Spatial dynamics in the Scandinavian wolf population
– effects of increased population size and culling

Rumslig populationsdynamik i den skandinaviska vargpopulationen
– effekter av ökad populationsstorlek och legal jakt

Håkan Sand, Olof Liberg, Camilla Wikenros, Mikael Åkesson, Barbara Zimmermann, Petter Wabakken

Sveriges lantbruksuniversitet, SLU
Institutionen för ekologi, Grimsö forskningsstation
2022

Spatial dynamics in the Scandinavian wolf population – effects of increased population size and culling

Rumslig populationsdynamik i den skandinaviska vargpopulationen – effekter av ökad populationsstorlek och legal jakt

Håkan Sand	Sveriges lantbruksuniversitet, Grimsö
Olof Liberg	Sveriges lantbruksuniversitet, Grimsö
Camilla Wikenros	Sveriges lantbruksuniversitet, Grimsö
Mikael Åkesson	Sveriges lantbruksuniversitet, Grimsö
Barbara Zimmermann	Høgskolen i Innlandet, Norge
Petter Wabakken	Høgskolen i Innlandet, Norge

Utgivare:	**Sveriges lantbruksuniversitet, Institutionen för ekologi**
Utgivningsår:	**2022**
Utgivningsort:	**Grimsö**
Bild framsida:	**Åke Aronson**
ISBN:	**978-91-576-9953-4**
Nyckelord:	**wolves, territory, time to re-occupation, dispersal, culling, density, population size, establishment, mortality**

Denna rapport har producerats av SLU på uppdrag av Naturvårdsverket som ett underlag till deras arbete med den nya förvaltningsplanen för varg

A special thanks to Wildlife Damage Center SLU Sweden, County administrative boards Sweden, Rovdata and SNO Norway for the systematic collection and documentation of wolf monitoring data.

Sammanfattning

Djurpopulationer uppvisar vanligtvis förändringar både i individuellt beteende och demografi när de ökar i storlek och täthet. Vargpopulationer är speciella på grund av det revirhävdande beteendet, där vargar försvarar exklusiva områden (revir) gentemot andra obesläktade vargar. Detta innebär att den rumsliga fördelningen av varg kan definieras i form av en närvaro-frånvaro karaktär av revir snarare än en kontinuerligt föränderlig täthet av individer. Detta revirhävdande beteende har viktiga konsekvenser för bevarandet och förvaltningen av vargpopulationer, eftersom jakt eller annan typ av dödlighet bland vuxna revirhävdande individer kan resultera i en komplex rumslig dynamik, som kan liknas vid ett schackbräde av områden som successivt växlar mellan att vara tomma eller ockuperade av olika grupper av varg.

Den skandinaviska vargpopulationen har inventerats vad gäller storlek och utbredning av revir sedan början av 1980-talet. Inventeringen har baserats på omfattande spårning och registrering av revirhävdande individer på snö och senare kombinerat med DNA-analyser av s.k. icke-invasiva prover (spillning, urin) insamlade under inventeringssäsongen. Detta inventeringsförfarande har resulterat i en nästan komplett stamtavla över vargpopulationen, där de individuella genetiska profilerna för reproducerande individer har registrerats och kopplats till ett specifikt geografiskt område (vargrevir) för respektive år. Detta gjorde det möjligt att genomföra en detaljerad analys av spridningsavstånd och släktskap bland reproducerande individer i etablerade vargrevir under perioden 1999 till 2020. Dessutom kunde även föräldrarna fastställas för icke-revirhävdande individer som dog under studieperioden, vilket möjliggjorde en geografisk analys av dödlighet i förhållande till deras födelserevir och till populationsdemografiska faktorer, såsom populationsstorlek och lokal täthet.

Syftet med denna rapport var att besvara fyra specifika forskningsfrågor formulerade av Naturvårdsverket genom att undersöka data över populationsutvecklingen kombinerat med information på individnivå som erhållits från det omfattande inventeringsverksamheten i Skandinavien. Först undersökte vi det rumsliga spridningsmönstret för alla vargar som lyckades etablera nya vargrevir under perioden 1999-2020, oavsett om de sedan lyckades reproducera sig eller ej. Sedan uppskattade vi hur snabbt revir återkoloniserades efter att ha upphört på grund av jakt eller av andra orsaker och vilka populationsfaktorer som kan påverka detta. För det tredje undersökte vi hur stor andel av helt tömda revir som därefter återbesattes av minst en individ från angränsande respektive icke-angränsande revir. Slutligen undersökte vi hur vargpopulationens storlek och täthet påverkade sannolikheten hos unga utvandrande vargar att överleva och etablera ett revir inom vargens huvudsakliga utbredningsområde.

Under studieperioden registrerades etableringar av 468 olika vargpar, varav 259 (56%) fall visade att båda vargarna härstammande från ett annat revir, 185 (39%) fall där en av vargarna var lokal (änka/änkling eller avkomma) från samma revir, och 24 (5%) fall där båda vuxna vargarna var lokalt rekryterade dvs resulterade från olika former av incestuös parning. Det var vanligare att tikar födda i reviret tog över föräldrarnas revir tillsammans med en ny hane (10%) jämfört med att en ung hane tog över reviret tillsammans med en ny tik (3%). Om man undantar lokalt rekryterade vargar (änkor/änklingar och avkommor) var det genomsnittliga linjära spridningsavståndet från centrum av födelserevir till centrum på det etablerade nya reviret 131 (10-553, min-max) km för hanar och 90 (6-424, min-max) km för tikar. Spridningsavstånden från födelsereviret minskade med en ökning av

den lokala tätheten av vargrevir för båda könen, men andelen av den totala variationen i individuella spridningsavstånd som kunde förklaras av skillnader i lokal täthet var låg (<13%).

Under tidsperioden 1999-2017 upphörde totalt 159 vargrevir och av dessa hade 21 (13%) inte återkoloniserats till och med inventeringsperioden 2020/21. Av de återstående 138 reviren som återkoloniserades var antalet år till återkolonisering i genomsnitt 1,1 år och varierade från 0 till 11 år. Det genomsnittliga antalet år från upphörande till återkolonisering av reviren minskade både över tid och med total populationsstorlek från ca tre år under perioden 2002-2009 till mindre än ett år för perioden 2015-2017. Revir med flockar återkoloniserades i genomsnitt 1,2 år snabbare än revir med endast ett revirmarkerande par. Även orsaken till upphörande av olika revir visade en tendens att påverka tiden till återkolonisering av samma revir, där det genomsnittliga antalet år till återkolonisering efter laglig jakt på båda de vuxna individerna var kortare jämfört med när den ena eller båda individerna försvunnit av okänd anledning.

I 133 vargrevir belägna inom vargens huvudsakliga utbredningsområde försvann båda vuxna vargarna under samma år och reviret upphörde därför. Av dessa återbesattes 37 (28%) senare av minst en individ från ett angränsande revir. Åttiotre (62%) återbesattes senare av individer från ett icke-angränsande revir, medan tretton (10%) aldrig återkoloniserades under studieperioden. För 25 av vargreviren var laglig jakt på båda de vuxna vargarna orsaken till att reviret upphörde och alla dessa revir återkoloniserades under studieperioden. Revir som upphörde genom laglig jakt eller andra kända dödsorsaker (utom känd illegal jakt) hade högre sannolikhet (41%) att återkoloniseras av minst en varg från ett grannrevir jämfört med revir där en eller båda de vuxna vargarna försvunnit på grund av okänd orsak (23%).

Utöver de vargar som dött till följd av licensjakt, var det totala antalet döda vargar i Skandinavien under studieperioden 634, vilket motsvarade 11% av den beräknade årliga populationsstorleken. Det fanns ingen trend över tid i andelen av dessa vargar som dog i förhållande till populationens storlek. 217 (34%) av dessa vargar registrerades döda utanför vargens huvudsakliga utbredningsområde och andelen av denna kategori ökade i populationen både över tid och med ökande populationsstorlek från ca 1% till 5%. Däremot minskade andelen döda vargar som hittades inom vargens huvudsakliga utbredningsområde både över tid och med ökande populationsstorlek från ca 10% till 5%. Under samma period lyckades 718 individer etablera sig som revirhävdare, vilket var lika med ett årligt genomsnitt på 13% av den totala populationsstorleken föregående år men denna andel förändrades inte signifikant över tid eller med ökad populationsstorlek. Däremot ökade kvoten ”antal vargar som dog utanför vargområdet/antal vargar som etablerade sig innanför detta”, i relation till populationsstorleken, vilket kan tolkas som vargpopulation börjar närma sig mättnad inom sitt nuvarande utbredningsområde.

Denna studie visar att den skandinaviska vargpopulationen nu har nått en storlek där de flesta revir som upphör i det huvudsakliga utbredningsområdet snabbt återkoloniseras. Jakt på hela flockar i specifika revir kommer i de flesta fall endast att ha en tillfällig effekt eftersom nya individer snabbt kommer att återkolonisera området. Det finns indikationer på en mättnadseffekt på populationen med en högre andel vargar som utvandrat ut ur det huvudsakliga utbredningsområdet under senare år trots att en stor del av detta fortfarande ej täcks av vargrevir. Unga utvandrande vargar har dock haft samma sannolikhet att etablera ett revir inom det huvudsakliga utbredningsområdet under senare jämfört med tidigare år. I likhet med andra vargpopulationer är spridningen av unga vargar i den skandinaviska populationen omfattande och uppvisar stor variation i avstånd. Detta ger förutsättningar för hög populationstillväxt och motståndskraft mot större nedgångar under år med hög dödlighet genom etablering av nya revir eller genom återkolonisering av nyligen försvunna revir.

Nyckelord: varg, spridning, återkolonisering, revir, lokal täthet, jakt, upphörande av revir, populationsstorlek, mortalitet, etablering

Abstract

Animal populations commonly show changes in individual behaviour and demography as they change in size and density. For wolves, this process is strongly affected by their territorial behaviour, making them defending exclusive areas (territories) towards conspecifics. This means that wolf distribution may be better defined by a presence-absence of territories rather than a continuously changing distribution of individuals. This territorial behaviour also has important consequences for the conservation and management of wolf populations because culling or other mortality of adult territorial individuals may result in complex spatial dynamics similar to a chess-board of areas successively changing between being vacant or occupied.

The Scandinavian wolf population has been intensively monitored in terms of size and distribution of wolf territories since the early 1980's. The monitoring has been based on extensive tracking and registration of scent-marking individuals on snow and later combined with DNA-analyses of non-invasive samples (scats, urine) collected during the monitoring season. This monitoring procedure has resulted in an almost complete pedigree of the wolf population, where the individual genetic profiles of reproducing individuals have been registered and linked to a specific geographic area (wolf territory) each year. This allowed a detailed analysis of dispersal distances and relatedness among breeding individuals in established wolf territories during 1999-2020. In addition, the identity of parents of non-breeding individuals that died during the study period was also determined, which allowed an analysis of the location of mortality in relation to their natal territory and to population demographic characteristics, such as population size and local density.

The objective of this report was to answer four specific research questions formulated by the Swedish Environmental Protection Agency, by investigating data on population development combined with information at the individual level as received from the extensive wolf monitoring program in Scandinavia. First, we investigated the origin and natal dispersal of all territorial wolves in the population from 1999 to 2020. The second concerned how fast territories were re-occupied after being terminated by culling or due to other reasons, and what factors that may affect this. Third, we examined the probability of re-occupation of terminated territories by dispersing individuals from neighbouring versus non-neighbouring territories. Finally, we examined how wolf population size and density affected the proportion of young dispersing wolves to survive and establish a territory within the main wolf distribution area.

During the study period we recorded territory establishment of 468 different wolf pairs of which 259 (56%) cases showed both partners to have a distant origin, 185 (39%) cases with one of the partners being local (widow/widower or offspring from the same territory), and 24 (5%) cases where both adults were locally recruited, i.e. with different forms of incestuous mating. It was more

common for female offspring to take over the parental territory together with a new male (10%) as compared to a male offspring taking over together with a new female (3%). Excluding locally recruited territorial wolves (widow/widowers and offspring), average dispersal distance from natal territory to established new territory was 131 (10-553, min-max) km for males and 90 (6-424 min-max) km for females. Dispersal distances from the natal territory decreased with an increase in local density of breeding territories for both sexes, but the percentage of the total variation in individual dispersal distances explained by local density was low (<13%).

During 1999-2017 a total of 159 wolf territories were terminated and of these, 21 (13%) had not been re-occupied by 2020. Of the remaining 138 territories that were re-occupied, the number of years from termination to re-occupation was on average 1.1 years and ranged from 0 to 11 years. The average number of years from termination to re-occupation decreased with both time and total population size ranging between one and three years during the 2002-2009 period but was reduced to less than one year for the 2015-2017 period. Territories with packs was on average re-occupied 1,2 years faster than territories inhabited by a territorial pair. The cause of termination of territories also showed a tendency to affect the time to re-occupation, with faster re-occupation after legal culling of both individuals as compared to territories where both individuals disappeared for unknown reasons.

