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The recolonization of Eurasian lynx from central to southern Sweden

A success story

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Cover: Lynx in colored pencil
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Abstract

The recolonization of large carnivores into their historic range is characterized by ecological and anthropogenic challenges. This thesis explores the natural range expansion of the Eurasian lynx (*Lynx lynx*) into southern Sweden, the last region to be recolonized following near extirpation from Sweden in the 20th century. I first define three criteria for a recolonization to be successful: there must be 1) availability of quality habitat, 2) sufficient mate availability to facilitate growth, and 3) sufficient genetic diversity to prevent inbreeding. Underpinning these requirements is the need for connectivity to ensure animals can reach suitable habitat and remain connected to the source population. To answer the question as to whether this recolonization event was successful, I first used resource selection functions to identify suitable habitat (Paper I), then used Bayesian population growth models to assess whether inverse density dependence affected population growth during population establishment (Paper II). I then used population genomics to check for genetic structure resulting from recolonization (Paper III), and examined the network of individual relatedness to better understand connectivity during recolonization (Paper IV). The resource selection study predicted extensive suitable habitat in southern Sweden, which was validated with establishment data during recolonization. It also revealed that dispersing individuals were less selective than established lynx (Paper I). Our Bayesian population growth models found that the population in southern Sweden grew more slowly than that of central Sweden during prior recolonization, although an Allee effect was unlikely, indicating sufficient connectivity even at low population densities (Paper II). The genomic analysis showed no spatial or temporal population structure, again indicating connectivity (Paper III). Individual relatedness patterns found no isolation by distance or resistance (Paper IV). The lynx population was able to establish in southern Sweden despite legal quota hunting and poaching. These findings demonstrate that wide-ranging carnivore populations can expand in the absence of protected areas and despite hunting pressure. It is my hope that this case study proves useful to managers and conservation planners who seek to facilitate the recovery of other animal populations in human-dominated landscapes.

Keywords: range expansion, connectivity, logistic regression, population genomics, spatial principal component analysis, isolation by distance, isolation by resistance

Återkoloniseringen av lodjur från centrala till södra Sverige: En framgångssaga

Sammanfattning

Återkoloniseringen av stora rovdjur till deras historiska utbredningsområde präglas av ekologiska och antropogena utmaningar. Denna avhandling studerade den naturliga återkolonisationen av det eurasiska lodjuret (Lynx lynx) av södra Sverige, den sista regionen att återkoloniseras efter att nästan ha utrotats från Sverige under början av 1900-talet. Först definierar jag tre kriterier för en framgångsrik återkolonisering: det måste finnas 1) tillgänglighet av lämpliga livsmiljöer, 2) tillräcklig många parningspartners för populationstillväxt och 3) tillräcklig genetisk mångfald för att förhindra inavel. Grundläggande för dessa krav är behovet av kontakt mellan kärnpopulationen och området för återkolonisation för att säkerställa att individerna kan nå lämpliga livsmiljöer. För att svara på frågan om återkolonisationen var framgångsrik använde jag först studier av habitatval för att identifiera lämpliga livsmiljöer (Artikel I), och populationsmodeller för att beräkna tillväxttakten under etableringsfasen (Artikel II). Jag använde sedan populationsgenomik för att studera genetisk struktur under återkolonisering (Artikel III) och individuell släktskap för att bättre förstå den genetiska kontakten mellan kärnområdet och området för återkolonisering (Artikel IV). Habitatvalsstudien visade att det fanns omfattande lämpliga livsmiljöer i södra Sverige, vilket bekräftades med inventeringsdata under återkolonisering. Den visade också att individer under spridning var mindre selektiva än etablerade lodjur (Artikel I). Populationsmodellerna visade att populationen i södra Sverige tillväxte långsammare än den i centrala Sverige under tidigare återkolonisering, och att en Allee-effekt var osannolik, vilket indikerar tillräcklig kontakt även vid låga populationstätheter (Artikel II). Den genetiska analysen visade ingen rumslig eller tidsmässig populationsstruktur, vilket återigen indikerar god kontakt mellan populationerna (Artikel III). Mönster av individuell släktskap visade ingen isolering med geografiskt avstånd (Artikel IV). Lodjurspopulationen kunde etablera sig i södra Sverige trots viss laglig jakt och tjuvjakt. Dessa resultat visar att stora rovdjurspopulationer kan expandera i frånvaro av skyddade områden. Jag hoppas att denna fallstudie är användbar för förvaltare och i naturvårdsarbete för att underlätta återhämtningen av andra djurpopulationer i människodominerade landskap.

Dedication

To Jeffrey Graham, my partner in this adventure called life and the other half of my *duprass* (Kurt Vonnegut, Cat's Cradle, 1963). Thank you for coming to Sweden with me.

Not all those who wander are lost.
J.R.R. Tolkien, The Fellowship of the Ring, 1954

Contents

List of Publications

This thesis is based on the work contained in the following papers, referred to by Roman numerals in the text:

I. Hemmingmoore, H., Aronsson, M., Åkesson, M., Persson, J., Andrén, H. (2020). Evaluating habitat suitability and connectivity for a recolonizing large carnivore. *Biological Conservation*, 242 (2020), 108352.

II. Andrén, H., Hemmingmoore, H., Aronsson, M., Åkesson, M., Persson, J. (2022). No Allee Effect detected during the natural recolonization by a large carnivore despite low growth rate. *Ecosphere*. *13*(3), e3997.

III. Hemmingmoore, H., Spong, G., Aronsson, M., Persson, J., Andrén, H., Åkesson, M. No population genetic structure in Eurasian lynx during the recolonization of southern Sweden (*Manuscript*).

IV. Hemmingmoore, H., Spong, G., Aronsson, M., Persson, J., Andrén, H., Åkesson, M. Long-distance dispersal drives the recolonization of lynx in Sweden (*Manuscript*).

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The contribution of Heather Hemmingmoore to the papers included in this thesis was as follows:

I. Designed the study together with JP, MA, MÅ, and HA. Performed the spatial analysis. Performed statistical analysis with support from MA and HA. Wrote the manuscript with contribution from JP, MA, MÅ, and HA.

II. Worked closely with HA to perform the statistical analysis and write the manuscript, with contributions from JP, MA, and MÅ.

III. Designed the study together with MÅ and HA, with input from JP, MA, and GS. Requested DNA samples from the Swedish Veterinary Institute (SVA) with support from HA. Extracted and digested the DNA, and trained & supervised lab assistants who extracted and digested DNA. Performed the genomic analysis with support from MÅ and GS. Wrote the manuscript with contribution from JP, MA, HA, and GS.

IV. Designed the study together with MÅ and HA, with input from JP, MA, and GS. Requested DNA samples from the Swedish Veterinary Institute (SVA) with support from HA. Extracted and digested the DNA, and trained & supervised lab assistants who extracted and digested DNA. Performed the genomic analysis with support from MÅ and GS. Wrote the manuscript with contribution from JP, MA, HA, and GS.

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Abbreviations

DAPC	Discriminant analysis of principal components
F_{IS}	Inbreeding coefficient
F_{ST}	Fixation index
H_E	Expected Heterozygosity
H_O	Observed Heterozygosity
PCA	Principal component analysis
RSF	Resource selection function
sPCA	Spatial principal component analysis

1. Introduction

Many populations of large carnivores are decreasing in both size and range, largely due to interference with human interests (Ripple et al. 2014). However, all four of Europe’s large carnivores (Eurasian lynx (*Lynx lynx)*, wolverine (*Gulo gulo*), wolf (*Canis lupus*) and brown bear (*Ursus arctos*)) have increased in both population size and geographic range over the last 50 years, in spite of high human population density and lack of protected areas in Europe (Chapron et al. 2014, Cimatti et al. 2021). This expansion of large carnivores in European multi-use landscapes suggests that the concept of “land sharing,” the coexistence of humans and animals in landscapes that are not expressly set aside for conservation (Phalan et al. 2011), is possible.

As wide-ranging mammals push to expand their range, either into new areas or those from which they were previously extirpated, they can be constrained by anthropogenic barriers, as in the case of pumas (*Puma concolor*) in southern California facing habitat fragmentation due to highways and other human infrastructure (Gustafson et al. 2017). Habitat loss and fragmentation due to human infrastructure can prevent recolonization, and is also a threat to those species whose ranges are contracting (Fahrig 2001, Fahrig 2007, Tucker et al. 2018). Roads are especially problematic, as they create barriers, fragment habitat, and cause mortality (Kramer-Schadt et al. 2004, Basille et al. 2013). In addition to physical barriers, direct human persecution can contribute to population decline and range contraction (Treves and Karanth 2003, Karanth and Chellam 2009).

At low population densities, an Allee Effect can cause a slow population growth rate; for example, the mate encounter rate could be so low that animals have a hard time finding each other, or stochastic events that affect relatively few individuals can have an outsize impact on small populations, e.g. a local decrease in prey availability due to weather or anthropogenic factors (Courchamp et al. 1999, Berec et al. 2007). As animal populations become isolated, genetic drift can occur, leading to small, inbred groups (Berec et al. 2007, Cushman et al. 2015). During recolonization, a similar effect can occur if few founders populate a new area; if they are cut off from the source population, rapid genetic differentiation can occur, the signature of which remains genetically visible generations later (Ibrahim et al. 1996).

As wildlife managers and conservation planners seek to facilitate the recolonization of large mammals into areas of their former range, especially in land sharing situations within anthropogenic landscapes, the question arises as to what criteria need to be fulfilled in order for a successful recolonization to occur. For the purpose of this thesis, I have defined a successful recolonization as follows:

1. Sufficient suitable habitat must be available for the species in question to recolonize, including sufficient food availability (Fahrig 2001, Tucker et al. 2018).
2. There must be sufficient mate availability on the frontier of recolonization for reproduction to occur and the population to grow (Berec et al. 2007).
3. The genetic health of the newly established population must be maintained to not suffer fitness consequences due to inbreeding (Cushman et al. 2018).

Underlying all these criteria is the need for connectivity (Beier et al. 2008, Tucker et al. 2018). Adequate legal protection must also be in place to prevent population decline due to human hunting, legal or otherwise (Treves and Karanth 2003, Chapron et al. 2014, Karanth and Chellam 2009). In terms of landscape, high quality habitat patches are of no use if the animals cannot reach them. In terms of demographics, pushing forward will not benefit the recolonizers if they do not retain connectivity to potential mates. Genetically, sufficient connectivity to the source population is important to prevent isolation and inbreeding (Excoffier et al. 2009, Cushman et al. 2018).

Barriers need not be physical to impede range expansion. Even in areas with sufficient available habitat and connectivity between patches, human persecution of wide-ranging carnivores is common due to the perception of conflict, often over livestock and game (Treves and Karanth 2003, Karanth and Chellam 2009, Redpath et al. 2013). In Europe, protections have played a major role in enabling the recovery of all four species of large mammals (Chapron et al. 2014). However, poaching can limit range expansion even in areas with robust legal protections in place. The Eurasian lynx population growth stagnated after being reintroduced to the Bohemian Forest despite sufficient habitat and prey, largely due to illegal hunting (Heurich et al. 2018), and 25% of the population might be poached annually (Červený et al. 2019). However, high poaching rates do not necessarily prevent recolonization, as in Scandinavia where poaching accounts for up to 46% of mortality in adult lynx (Andrén et al. 2006).

A recolonization can be considered successful if a wildlife population expands its range into a previously extirpated area and successfully establishes, while not becoming genetically isolated. In some cases, populations recolonize areas of their former range but face challenges due to low population numbers and genetic isolation. For example, the Scandinavian wolf population recovered in Sweden and Norway from just two individuals in 1978 (Wabakken et al. 2001) to about 500 wolves in 2022 (Wabakken et al. 2022). Although this could be considered a success demographically, they remain inbred, such that two wolves arriving from the Finnish population had a significant genetic effect on the population (Åkesson et al. 2016). While this recolonization is not a failure because the populations did establish and grow, it continues to face genetic challenges due to isolation, and is therefore not a complete success according to the above criteria.

This thesis examines the recolonization of Eurasian lynx from central to southern Sweden based on the success criteria defined above. Lynx were hunted nearly to extinction on the Scandinavian Peninsula in the early part of the 20th century due to the management goal of eradication, with as few as 30 to 100 individuals remaining in one or two isolated pockets in north central Scandinavia (Lönnberg 1930, Curry-Lindahl 1951, Spong and Hellborg 2002, Rueness et al. 2003a). In Sweden, legal protections were implemented in 1928 (Curry-Lindahl 1951), and the population has since recovered to between 1200 and 1600 individuals in the winter of 2021/2022 (Odden and Frank 2022). The lynx population has gone through periods of complete protection and periods in which hunting has been permitted through managed quotas (see section 3.3 for further detail). As the lynx population recovered, its range expanded southward, and southern Sweden was the last region to be recolonized (Figure 1a). The first documented reproduction in southern Sweden in modern times took place in 2003, and the population in this region was estimated to between 300 and 400 individuals in winter 2021/2022 (Odden and Frank 2022). Although it was clear that lynx were able to reach southern Sweden, to what extent connectivity was maintained between the populations of central and southern Sweden was unclear. It was unknown to what extent sufficient habitat was available for lynx in southern Sweden and whether the population faced slower growth due to low population density (an Allee Effect). Therefore, the resultant population genetic structure of the newly recolonized south was unknown. For this thesis, I had the unique opportunity to use data that was collected during this natural recolonization event as it occurred, to answer these questions from a landscape, demographic, and genetic perspective.

