anthropogenic features Scandinavian wolves tend to avoid these as part of a risk avoiding behaviour (Carricondo-Sanchez *et al.* 2020). However, thanks to the same study we know that this behaviour can be affected by local and temporal factors, as it has been found that wolf avoidance of anthropogenic features decreased at higher latitudes, during winter, and during the night. This is nothing strange, as adapting to a nocturnal life-style to avoid humans is quite typical for large carnivores in human-dominated landscapes (Chapron *et al.* 2014). Furthermore, wolves have been observed elsewhere to utilize low-use roads to reduce energy costs of travelling and to more effectively take advantage of a territory's resources, leading to smaller territories (Sells *et al.* 2021).

Finally, the total population variable is interesting as it was not statistically significant, yet was key for the final model, meaning it is still important for explaining differences in territory size. While it is not a huge change from the previous study (Mattisson *et al.* 2013), something has definitely happened. It could be that wolf numbers have reached a level where intraspecific competition has become more important in influencing territory size. Comparing the wolf year 2010/2011 (the final year of the 2013 study) to 2020/2021 (the final year of this study), there is a 23-80% increase from an estimated 289-325 individuals (Wabakken *et al.* 2011) to 356-585 individuals (Svensson *et al.* 2021). Indeed, when comparing the two past decades, the 2000s saw a population steadily increasing from below a hundred wolves to close to around 300 at the start of the 2010s (Wabakken *et al.* 2010), while the recent decade saw a total population that by conservative estimates only fell below 300 in the early years, and possibly reached a size close to 600 individuals at its peak 2014/2015 (Svensson *et al.* 2021). During the study periods wolves expanded very little outside of south-central Scandinavia, with certain areas seeing no new packs established (primarily central-north-western Dalarna county, Figure 6).

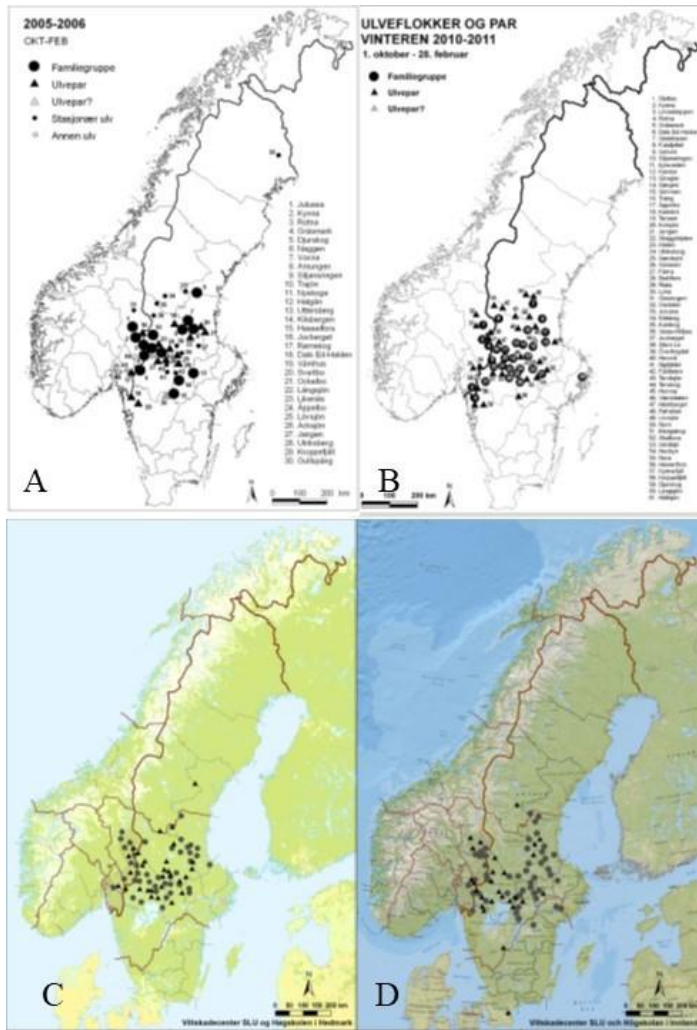


Figure 6. The range of the Scandinavian wolf population from 2005-2006 (A), 2010-2011 (B), 2015-2016 (C) and 2020-2021 (D). The black dots on the maps are confirmed packs and mated pairs. Maps were taken from the wolf population reports for each year.