In 133 wolf territories located within the main wolf distribution area, both adult breeding wolves disappeared during the same year and the territory was therefore terminated. Of these, 37 (28%) were later re-occupied with at least one individual from a neighbouring territory. Eighty-three (62%) were later re-occupied by individuals from a non-neighbouring territory, whereas thirteen (10%) were never re-occupied during the study period. For 25 of the wolf territories, culling of both breeding adults was the reason for the termination of the territory and of these all were re-occupied during the study period. Territories that were terminated by culling or other known causes, except known illegal killing, had a higher (41%) chance to be re-occupied by a neighbour as compared to territories that were terminated due to the disappearance of both adults for unknown reason (23%).

Excluding wolves that died from license culling, the total number of recorded dead wolves in Scandinavia during the study period was 634. On average, the number of dead wolves recorded per year corresponded to 11% of the estimated annual population size. There was no trend over time in the proportion of wolves that died relative to population size. The proportion wolves registered dead outside the main wolf distribution area increased in the population both over time and with total population size from approximately 1% to 5%. In contrast, the proportion of dead wolves found within the main wolf distribution area decreased both with time and population size from approximately 10% to 5%. During the same period, 718 individuals succeeded to establish as a territorial wolf, which was equal to an annual average of 13% of the total population size in the previous year, and this proportion did not change significantly over time, nor with increased population size. However, the ratio "dead wolves found outside the wolf area/new wolves establishing territories inside the wolf area" increased significantly with population size, which could indicate that the population is approaching saturation within its present distribution area.

This study shows that, similar to other wolf populations, dispersal of young wolves in the Scandinavian population is extensive with large variation in distances, and that the population now has reached a size where most terminated territories in the main wolf distribution area rapidly are re-occupied. This provides conditions for high rates of population growth or resilience of population

size in years with high rates of mortality. Actively terminating territories, i.e. through directed culling, to remove “problem wolves” will in most cases only have a temporary effect, as new occupants will rapidly re-colonize the area. There are indications that the wolf population now is approaching saturation with an increasing proportion of young wolves dispersing out of the main distribution area despite that a large portion of the current main wolf distribution area is still un-occupied by wolves. Counter to this, young dispersing wolves seem to have the same probability for establishing a territory within the main distribution area during more recent years.

Keywords: wolves, dispersal, re-occupation, wolf territory, local density, termination, culling, population size, mortality, establishment

Table of contents

Description of the assignment

The assignment from the Swedish Environmental Protection Agency to SKANDULV was to compile and analyse relevant data in order to better understand the effects of increased wolf density and culling of wolves. The assignment contains four parts.

1. The origin of established wolves. A compilation of where wolves, divided by sex, that establish themselves in new territories come from. The compilation shall, for each new couple that has established a territory, state the original territory for the female and the male and the distance between the original and the established territory, or when this has occurred, state whether any of the newly established are either widow / widower, or offspring from a previous territorial pair in the same area. The compilation must also contain an analysis of possible factors that may have influenced the pattern of establishment, such as the size / density of the wolf population, time since the wolf was established in Scandinavia, the location of the territory in the wolf population's distribution area (central vs. peripheral), re-occupation of a previous territory in the same area or establishment in new area.

2. Re-occupation of terminated territories. Analysis of how fast and from where terminated territories are re-occupied. The analysis shall include all territories in which one or both of the territorial wolves have died or disappeared, regardless of the reason for the disappearance. The analysis should test for differences between territories where only the female, only the male, or both animals have died / disappeared. Possible factors that may have affected the time to re-occupation should be identified, e.g. cause of termination (legal culling, poaching, other causes), population size, local density, location of the territory in the distribution area (central / peripheral) etc.

3. Can hunting facilitate the establishment of F1:s (first generation offspring)? Does termination of a wolf territory through culling have any effect on the probability for young wolves from adjacent territories to establish in the vacant territory? This has a management interest, as a tool to possibly make it easier for genetically valuable young wolves to establish themselves in the near area, and thereby contribute to the gene pole.

4. Does population size and density affect the probability for young dispersing wolves to establish in the main wolf distribution area? Analysis of how the population size / density affects the proportion of known deaths (excluding licence killed), which occur inside and outside the area that could be defined as the main distribution area for wolves in Scandinavia. A hypothesis is that an increasing population size means that an increasing proportion of young wolves seek out this area. The hypothesis predicts that the proportion of dead wolves of the entire population should be constant or decrease within the main distribution range but increase outside this range along with

an increase in population density. Deaths due to license culling should be excluded, as these are completely controlled by the administration and have nothing to do with the behaviour of the individual wolves. The analysis is intended to explore the importance of population density for the opportunity of young wolves to establish within or outside this area, respectively. This is of interest for the probability of genetically important individuals to establish and thereby contribute to the gene pole.

A preliminary oral report of the various sub-assignments must be presented during September 2021 and a final report must be received by NV on 2022-02-28.

Uppdragsbeskrivning

Uppdragsbeskrivning från Naturvårdsverket till SKANDULV för att ta fram, sammanställa och analysera relevanta data i syfte att bättre förstå effekterna av ökad vargtäthet och licensjakt på varg. Uppdraget innehåller fyra delar.

1. Etablerade vargars ursprung. En sammanställning av var de vargar, uppdelat på kön, som etablerar sig i nya revir kommer ifrån. Sammanställningen ska för varje nytt par som etablerat sig i revir, ange ursprungsrevir för tiken och hanen och avstånd mellan detta och etableringsreviret, eller när detta förekommit, ange om någon av de nyetablerade är antingen änka/änkling, resp. avkomma, från ett tidigare revirpar i samma område. Sammanställningen ska också innehålla en analys av tänkbara faktorer som kan ha påverkat etableringsmönstret, såsom vargstammens storlek/täthet, tid sedan vargetableringen i Skandinavien, revirets läge i vargpopulationens utbredningsområde (centralt vs perifert), återbesättning av tidigare revir i samma område resp. etablering i nytt område.

2. Återbesättning av tömda revir. Analys av hur snabbt och varifrån tömda revir återbesätts. Analysen ska omfatta alla revir där den ena eller båda de revirhävdande individerna dött eller försvunnit, oavsett anledning till försvinnandet. Analysen ska visa på eventuella skillnader mellan revir där bara tiken, bara hanen, eller båda djuren dött/försvunnit. Tänkbara faktorer som kan ha påverkat tid till återbesättning ska identifieras, t.ex. orsak till revirets upphörande (laglig jakt, olaglig jakt, andra orsaker), populationens storlek, lokal täthet, revirets läge i utbredningsområdet (centralt/perifert), etc.

3. Kan jakt underlätta för etablering av F1-or (avkommor till immigranter)? Har tömning av revir genom jakt någon effekt på sannolikheten för valpar från angränsande revir att etablera sig i det vakanta reviret? Detta har ett förvaltningsintresse, som ett redskap att eventuellt underlätta för genetiskt viktiga ungvargar att etablera sig i närområdet, och därmed bidra till genpolen.

4. Påverkar populationsstorlek och täthet F1-ors möjlighet att etablera sig inom det nuvarande vargutbredningsområdet? Analys av hur populationens storlek/täthet påverkar andelen kända dödsfall (exkl. licensjakter), som sker innanför respektive utanför det område som skulle kunna definieras som ett toleransområde för varg i Skandinavien. En hypotes bakom analysen är att en ökande population inom toleransområdet medför att en allt större andel ungvargar söker sig ut ur detta. Hypotesen predikterar att proportionen döda vargar av hela populationen ska vara konstant eller sjunka med ökande populationstäthet inom toleransområdet, men öka utanför. Dödsfall p.g.a. licensjakterna undantas, eftersom dessa fullständigt styrs av förvaltningen och

inte har med de enskilda vargarnas beteende att göra. Analysen är tänkt att undersöka täthetens betydelse för möjligheten att etablera sig inom resp. utanför detta område. Detta är av intresse för genetiskt viktiga individers möjlighet att etablera sig och därmed bidra till genpolen.

En preliminär muntlig rapport av de olika deluppdragen skall redovisas under september 2021 och en slutrapport skall vara NV till handa 2022-02-28.

Background

The Scandinavian wolf (*Canis lupus*) population was established in the early 1980s and has grown from a single pair to an estimated 480 individuals in the 2020/21 monitoring season (Wabakken et al. 2001, Svensson et al. 2021). Population growth has been generally positive up to 2014 when it temporarily stagnated, partly as a result of the initiation of several years with license culling, starting in 2010. However, in the last two years, the population has been increasing again, and reached a new all-time high in 2020/21 with 480 wolves. Approximately, 85% of the population has been located to south-central Sweden with the remaining part in the adjacent parts of south-east Norway.

Whereas the population growth has been generally positive, the distribution of the population in Sweden has been concentrated to central Sweden south of the reindeer herding area, and in a smaller corresponding area in Norway, i.e. the "wolf zone" (Recio et al. 2020, Åkesson et al. 2022a). Permanent establishment of wolves have not been allowed in the reindeer herding area and wolves established in this area have therefore been regularly removed through protective culling. In contrast, the population has been allowed to expand further south in Sweden, but this expansion has been slow or absent and has, until recent years, mainly included single stationary individuals (Recio et al. 2020). This pattern has therefore resulted in that the population's main distribution area has remained largely the same during the last two decades. The positive growth of the population has therefore mainly resulted in an increased density of wolf territories within the main distribution area with certain parts obtaining a significantly higher density of wolf territories than other parts.

In order to control population size, reduce concentration of wolf territories, and prevent wolf depredation on domestic animals in certain areas/counties, the population has been exposed to both licensed culling and protection culling. However, an observed pattern is that territories where wolves have been removed by culling, or where territorial wolves had disappeared for other reasons, relatively quickly became re-occupied by new territorial individuals, especially in areas with a high density of territories. From a management perspective, it is relevant to know how fast vacant territories are re-occupied and from where the individuals that re-occupy these terminated territories come from, and to find out whether the reason for termination of an existing territory affects the time to new establishment.

An important national management goal is that the Swedish wolf population has so-called favourable conservation status (FCS) in accordance with the EU

Habitats Directive. In short, this means that i) the Swedish population should have a minimum population size of 300 individuals and ii) there should be a frequency of successful immigration from the source population in Finland/Russia that entails at least one new reproducing immigrant per wolf generation, i.e. one every five years (Linnell et al. 2008, Liberg et al. 2015). The latter condition results from the fact that the Scandinavian wolf population is separated by land distance of more than 1000 km from the larger and more continuous source population in Finland/Russia. This semi-isolation of the population has resulted in a high level of inbreeding which has been counteracted by occasional successful immigration events. Seen over the entire period from the beginning of the 1980s to present, the immigration goal has been met, leading to a reduced inbreeding level in the population (Åkesson et al. 2016, Åkesson and Svensson 2021).

For inbreeding decrease in the population, it is required that both immigrants and their offspring succeed to establish territories and reproduce. However, with increased density of territories in the main distribution area, competition for access to vacant territories is likely to increase. One option for the management may therefore be to increase the possibilities for young offspring to immigrants (F1) to establish, by removing (culling) territorial individuals or total packs that are not genetically valuable but hold territories adjoin a territory containing reproducing immigrants or their first-generation offspring (F1).

Linked to the question above, although at a larger spatial scale, is whether the actual density of wolf territories in the total distribution area is an important factor affecting the probability for young wolves to establish and reproduce. A generally higher density in this area may reduce the probability for genetically important individuals to successfully contribute to the population by reproduction. It is therefore of interest to the management to investigate whether the recent increasing density of wolf territories has resulted in a lower probability for young dispersing wolves to establish in the main distribution area.

The objective of this report was to focus on the four specific research topics listed above by analysing data on population development combined with information at the individual level, received from the extensive wolf monitoring program of Scandinavia during 1999-2020. First, we investigated the spatial pattern of origin (natal territory) and dispersal for all wolves that have succeed to establish new territories and reproduce. Second, we estimated at what rate territories are re-occupied after being terminated by culling or due to other reasons and what factors that may be important for this process. Third, we examined the effects of culling and other causes to territory termination on the possibilities for dispersing individuals from neighbouring or non-neighbouring territories to establish in the terminated territory. Fourth, we tested if wolf population size and density affect the possibilities for young dispersing wolves to survive and establish within the main wolf distribution area.

Study area and methods

Study area and population development

Wolves in Sweden belong to the Scandinavian population which also includes wolves in Norway, where approximately 85% of the population is residing on the Swedish side (Wabakken et al. 2001; Svensson et al. 2021). The population is geographically separated from the Finnish-Karelian wolf breeding range (Åkesson et al. 2022b) with a minimum gap of 1000 km distance of land travelling (Wabakken et al. 2007). This gap between the two populations is largely made up by the Fennoscandian reindeer herding area, where DNA-identified wolves typically have been legally culled due to political goals of not having territorial wolves within the reindeer husbandry area or poached or disappeared for unknown reasons without being later identified (Liberg et al. 2020).

The main distribution area of the population is concentrated to the south-central part of Sweden and the adjacent areas in south-east Norway, and is dominated by boreal forest, with moose (*Alces alces*) and roe deer (*Capreolus capreolus*) as main prey. The current study uses data and information from the monitoring reports of 1999/00 up to 2020/21, because 1999 was the start of regular collection of DNA-samples from the wolf population which later has been used for building a nearly complete pedigree of the population (Liberg et al. 2005, Åkesson et al. 2016).