2. Objectives

The aim of this project is to increase the general knowledge of connectivity, habitat selection, dispersal patterns, genetic structure and establishment of large carnivores into unoccupied areas that are part of the historic distribution of the species. To achieve this aim, I assessed the available habitat, population growth, population genetic structure, and connectivity of the Eurasian lynx for more than a 20-year period during their natural recolonization in Sweden.

My thesis is comprised of the following objectives:

To identify available habitat for dispersing and established lynx in southern Sweden (*Paper I*).

To identify potential dispersal barriers and corridors between central and southern Sweden that could inhibit or facilitate lynx recolonization (*Paper I*).

To assess whether the lynx population growth in southern Sweden was influenced by an Allee Effect during recolonization (*Paper II*).

To investigate the genetic structure of the newly established population in southern Sweden (*Paper III*).

To investigate how individual dispersal patterns have influenced the spatial and genetic structure of the newly established population in southern Sweden (*Paper IV*).

3. Study system

3.1 Lynx ecology

The Eurasian lynx is found across Eurasia, and occurs in 11 distinct populations in Europe, which extend from the Balkans and Carpathian region in the southeast to Finland and Scandinavia in the north (Schmidt et al. 2011, Chapron et al. 2014). Lynx are solitary and territorial felids (Nilsen et al. 2012). They follow a polygamous mating system, breeding once per year in March. Females give birth to approximately two kittens around late May or early June (Nilsen et al. 2012).

The Scandinavian lynx of Sweden and Norway is the least genetically diverse subpopulation of Eurasian lynx due to its relative isolation from the rest of the continent (Schmidt et al. 2011, Rueness et al. 2014). They have the largest home ranges documented among Eurasian lynx (Herfindal et al. 2005), with females and males occupying an average of 300–700 km² and 600–1700 km² respectively (Aronsson et al. 2016).

Lynx are solitary ambush predators. Their main prey in central and southern Scandinavia is the roe deer (*Capreolus capreolus*) (Odden et al. 2006). Semi-domestic reindeer (*Rangifer tarandus*) form the bulk of their diet in northern Scandinavia (Mattisson et al. 2011). They prey on smaller animals where larger ungulates are unavailable (Khorozyan and Heurich 2023). In terms of habitat, lynx select for forest cover and rugged terrain. Although they are elusive, they can tolerate human-modified landscapes, and regularly use areas of moderate anthropogenic influence (Basille et al. 2009, Bouyer et al. 2015a, Gehr et al. 2017, Oeser et al. 2023).

Lynx typically leave their mother's home range and begin their natal dispersal at approximately 10–11 months of age. Most establish their own home range by the age of 18 months, although it can take up to 24 months (Samelius et al. 2012). Scandinavian lynx are also the furthest dispersers among Eurasian lynx, with a mean dispersal distance of 46 ± 38 SD and 204 ± 89 SD km for females and males respectively in central Sweden, and 47 ± 42 SD females, 130 ± 123 SD km for males in northern Sweden (Samelius et al. 2012). The greatest dispersal distance recorded of 550 km was a female lynx that dispersed from central Norway to northern Sweden (Rovdata 2012). As in closely related species, e.g. Canadian lynx (*Lynx canadensis*) and Iberian lynx (*Lynx pardinus*) (Gastón et al. 2016, Vanbianchi et al. 2018), dispersing Eurasian lynx are even more tolerant of anthropogenic landscapes than those with established home range, although fenced highways can act as barriers to lynx dispersal (Zimmermann et al. 2007).

3.2 Monitoring, management and recolonization

3.2.1 Lynx monitoring

Sweden and Norway use a common lynx monitoring methodology based on un-replicated counts of family groups (Linnell et al. 2007a, 2007b, Gervasi et al. 2013). Lynx monitoring follows a protocol regulated by the Swedish Environmental Protection Agency (SEPA) and Rovdata (SEPA 2016), and is conducted by authorized personnel from October to February each year. The monitoring is primarily based on snow tracking of lynx tracks from two or more individuals moving together, which are assumed to be a family group consisting of an adult female and her kittens from the same year (Linnell et al. 2007a). Other observations that confirm reproduction can also be used, e.g. photographs of kittens, or kittens killed by hunting or in traffic. Monitoring results are reviewed by an independent central coordinator to validate that they fulfill the criteria to be considered as a lynx family group before the final population size estimates are presented (SEPA 2019).

Distance criteria based on home-range sizes and movement patterns from radio-marked female lynx have been used to distinguish observations of separate family groups, to assure that counts of family groups are distinct (Linnell et al. 2007a, Gervasi et al. 2013). The number of monitored family groups is multiplied by a conversion factor to estimate the number of lynx in the population including males and non-reproductive females. This conversion factor varies by region, with the average being 5.48 (± 0.40 SD) to get the total number of lynx in the population in central and southern Sweden (Andrén et al. 2002).

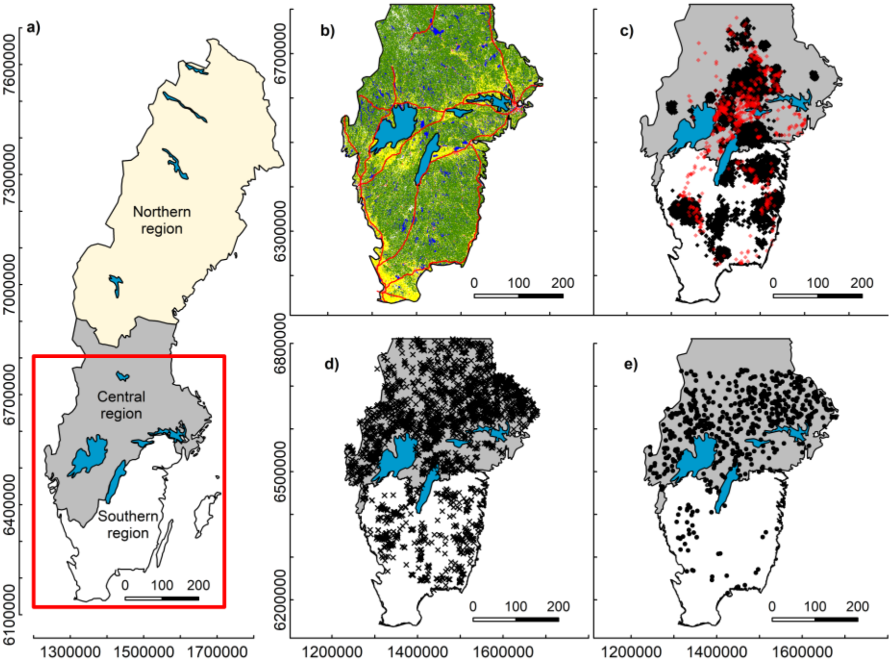

Figure 1: a) Swedish lynx management regions, our study area outlined in red. b) Land cover type (green = forest, yellow = agricultural or grassland, red = urban areas blue = water, white = other, red lines = highways). c) Telemetry locations from established lynx in black and dispersers in red (Paper I); grey background = central Sweden, white background = southern Sweden. d) Government lynx monitoring locations of family groups 2002-2019 (Paper II); grey background = central Sweden, white background = southern Sweden. e) DNA sample locations (Papers III & IV); grey background = central Sweden, white background = southern Sweden.

3.3 Population and management

Lynx management in Sweden is governed centrally by the Swedish Environmental Protection Agency (SEPA) and grouped into three management regions in northern, central, and southern Sweden respectively (Figure 1a). A nationwide population target is set by SEPA, which is divided into regional targets in each of these three areas. Hunting quotas are set annually at the county level if the previous year's lynx population estimate exceeds the regional target, and permission for counties to set hunting quotas is not granted by SEPA if the regional population estimate is lower than the target. During the years in which quota hunting is permitted, the hunting season takes place in the month of March. In addition to granting hunting quotas, county administrative boards grant permission for lethal control on a case-by-case basis when lynx threaten domestic animals. In this case, a person may apply for permission from their local county administrative board to shoot a problem animal. If the lynx in question is currently threatening a domestic animal, the owner can shoot it without prior permission.

A focus of Swedish lynx management this century has been to facilitate the southward spread of the lynx population, to occupy their historic distribution and ease predation pressure on semi-domestic reindeer in northern Sweden, the herding of which represents an important cultural activity by the indigenous Sámi people (SEPA 2014). A nationwide lynx population target of 300 family groups was set in 2001 (Swedish Government 2000), reduced to 250 family groups in 2011, at which time the three management regions were implemented (SEPA 2011) (Figure 1, Figure 2). At that time, monitoring results showed 245 family groups nationwide, with 135 in northern Sweden. The regional target for northern Sweden was set to 75 family groups at the time (Zetterberg and Svensson 2012), leading to high harvest rates of lynx in the northern region (Figure 2).

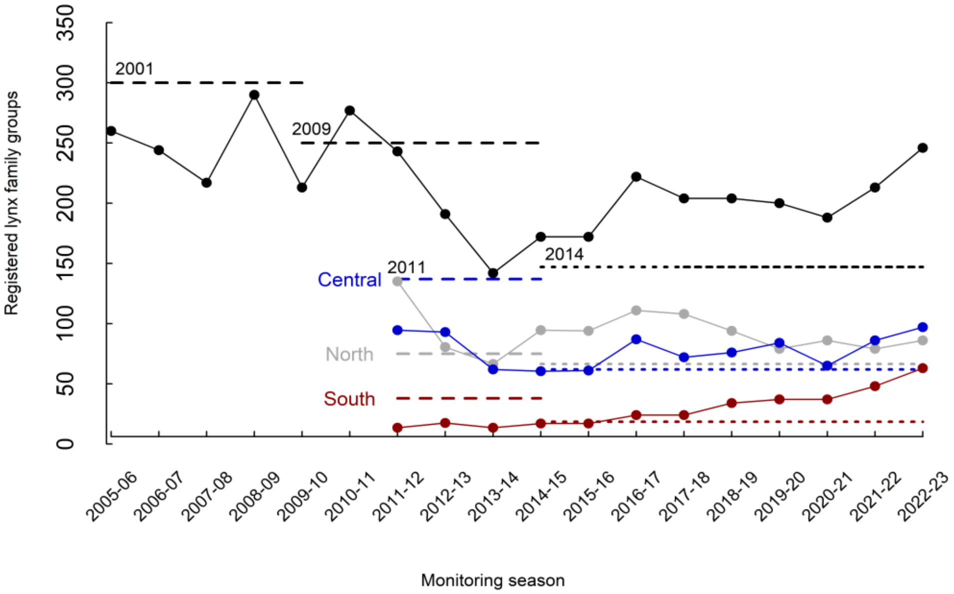

Figure 2: Swedish Environmental Protection Agency (SEPA) population targets for lynx (dashed lines prior to 2011), absolute minimum population levels (dashed lines after 2011), population estimates (dots connected by solid lines). Targets and estimates are shown at the national level (black) and for the management regions (northern region [grey], central region [blue], and southern region [red].

In 2014, favorable conservation status (a requirement for species listed in Appendix 2, EU Habitat Directive 92/43/EEG) for lynx in Sweden was reassessed and the minimum national population was set to 870 individuals, which corresponds to 147 family groups (SEPA 2014). Regional absolute minimum numbers of family groups were reduced to 66.5, 62 and 18.5 family groups in the northern, central and southern management region, respectively. To minimize the risk of coming below the absolute minimum population level, the different management regions set up population target ranges that were higher than the absolute minimum level (northern region, management interval to 68 – 127 family groups; central region, management interval to 72 – 92 family groups; southern region, a target of 40 family groups). In 2018, the monitoring showed that the lynx population was within the management intervals for northern and central regions, while it still had not reached the target of 40 family groups in the southern region (Tovmo and Zetterberg 2018). In 2019, the regional minimum levels were reassessed to 58, 62 and 27 family groups in the northern, central and southern management region, respectively (SEPA 2019). The purpose of the reduction in the northern region is to reduce predation on semi-domestic reindeer.

3.4 Study area

The study area for this thesis encompasses approximately the southern third of Sweden, situated beneath the latitude of 6738000 as per the Swedish National Grid RT90 projection, and encompassing most of the central lynx management region and the entire southern management region (Figure 1). Intensively managed boreal forests primarily composed of Norway spruce (*Picea abies*) and Scots pine (*Pinus sylvestris*) occupy over 60% of the landscape in this area. Additional tree species present in the region include birch (*Betula pubescens* and *Betula pendula*), aspen (*Populus tremula*), ash (*Fraxinus excelsior*), elm (*Ulmus glabra*), oak (*Quercus robur*), and beech (*Fagus sylvatica*). Most land in southern Sweden is privately owned (63%), followed by corporate and state ownership. Only 3% of the land in southern Sweden is protected, and the largest protected area is only 78.5 km^2, which is smaller than a single lynx home range. Therefore, lynx rely heavily on land sharing, in which they use potentially human-modified landscape that is not set aside for wildlife.