While total population size worked well in this study, improving our method for a future study could be of interest. In a study published in 2012 (and then followed up by a study published in 2021) with similar focus on factors affecting wolf territory size in Montana, the teams consciously scaled the number of neighbouring packs to the size of the studied territories, as to off-set the factor of larger territory meaning more area which can come into contact with neighbouring groups (Rich *et al.* 2012, Sells *et al.* 2021). Both of these studies found that there was a direct negative relation between the number of neighbours and territory size. It would therefore be quite interesting if in a future study both total population size and the number of neighbouring packs could be considered.

When looking at the yearly reports by SKANDULV on the Scandinavian wolf population covering the study period (1999-2021) only 5 individuals were

potentially killed by other wolves, with only 2 having strong evidence. These were a juvenile found dead in an area where two territories overlapped and an adult male thought to have been killed by a neighbouring pack (Wabakken *et al.* 2004, Wabakken *et al.* 2009).

In the end this study has given us a great overview over what factors have influenced wolf territory size these past decades, nicely complementing the previous study published in 2013. The consistent importance of latitude is interesting, as is the increased importance of pack size and population size. Social factors clearly play a vital part in explaining territorial behaviour amongst these apex predators and should be considered going forward with both research and management decisions.

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Appendix 1

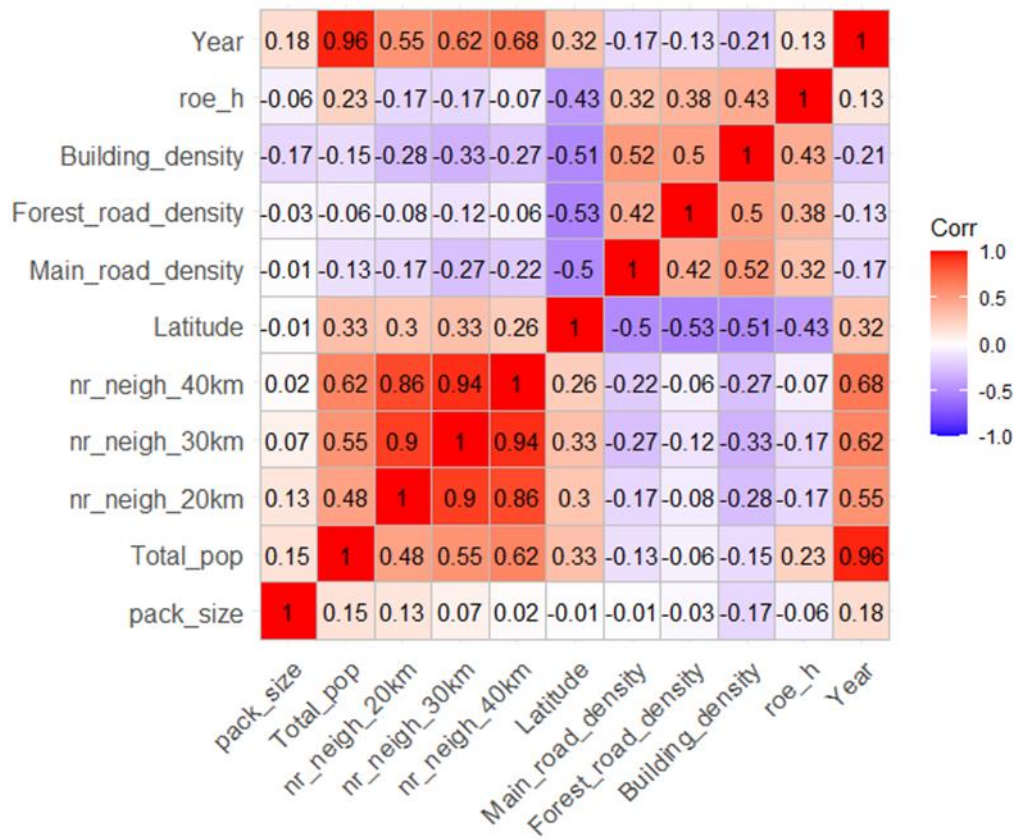


Figure 1. Correlation-index between factors.