We differentiated between data collected inside and outside of the main wolf distribution area which here is defined as the total area or parts of nine counties outside the reindeer husbandry area in central Sweden and the wolf management zone in Norway (Figure 1f). This area comprises the majority of the wolf territories that were established during the study period but constitute only the northern half of the area where wolves have been allowed to establish by the national management in Sweden (National wolf management plan 2016).

Definition of terms

For the sake of simplicity, when we use the term "year" for the establishment or termination of a certain territory, we refer to the calendar year of the autumn in the respective monitoring year, i.e. a territory that is established in the monitoring year of 2011/12, and is last recorded in the monitoring year of 2013/14, is here referred to as established in 2011 and terminated in 2013. A territory was classified as "new" the first time it was established in a certain area and continued to be so as long as it was held by the original pair. However, if one or both wolves in the original pair were replaced, (with the center point maximum 18 km from the former, see below) the same territory was classified as "old".

To determine the distance between different territories, between the locations of the same territory in different years, and for the analyses of patterns of dispersal and establishment we calculated the distance between the geometric center points of the respective territories, verified within the annual wolf monitoring programme. For some analyses we also used the term "population center", which is defined as the geometric center point of the center points of all territories for each year. Dispersal distance was defined as the distance from the natal territory of a dispersing young wolf to the place where it establishes its first territory. We distinguished between "local" and "outside" origin of the two partners in a new pair. "Local origin" is either a widow or a widower continuing as a territorial wolf after the death/disappearance of its partner with a new partner in the same territory, or an offspring born in the territory.

A territory is defined as "being the same" (re-occupied) if its annual center point, verified within the annual wolf monitoring programme, is not further away from the center point of the preceding territory than the radius (18 km) of an averaged sized territory, as determined by Mattisson et al. (2013) with the Minimum Convex Polygon method. "Outside origin" are all other cases. Definitions of the terms "Neighbor", "Near" and "Long distance" are given in the table head for Table 1b.

The number of years to re-occupation was defined as the difference between the year for termination of the first territory and the year of re-occupation of the same territory minus one, i.e. if a territory terminates in 2016, and is re-occupied in 2018, the number of years to re-occupation is 1. We distinguished between four different causes of termination, "legal culling" including all forms of legal intentional killing by humans (i.e. protective and license culling), "traffic" including deaths by collision with road or railway vehicles, "natural" including all known mortalities inferred by non-human causes (e.g. disease, accidents, old age (either determined by a veterinary post mortem examination, or assumed dead if the wolf disappear without known cause after the age of 10 years), or killing by conspecifics), and "unknown or illegal", including all cases with known illegal killing and cases where the wolf was assumed dead but for an unknown reason.

Genetics
The population origin, natal territory and sex of individuals establishing new territories were retrieved from data collected within the annual monitoring

programme of the population. From 2001 this became a part of the annual monitoring of the wolf population in which non-invasive samples were collected during the monitoring period and later analysed in the lab in SLU Grimsö or at NINA Trondheim. This type of data before 2001 was available from the database of SKANDULV.

From these data a near complete pedigree has been reconstructed for the total Scandinavian wolf population. Up to 2020 it contained 336 different breeding pairs, of which full kin relationships could be reconstructed for 331 (Åkesson and Svensson, 2021). The pedigree reconstruction is described in (Åkesson et al., 2016) and was based on approximately 21,000 successfully analysed DNA-samples. In total, 2258 individuals have been identified, and only 6 could not be assigned to parents included in the pedigree (Åkesson and Svensson, 2019).

Statistical analyses
To test if male or female wolves were more likely to remain in the territory once being a widow and for offspring taking over a parental territory, we used the Pearson Chi-square test (cross tabulated data) and reported the two-sided significance level. The same type of test was also used for comparing males and females with regard to the time to re-occupation of a territory and the cause of disappearance. A similar test (contingency table) was also used for comparing if there were differences in the distribution of re-occupied territories by wolves from neighbouring and non-neighbouring territories in relation to the cause of termination (culling vs. other). We also tested for differences in the time to re-occupation for territories within versus outside of the main wolf distribution area using a Mann Whitney U-test.

For an estimation of the linear relationship between single dependent variables which were approximately normally distributed, we used linear regression and reported the strength of the relationship by r^2 (which is equal to the proportion of the total variance of the dependent variable that can be explained by an explanatory variable) and the statistical significance level (P-value) for the same relationship. Variables included in this type of test were dispersal distance, the proportion of dead wolves found, year, total population size, local population size, and the proportion of the population in the previous year that succeeded to establish as territorial wolves.

For a test of multiple explanatory factors on dispersal distances, we used a general linear model and estimated their partial effect on the dependent variable. We then quantified the effect of variables by plotting the predicted values from the full model using the parameter estimates (B) for each independent variable while keeping other variables in the model constant at median values.

Finally, we used a negative binomial regression analysis with a log-link function to examine the effect of single and multiple independent variables on the time to re-occupation of territories because this variable showed to be over-dispersed, i.e. strongly biased towards small numbers. We tested model effects of each variable by using the Wald Chi-square test and reported the statistical significance of each dependent variable. We quantified and reported the effect of each dependent variable using the same procedure as in the general linear model. For all statistical tests of the effect of independent variables or differences between groups we refer to probability (P) values less than 0.05 as being statistically significant and for those between 0.05 and 0.10 as having a tendency to being statistically significant. All tests were performed in SPSS version 27.0.

Results

1. What is the geographical pattern of origin for wolves establishing new wolf territories?

In the period 1999-2020, we recorded territory establishment of 468 different wolf pairs. The annual number of newly established pairs increased during the first part of the study period, from 3 in 1999 to 34 in 2012, after which it fluctuated between 26 and 38. This pattern seems to have been in congruence with the development of the population size (Figure 1a).

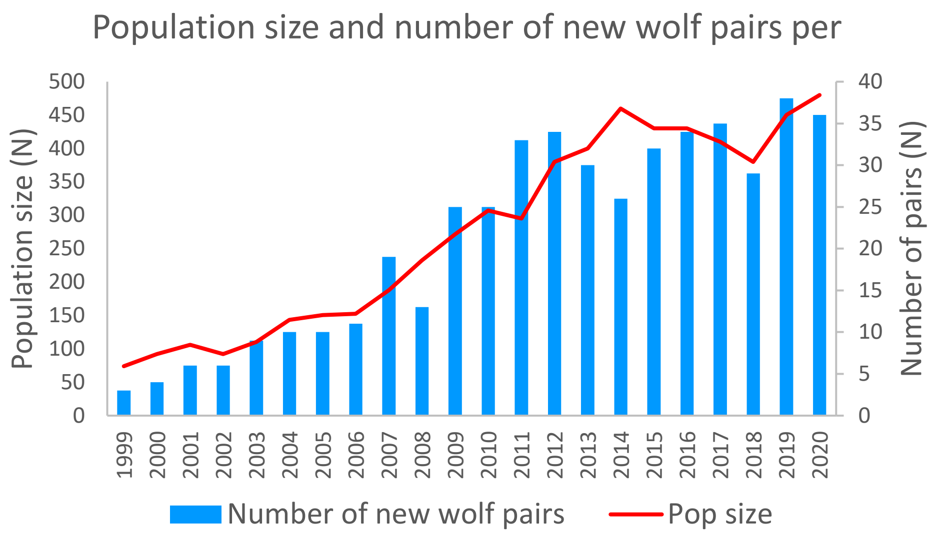


Figure 1a. Number of new established wolf pairs in Scandinavia annually in the period 1999-2020. The year refers to the autumn of the respective monitoring year, i.e. with 2020 referring to the monitoring year of 2020/21.

In 259 (55%) cases, both partners had a distant origin, in 185 (39%) cases one of the partners was local (widow/widower or offspring from the same territory), and in 24 (5%) cases, both adults were locally recruited (Table 1a).

It was nearly twice as common with a female widow remaining in the territory (111 cases, 24%) as compared to a male (59 cases, 13 %) (Table 1b, Chi-square=25.7, P<0.001). Also, the frequency of female offspring taking over the parental territory together with a foreign male (46 cases, 10 %) was more common than cases when a male offspring took over together with a foreign female (16 cases, 3 %) (Chi-square=14.3, P<0.001). For the 24 cases (5 %) where both replacers of a territory were local, 11 were father-daughter, 5 were mother-son, and 2 cases were siblings.

Included in the category of both partners being locally recruited were also 3 cases where a male paired with a step-daughter and 2 cases where a female paired with a step-son and one case where the remaining widow and widower in two neighbouring territories paired and merged their respective previous territory into one new.

Table 1a. Origin of the two partners in new territorial wolf pairs, referring to whether they continued in a territory they already inhabited (widow, widower or offspring) or they arrived from outside.

	Male locally recruited	Female locally recruited	Both locally recruited	Both from outside	Total
N	52	133	24	259	468
Proportion	0.11	0.28	0.05	0.55	1.0

We also recorded 24 cases where full siblings established pairs in non-natal areas (i.e. included in the category with both partners having a distant origin), and 4 cases with half siblings (i.e. sharing only one of the parents). We do not know whether any of these had dispersed together from their natal territory or later met to form a pair.

Females did not only establish locally at a higher rate than males, but also dispersed shorter distances than males if establishing outside their natal territory. More than twice the proportion of females as compared to males were classified to arrive from a neighbouring territory, while more than twice the proportion of males as compared to females were classified to have performed a long-distance dispersal (Table 1b).

Table 1b. Characteristics of the origin of territorial wolves. "Widow" refers to pairing up with a new partner in the home territory, "Offspring" refers to taking over the natal territory, "Neighbor" refers to dispersal distances within the diameter of one average territory (36 km), "Near" refers to dispersal distances in the interval of 37-108 km (2 - 3 average territories) and "Long distance" to dispersal distances > 108 km. Not included are 26 males and 5 females that switched territory after their first establishment as territorials (so called breeding dispersal as opposed to natal dispersal).

	Characteristics of origin					
	Widow	Offspring	Neighbor	Near	Long distance	Total
N males	59	16	53	123	191	442
Proportion	0.13	0.03	0.11	0.26	0.41	1.0
N females	111	46	112	107	87	463
Proportion	0.24	0.10	0.24	0.23	0.19	1.0

When locally recruited territorial wolves (widow/widowers and offspring) were excluded, the average dispersal distance from natal territory to established territory was 131 km (122-141 km 95% CI, n=363) for males and 90 km (80-99 km 95% CI, n=306) for females. Average annual male dispersal distances decreased with time during the study period (n=22, $r^2 = 0.26$, P=0.016), while female distances did not (n=22, $r^2 = 0.005$, P=0.75) and therefore, the difference between sexes decreased with time (Figure 1b).

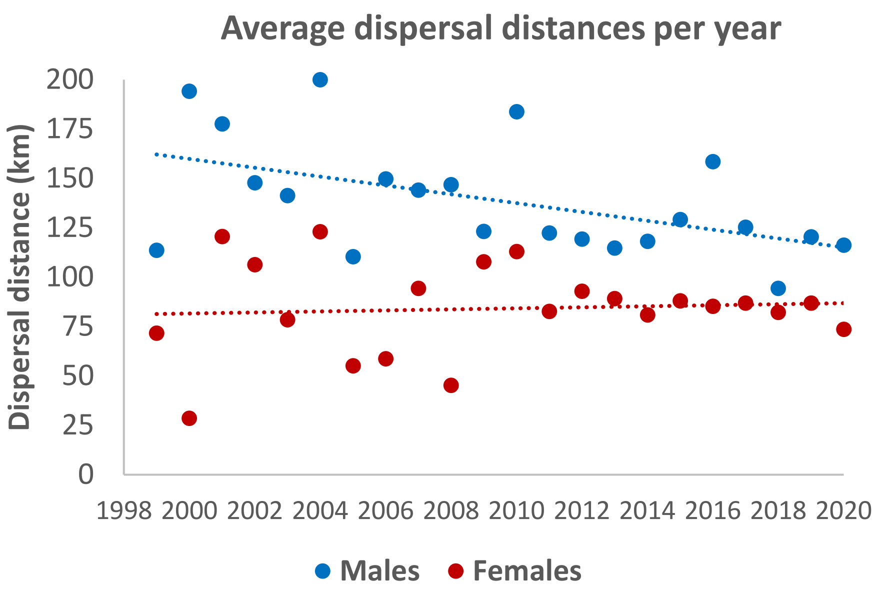


Figure 1b. Average annual dispersal distances from natal territory to established territory, for wolves establishing in territorial pairs during 1999-2020, for males (blue) and females (red). Local recruitments (= zero dispersal distance) are not included.

Similar to time (year), average annual dispersal distances were also negatively related to population size for males (n=22, r^2=0.22, P=0.026) but not for females (n=22, r^2=0.009, P=0.67). For males, this relationship was slightly stronger (r^2=0.24) using population size for the year preceding the dispersal event (t-1) as compared to population size for the same year (t) (Figure 1c) although this was not as strong as the relationship with time (year).