3.4.1 Potential barriers to recolonization

The relatively continuous forest of central and southern Sweden is intersected by a large agricultural zone making up 12% and 19% of central and southern Sweden respectively (Hemmingmoore et al. 2020) (Figure 1b), consisting primarily of wheat and barley production. This area is characterized by the relatively narrow stretches of land between four of Sweden’s largest lakes (Lake Vänern, Lake Vättern, Lake Hjlämaren, Lake Mälaren). Two and three percent of the landscape is occupied by human infrastructure in central and southern Sweden respectively, which includes cities and roads (Hemmingmoore et al. 2020). Four of Sweden’s major highways pass through this area; the E20 passes south of Mälaren and runs between Vänern and Vättern, with the E18 north of Mälaren and Vänern, and the E4 passing south of Vänern. The top ten most populous Swedish cities are situated within the southern third of the country, where human population density is higher than in the rest of Sweden.

These potential barriers, both natural and human-made, could potentially limit lynx dispersal and create impediments to moving between southern and central Sweden. Previous studies have shown that lynx avoid open agricultural fields and need sufficient forest to expand their range (Niedziałkowska et al 2006), and largely avoid human infrastructure, although it can be use during dispersal (Basille et al. 2009). Furthermore, lynx avoid areas of high road density (Basille et al. 2013), and highways can create barriers to lynx dispersal (Zimmermann et al. 2007).

4. Methods

4.1 Lynx data

4.1.1 Landscape – capturing and collaring (Paper I)

VHF and GPS collars were used to monitor lynx in the central study area beginning in 1996, and followed their expansion southward throughout the study period as part of a long-term lynx study. All lynx were captured, immobilized, and equipped with collars following a Swedish Animal Welfare Agency's ethically approved protocols (Andrén et al. 2006; Arnemo and Evans 2017, permits C275/95 and C16/0). VHF collars were used between 1996 and 2008 (MOD335 and MOD400NH Telonics, Mesa, AZ, USA) and GPS collars were used between 2003 and 2015 (GPS plus mini, Vectronics Aerospace, Germany; Televilt Posrec 300 and Tellus 1C, Followit, Sweden).

I used 26,569 locations from 108 individuals (59 males and 49 females) monitored in central (1996-2015) and southern (2007-2015) Sweden. Two individuals were fitted with both a GPS and VHF collar at different times, resulting in 75 VHF-collared individuals (216 ± 364 locations/individual) and 36 GPS-collared individuals (295 ± 200 locations/individual). (Figure 1c).

4.1.2 Demographic – monitoring data (Paper II)

I used lynx monitoring data from the Swedish lynx monitoring system for lynx family groups between the years of 1993/1994 and 2018/2019 in central and southern Sweden (available in the carnivore database Rovbase;

rovbase30.miljodirektoratet.no) (Figure 1d). Lynx monitoring in Sweden is based on non-replicated counts of family groups, as described above.

4.1.3 Genetic – tissue samples (Papers III and IV)

The Swedish National Veterinary Institute (SVA) collects tissue samples from all lynx that are killed in Sweden, including road and train accidents, licensed hunting, lethal control, or animals that are found dead. The location, sex of the animal, and an approximate age are recorded and associated with the sample in every case. In Paper IV, I used 609 tissue samples from the SVA, which included all samples from southern Sweden and 70% of samples from central Sweden between 1993 and 2017. All samples were from lynx that were legally shot, killed in traffic, or found dead of other causes (Figure 1e). In paper III, known parent/offspring relatives were excluded to avoid bias toward related individuals, bringing the total number of samples to 600.

I extracted DNA from all the lynx tissue samples using the phenol-chloroform extraction method at Grimsö Wildlife Research Station. All samples were sequenced at Science for Life Laboratory, using the next-generation sequencing method “Restriction Site Associated DNA Sequencing,” or RADseq (Catchen et al. 2013, Andrews et al. 2016, Rochette et al. 2017). RADseq sequences short strands of DNA for the purpose of identifying single nucleotide polymorphisms, or SNPs.

Sequencing data was assembled de-novo, without a reference genome, using the Stacks software pipeline (Catchen et al. 2013, Andrews et al. 2016, Rochette et al. 2017). The SNP data was filtered using VCFtools v0.1.16 (Danecek et al. 2011) to exclude markers with lower than 15x coverage, more than 25% missing data, individuals with more than 25% missing data, markers with a minor allele frequency below 5%, and markers that were significantly out of Hardy-Weinberg Equilibrium with $p<.005$. The data was thinned to include only a single SNP per 126 base pairs, which is the sequence read length, to exclude linked markers.

4.2 Analysis

4.2.1 Landscape

Habitat data

Eight predictor variables were chosen based on previous studies of lynx resource selection (Table 1).

Table 1: Resource variables used in the resource selection functions

Category	Variable	Measure	Scale	Biological Meaning
Prey	Roe deer hunting bag	Number of roe deer shot per 1000 ha	Swedish hunting district, 54 to 6 704 km^2	Main prey of lynx in this area (Herfindal et al. 2005, Odden, Linnell and Andersen 2006, Gervasi et al. 2014)
Human disturbance	Distance to large roads	Distance from primary and secondary roads	Euclidean distance in meters	Possible avoidance of human activity (Basille et al. 2009, Basille et al. 2013, Kramer-Schadt et al. 2004)
	Distance to small roads	Distance from tertiary roads	Euclidean distance in meters	Possible avoidance of human activity (Basille et al. 2013, Basille et al. 2009, Kramer-Schadt et al. 2004)
	Human population density	Human population per km^2	25 x 25 meter grid cells	Possible avoidance of human activity (Bouyer et al. 2015a, Andrén et al. 2006, Bunnefeld et al. 2006, Gehr et al. 2017)
Land cover	Land cover class	Land cover category,	25 x 25 meter grid cells	Possible preference for certain land cover types and avoidance of others (Rauset et al. 2013, Samelius et al. 2013)
	Distance forest to edge	Distance from edge between forest and agriculture or grass land	25 x 25 meter grid cells	(Zimmermann, Breitenmoser-Würsten and Breitenmoser 2007)

Category	Variable	Measure	Scale	Biological Meaning
Terrain	Elevation	Meters above sea level	50 x 50 meter grid cells	(Bouyer et al. 2015b)
	Ruggedness	Terrain ruggedness index (TRI)	50 x 50 meter grid cells	Possible preference due to concealment (Bouyer et al. 2015b, Rauset et al. 2013)

Resource selection modelling

I used conditional logistic regression to estimate resource selection functions (RSFs) by sex, study area, and dispersal status (Chetkiewicz and Boyce 2009). RSFs rely on a use-availability design, wherein locations used by the animal (hereafter "used points") are compared to the available surrounding landscape (Boyce and McDonald 1999; Johnson et al. 2006; Manly et al. 2007). For availability data, I generated circular buffers around each VHF or GPS location using a radius of 16 km for established lynx and 5 km for dispersers, to approximate home range size and daily step length respectively. Five random points were generated within each buffer to represent available locations (Boyce et al. 2003). I used binomial generalized linear mixed effects models with logit links in the lme4 package (Bates et al. 2014) for R Studio 1.0.40 (R Core Team 2021) to model RSFs. All predictor variables were checked for collinearity using Pearson's correlation coefficient (Crawley 2014), and all continuous variables were standardized around their mean.

To test the predictive ability of our RSF models, I generated predictive surfaces (raster maps) wherein every pixel is assigned a resource value according to the model coefficients for the model with the best fit (Chetkiewicz and Boyce 2009; Hebblewhite et al. 2011; Inman et al. 2013). I validated the predictive power of these surfaces by checking the mean predicted habitat quality score of the lynx monitoring data that was not used in training each model, and comparing it to the predicted values from the training data using Welch two-sample t-tests in R (R Core Team 2021).

Habitat patch and connectivity

To test whether core habitat patches in southern Sweden are identifiable based on data from lynx in central Sweden, I used the results of the central area RSF to identify patches of contiguous habitat large enough to encompass three female home ranges (Aronsson et al. 2016; Herfindal et al. 2005), with greater than a 0.15 habitat quality score (0.167 being neutral selection). This probability was chosen because lynx can tolerate some non-optimal habitat in their home ranges, as mean habitat values for 95% kernels and 95% minimum convex polygons for established individuals are 0.170 (± 0.018 SD) and 0.174 (± 0.019 SD), respectively.

To evaluate connectivity, I used cost distance analysis to assess the resistance of the landscape between core habitat patches (Sawyer et al. 2011). I assessed connectivity between all habitat patches based on resistance values across the whole landscape, instead of using least cost path or corridors, so as to not artificially constrain the width of the passable landscape. Cost distances were calculated based on the habitat values assigned to each 25 by 25 meter map pixel, based on the RSF model results. I used Linkage Mapper 1.1.1 (McRae and Kavanagh 2011) to generate cost distance values for the matrix habitat between identified core habitat patches. I separately assessed these cost weighted distance values based on dispersing and established lynx RSF models, and created a raster map for each, wherein pixel values provide the cost-weighted distance to the nearest core habitat patch (McRae and Kavanagh 2011). I calculated the ratio between these rasters to test whether predictions made based on a group of established animals are sufficient to identify landscape that can facilitate dispersal.

4.2.2 Population growth

Population modelling

To assess the presence of an Allee Effect, or a lower growth rate at low population density, during lynx colonization of southern Sweden, we used Bayesian hierarchical population models, with four different process equations. In all process models μ_t is the deterministic prediction of the log lynx population at time t, N_t is the unobserved population size a time *t*, $H_{(t-1)}$ is the observed legal harvest of lynx at time *t-1* (i.e. legal harvest from the previous hunting season in February and March), and σ_{proc} is the standard deviation of the unobserved population size.

Process model 1 – Linear density-dependent growth rate

$\mu_t = \log[(N_{(t-1)} - H_{(t-1)}) \times \exp(a_0 + a_1 \times N_{(t-1)})]$

$N_t \sim \text{lognormal}(\mu_t, \sigma_{proc})$

Process model 2 - Quadratic density-dependent growth rate

$\mu_t = \log[(N_{(t-1)} - H_{(t-1)}) \times \exp(b_0 + b_1 \times N_{(t-1)} + b_2 \times N_{(t-1)}^2]$

$N_t \sim \text{lognormal}(\mu_t, \sigma_{proc})$

Process model 3 – Density-independent growth rate and comparing southern and central Sweden

$\mu_t = \log[(N_{(t-1)} - H_{(t-1)}) \times \exp(c_0)]$

$N_t \sim \text{lognormal}(\mu_t, \sigma_{proc})$

Process model 4 – Density-independent growth rate, including lynx killed in vehicle collisions and comparing southern and central Sweden

$\mu_t = \log[(N_{(t-1)} - H_{(t-1)} - T1_{(t-1)}) \times \exp(d_0) - T2_{(t-1)}]$

$N_t \sim \text{lognormal}(\mu_t, \sigma_{proc})$

In Process Model 1, a_0 represents the growth rate (log(λ)) at zero density and a_1 the per capita change in growth rate. If $a_1<0$, then a_0 is the maximum growth rate; r_max. However, if $a_1 >0$, then a_0 is the growth rate at zero density, and the growth rate increases as density increases. An Allee Effect would result in a positive a_1 estimate ($a_1 > 0$), while for classical density dependence the a_1 estimate would be negative ($a_1 < 0$).

In Process Model 2, b_0 represents the growth rate at zero density, b_1 and b_2 describe to shape of the quadratic curve. We added the quadratic term to test if the growth rate was first positive at low densities (i.e. Allee Effect), and then changes to negative when density increases (i.e. classic density-dependence), resulting in a hump-shaped growth rate curve, resulting in a negative b_2 estimate ($b_2 < 0$).

In Process Model 3, c_0 represent the estimated constant (density-independent) growth rate (log(λ)). We used one model to estimate the density-independent growth rate and included two region specific growth rates in the model: $c_{0\text{-}southern}$ (for southern Sweden) and $c_{0\text{-}central}$ (one common for Regions A, B and C in central Sweden).

In Process Model 4, d_0 represent the estimated constant growth rate when lynx killed in vehicle collisions (T) are included in the yearly mortality estimate, along with legal harvest. We used one model to estimate the density-independent growth rate, including lynx killed in vehicle collisions and included two region specific growth rates in the model; $d_{0\text{-}southern}$ and $d_{0\text{-}central}$. $T1_{(t-1)}$ is the observed number of lynx killed in vehicle collisions after the census in February but before the birth pulse in late May at time $t-1$ and $T2_{(t-1)}$ is the observed number of lynx killed in vehicle collisions after the birth pulse in late May but before the census in February at time t.

Observation model

All four process equations were linked to data using the same observation equation:

$alpha_t = N_t^2 / \sigma^2_{Nobs}$ and $beta_t = N_t / \sigma^2_{Nobs}$
$\varphi_t \sim \text{gamma}(alpha_t\ , beta_t)$
$FGobs_t \sim \text{Poisson}(p \times \varphi_t)$

$FGobs_t$ is the observed number of family groups at time t, p is the number of family groups per total number of lynx, σ_{Nobs} is the estimated observation error of the population size. This formulation views the count data hierarchically, where the mean observed count of lynx family groups at time t is Poisson distributed with mean φ_t multiplied by p and this mean (φ_t) is drawn from a gamma distribution with mean equal to the prediction of the process model and a standard deviation for observation error (σ_{Nobs}). We chose this approach because it allows the uncertainty in the data model to be larger than the variance of the Poisson parameter φ_t.

Model fitting and evaluation

Vague prior distributions were assigned to, a_0, a_1, b_0, b_1, b_2, c_0, and d_0, ~ normal(0, 100), σ_{proc} ~ uniform(0, 10) and σ_{Nobs} ~ uniform(0, 100). On average, one lynx family group represents 0.184 ± 0.013 SD of total number of lynx in the population (Andrén et al. 2002). The prior for the number of family groups per total number of lynx (p) was calculated from this using moment matching; $p \sim \text{beta}(152, 677)$. For all modelling and calculations of associated probabilities we used a Bayesian framework implemented in JAGS (Plummer 2003) called from R (www.r-project.org) using the 'rjags' package (Plummer et al. 2016). We ran three independent chains of 100,000 iterations following a 50,000 burn in. Convergence was assessed by visual inspection of trace plots and by the diagnostics of Heidelberger (Heidelberger and Welch 1983) and Gelman (Brooks and Gelman 1997). We used posterior predictive checks using Bayesian p-values (Hobbs and Hooten 2015). We present posterior means and SD with associated 95% Bayesian credible intervals (BCI).

4.2.3 Genetics

Individual heterozygosity and inbreeding coefficient

I assessed the spatial and temporal development of genetic diversity within the population by looking at heterozygosity and its implications for inbreeding. Expected heterozygosity (H_E) at the individual level is the probability that two randomly selected alleles from a given locus would be different if the population is in Hardy-Weinberg equilibrium (HWE) (Waits and Storfer 2015). Observed heterozygosity (H_O) is the actual proportion of heterozygous genotypes in the sample. The F statistic, F_{IS} or inbreeding coefficient, calculated as $F_{IS} = (H_E - H_O)/ H_E$, is a measure of the deviation of an individual from what would be expected under HWE (Waits and Storfer 2015). An inbreeding coefficient close to zero indicate low levels of inbreeding, and values close to one indicating high levels of inbreeding, respectively (Welles and Dlugosch 2019). Observed and expected heterozygosity per individual as well as the inbreeding coefficient were calculated using Plink version 1.9 (Chang et al. 2015).

Population structure

Population cluster analysis, spatial principal component analysis (sPCA), and discriminant analysis of principal components (DAPC) were conducted using the package “adegenet” (Jombart and Ahmet 2011) in R (R Core Team 2021) in order to assess structure within the population. Cluster analysis uses genetic distance metrics to group the samples into the most likely genetic clusters. Spatial PCAs are principal component analyses that use spatial information between samples to account for autocorrelation and identify spatially structured genetic variation. It first calculates a covariance matrix based on the genomic and spatial information of each individual, then identifies the principal components of this variation. I used the K nearest neighbor connection network with 4 neighbors and 10 axes each of positive and negative spatial autocorrelation.

Unlike the other two methods, DAPC relies on a-priori population definitions to assess the assignment of all individuals in the data set to one of the pre-defined populations. It does not rely on an assumption of HWE or linkage disequilibrium, which makes it especially applicable to an expanding population (Jombart and Ahmet 2011). In a DAPC, a PCA first transforms the data into a set of uncorrelated principal components, then uses these principal components to find linear combinations that maximize between-group variance and minimize within-group variance with the goal of separating genetic clusters. I used the central and southern regions of our study area as the two populations. I then divided the results of all three analyses into the three time periods representing pre-colonization (1993-2003), the colonization period (2004-2010), and the establishment period (2011-2017). This was done so the structure would be comparable over time, to be able to identify persistent or changing population structure.

I tested the F_{ST} value, which measures the proportion of the total genetic variance contained within a subpopulation relative to the total genetic variance (Holsinger and Weir 2009). For this analysis, I tested the differences when the population was divided by study area (n=2), by time period (n=3) using the –fst function in Plink.

Individual relatedness

I calculated individual relatedness using the –genome flag in Plink version 1.9 (Chang et al. 2015), which estimates pairwise kinship coefficients by using a method-of-moments approach to calculate the probability of sharing zero, one, or two alleles by identity by descent at each locus between any two individuals in a randomly-mating population (Purcell et al. 2007). A value of one indicates that the two individuals are identical by descent (IBD) at all loci, meaning they inherited the same alleles from a common ancestor. A value of zero indicates that the two individuals are unrelated, meaning they did not inherit any alleles IBD from a common ancestor. A value of .5 indicates they share half their alleles from a common ancestor. I calculated pairwise kinship coefficients using both these methods for every pair within our data set. Primary or first-order relatives are those that share 50% of their alleles, i.e. parent/offspring or full siblings. Secondary or second-order relatives are those that share 25% of their alleles, i.e. grandparent/ grand offspring or half siblings, and tertiary or third-order relatives are those that share approximately 12.5% of alleles, such as a great-grandparental relationship or first cousins.

Isolation by distance and resistance

I calculated geographic distance between all pairs of individual sampling locations using QGIS 3.18.2 (2021). I also calculated the cost distance between each pair of lynx in the data set using the model predictions for habitat selection for dispersing lynx taken from Paper I. I used Mantel tests to assess the correlation between relatedness and geographic distance, and relatedness and cost distance in the vegan R package (Oksanen et al. 2013). I also calculated this correlation for pairs within each sex (male-male pairs, n=336, female-female pairs, n=263), to look for sex-based differences. I also did this calculation within regions, i.e. for pairs that are both in central Sweden (n=558) or both in southern Sweden (n=52) to capture any difference between the source population and the area of expansion.

Kinship assignment

For each dyad, I assessed the number of alleles that are shared by IBD to assign a most likely relationship category for the pair, using the Z0, Z1, and Z2 statistic (collectively called Z statistics) in Plink version 1.9 (Chang et al. 2015) using the –genome flag. Z0, Z1, and Z2 give the proportion of sites at which the two individuals share zero, one, or two alleles by IBD respectively. I then calculated the Euclidean distance between the Z0, Z1, and Z2 values for each pair with the expected values for each relationship type using the following formula[2]:

$$\sqrt{\left(Z_0 - Z_{0[Expected]}\right)^2 + \left(Z_1 - Z_{1[Expected]}\right)^2 + \left(Z_2 - Z_{2[Expected]}\right)^2}$$

The relationship type with the shortest distance was assigned as the most likely relationship type.

Dispersal distances

For primary relatives, which are parent/offspring or full sibling pairs, I assessed the geographic difference in distance between male-male, male-female, and female-female pairs. I did not do this for secondary and tertiary relatives, as the sex of the intervening relative is not known, and therefore sex-based dispersal patterns cannot be established.

5. Results and discussion

5.1 Landscape

The purpose of this study (Paper I) was to identify available habitat for dispersing and established lynx in southern Sweden, and to identify barriers or corridors that could inhibit or facilitate lynx recolonization. I found that lynx with established home ranges select for forest and against areas of human infrastructure, which is consistent with previous findings (Niedziałkowska et al. 2006). I also found that more than half of the land in southern Sweden provides sufficient habitat quality in large enough patches for a lynx population to establish. Additionally, the matrix landscape between these patches, and between habitat patches in central and southern Sweden, is sufficiently permeable for lynx to disperse between them, therefore maintaining connectivity to the source population in central Sweden. Therefore, the first criteria I established in the introduction to this thesis with regard to defining a successful recolonization, that there must be sufficient suitable habitat for the population to establish in the recolonization area, is fulfilled in the case of the lynx in southern Sweden.

5.1.1 Resource selection

I found that female and male lynx select similar habitat. All variables were included in the best models best describing resource selection for both female and male adult lynx with established home ranges (Table 2). Both sexes selected for forest and against semi-natural areas, marshland, human infrastructure, and waterways. Male and female lynx selected more similarly within each region, whereas the differences in selection between central and southern Sweden were more pronounced than between the sexes within either study area. Established lynx of both sexes selected against grassland and agricultural land in the central area, whereas, surprisingly, lynx selected for these land cover types in the south. Southern established lynx of both sexes and central males selected against areas of higher roe deer availability, whereas central females selected for roe deer availability. This selection against prey availability may indicate that prey is sufficiently abundant across the whole region that the lynx can select for areas in which fewer roe deer are present.

Lynx were less selective during their natal dispersal than were established adults. The resource selection models for dispersers did not include anthropogenic or prey-related variables as they did for adult lynx. However, when the locations of dispersing lynx were assessed against the predictive surface based on the central established lynx model, the mean habitat quality score was not significantly different (p=0.28) from the central established lynx. This result indicates that although our model selection process tells us dispersing lynx are less selective than established lynx, they do select the same habitat as their older and more established conspecifics. For variables that were identified as important for both established and dispersing lynx, dispersers tended to select in accordance with established lynx. Selection information for all variables is given in Table 2.

Table 2: Direction and significance of selection of each resource selection variable, by region and establishment status. Plus signs (+) indicate selection for a resource, minus signs (-) indicate selection against a resource, and slashes (/) indicate neutral selection. The number of asterisks indicate the p value significance, with (.), (*), (**), and (***) indicating p value of <.1, .05, .01, and .005 respectively. Blanks indicate variables that were not in the final model.

	Coniferous Forest	Deciduous Forest	Young Forest, Thicket	Mixed Forest	Grassland, Pasture	Semi-Natural	Bare Ground, Rock	Agracultural Land	Human Ifrastructure	Bog and Water	Distance to Forest Edge	Human Population	Distance to large road	Distance to small road	Terrain Ruggedness	Elevation	Roe Deer Hunting Bag
Model	Land cover											Anthropogenic			Terrain		Prey
Established Central (All)	+ ***	+ ***	+ ***	+ ***	– ***	– ***	+	– ***	– ***	– ***	– ***	– ***	+ ***	– ***	+ ***	– ***	+ ***
Established Central (M)	/ ***	+ ***	+ ***	+	– **	– .	+	– ***	– ***	– ***	– *	– ***	+ ***	– ***	+ ***	– ***	– *
Established Central (F)	+ ***	+ ***	+ ***	+ ***	– ***	– ***	–	– ***	– ***	– ***	– ***	– ***	+ ***	– ***	+ ***	– ***	+ ***
Established South (All)	– ***	+ ***	+ ***	+ ***	+ ***	– *	+ **	+ ***	– ***	– ***	– ***	– ***	+ ***	+ ***	+ ***	+ ***	– ***
Established South (M)	– ***	+ ***	+ ***	+ **	+ ***	–	+ **	+ *	– ***	– ***	– ***	– ***	+ ***	+ ***	+ ***	+ ***	– ***
Established South (F)	– ***	+ ***	+ ***	+ .	+ ***	–	–	+ ***	– ***	– ***	– *	– ***	+ ***	– ***	+ ***	+ ***	– ***
Disperser (All)	+ ***	+ **	+ **	+	–	–		– ***	– **	– ***	– *				+ ***	– *	
Disperser (M)	– ***	+ ***	+ **	+	–	–		– **	– .	– **	–				+ ***	–	
Disperser (F)	+ ***	+	+	+ .	–	–		– ***	– *	– *	– *				+ ***	– *	

5.1.2 Habitat availability

Our resource selection study found eight contiguous patches of habitat larger than three female home ranges and therefore suitable for lynx population establishment (Figure 3). They ranged in size from 1,388 to 26,720 km^2, covering 49% of the landscape and spanning both central and southern Sweden, including 52% of southern Sweden. Five patches as large as one female home range each were also identified (Figure 3b). Although these were not considered establishment areas due to their size, they demonstrate that sufficiently suitable habitat for lynx to pass between central and southern Sweden is available even within this narrow area of land with sparse forests and a relatively high anthropogenic footprint.

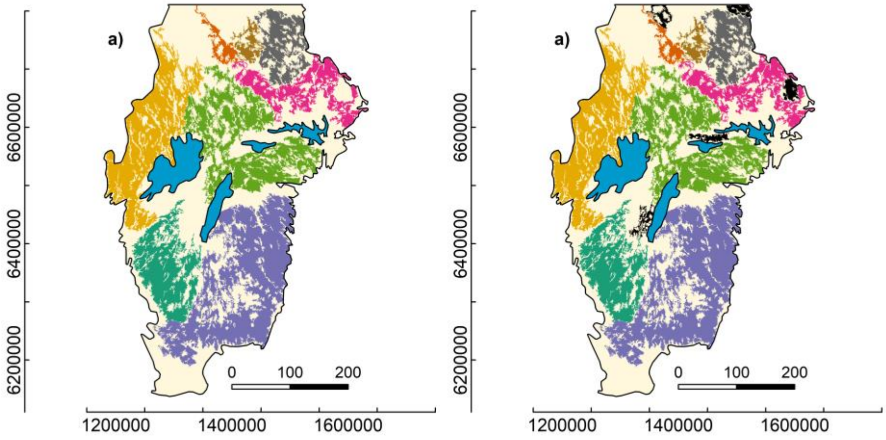

Figure 3: a) Core habitat patches identified based on a size threshold of three female home ranges. b) Core habitat patches based on a size threshold of one female home range. Patches that are smaller than two female home ranges are shown in black.