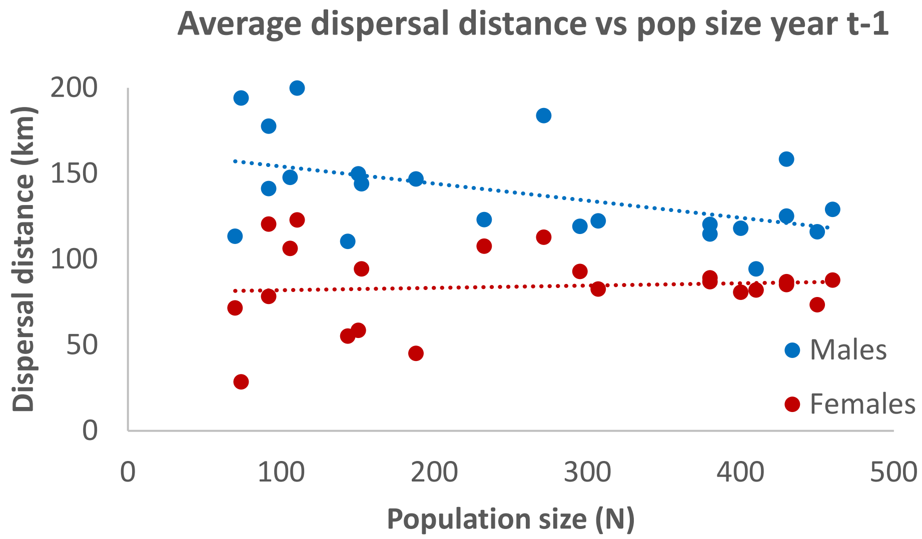


Figure 1c. Average annual dispersal distances against population size for year t-1, for wolves establishing in territorial pairs during 1999-2020, plotted for males and females. Local recruitments (= zero dispersal distance) are not included.

We also tested if dispersal distances from the natal to the establishment of a new territory for individual wolves were related to the local density of breeding territories one year before the dispersal event (t-1). As an estimate of local density, we used the number of wolf territories within a 108 km distance from the center point of the natal territory, i.e. three times the diameter of an average sized (1000 km^2) circular wolf territory. Local density of territories (t-1) ranged between 0 and 30 with a mean of 9.5 (9.0-10.0, 95% CI, n=695) during the study period and the annual mean was strongly positively related to both year (r^2=0.75, P<0.001) and total population size (r^2=0.86, P<0.001) among years.

Results showed that dispersal distances decreased significantly with an increase in the local density of breeding territories for both males (n=363, P<0.001, Figure 1d) and females (n=306, P<0.001, Figure 1e). However, the amount of variation in individual dispersal distances explained by the local density was relatively small (male: r^2 = 0.12, female: r^2 = 0.11) in relation to the total variation in dispersal distances observed among individuals (Figure 1f).

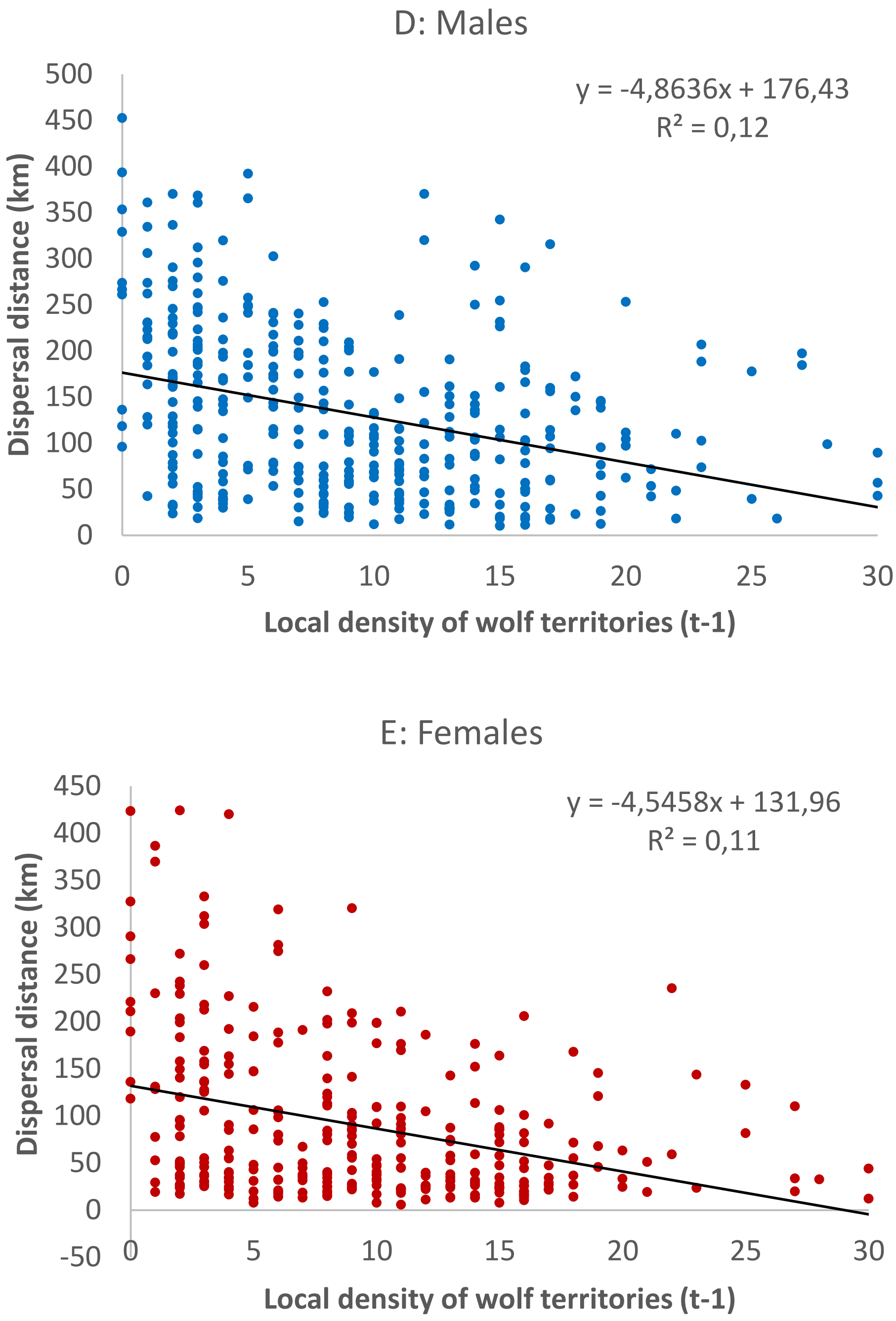
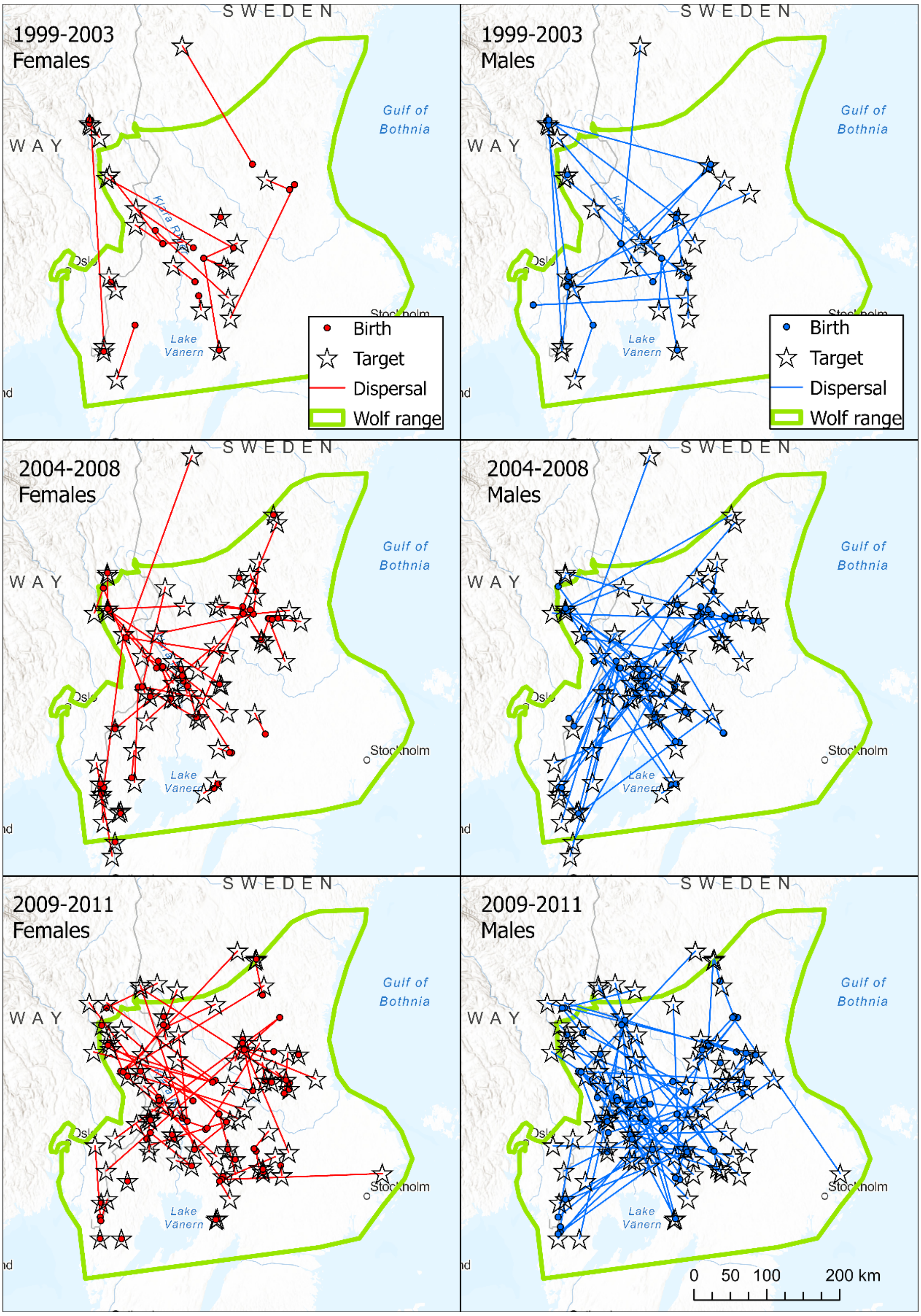


Figure 1 d and e. Dispersal distance from the center point of the natal territory to the center point of an established new territory for 363 males (d=upper) and 306 females (e=lower). Data on dispersal distances are plotted against the local density of natal territories in the previous year (t-1), estimated as the number of territories within a radius of 108 km from the center point of the natal territory (i.e. equal to a circular diameter of three average wolf territories).


1999-2003
Females
1999-2003
Males
2004-2008
Females
2004-2008
Males
2009-2011
Females
2009-2011
Males
SWEDEN
WAY
Gulf of
Bothnia
Oslo
Stockholm
Lake
Vanern
Birth
Target
Dispersal
Wolf range
0 50 100 200 km

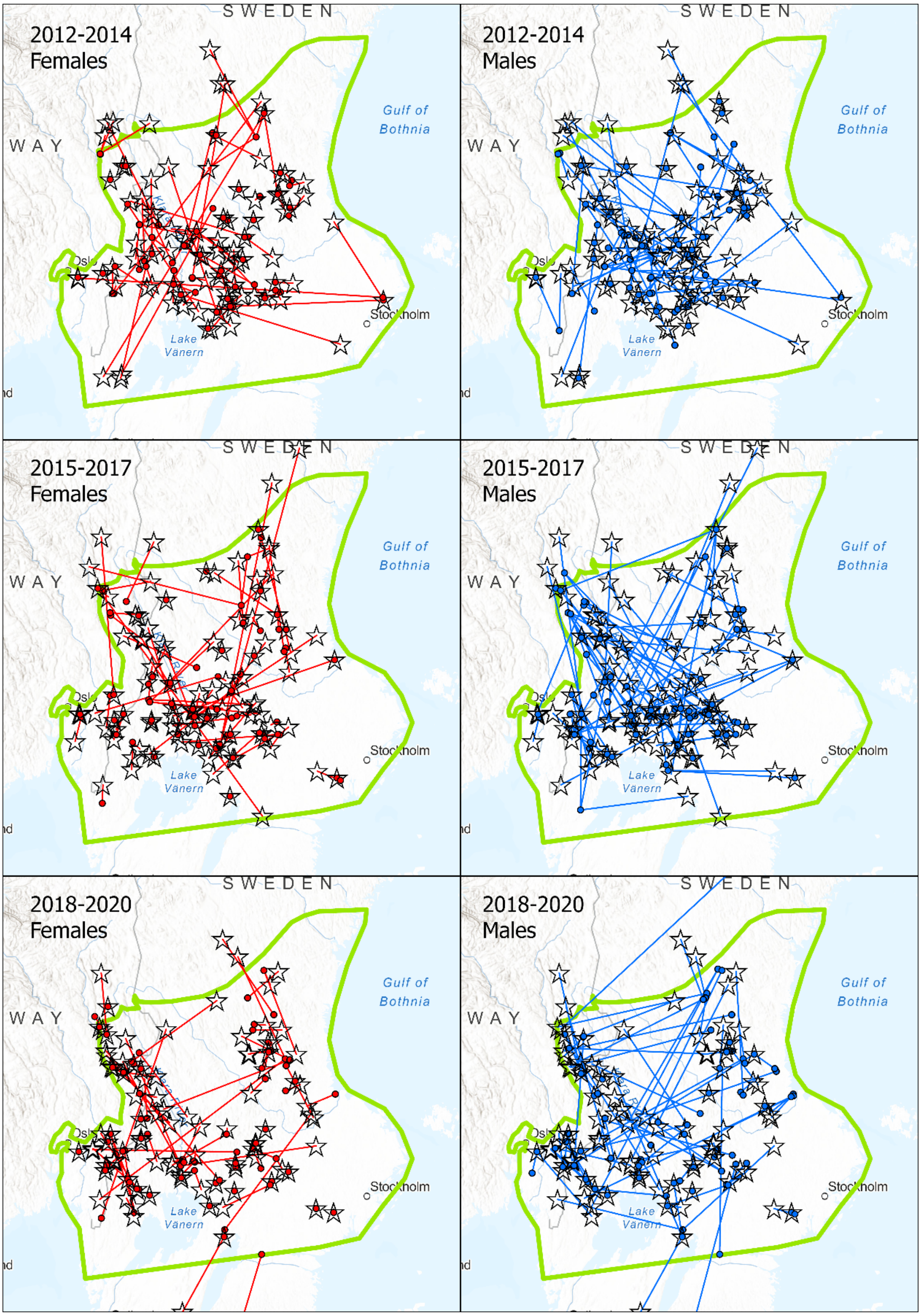


Figure 1f. Map illustrating dispersal from natal territory (birth) to the establishment of a new territory (target) for 363 males (blue) and 306 females (red) during six time periods between 1999 to 2011 (first) and 2012 to 2020 (second) in the main wolf distribution area (green line) in Scandinavia.