Southern established lynx selected higher quality habitat (0.218 ± 0.105 SD) compared to central established lynx irrespective of the predictive surface used ($p<0.001$). We would expect this result because the lynx population in central Sweden is denser (Andrén 2022), whereas those in southern Sweden were expanding into available territory. These results indicate that there is sufficient suitable habitat in southern Sweden for a lynx population to establish. The large amount of available habitat, covering more than half of land area, is comparable to central Sweden where lynx have been present for decades. Additionally, the propensity of lynx in southern Sweden to establish in high quality habitat indicates that the area is not yet saturated, and lynx are selecting the best possible habitat to establish their home ranges.

5.1.3 Connectivity between habitat patches

Cost-weighted distances between core habitat patches identify very similar areas of permeability regardless of whether the assessment was based on established or dispersing lynx, although the resistance of the landscape was estimated to be higher, i.e. less permeable, for surfaces based on established lynx models. This result could be expected since dispersers select the same as established lynx. In all cases, the matrix habitat between core habitat patches is permeable, suggesting full connectivity across the entire study area. The median cost distance value based on established lynx was 26% higher than for dispersing lynx, with minimum, first quartile, third quartile, and maximum of 0%, 22%, 31%, and 94% higher values respectively for established lynx.

5.2 Population growth

An Allee Effect is the situation in which low population density leads to slower population growth. Allee Effects in wide-ranging, solitary species can result from limits in reproduction (i.e. low mate encounter rate), survival (i.e. local stochastic effects on the population), or genetics (i.e. inbreeding depression resulting from genetic drift in an isolated population) (Courchamp et al. 1999, Berec et al. 2007). A key goal of Swedish lynx management has been to encourage a population shift toward the south, to ease reindeer predation pressure in the north. In this study (Paper II), we set out to assess whether an Allee Effect, or inverse density dependence, was slowing lynx population growth in southern Sweden. We found a 94% probability that the population of southern Sweden did grow more slowly than that of central Sweden during its recolonization (Figure 4), but we found that inverse density dependence, i.e. an Allee Effect, was unlikely to be driving this slower growth rate. However, although our population simulations revealed a non-negligible (30%) chance that population observed development could include an Allee Effect.

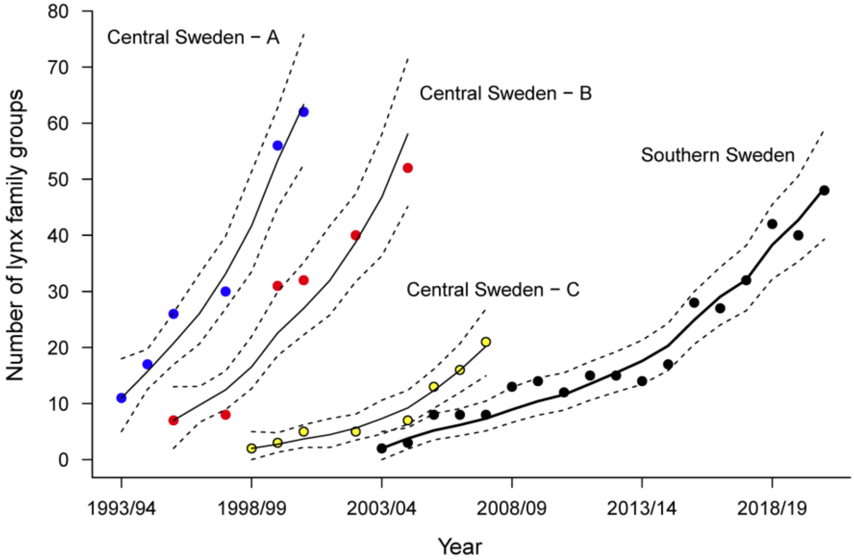

Figure 4: Number of lynx family groups in relation to year in central Sweden (Region A, blue dots; Region B, red dots; and Region C, yellow dots) and southern Sweden (black dots). Medians of posterior distributions of the estimated number of lynx family groups (solid line) and 95% Bayesian credible intervals (dashed lines).

A low mate encounter rate would be the most likely mechanism to drive an Allee Effect due to the low population density in southern Sweden, leading to a low population growth rate (Berec et al. 2007, Deredec and Courchamp 2007). However, lynx were recorded in southern Sweden prior to 2003 when the first reproduction was documented, with a male lynx killed in the year 2000 in southwest Sweden (Paper III and IV), and six VHF-collared males and one female between 1999 and 2002 (Paper I). Lynx display a male-biased dispersal pattern, in which many females (ca. 55 %) but few males settle in areas neighboring their natal home range, males disperse further (mean 149 km, 32 – 428 km) than females (mean 46 km, 3 – 215 km; (Samelius et al. 2012)). Although our data for lynx in southern Sweden prior to 2003 are few, they align with this expectation, in that seven of the eight lynx recorded in southern Sweden were male. Therefore, it is likely that female lynx faced no shortage of mate choice when they moved southward. Additionally, males roam over larger home ranges, especially at low population density (Aronsson et al. 2016), increasing the likelihood of mate encounters and decreasing the likelihood of local stochastic effects influencing the population. Since we found a high degree of connectivity between central and southern Sweden (Paper I, Paper IV), it could be the case that lynx in southern Sweden did not face the risks associated with a small population size because they were not cut off from the established population in central Sweden.

The second criteria I defined in the introduction to identify a successful range expansion is that the animals in question need to have sufficient mating opportunities when they arrive at the recolonization area, i.e. they need to be able to find each other. In this case, we found that the lynx in southern Sweden have no trouble with that, and therefore this recolonization can be considered successful in this regard.

5.2.1 Population growth during recolonization

We found that the population of southern Sweden did grow more slowly than that of central Sweden during its previous recolonization. Of our four population growth models, the two that used density-independent growth rates (models three and four, see methods) displayed the best model fit. Model three, which did not include an Allee Effect, gave a 94% probability that the growth rate in southern Sweden was lower than in central Sweden during its recolonization phase. Model four, which differed from model three only in that it included traffic mortality, gave a 93% probability.

Models one and two, which included a linear and quadratic density-dependent growth rate respectively, failed the Heidelberger diagnostic, while model 1 also failed to converge and model two's posterior distributions were centered around zero with large standard deviations, indicating that neither fit the data. Models three and four used a density independent growth rate, and compared growth between central and southern Sweden. The results of Models 3 and 4 were almost identical, with a growth rate in southern Sweden ($c_{0\text{-southern}}$) estimated at 0.19 and central Sweden ($c_{0\text{-central}}$) during the recolonization (1994 – 2008) estimated at 0.25. For Model 4, this growth rate corresponds to a lambda ($\lambda = \exp(c_{0\text{-southern}})$) of 1.20 (± 0.04 SD) and ($\lambda = \exp(c_{0\text{-central}})$) of 1.29 (± 0.04 SD). The mean lambda in Model 4 was (λ =

exp($d_{0\text{-}south}$)) for southern Sweden was 1.24 (± 0.04 SD) and for central Sweden was 1.31 (± 0.03 SD).

5.3 Genetics

The purpose of this study was to investigate the genetic structure of the lynx population in central and southern Sweden (Paper III), and to investigate how individual dispersal patterns have influenced this structure (Paper IV). I found the population across central and southern Sweden to be essentially panmictic, with no spatial or temporal clustering, and no effect of latitude or date on individual heterozygosity or inbreeding. I found no effect of isolation by distance or isolation by resistance, with primary relatives, or those related within a single generation, across the study area from one another.

The third criteria I defined with regard to a successful recolonization is the maintenance of genetic connectivity to the source population, to prevent isolation and resultant inbreeding. In this case, I found perfect connectivity between lynx in the source population in central Sweden and the recolonizers in the south, to the point that there is no distinction between the two areas. Although Scandinavian lynx are less genetically diverse than other Eurasian lynx populations due to their relative isolation from the rest of Eurasia (Schmidt et al. 2011, Rueness et al. 2013), there has been no further loss of diversity in comparison with the source population as lynx have spread southward. Therefore, this has proven to be a successful recolonization from a genetic standpoint.

5.3.1 Individual heterozygosity and inbreeding

Neither individual heterozygosity nor inbreeding displayed any change by latitude or through time, suggesting that at no point during the recolonization was a group of lynx isolated from the others (Figure 5). Our results showed that mean expected heterozygosity (H_E) was slightly higher than mean observed heterozygosity (H_O) at 0.347 ± 0.001 SD and 0.343 ± 0.034 SD respectively ($p=0.002$; Welch’s two-sample t-test). Expected and observed heterozygosity are the same in populations with perfect mate choice, which are at HWE (Waits and Storfer 2015). If the southern population was established by a limited number of founders or in isolated pockets, allele frequencies would change due to genetic drift, and we would expect to find lower observed heterozygosity further south. The mean inbreeding coefficient F_{IS} value was 0.014 ± 0.097 SD, (p=0.002, one-sample t-test), whereas we would expect it to not differ from zero if no inbreeding were occurring. Although we found significant p values in both cases, the standard deviations both far exceeded the difference in means, which indicates that for any individual sample, the mean of the other group is within its standard deviation. This effect suggests that H_E and H_O effectively overlap, and F_{IS} effectively overlaps with 0, suggesting no isolation between the central source population and newly recolonized southern Sweden.

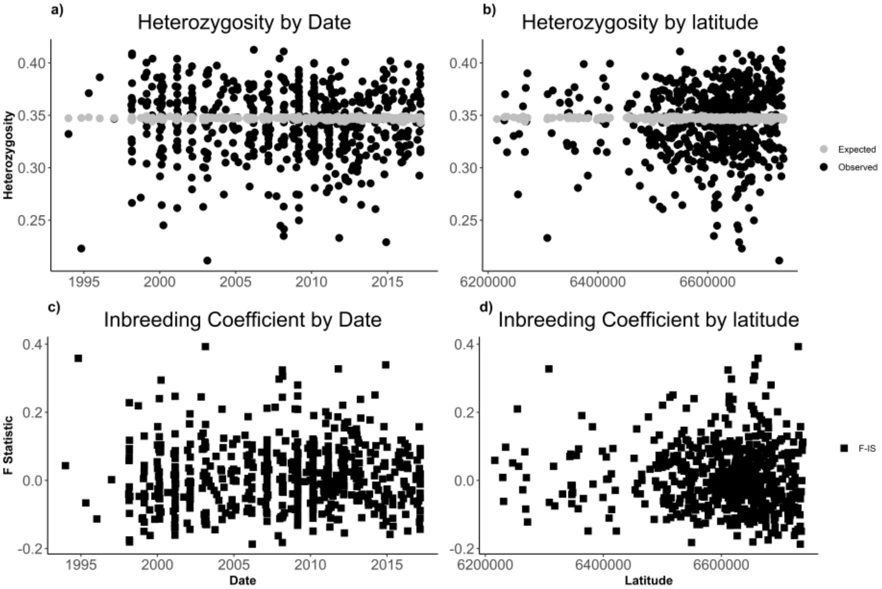

Figure 5: A) Observed and expected heterozygosity by individual, plotted by date. B) Observed and expected heterozygosity plotted by latitude. C) FIS inbreeding coefficient, plotted by date. D) FIS inbreeding coefficient, plotted by latitude.

5.3.2 Population cluster analysis

The results of cluster analysis and spatial PCA (sPCA) showed no indication of population structure developing during the recolonization (Figure 6), nor did discriminant analysis of principal components (DAPC). These results corroborated my findings at the individual level given in section 5.3.1. As the population spread southward, neither the cluster analysis nor sPCA suggested structure. The cluster analysis suggested two genetic groups, but these groups did not cluster together spatially, while no structure was apparent from the sPCA. The DAPC population assignments did not group together according to latitude, therefore suggesting no population distinction between central and southern Sweden.

When spatial and temporal groups are compared using fixation index, F_{ST} estimates show low differentiation between spatial and temporal groups. Between central and southern Sweden, the mean F_{ST} was 0.011. This means that just 1.1% of the genetic variation observed between lynx in this sample set is due to their assignment to central or southern Sweden. When the populations were divided by time period rather than geographically, the mean F_{ST} estimate was even lower, at 0.003, meaning that 0.3% of the genetic difference is due to which temporal group the samples were in.

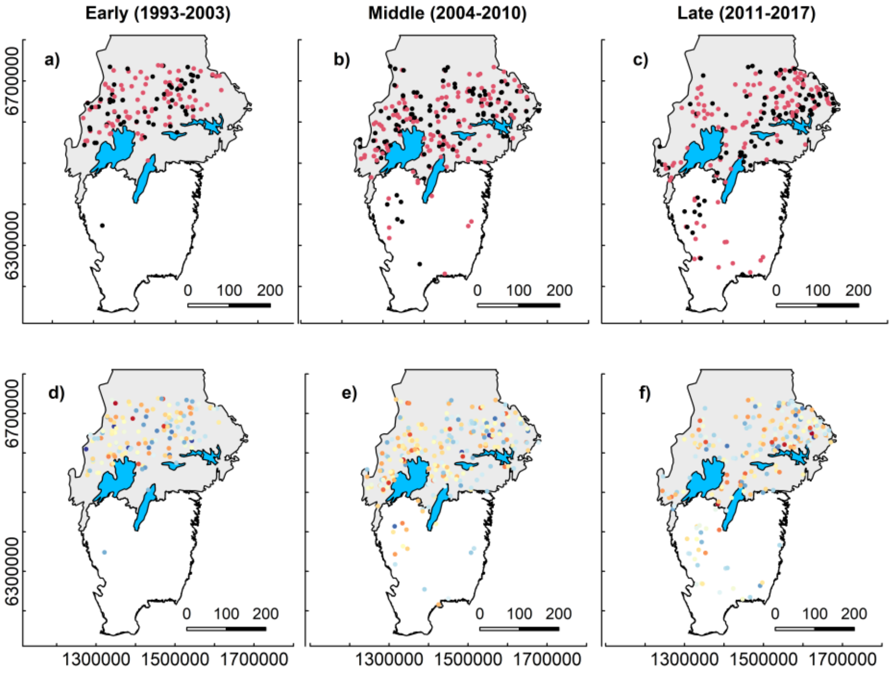

Figure 6: Spatial distribution of cluster analysis and spatial PCA analysis. a-c) Cluster analysis results for each of the three time periods. d-f) Spatial PCA results for each of the three time periods. The colors represent the same cluster in a-c) and the same sPCA value in d-f). The central study area is grey and the southern study area is white.

5.3.3 Individual relatedness and dispersal

Of the 609 lynx in the data set, 366 had at least one primary relative (parent-offspring or full sibling) within the data set, with a maximum of seven primary relatives for one individual. Members of related pairs occurred across the entire study area for both males and females, with no discernible spatial pattern. Every lynx in our data set except one had at least one secondary relative in the data set.

Members of primary relative pairs were found across the study area from one another, with a mean distance of 50 ± 62 SD km for females (n=73 pairs) and 82 ± 86 SD km for males (n = 82), with a maximum of 215 and 428 kilometers for females and males respectively (Figure 7).

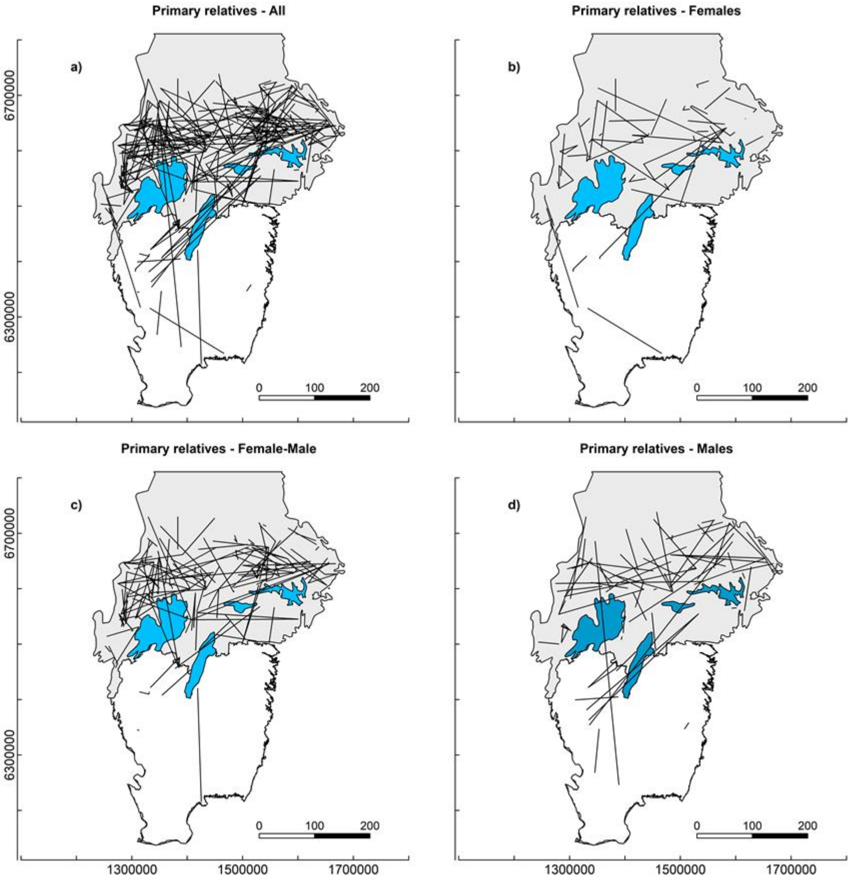

Figure 7: Spatial distribution of primary relative pairs of lynx by sex. Primary or first-order relatives have a relatedness coefficient of 0.4-0.75. The central study area is grey and the southern study area is white.

5.3.4 Isolation by distance and resistance

There was no significant correlation between genetic distance and geographic distance for the whole population, regardless of sex or regional pairings (Figure 8). In all cases, the Mantel statistic r values were negative, suggesting a weak negative relationship, but the p-values were all 0.96 or greater, indicating no statistically significant correlation. There was also no significant correlation between genetic distance and cost distance, controlled for geographic distance, for the whole population, female-female pairs, male-male pairs, pairs within the central region, and pairs within the southern region. This lack of correlation held true when distances were restricted to known sex-specific dispersal distances from this region. In all cases, the Mantel statistic r values were close to zero, indicating a very weak relationship. The p-values were all 0.375 or greater, suggesting no statistically significant correlation. The geographic distance and cost distance values are highly correlated at over 97%. The similarity of the cost distance and Euclidian distance values indicate that lynx do not face impediments to moving through the landscape, even in areas of high human development.

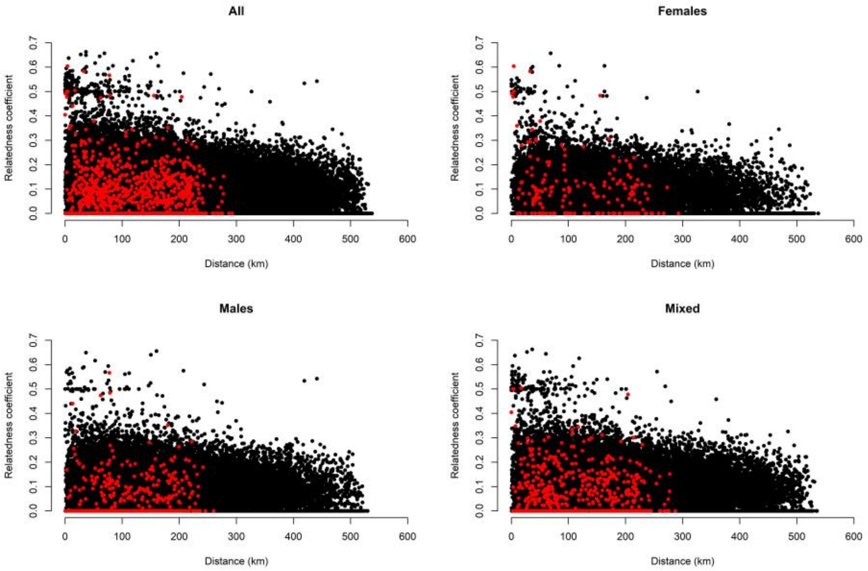

Figure 8: Geographic distance and relatedness coefficient for all pairs of lynx in the data set, by sex and region (pairs in which one or both lynx are in central Sweden are black, pairs in which both lynx are in southern Sweden are red).

6. Conservation implications

Wildlife managers and conservation planners worldwide face the challenge of protecting populations of wide-ranging mammals and facilitating their recovery (Treves and Karanth 2003, Beier et al. 2008, Karanth and Chellam 2009, Chapron et al. 2014, Tucker et al. 2018). Forty-eight percent of carnivore species are decreasing according to the IUCN Red List, while 29 of the 38 extant felid species (76%) are in decline (Fernández-Sepúlveda and Martín 2022). This thesis provides an example in which the Eurasian lynx recolonized southern Sweden. In the introduction to this thesis, I defined a successful recolonization as one that fulfills the following criteria:

1. Sufficient suitable habitat must be available for the species in question to recolonize, including sufficient food availability (Fahrig 2001, Tucker et al. 2018).
2. There must be sufficient mate availability on the frontier of recolonization for reproduction to occur and the population to grow (Berec et al. 2007).
3. The genetic health of the newly established population must be maintained to not suffer fitness consequences due to inbreeding (Cushman et al. 2018).

This recolonization was successful because there was a robust management structure in place to encourage growth, suitable habitat available for the population to establish, and sufficient connectivity between the source population and destination area. The lynx population was able to maintain near perfect connectivity to the source population in central Sweden despite a belt of agricultural land, highways, and towns, which are all avoided by lynx (Kramer-Schadt et al. 2004). As human infrastructure increasingly encroaches on wildlife habitat globally, and roads cut through previously natural areas, such a land-sharing success story provides hope for other wide-ranging carnivores. Let us examine what lessons from this recolonization can be applied more broadly to help facilitate wildlife range expansion elsewhere.

Firstly, species with a higher ability to use non-optimal matrix habitat are less vulnerable to habitat fragmentation and human encroachment (Fahrig 2001). Although the Eurasian lynx is considered a habitat generalist

(Schmidt et al. 2011), it does rely on forest (Niedziałkowska et al. 2007, Cimatti et al. 2021, Oeser et al 2023). Although lynx have a relatively high tolerance for human infrastructure, they are not impervious to human disturbance (Cimatti et al. 2021, Ripari et al. 2022), and they need refuge habitat nearby in order to use heavily human-modified landscape (Basille et al. 2009, Ripari et al. 2022, Oeser et al. 2023). Interestingly, Canadian lynx show gradual genetic structure with a few overlapping clusters across North America, with lower expected heterozygosity but not observed heterozygosity in peripheral populations (Schwartz et al. 2003). They are not separated into small, fragmented populations like their European counterparts (Rueness et al. 2003b). Although Canadian lynx are considered habitat and prey specialists, they disperse through matrix habitat that would never be considered suitable for establishment (Vanbianchi et al. 2018). Therefore, the ability of dispersing individuals to pass through non-optimal matrix may be more important than the degree of habitat specialization that adults display in establishing their home ranges.

Even for species that are able to move through sub-optimal habitat, there are limits. While I found no impediments to recolonization and no genetic structure during recolonization in this study system (Papers III and IV), small populations of reintroduced Eurasian lynx in central Europe have faced challenges due to small population sizes, poor connectivity, and human persecution (Sindičić et al. 2013, Chapron et al. 2014, Bull et al. 2016, Gajdárová et al. 2021). Pumas in North America are similarly wide-ranging felids that face genetic isolation when faced with anthropogenic barriers, as in southern California (Gustafson et al. 2017) and Florida (Johnson et al. 2010). Like Eurasian and Canadian lynx, puma populations can remain essentially panmictic over large areas, such as in Wyoming, USA (Anderson et al. 2004). However, when small groups are cut off from the source population by highways, they lose genetic diversity. Therefore, maintaining connectivity to a large source population appears to be a defining characteristic of successful recolonization.

Encouragingly, the complete avoidance of humans and human infrastructure is not necessary, even for elusive species that require forest or other natural habitat. The largest protected area in southern Sweden is smaller than a single lynx home range (Paper I), and yet lynx have successfully recolonized Sweden using a land sharing model. Many carnivore populations elsewhere in the world are decreasing due to the habitat fragmentation, prey depletion, and direct elimination by humans, with the only viable solution perceived to be the sparing of large protected areas away from human settlement, which is not always feasible (Karanth and Chellam 2009).

Carnivore conservation is as much a social endeavor as an ecological one, because conflicts are fraught with social and political implications, as well as deeply rooted cultural values (Treves and Karanth 2003). In the 1920s, Sweden officially considered lynx to be pests, and had the explicit management policy of total eradication (Lönnberg 1930). Today, lynx occupy the entire length of the country, and the population is the highest it has been in a century. The Swedish Environmental Protection Agency publishes clear, scientifically informed population targets (SEPA 2019, Odden and Frank 2022). Monitoring data is public (rovbase.com). Management is decentralized at the level of the county administrative board and includes Wildlife Management Delegations, which were formed for the purpose of strengthening the legitimacy of wildlife management institutions through local engagement between stakeholders with different views (Lundmark and Matti 2015). Redpath et al. (2013) assert that difficult conflicts can be overcome when all stakeholders can agree to work together on the issue and define clear goals, maintain access to transparent evidence, and acknowledge trade-offs for the other stakeholders as well as themselves. Although Sweden's management system may not perfectly fit this model, it has provided a regulatory background against which the lynx population has been able to recover. This is not to say that all of society agrees or even complies. Legal and illegal hunting is the primary cause of death in adult lynx in Sweden (Andrén et al. 2006, Andrén et al. 2022b). Poaching causes up to 46% of adult mortality in north and central Scandinavia (Andrén et al. 2006), and is a significant factor in southern Sweden (Andrén et al. 2022b). This figure is similar to more fragmented lynx populations in central Europe (Heurich et al. 2018, Červený et al. 2019, Arlettaz et al. 2021). Interestingly, the region in Scandinavia that had the highest legal harvest of lynx also had the lowest incidence of poaching, although there is not a simple relationship between increased legal harvest and decreased illegal harvest across Scandinavia (Andrén et al 2006). A culture of tolerance toward large carnivores is frequently cited as a contributing factor to lynx recovery in Europe (e.g. Chapron et al. 2014, Cimatti et al. 2021). Although tolerance is important, this study shows that adherence to a policy of total compliance with conservation goal is not a necessary condition for large carnivore recovery.