Finally, we included sex, type of territory (new, old), local density of territories (t-1), and the distance of the natal territory to the estimated population center in one multi-factorial model and tested for their separate (main) effect on dispersal distance. This model confirmed the longer dispersal distances for males compared to females and that this distance increased with the distance from the natal territory to the estimated population center (Figure 1g). The model also showed that a higher local density of territories (t-1) resulted in reduced dispersal distances. The type of territory (old or new) was not a significant factor in this model

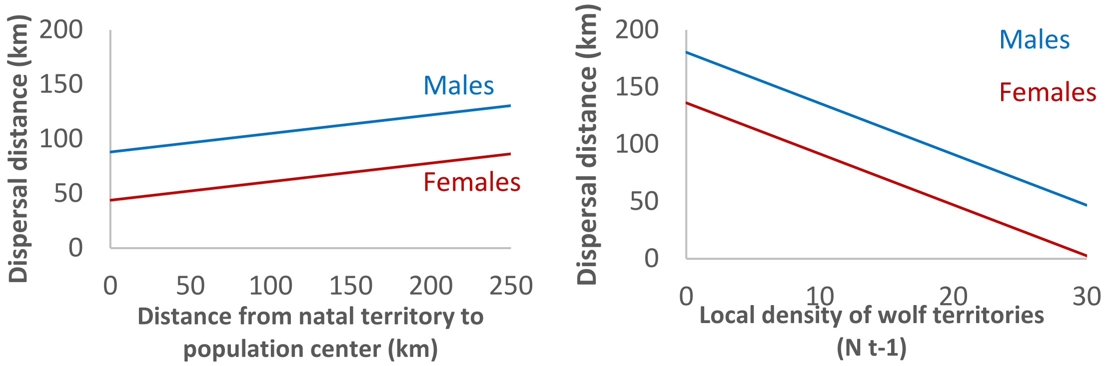


Figure 1g. The relationship between mean estimated dispersal distances for both sexes and the distance from the natal territory to the population center (left panel) and the local density of territories in relation to the natal territory (right panel) för 363 males and 306 females in Scandinavia during 1999-2020. In the left figure distance from natal territory to population center is held constant at 150 km and in the right figure local density is held constant at 15 territories.

2. Re-colonization of terminated territories

Time to re-occupation – both adults gone

During 2002-2017, a total of 159 wolf territories were terminated where both individuals were confirmed missing during the following monitoring season. Of these, 21 (13%) had not been re-occupied by 2020.

Of the remaining 138 territories that were re-occupied up to 2020, the number of years from termination to re-occupation was on average 1.1 (median=0) years and ranged from 0 (re-occupation occurred the following monitoring season) to 11 years (Figure 2a).

Figure 2a. Distribution of the number of years until confirmed re-occupation of 138 wolf territories where both territorials had disappeared during 2002-2017 in Scandinavia.

A geographical division of the 138 territories into i) their main distribution area (n=124) and ii) those that were located either within the reindeer herding area in Sweden or outside of the wolf zone in Norway (n=14) showed a different pattern. The first group (i) had an average number of years to re-occupation of 0.9 (0.62-1.18, 95% CI) whereas the corresponding estimate for latter group (ii) was 2.2 years (1.04-4.16, 95% CI) and this difference was statistically significant (M-W U, P=0.033). Out of the total sample, 91% of the terminated territories in the main distribution area (i) were re-occupied until 2020 whereas only 61% of the territories outside this area (ii) were re-occupied during the same period.

Another factor of importance was whether reproduction had occurred in the terminated territory, i.e. whether the territory was occupied by a pair or a pack. Time to re-occupation for the 110 lost pairs where both adults were replaced from outside was 1.36 years, whereas for 28 packs where the adults were replaced by at least one offspring was 0.07 years.

An analysis of the relationship between the number of years to re-occupation and time (year of termination), total population size, and local density (see above for definition), showed that the number of years to re-occupation decreased with both time (Wald Chi-Square test P=0.008), total population size (P=0.005) (Figure 2b and c) but not with local population density (P=0.129).

Plotting a moving average over three-years (weighted for the sample size for each year) showed that the average time to re-occupation ranged between one and three years during the 2002-2009 period (100-300 wolves) but was reduced to less than one year for the 2015-2017 period. The latter means that most territories that were terminated in this period were re-occupied by a new pair during the same or the following monitoring season as the termination of the territory occurred.

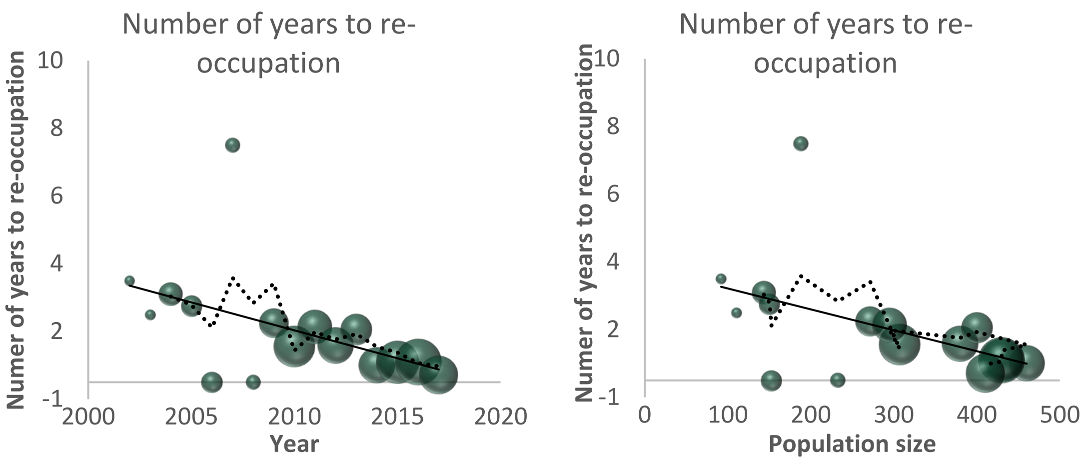


Figure 2b and c. The number of years from termination of a territory to the same territory was re-occupied by other wolves in relation to year (left) and total population size (right). The dotted line represents a moving average of three years with the size of plots indicating the samples size for a particular year and population size, with the largest plot representing a sample size of n=20 (2016) and the smallest n=1 (2002).

Time to replacement – one adult gone

During the same period 142 other cases were registered where only one of the earlier confirmed adult territorial individuals were missing in the territory during the monitoring season. By the end of the study in 2020, 138 of these (97%) had been replaced by a new adult territorial individual. Of these, 126 (91%) were replaced during the following monitoring season and another 6 (4%) after the second monitoring season (Figure 2d). At the fifth monitoring season after the disappearance (4 years) the missing partner had been replaced in all 138 territories. This is equal to an average/median time to re-colonisation of 0.15 (0.06-0.24, 95% CI) / 0 years.

In 84 cases out of a total of 89 (94%) where the male was missing, another male replaced the first male within one year, i.e. during the same or the following monitoring season (Figure 2d). In 42 of 53 (79%) cases a missing female was replaced within one year. A chi-square test showed that there was a tendency to statistically significant differences between sexes (Chi-square=10.2, P=0.07).

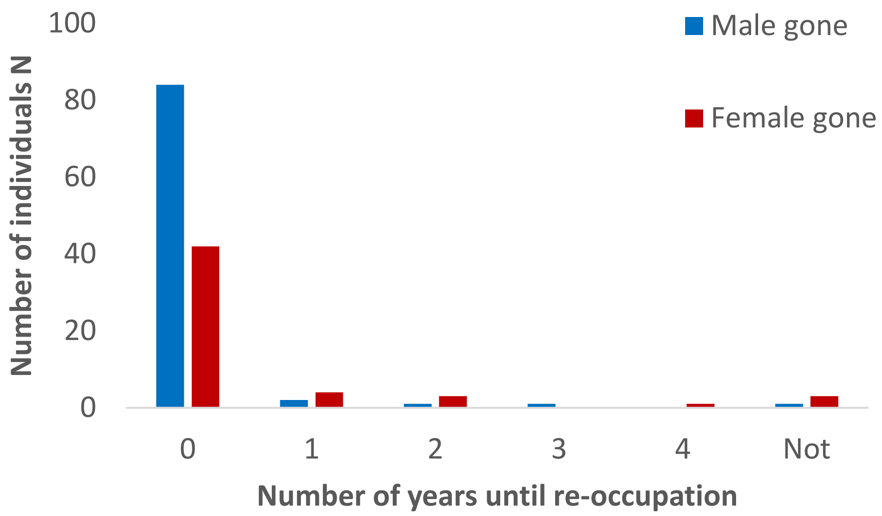


Figure 2d. The number of years to replacement of one missing adult individual in 142 wolf territories during 2002-2020 in Scandinavia. Zero number of years (x-axis) means that the replacement had occurred during the same or the next monitoring season following disappearance.

Causes of loss of adult territorial wolves

Among the 138 wolf territories that were terminated (both adult individuals gone) and later re-occupied, 49% of the causes for both adult individuals were known whereas

51% of the individual disappearances were classified as unknown with the latter group including verified and assumed poaching.

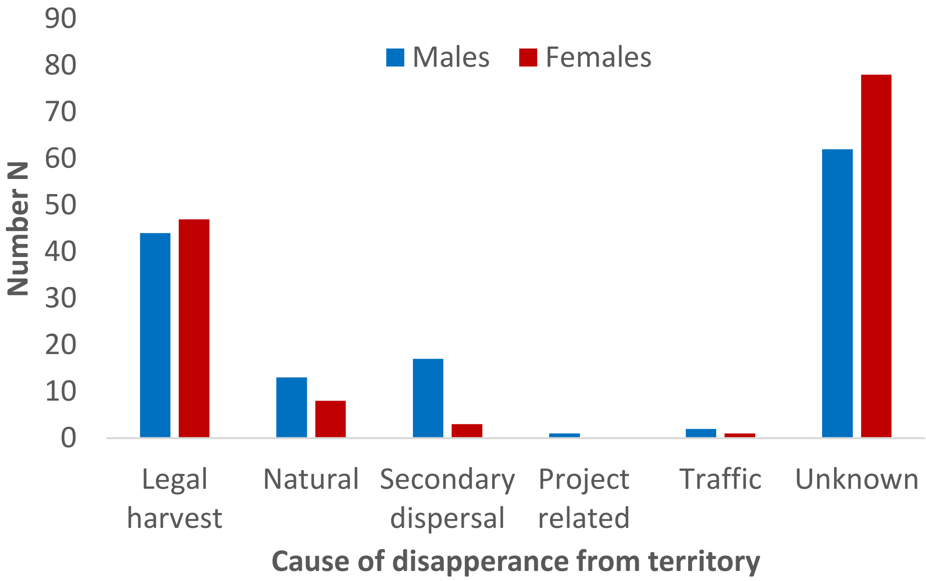


Figure 2e. The cause of disappearance for each individual and sex among the 138 wolf territories that were terminated during 2002 and 2017 and had been re-occupied by 2021 in Scandinavia. "Secondary dispersal" includes wolves that left a territory they were established in and moved to a new territory and new partner, usually in connection with the death of their former partner. "Project related" includes one wolf that died from anaesthesia during a capture/marking event.

In an analysis investigating if and how the cause of disappearance affected time to re-occupation of the territory, we included also observations of territories that had not yet been re-occupied and for those used the number of years without occupations so far registered up to the monitoring season of 2020. We geographically restricted our sample to the main wolf distribution area in Scandinavia, i.e. excluded areas outside of the wolf zone in Norway and within the reindeer herding area in Sweden. This was because wolves in these areas were repeatedly removed by the management and also geographically more distant to other territories in the main distribution area.

Because the two adult individuals disappeared for different reasons in many of the terminated territories, we created a subsample (n=121) consisting of three classes of cause of disappearance. These included those where both wolves were removed by legal culling (1; n=24), where both wolves had disappeared for an unknown reason (2; n=61), and those where one of the adult wolves had disappeared for an unknown reason and the other for a known reason (3; n=36) (Figure 2f). We refer to the discussion for the motivation of this classification.

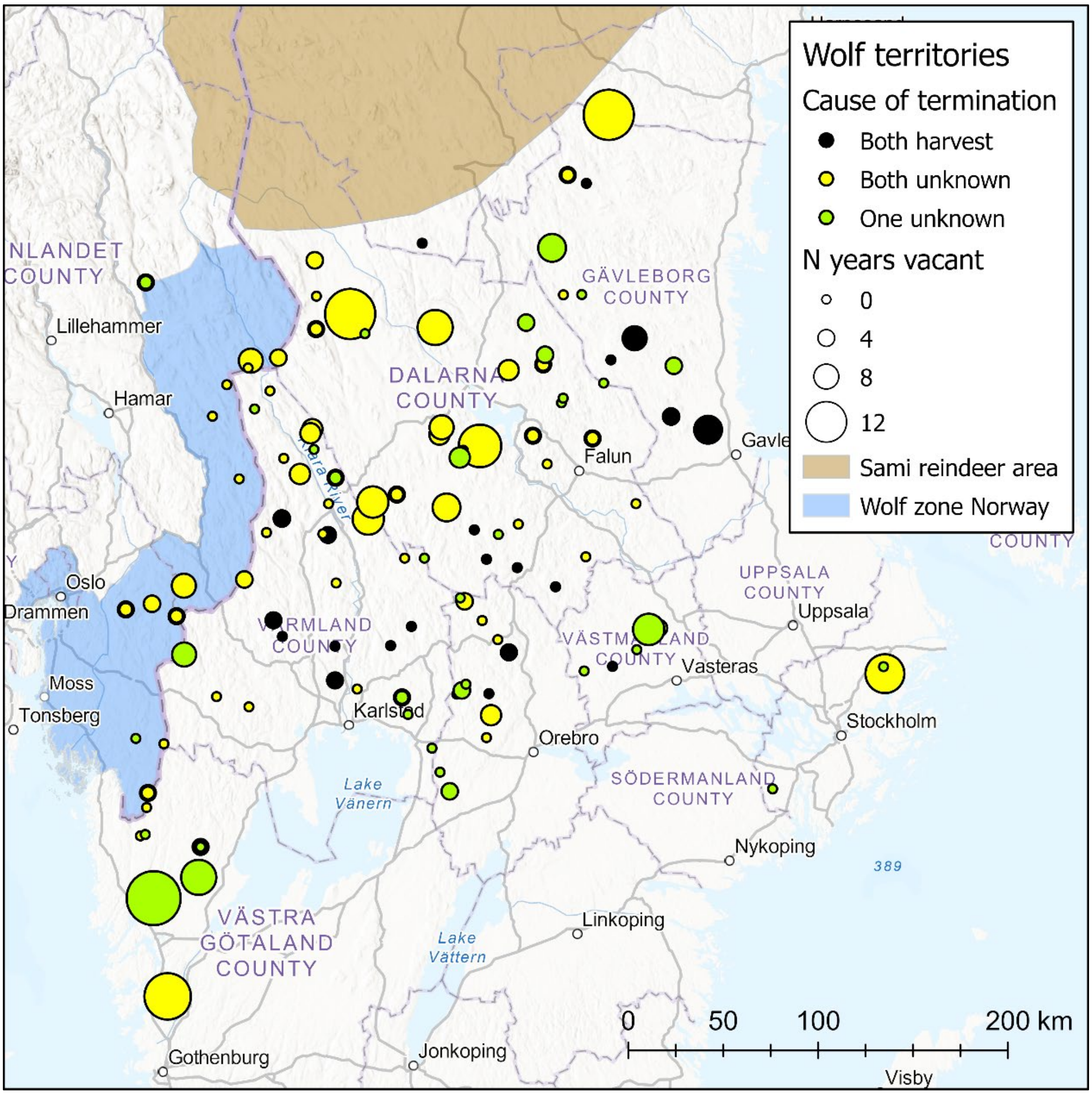


Figure 2f. The geographical distribution of 121 wolf territories within the main distribution area that were terminated and later re-occupied. Data include only cases where 1) both adults were legally culled (black), 2) both adults disappeared for unknown reason (yellow), and 3) one of the adults disappeared for unknown reason and the other adult for a known reason (green). Size of dots indicate the time in years to re-occupation of the same territory. Also marked in the map are the Sami reindeer area and the wolf management zone in Norway.

The average number of years until re-occupation of the territory after both wolves were removed by legal culling was 0.74 years, after both disappeared for unknown reason 2.02 years, and 1.44 years after the disappearance of one individual that disappeared for unknown reason and the other for a known reason (Figure 2g). This difference between groups also showed to be statistically significant (Wald Chi-square, P=0.010).

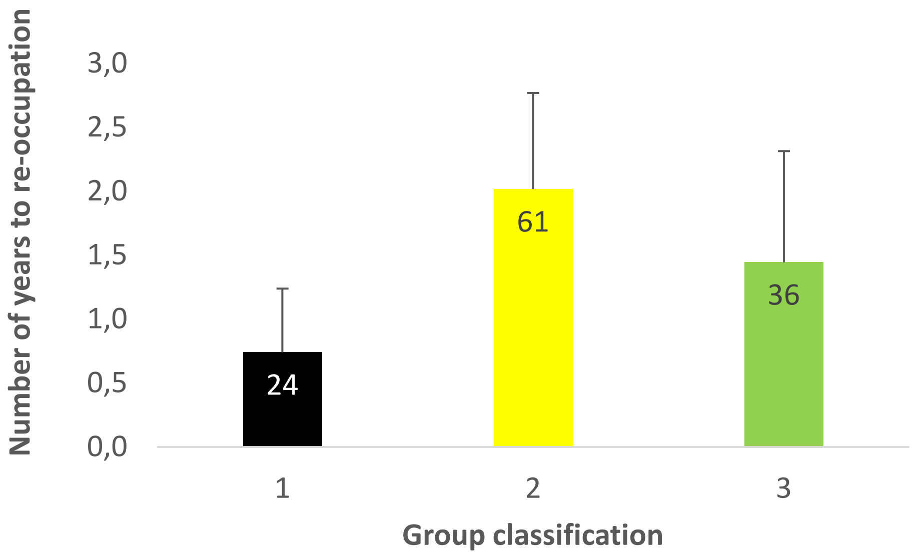


Figure 2g. The average number of years to re-occupation of a wolf territory for the three groups representing different causes to disappearance of the two adult individuals in Scandinavia during 2002-2020. Group 1 included those where both wolves were removed by legal culling, group 2 those where both wolves had disappeared for an unknown reason, and group 3 those where one of the adult wolves had disappeared for an unknown reason and the other for a known reason. Sample size is given within bars and sample error is given by 95% confidence intervals.

Finally, we used the same dataset (n=121) and included several of the factors listed above into one analysis and tested for their effect on the number of years to re-occupation. These factors were group size (pair or pack), cause of disappearance (classes 1 (both known), 2 (both unknown) to 3 (one known, the other unknown)), and local population density (number of wolf territories within 108 km). The results showed that the group size was the most important factor related to the number of years to re-occupation (Wald Chi-Square, P<0.001), with pairs having on average 1.2 years longer time to be replaced, as compared to packs, given the local territory density was 5 and cause of termination was 1 = culling (Figure 2h). Also, the local density of wolf territories was important (P=0.013) reducing the time to re-occupation with 1 year with an increase from 1 to 10 local territories (group size set to 1 = pairs, and cause of termination to 1 = culling). In this multi-factorial model, the time to re-occupation in territories where both adults were legally culled showed a tendency to be significantly shorter as compared to territories where both disappeared for unknown reason (test between group 1 vs 2, P=0.062) but there was no significant difference between the groups 1 and 3 (test between group 1 vs 3, P=0.345).

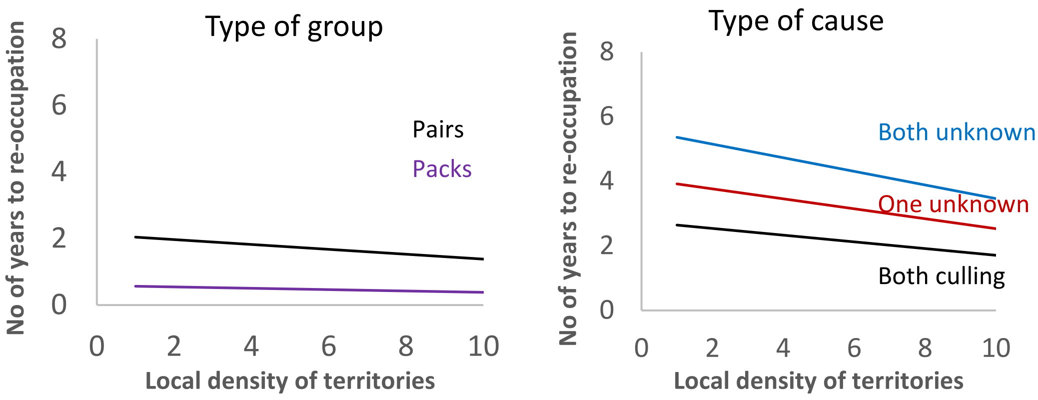


Figure 2h. The number of years to re-occupation of a territory as an effect of the local density of wolf territories (count within 108 km) and wolf group size (pair or family group, left panel), and as an effect of the type of cause for disappearance of both adult individuals (culling, both unknown, one unknown, right panel) in Scandinavia during 2002-2020. In the left figure the type of cause was set to "both culling" whereas in the right figure group size was set to "pairs".

3. **Can culling in specific territories improve the possibilities for offspring (F1) neighbouring territories to establish in the terminated territory?**

During 1999-2017, there were in total data from 133 wolf territories within the main wolf distribution area where both adult breeding wolves disappeared during the same year and the territory was therefore defined as terminated.

For 25 of these 133 wolf territories, culling was the reason for the termination of the territory and all these were re-occupied during the study period. The remaining 108 territories were terminated for other reasons than culling and of these 13 (12%) were not re-occupied during the study period (Figure 3).

Among the 25 territories that were terminated by culling, 9 (36%) were later re-occupied with at least one individual from a neighbouring territory. For two of those (8%), the male originated from the neighbouring territory whereas in 6 cases (24%) the female originated from a neighbouring territory (Figure 3). Finally, there was one case (4%) where both new individuals came from the neighbouring territory. In the remaining 16 (64%) cases where legal culling was the cause of termination, the territory was replaced by individuals from a non-neighbouring territory.

Among the 108 territories that were terminated for other reasons than culling, 28 (26%) were later re-occupied with at least one individual from a neighbouring territory. In three cases (3%), the male came from a neighbouring territory, in 21 cases (19%), the female came from the neighbouring territory, and in four (4%) cases, both individuals came from the neighbouring territory (Figure 3a). In the remaining 67 (62%) cases with a non-culling cause of termination, the territory was replaced by individuals from non-neighbouring territories. In total for all causes, females re-occupied a neighbouring territory in 27 of the 32 cases (84%) (excluding five cases where both replacers came from a neighbouring territory) and this differed significantly from an expected equal sex ratio (Chi-square=8.6, P=0.003).

In summary, of the 133 wolf territories that were terminated for some reason, 37 (28%) were later re-occupied by at least one individual from a neighbouring territory. Thirteen (12%) were never re-occupied during the study period whereas 83 (62%) were later re-occupied by individuals from a non-neighbouring territory.

For 32 terminated territories where one of the adults was replaced from neighbouring territories (male or female neighbour in Figure 3) there was no difference between sexes depending on the cause of termination (Chi-Square=0.71, P=0.58). For the 50 territories that were terminated due to either culling (n=9) or other causes (n=41) there was a weak tendency that a higher proportion of those terminated due to culling was later re-occupied as compared to those terminated for other reasons (Chi-Square=3.9, P=0.09).

For the 120 territories that were later re-occupied, there was no significant differences (Chi-square=0.39, P=0.63) in the proportion of those that were re-occupied by a neighbour or a non-neighbour depending on the cause of termination (legal culling vs other). This means that territories that are terminated by culling have the same chance to be re-occupied by a neighbour as territories that are terminated due to some cause other than culling.