Maintaining landscape connectivity between habitat patches and genetic connectivity between source areas and areas of recolonization allow a population to expand and remain genetically diverse. Therefore, connectivity is the defining characteristic of a successful recolonization. This finding is empowering for conservation planners. While we cannot realistically hope to follow the land-sparing model of setting aside enough untouched land for wide-ranging carnivores to maintain large populations, and we cannot prevent human encroachment on all natural areas or human persecution of wildlife, we can promote habitat connectivity. Wildlife underpasses and overpasses have been successfully used to avoid traffic mortality and connect populations of wide-ranging mammals that would otherwise be in danger of fragmentation (Smith et al. 2015, Simpson et al. 2016, Brennan et al. 2022). They have been used successfully to avoid traffic mortality and facilitate gene flow for pumas in Florida (Foster and Humphrey 1995), and are used by moose (*Alces alces*) in the same region as our study (Olsson et al. 2008). It is worth noting that following certain design guidelines, such as building overpasses 50 meters or wider, increase their effectiveness, and guidelines are available for conservation planners to maximize effectiveness (e.g. Simpson et al. 2016, Brennan et al. 2022).

In cases where populations are too small or fragmented to naturally recover, other interventions can be followed that seek to mimic natural dispersal between populations, thus helping fragmented or reintroduced populations to overcome isolation (Premier et al. 2021). These interventions include translocations and captive breeding and release programs, which have been followed and continue to be recommended for the disparate lynx populations in central Europe (Premier et al. 2021).

Every recolonization occurs within a unique cultural and ecological context. Therefore, these suggestions are not intended to be prescriptive, but rather to provide examples from which other managers and conservation planners can draw inspiration as they design solutions to increase connectivity for their respective species and systems of interest.

7. Conclusion

The recolonization of the Eurasian lynx from central to southern Sweden was a success. According to the first criterion I suggested, there must be sufficient suitable habitat for the population to establish in the recolonization area, which I found to be the case. Secondly, mates must be available and reachable to animals at the frontier of recolonization for the population to establish, which they were. We found that the population in southern Sweden likely did not face an Allee Effect, likely due to its connectivity to central Sweden. Therefore, the population should not become genetically isolated and face the resulting risk of inbreeding depression. We found no evidence of the development of population structure, decreasing heterozygosity, or increasing levels of inbreeding during recolonization. This success was enabled by strong landscape connectivity between the source area and the frontier of recolonization. No amount of suitable habitat or potential mates would make a difference if the lynx could not reach them. Finally, this entire range expansion was facilitated by a management policy that encouraged growth in southern Sweden and allowed the expanding population to retain connectivity to the established central population. It is my hope that this case study can serve as an example to help plan and facilitate wildlife recolonizations around the world.

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Popular science summary

Imagine hiking in the forest of southern Sweden, your path littered with bilberry bushes and fresh chanterelle mushrooms. As you stop to admire a patch of lichen on a birch trunk, you notice that the ambient bird songs have faded. A hush settles across the forest. You feel a pair of eyes on your back. As you turn around, a pair of piercing yellow eyes meets your gaze. You can hardly believe it – a lynx, Sweden's elusive big cat, is staring at you from across a clearing. This majestic feline sits atop a rocky outcropping sunning itself, with the pointed tufts on the ends of its ears cocked toward you. It yawns, arching its golden-brown back in a deep stretch. With one last glance at you, it climbs down from the rock, turns toward the tree line, and disappears into the underbrush.

Experiences like this are now possible in southern Sweden for the first time in more than one hundred years. The Eurasian lynx, once hunted to the brink of extinction in the early 20th century, has naturally recolonized Sweden, with a current population estimate of around 1200-1600 in Sweden. As recently as 2003, there was no permanent lynx population in southern Sweden. Since then, the population in the region has recovered to approximately 345 individuals in the winter of 2021/2022, which is more than double the minimum target of 148 lynx for the region.

The journey of lynx back to their former range, a process known as recolonization, poses a challenge for the animals attempting it. For a recolonization to be successful, there must be enough of suitable habitat for the population to establish, enough lynx in the recently recolonized area to sustain population growth, and enough genetic diversity within the population to prevent inbreeding. Connectivity between the source population and the area of recolonization is essential to enable lynx to reach new habitat, find mates, and therefore maintain a genetically diverse population. A favourable management regime is also necessary, because too much human persecution can doom even the strongest recolonization efforts to failure.

In my thesis, I strived to better understand the recolonization journey of the lynx from central to southern Sweden. The first part of the study involved identifying suitable habitats for lynx, using scientific techniques to analyze landscape features that the lynx select. Next, we explored the lynx population growth rate in the newly colonized areas to check whether recolonization occurred more slowly than in previous areas, and whether slower growth may have been driven by low population density (called an Allee effect). Finally, we analyzed the genetic diversity in the population using population genomics, a method that uses thousands of DNA snippets from each individual to learn about the population structure and development.

This research revealed a success story of recovery and resilience. There is an abundance of suitable habitat for lynx in southern Sweden, and they have successfully settled there. Despite initially slow growth, the population maintains close ties with lynx in central Sweden, which has led to no loss of genetic diversity in the south. Despite past hardships, the lynx population has re-established in southern Sweden, thanks to management policies that have favored its recolonization, a low level of human persecution, and the impressive ability of lynx to disperse for hundreds of kilometers, even across unfavorable habitat like farmland or areas with buildings and other human development.

It is our hope that this example of a successful recolonization serves as a template for the restoration of large carnivores worldwide. It illustrates the importance of connectivity and the need for careful management strategies that encourage human tolerance and facilitate population growth. As we look towards the future, the ability of lynx to reclaim their ancestral homeland reminds us that with the right conditions and protections, nature has an extraordinary ability to recover.

Populärvetenskaplig sammanfattning

Föreställ dig att du vandrar i skogarna i södra Sverige, din stig kantad av blåbärsris och kantareller. När du stannar för att beundra några lavar på en björkstam märker du att fåglarna har tystnat. En stillhet lägger sig över skogen. Du känner någons blick i nacken. När du vänder dig om möter ett par genomträngande gula ögon din blick. Du kan knappt tro det – en lo, Sveriges skygga stora katt, stirrar på dig från andra sidan en glänta. Detta majestätiska kattdjur sitter på en klippavsats och solar sig, med de spetsiga tofsarna på öronen riktade mot dig. Den gäspar, sträcker ut sin gyllenbruna rygg. Med en sista blick på dig klättrar den ner från klippan, vänder sig mot skogskanten och försvinner in i undervegetationen.

Upplevelser som denna är nu möjliga i södra Sverige för första gången på över hundra år. Den eurasiska lon, som en gång jagades till utrotningens rand i början av 1900-talet, har naturligt återkoloniserat Sverige med idag en population på cirka 1200-1600 individer i Sverige. Så sent som 2003 fanns ingen permanent lopopulation i södra Sverige. Sedan dess har populationen i regionen återhämtat sig till cirka 345 individer under vintern 2021/2022, vilket är mer än dubbelt så många som förvaltningens miniminivån på 148 loar för regionen.

Lons resa tillbaka till sitt tidigare utbredningsområde, en återkolonisering, har varit en utmaning. För att en återkolonisering ska lyckas måste det finnas gott om lämpliga livsmiljöer för att populationen ska kunna etablera sig, tillräckligt många loar i det nyligen återkoloniserade området för att upprätthålla populationstillväxt, och tillräcklig genetisk mångfald inom populationen för att förhindra inavel. Kontakten mellan kärnpopulationen och återkoloniseringsområdet är avgörande för att loarna ska kunna nå nya livsmiljöer, hitta parningspartners och därmed upprätthålla genetisk variation i populationen. En gynnsam förvaltningsstrategi är också nödvändig, eftersom hög dödlighet orsakade av människan kan förhindra återkolonisationen.

I min avhandling sökte jag efter en djupare förståelse av lons återkoloniseringsresa från centrala till södra Sverige. Den första delen av studien handlade om att identifiera lämpliga livsmiljöer för lo, genom att använda vetenskapliga metoder för att analysera landskapsegenskaper som loarna väljer. Sedan studerade vi lopopulationens tillväxttakt i de nyligen koloniserade områdena för att kontrollera om återkoloniseringen gick långsammare än i tidigare områden, och om långsammare tillväxttakt kan ha drivits av låg populationstäthet (en så kallad Allee-effekt). Slutligen analyserade vi den genetiska mångfalden i populationen med hjälp av populationsgenetik, en metod som använder tusentals DNA-segment från varje individ för att beskriva populationens struktur och utveckling.

Denna forskning avslöjade en framgångshistoria om återhämtning. Det finns gott om lämpliga livsmiljöer för lo i södra Sverige, och de har framgångsrikt etablerat sig där. Trots en ursprungligen långsam tillväxttakt upprätthåller populationen kontakt med loar i centrala Sverige, vilket har lett till att ingen genetisk mångfald har gått förlorad i söder. Trots tidigare svårigheter har lopopulationen återetablerat sig i södra Sverige. Detta tack vare en förvaltningsstrategi som har gynnat dess återkolonisering, en låg dödlighet orsakad av människan, samt loarnas imponerande förmåga att sprida sig över hundratals kilometer, även över olämpliga livsmiljöer som jordbruksmark eller områden med bebyggelse.

Det är vår förhoppning att detta exempel på en framgångsrik återkolonisering kan tjäna som en mall för återinförandet av stora rovdjur över hela världen. Det illustrerar vikten av kontakt mellan populationer och behovet av noggranna förvaltningsstrategier som uppmuntrar mänsklig tolerans och underlättar populationstillväxt. När vi blickar mot framtiden påminner lons förmåga att återhämta sig i sitt ursprungliga utbredningsområde oss om att med rätt förutsättningar och skydd har naturen en extraordinär förmåga att återhämta sig.

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Evaluating habitat suitability and connectivity for a recolonizing large carnivore

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ABSTRACT

The conservation of wide-ranging species presents challenges in a world of intensified human land use, forcing animals to occupy and recolonize human-modified landscapes. Although identifying suitable habitat and ensuring connectivity are important in supporting natural recolonization, these actions are rarely validated due to difficulties in monitoring such events. In Sweden, the Eurasian lynx (Lynx lynx) is now recolonizing its former range, after centuries of persecution. We investigated resource selection based on telemetry data from 108 lynx monitored over 20 years. We assessed the differences between the established population in central Sweden and the recolonizing population in southern Sweden, and between established and dispersing individuals. We found that models based on central Sweden successfully identified core habitat patches for establishment in southern Sweden, validated after recolonization. We also found that lynx selected for higher habitat suitability during the recolonization phase, and that dispersing individuals were less selective than established lynx. Using cost-distance analysis, we assessed connectivity between central and southern Sweden, and found that landscape permeability was higher when based on dispersing lynx compared to established lynx. Altogether, our findings suggest that when landscapes are sufficiently similar between source and recolonization areas, resource selection information from an established population can be useful for managers seeking to facilitate recolonization of wide-ranging species. We recommend more frequent use of validation during and after recolonization events, to improve our common understanding of habitat suitability and connectivity modeling, and therefore to enable more active management of recolonization events.

1. Introduction

Some large carnivores are currently recovering in human-dominated landscapes (Chapron et al., 2014; Gantchoff and Belant, 2017; LaRue and Nielsen, 2016); thus there is a growing need to predict their establishment and to facilitate management actions that help ensure their long-term viability and mitigate potential conflicts (Redpath et al., 2013). Large carnivore movements are increasingly constrained by human land use, forcing them to occupy or cross human-modified landscapes in search of suitable habitat (Fahrig, 2001; Fahrig, 2007; Tucker et al., 2018). Expansion may therefore be determined by animals' potential to successfully move through the landscape, especially in low-density populations exposed to high rates of human-caused mortality (Fahrig, 2007; Tucker et al., 2018). Consequently, identifying suitable habitat patches and ensuring population connectivity are vital for carnivore conservation and management (Beier et al., 2008; Brodie et al., 2015; McClure et al., 2016; Riordan et al., 2015).

Suitable habitat patches are often identified from resource selection functions (RSFs) (Boyce et al., 2002; Manly et al., 2007), and the potential for connectivity is evaluated by assessing the cost of passing through different habitat types based on RSF results (Abrahms et al., 2017; Beier et al., 2008; Chetkiewicz and Boyce, 2009; Sawyer et al., 2011). Dispersal is the main driver of both population connectivity and recolonization (Jackson et al., 2016; LaRue and Nielsen, 2016; Morrison et al., 2015). As dispersal events often involve long distance movements (Fahrig, 2007; Tucker et al., 2018), and resource requirements may differ between established and dispersing individuals (Abrahms et al., 2017; Chetkiewicz et al., 2006), connectivity should ideally be assessed using actual dispersal events (Beyer et al., 2010). However, studies on habitat connectivity often use data from resident individuals, which could overestimate landscape resistance when dispersers are more inclined than residents to use the low-quality matrix between core habitat patches (Abrahms et al., 2017; Jackson et al., 2016).