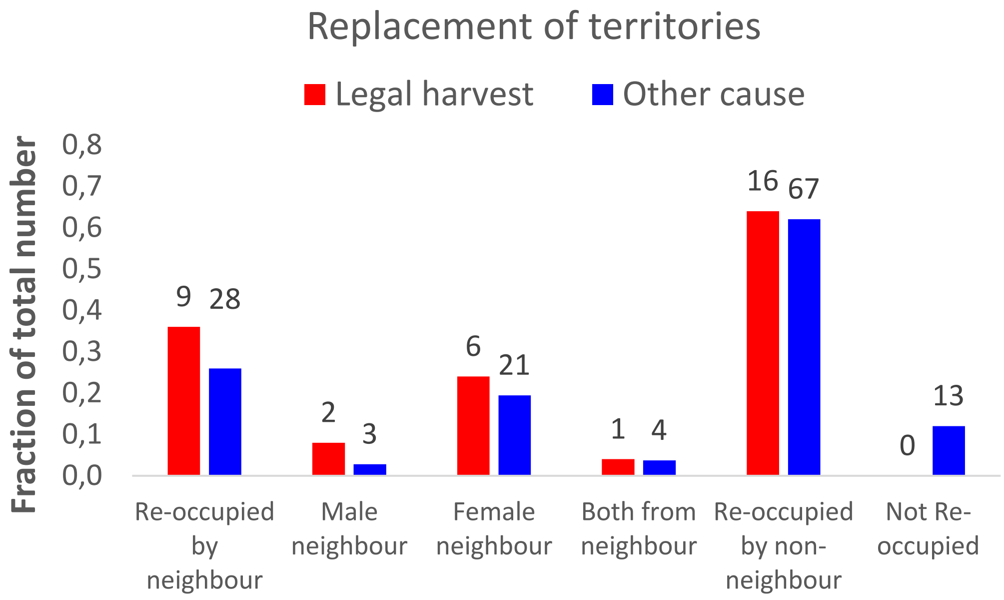


Figure 3. The fraction of the total number of terminated territories (n=133) that later were re-occupied (n=37) or not (n=83) by wolves from a neighbouring territory and those that was never re-occupied (n=13) during the study period 2002-2017 in Scandinavia. Red bars indicate territories that were terminated by culling (n=25) whereas blue bars indicate territories that were terminated for reasons other than culling (n=108). Sample sizes (n) for each group are given above bars.

Finally, we tested if there was a difference between territories where both wolves were lost by known cause of death, i.e. culling, traffic or natural causes, versus those where at least one was lost due to unknown cause. Results showed that territories where both wolves died from culling or other known causes had almost twice as high probability (41%, n=37) to be re-occupied by a neighbour as compared to territories where at least one of the two adult wolves disappeared for an unknown reason (23%, n=96) (Chi-square two-sided test=4.1, P=0.042).

4. **Does population size/density affect the possibilities for young wolves (F1) to establish within the current main wolf distribution area?**

Location of dead wolves found

To answer this question, we examined 1) the proportion of wolves that died for reasons other than license culling inside and outside respectively, of the main wolf distribution area in relation to population size during the 1999-2020 period and 2) the number of wolves that established a new territory for each year in relation to population size the previous year within the wolf distribution area during the same time period.

Excluding wolves that died from license culling, the total number of dead wolves registered in Scandinavia during the 1999-2020 period was 634. On average among years, the proportion of dead wolves found was 11% of the estimated population size. There was no apparent trend over time ($n=21$, $p=0.39$, $r^2=0.04$) in the annual mortality rate (proportion of wolves that died each year in relation to population size), irrespective of whether they died inside or outside the main wolf distribution area (Figure 4a).

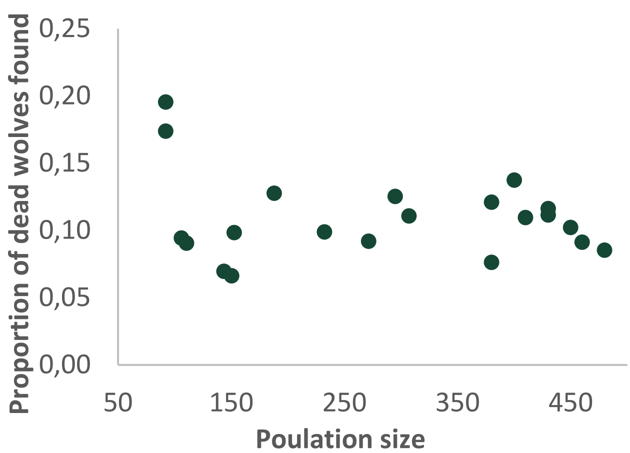


Figure 4a. Annual death rate, defined as number of dead wolves found per year (excluding license-killed) both inside and outside of the main wolf distribution area, divided by total population size the same year, plotted in relation to population size during the 2000-2020 period in Scandinavia.

In total during the same period, 217 wolves were found dead outside the main wolf distribution area, which constituted on average 3% of total population size among years. However, the proportion of this category in relation to total population size increased strongly both over time ($p<0.001$ $r^2=0.48$) and with increased population size ($p=0.001$, $r^2=0.44$) from approximately 1% to 5% (Figure 4b-c).

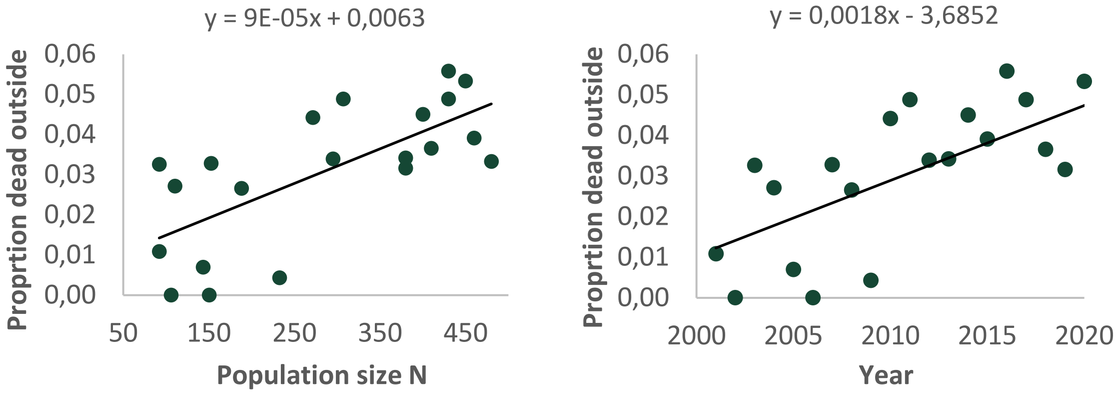


Figure 4 b and c. The proportion of dead wolves (excluding license-culling) found outside the main wolf distribution area for each year in relation to population size (left) and year (right) during the 1999-2020 period in Scandinavia.

In contrast, the proportion of dead wolves found of total population size within the wolf breeding range decreased both with time ($P=0.004$, $r^2=0.36$) and population size ($P=0.01$, $r^2=0.30$) from approximately 10% to 5% over the study period (Figure 4d-e).

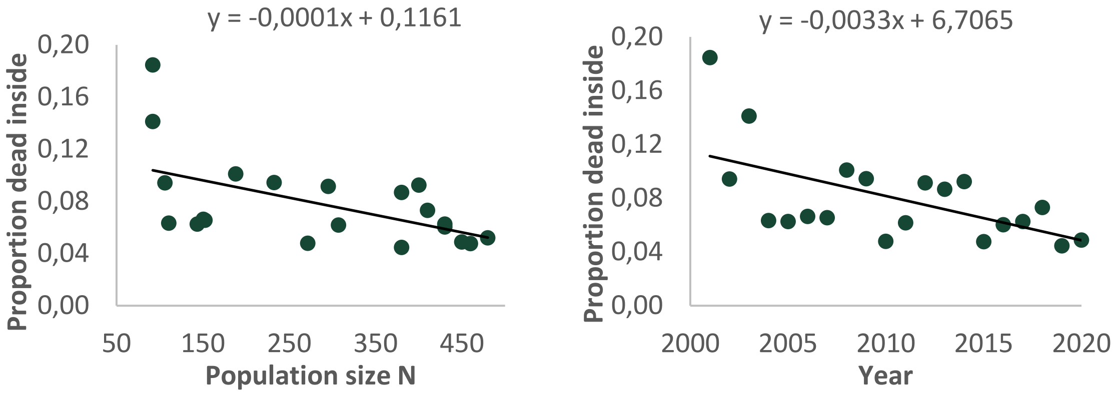


Figure 4 d and e. The proportion of dead wolves (excluding license-culling) found inside the wolf distribution range in relation to population size (left) and year (right) for each year during the 1999-2020 period in Scandinavia.

New territorial establishments

In total, 718 individuals succeeded to establish as a territorial wolf during the study period which was equal to an annual average of 13% of the population size in the previous year. We used the ratio between number of young wolves establishing their first territory in year 1 and the population size in the previous year (t-1), as a proxy for the success of establishment of young wolves. This ratio did not change significantly over time ($P=0.34$, $r^2=0.05$) nor with increased population size ($P=0.53$, $r^2=0.02$) (Figure 4 f and g).

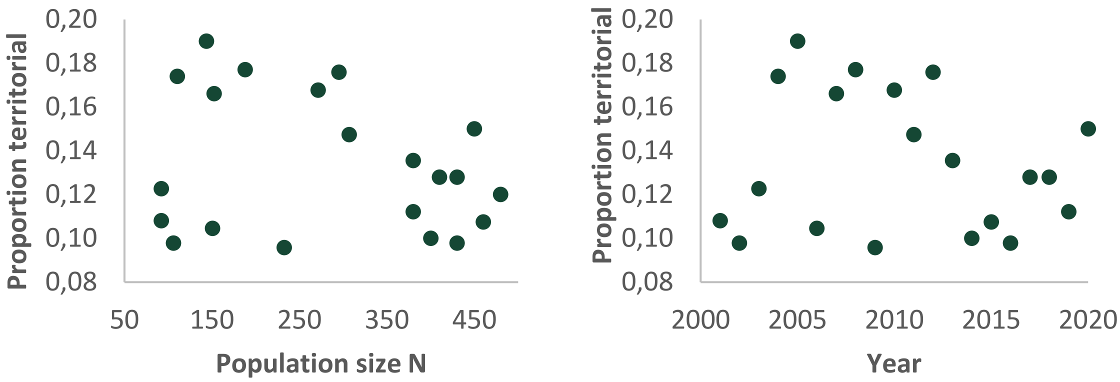


Figure 4 f and g. The proportion of the population in the previous year that succeeded to establish as territorial wolves the following year in relation to population size (left) and year (right) during the 1999-2020 period in Scandinavia.

However, the ratio between the number of wolves that died outside the wolf distribution range and the number that established as a territorial individual inside this range increased strongly with both time ($P<0.01$, $r^2=0.69$) and population size ($P<0.001$, $r^2=0.61$) from approximately 0.10 during the initial years/low population size to 0.40 at the end of the study period/high population size (Figure 4 h and i).

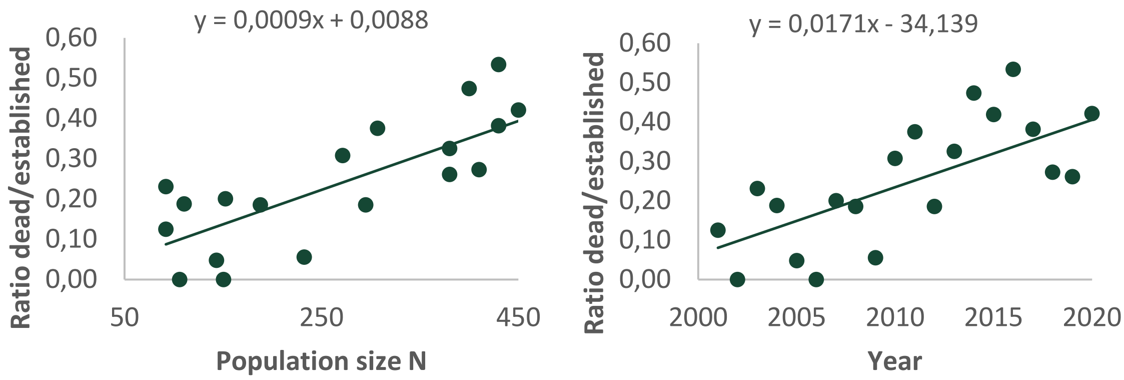


Figure 4 h and i. The ratio between the number of wolves found dead outside the wolf distribution range and the number that established as territorial wolves for each year, in relation to population size (left) and year (right) during the 1999-2020 period in Scandinavia.

Discussion and Synthesis

Wolves are known for having a high capacity for population growth that may exceed 40% annually if conditions are favourable, i.e. low rates of mortality (Mech and Boitani 2003). The demographic mechanisms responsible for this are large litters, early sexual maturation, and a relatively long reproductive life span. In addition, wolves may disperse at an early age and travel for long distances providing opportunities for single wolves of opposite sex to meet, pair, and establish a territory even in populations of low or almost zero density. The Scandinavian wolf population is an example of the latter that initiated the re-colonization of the Scandinavian peninsula in the early 1980's (Wabakken et al. 2001).

Although wolves have a monogamous mating system with territorial behaviour that normally only allows for the two adult wolves in their territory to reproduce, mortality of one or both adults provide opportunities for new wolves to replace the previous individual(s) and thereby prolong the succession of specific territories. Thus, the capacity of single dispersing wolves (e.g. vagrants) to quickly find and replace lost territorial wolves and vacant territories seems to have been important both for the persistence of specific wolf territories and for the growth of the total population. An earlier study of pair bond dissolution in the Scandinavian wolf population showed that wolf packs commonly dissolve and that this generally is linked to a mortality event of one or both of the adult pair and that the cause of mortality is mostly human-related (Milleret et al. 2016).

Pattern of dispersal and establishment

During the last two decades, replacement of adult territorial wolves in the Scandinavian wolf population showed to occur at a high rate, and results from wolves dispersing over a large range of distances. This study also confirmed a general pattern among terrestrial mammals, i.e. that males generally have longer natal dispersal i.e. dispersal from the natal to the established territory, than females (Greenwood 1980), although this is not always the case in wolves (Mech and Boitani 2003, Kojola 2006). Gese and Mech (1991) demonstrated that for shorter distances, there was no difference between males and females, while it was more common that males dispersed long distances (> 150 km), something we also could confirm in this report.

Dispersal distance was negatively correlated to population size for males but not for females, so that in the end of the study period when the population was close to 500 individuals, there was little difference between the sexes. This might suggest that a further increase in population size will not change dispersal distances much. Large individual variation will however continue to be the norm for both sexes. This means that young wolves will continue to disperse into areas currently not allowed for permanent wolf establishment in Scandinavia. The results presented in section 4 indicates that this number might also increase with a further increase in population size.

Dispersal distances also showed a significant negative correlation to the local density of territories in both sexes irrespective of the distance used for defining local density. This may be counter-intuitive, as one might expect longer dispersals for wolves born in high-density areas. One potential explanation is that it may be easier for young wolves to find potential mates in high-density areas perhaps in combination with the fact that there are still a significant number of areas available for wolves to establish a territory in. Inverse density dependent dispersal has also been demonstrated in other species as well, e.g. brown bear (Støen et al. 2006) and tundra vole (Ims and Andreassen, 2005).

Time to territorial replacement

Results from this study show that the Scandinavian wolf population now has reached a size which allows that the majority of the terminated territories, where either both or only one of the adult individuals were missing, to be re-occupied within one year. The time to re-occupation was also faster and more complete in the main distribution area for wolves as compared to more remote territories. The higher dispersal ability among males also shows that territories where the adult male has been lost are replaced with a new male at a faster rate than territories where the female was lost. This study also shows that the local density has some effect on the time to re-occupation but that total population size tends to have the same effect. Even more important for the time to re-occupation was whether the terminated pair had reproduced and formed a pack or not with packs having a shorter time to re-occupation. The most important reason was that if offspring were present in the territory, because one of these commonly inherited the position as one of the adult reproducing individuals. Of the 28 terminated territories where at least one of the replacers was an offspring, 26 were replaced during the same or next year, and the remaining two were re-occupied only after one year.

An interesting observation was that territories terminated due to culling or other known causes of mortality of both adult individuals tended to be more quickly re-occupied than territories where both of the adult individuals disappeared for an unknown reason. The reason for this difference is unknown and we can only speculate about the underlying cause to this difference. We have in an earlier study demonstrated that the majority of these unknown disappearances most likely is caused by poaching (Liberg et al. 2020). If this is the case, the explanation for a slower re-occupation in these territories could be that they occur in "risk areas", where the probability for a new territorial pair to disappear from poaching before being registered during the regular monitoring period is higher. An alternative, but less likely explanation is that a significant part of these individuals was exposed to some, so far, unknown mortality factor that may be important for the persistence of territories. Either way, the reason these territories show a longer time to re-occupation may be that new wolves settling there disappear before they even are registered as a territorial pair.

Replacement of lost territorial wolves by neighbours

Our findings have implications for how and when different management actions such as culling may be used in order to enhance the possibilities for genetically valuable individuals in a neighbouring territory to pair up with a widow/widower or completely re-colonize the vacant territory.

For example, there may be an ambition by the management to improve the possibility for young "genetically valuable" wolves (F1), to successfully establish themselves as breeding members of the Scandinavian wolf population. The hypothesis is that termination of an existing territory adjoining the natal territory of these genetically valuable wolves, will enhance the probability for their offspring to successfully establish as territorial wolves and subsequently breed. Our results give some support for this hypothesis. On average 28% of the terminated territories were replaced by at least one neighbour and there was no difference between those terminated by legal culling or by other reasons. However, if territories where one or both wolves had disappeared due to unknown causes were excluded, the proportion replaced by at least one neighbour increased to 41%. This may suggest that at least some of the wolves disappearing by unknown causes occur in a "risk area", as discussed above.

A frequency of 41% replacement from a neighbour territory might seem encouraging for a manager looking for tools to improve the chances for genetically valuable young wolves to settle and breed. However, purposely terminated territories through culling often have more than one neighbouring territory and therefore one need to consider the risk that the target territory therefore might be re-occupied by the "wrong" neighbour. However, vacating more than one neighbouring territory will increase the chance to obtain the desired result.

As expected, females showed to be three times more likely to establish in a vacated neighbouring territory than males. This illustrates the stronger philopatric tendency in females compared to males, as also seen in dispersal distances and the frequency of local recruitment discussed above. This phenomenon also has implications for the desired outcome of which individuals that may re-occupy a terminated territory.

Therefore, if the territory containing genetically valuable offspring consists of males only, this management option might be less interesting.

Does the Scandinavian wolf population show signs of saturation?

As animal populations grow and increase in density, free space or important food resources will become limiting. This is likely to force young animals to leave the present population distribution area and disperse to areas of lower density and more abundant resources. This may be referred to as a saturation effect on dispersal or saturation dispersal (Fryxell et al. 2014). In Scandinavia, the number of dead wolves found per year outside the main wolf distribution area has increased faster than the population increase, and the ratio between wolves found dead outside of this area and the number of young wolves managing to establish territories inside the main wolf distribution area the same year, was significant.

We conclude that this indicates that the Scandinavian wolf population now shows signs of saturation, and that an increasing proportion of young wolves born within the main distribution area are now forced out of the population. However, although present, this process is so far relatively limited as large areas within the current main wolf distribution area are still un-occupied by wolf territories and allow for new establishments before fully saturated. This is also supported by the observation that the proportion of wolves of the total population that succeeded to established themselves as new territorial individuals within the main distribution area did not change significantly over time or with population size. However, with further increased population size and density within the main distribution area, we anticipate increased rates of dispersal into areas where permanent presence of wolf territories is limited to one reproducing pack by the management, i.e. into the reindeer husbandry area in Sweden and outside of the wolf management zone in Norway. In contrast, southern Sweden is a possible expansion zone and currently has a low density of wolf territories, but future establishments in this region may turn out to be even more problematic and controversial, mainly due to the relatively higher density of humans and domestic sheep farms in this region.

Synthesis and conclusion

The objective of this report was to provide the management with new knowledge and guidance regarding when to apply decisions on culling of wolves. Especially two reasons for culling wolves are central in this context, i.e. 1) removing "problem wolf pairs or packs" to reduce damage on livestock or in other way dampen local conflicts, and 2) strengthen the genetic health of the wolf population, especially by facilitating the establishment and breeding of young genetically valuable wolves.

When removing a wolf pack in order to reduce conflict, it is of interest to know for how long the terminated territory can be expected to remain un-occupied by wolves.

However, almost all terminated territories were replaced within a few years and if only one of the two territorial individuals was removed, the re-establishment of an intact pair was even faster. The only factors that seemed to retard this process were a peripheral position, i.e. outside the main wolf distribution area and low local density. Keeping specific areas vacant of wolf territories within the main distribution area therefore, in most cases, requires repeated culling of entire packs or pairs in the area of interest.

More encouraging was the replacement of terminated territories where the frequency of replacements from a neighbouring territory was so high that this may constitute a useful management tool. The probability for this to happen can be further increased if several neighbouring territories are terminated.

Finally, our data also indicate that we are approaching saturation in the main distribution area where more young wolves disperse out of the population at the present wolf density than was the case some years ago. With a continuation of population growth, we expect this force to increase, and thus affect the possibility for young genetically valuable wolves to establish and breed within the present main wolf distribution area.

References

Fryxell JM, ARE Sinclair and G Caughley. 2014. Wildlife ecology, Conservation and Management, Third edition, Wiley, Blackwell. 509 pp.

Gese, E. M., and L. D. Mech. 1991. Dispersal of wolves in north-eastern Minnesota, 1969–1989. Canadian Journal of Zoology 69:2946-2955.

Greenwood, P. J. 1980. Mating systems, philopatry, and dispersal in birdsand mammals. Animal Behaviour 28:1140-1162.

Ims, R. A., & Andreassen, H. P. (2005). Density-dependent dispersal and spatial population dynamics. Proceedings of the Royal Society B: Biological Sciences, 272(1566), 913-918.

Kojola, I., J. Aspi, A. Hakala, S. Heikkinen, C. Ilmoni, and S. Ronkainen 2006. Dispersal in an expanding wolf population in Finland. Journal of Mammalogy 87:281–286.

Liberg O, Andrén H, Pedersen HC, Sand H, Sejberg D, Wabakken P, Åkesson M, and Bensch S. 2005. Severe inbreeding depression in a wild wolf (*Canis lupus*) population. Biology Letters 1: 17-20.

Liberg O, Chapron G, Wikenros C, Flagstad Ø, Wabakken P, and Sand H. 2015. Bilaga 2 "Joint statement från syntes-författarna" och bilaga 3 "An updated synthesis on appropriate science-based criteria for “favourable reference population” of the Scandinavian wolf (Canis lupus) population" i "Delredovisning av regeringsuppdraget att utreda gynnsam bevarandestatus för varg (M2015/1573/Nm)". Rapport från Naturvårdsverket, NV-02945-15.

Liberg O, Suutarinen J, Andrén H, Åkesson M, Wabakken P, Wikenros C, and Sand H. 2020. Poaching-related disappearance rate of wolves in Sweden was positively related to population size and negatively to legal culling. Biological Conservation 243: 108456.

Linnell JDC, Salvatori V, and Boitani L. 2008. Guidelines for population level management plans for large carnivores in Europe. A Large Carnivore Initiative for Europe report prepared for the European Commission (contract 070501/2005/424162/MAR/B2).

National wolf management plan 2016. Swedish Environmental Protection Agency, 109 pp.

Mattisson J, Sand H, Wabakken P, Gervasi V, Liberg O, Linnell JDC, Rauset GR, and Pedersen HC. 2013. Home range size variation in a recovering wolf population: evaluating the effect of environmental, demographic, and social factors. Oecologia 173: 813-825.

Mech, L. D., and L. Boitani. 2003. L.D. Mech and L. Boitani, editors. Wolves: behavior, ecology, and conservation. Chicago University Press, Chicago, Illinois, USA.

Milleret C, Wabakken P, Liberg O, Åkesson M, Flagstad Ø, Andreassen HP, and Sand H. 2017. Let's stay together? Intrinsic and extrinsic factors involved in pair bond dissolution in a recolonizing wolf population. Journal of Animal Ecology 86: 43-54.

Recio MR, Singer A, Wabakken P, and Sand H. 2020. Agent-based models predict patterns and identify constraints of large carnivore recolonizations, a case study of wolves in Scandinavia. Biological Conservation 251: 108752.

Støen, O. G., Zedrosser, A., Sæbø, S., & Swenson, J. E. 2006. Inversely density-dependent natal dispersal in brown bears Ursus arctos. Oecologia: 148(2), 356-364.

Svensson L, Wabakken P, Maartmann E, Cardoso Palacios C, Flagstad Ø, och Åkesson M. 2021. Inventering av varg vintern 2020-2021. Bestandsovervåking av ulv vinteren 2020-2021. Beståndsstatus för stora rovdjur i Skandinavien. Bestandsstatus for store rovdyr i Skandinavia. 1-2021. 55 s.

Wabakken P, Sand H, Liberg O, and Bjärvall A. 2001. The recovery, distribution, and population dynamics of wolves on the Scandinavian peninsula, 1978-1998. Canadian Journal of Zoology 79: 710-725.

Wabakken P, Sand H, Kojola I, Zimmermann B, Arnemo JM, Pedersen HC, and Liberg O. 2007. Multistage, long-range natal dispersal by a global positioning system-collared Scandinavian wolf. Journal of Wildlife Management 71: 1631-1634.

Åkesson M, Liberg O, Sand H, Wabakken P, Bensch S, and Flagstad Ø. 2016. Genetic rescue in a severely inbred wolf population. Molecular Ecology 25:4745-4756.

Åkesson M, och Svensson L. 2019. Sammanställning av släktträdet över den skandinaviska vargpopulationen fram till 2018. Rapport från Viltskadecenter 2019-3. 12 s.

Åkesson M, och Svensson L. 2021. Sammanställning av släktträdet över den skandinaviska vargpopulationen fram till 2020. Rapport från Viltskadecenter 2021-2. 14 s.