Like many carnivores, Eurasian lynx (*Lynx lynx*) declined across Europe in the 19th and early 20th centuries due to human persecution (Chapron et al., 2014). Lynx have recovered in much of Europe, through both natural recolonization and a few successful reintroductions (Chapron et al., 2014; Linnell et al., 2009). The Scandinavian lynx is a distinct subpopulation of Eurasian lynx, which has recovered after near extirpation in the early 20th century (Chapron et al., 2014; Liberg, 1997; Linnell et al., 2010; Linnell et al., 2007). Lynx recolonized central Sweden from northern Scandinavia during the 1990s, and the first documented lynx reproduction in southern Sweden occurred in 2003 (Viltskadecenter, 2005). Today, lynx occupy most of Sweden (Fig. 1a)

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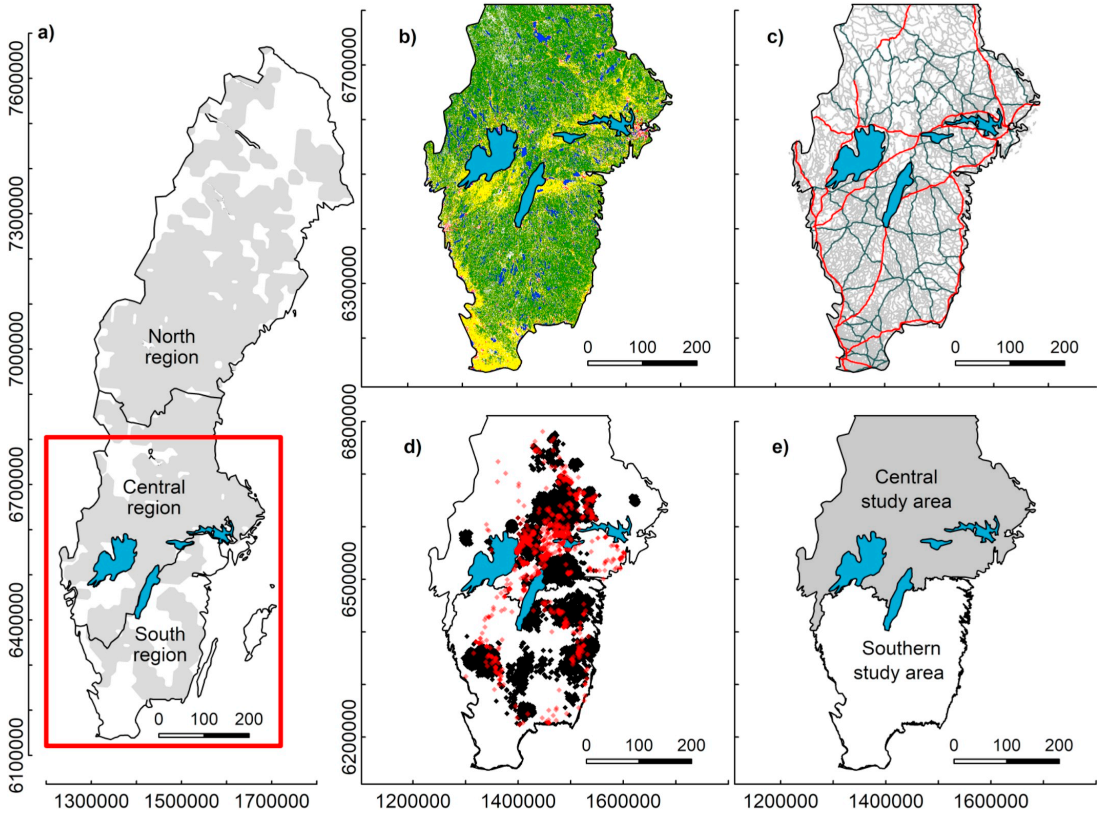

Fig. 1. a) Swedish lynx management regions, our study area outlined in red, and lynx distribution in gray. b) Land cover type (green = forest, yellow = agricultural or grassland, red = urban areas blue = water, white = other). c) Roads, with small roads in light gray, primary roads in black, and national highways in red. d) Telemetry locations from established lynx in black (*n* = 101 individual) and dispersers in red (*n* = 35 individuals). e) Study areas used in this analysis. Scale bar distances are in kilometers and the X- and Y-axes are coordinates in the Swedish grid RT90. (For interpretation of the references to color in this figure legend, the reader is referred to the web version of this article.)

and are estimated at approximately 1200 individuals (Zetterberg and Tovmo, 2017) based on annual monitoring (Supplementary material). Swedish lynx management is decentralized to three regions (Fig. 1a), each with a specified target for minimum yearly count of family groups (females with kittens) (Fig. A1). Population estimates based on monitoring results directly inform management, and lynx hunting is permitted if the population exceeds the regional target on an annual basis (Andrén et al. in press) (see also Supplementary material).

One goal of the Swedish national lynx management plan is to redistribute the population between the central and southern management regions (SEPA, 2016). Connectivity and habitat suitability were not assessed in the management plan. This goal was based on assumed habitat and prey availability in the south as well as sufficient connectivity (SEPA, 2016), although the area between the central and southern management regions consists of a potentially unsuitable matrix landscape for lynx, i.e. densely populated agricultural land interspersed with highways and large lakes (Fig. 1b, c) (Basille et al., 2013; Kramer-Schadt et al., 2004; Zimmermann et al., 2007).

In this study, we took advantage of long-term data from 108 lynx, including both resident and dispersing individuals, fitted with VHF/GPS collars throughout the recolonization of southern Sweden (1996–2015; Fig. 1d). Thus, we had a unique opportunity for an inferentially strong observational study of the recolonization patterns of a historically persecuted carnivore, more specifically to identify and validate suitable habitat and assess connectivity between source and re-establishment areas. Our first aim was to predict suitable habitat in southern Sweden based on lynx in central Sweden, and to validate these predictions after recolonization of the south. Based on the similarity in habitat composition between the two areas (Table 1, Table A1) we expected that models based on the source area would successfully predict establishment (Guisan et al., 2017). Our second aim was to identify potential areas of connectivity between central and southern Sweden, and to test whether corridors predicted from established lynx differed from those predicted by dispersers. We expected dispersers to be less selective than established lynx and therefore to predict higher landscape permeability, because previous studies suggest that dispersers are more inclined to move through suboptimal habitat than adults (Abrahms et al., 2017; Gastón et al., 2016; Palomares et al., 2000; Vanbianchi et al., 2018).

We first modeled lynx resource selection by sex, region, and status (established vs. dispersing), to assess what resources lynx are selecting for in the landscape. We used these models to spatially predict habitat suitability across both study areas, and used these habitat suitability values to identify large core habitat patches supporting lynx establishment. We then used these predictions to create cost-distance surfaces across the landscape, to assess connectivity between identified habitat patches.

Table 1

Resource variables used in resource selection function (RSF) models, which informed core habitat patch identification and cost-weighted distance analysis.

Category	Variable	Measure	Scale	Source	Biological meaning/hypothesis	Values
Prey	Roe deer hunting bag	Number of roe deer shot per 1000 ha, for the year in which the lynx location was taken	Swedish hunting district, 54 to 6704 km^2	Swedish Association for Hunting and Wildlife Management	Possible selection for higher roe deer availability because they are the main prey in this area. (Herfindal et al., 2005, Odden, Linnell and Andersen 2006, Gervasi et al. 2014).	Central study area: Min/Max/Mean 0.01/210/57 South study area: Min/Max/Mean 22/337/93
Human disturbance	Distance to large roads	Distance from primary and secondary roads (Swedish Transport Agency Road numbers up to 499)	Euclidean distance in meters	National Land Survey of Sweden, raster calculated in QGIS 2.18.2	Possible avoidance of human activity (Basille et al., 2009, Basille et al., 2013, Kramer-Schadt et al., 2004)	Central study area: Min/Max/Mean 0/33 139/5000 South study area: Min/Max/Mean 0/23 975/3958
	Distance to small roads	Distance from tertiary roads (Swedish Transport Agency road numbers 500 +)	Euclidean distance in meters	Swedish Land Survey Authority (*Lantmäteriet*), raster calculated in QGIS 2.18.2	Possible avoidance of human activity (Basille et al., 2013, Basille et al., 2009, Kramer-Schadt et al., 2004)	Central study area: Min/Max/Mean 0/13 077/1833 South study area: 0/10 310/1181
	Human population density	Human population per km^2	25 × 25 meter grid cells	Center for International Earth Science Information Network (CIESIN), Columbia University	Possible avoidance of human activity (Bouyer et al., 2015a, Andrén et al., 2006, Bunnefeld et al. 2006, Gehr et al., 2017)	Central study area: Min/Max/Mean 0/4076/42 South study area: Min/Max/Mean 0/1662/48
Land cover	Land cover class	Land cover category,	25 × 25 meter grid cells	National Land Survey of Sweden	Possible selection for certain land cover types (e.g. forest) and avoidance of others (e.g. agricultural land and urban areas) (Rauset et al., 2013, Samelius et al. 2013)	See Table A1
	Distance forest to edge	Distance from edge between forest and agriculture or grass land	25 × 25 meter grid cells	Calculated in QGIS 2.18.2 based on SMD land cover classes, National Land Survey of Sweden	Possible selection for forested areas and areas immediately outside the forest (Zimmermann, Breitenmoser-Würsten and Breitenmoser 2007)	Central study area: Min/Max/Mean 0/8342/235 South study area: Min/Max/Mean 0/6319/259
Terrain	Elevation	Meters above sea level	50 × 50 meter grid cells	Digital Elevation Model	Possible preference for areas of high elevation in flatter study areas, as this one is (Bouyer et al., 2015b)	Central study area: Min/Max/Mean −5/948/163 South study area: Min/Max/Mean −5/374/128
	Ruggedness	Terrain ruggedness index (TRI)	50 × 50 meter grid cells	(Riley 1999) calculated in QGIS 2.18.2	Possible preference for rugged terrain due to concealment (Bouyer et al., 2015b, Rauset et al., 2013)	Central study area: Min/Max/Mean 0/173/5 South study area: 0/127/5

2. Methods

2.1. Study system and data

The central and southern study areas (Fig. 1e) are divided where an agricultural belt (78% wheat and barley) and the two largest lakes in Sweden interrupt otherwise continuous forest (Fig. 1b). This biogeographic border does not follow county borders, as do the lynx management regions. Consequently, our southern study area overlaps most of the southern management region and the southwest area of the central management region (Fig. 1a, e). The central and southern study areas are characterized by 70% and 63% forest, respectively (Table A1), most of which is intensively managed Norway spruce (*Picea abies*) and Scots pine (*Pinus sylvestris*) (Andrén et al., 2002). Agricultural land (cropland and grazing areas) and natural grassland together constitute a larger proportion of the south (24%) compared to the central study area (14%) (Table A1). Most land in southern Sweden is privately owned (63%), followed by corporate and state ownership. Only approximately 3% of the land in southern Sweden is protected, and the largest protected area is 78.5 km^2. In both study areas, the main prey is roe deer (*Capreolus capreolus*) (Andrén et al., 2006; Aronsson et al., 2016).

We used 26,569 locations from 108 individuals (59 males and 49 females) monitored in the central (1996–2015) and southern (2007–2015) study areas (Fig. 1d). All lynx were captured, immobilized, and equipped with collars following Swedish Animal Welfare Agency's ethical-approved protocols (Andrén et al., 2006; Arnemo and Evans, 2017). Animals were fitted with VHF collars (1996–2008: MOD335 and MOD400NH Telonics, Mesa, AZ, USA) or GPS collars (2003–2015: GPS plus mini, Vectronics Aerospace, Germany; Televilt Posrec 300 and Tellus 1C, Followit, Sweden). Two individuals were fitted with both GPS and VHF collars, at different times, resulting in 75 VHF-collared individuals (216 ± 364 SD locations/individual) and 36 GPS-collared individuals (295 ± 200 SD locations/individual). One location per day per individual was randomly selected to reduce temporal autocorrelation and reduce potential biases due to differences in sampling frequency between animals (Aronsson et al., 2016; Frair et al., 2004; Nielsen et al., 2002).

Lynx natal dispersal events typically start at 10–11 months of age, and most individuals establish their own home range by 18 months of age (Samelius et al., 2012). We used net squared displacement (NSD) (Bunnefeld et al., 2011) to separate dispersing individuals (hereafter "dispersers," $n = 35$) from those with established home ranges (hereafter "established," $n = 101$) based on movement pattern. Locations that were classified as unknown or in a pre-dispersal phase were omitted. NSD is a method used for identifying movement behavioral states of animals based on the squared distance they have travelled from their first location, with distinctly different patterns for various movement states (Bunnefeld et al., 2011).

Lynx monitoring locations of family groups collected between December 2002 and March 2018 (www.rovbase.se, accessed 2 April 2018, see Supplementary materials) were used as validation data ($n = 645$ in the central and $n = 441$ in southern study area).

2.2. Resource selection

Predictor variables were chosen based on previous studies of lynx resource selection (Table 1). Land cover classes were consolidated using prior categorizations of the 2000 Swedish Land Cover National Land Survey of Sweden maps (i.e. the latest available update of Swedish land cover) (Rauset et al., 2013) and modified to provide further granularity regarding forest type (Table A1) because lynx may use deciduous and coniferous forest differently. Prey availability was assessed from regional roe deer hunting bag sizes, which is a proxy for roe deer abundance (Aronsson et al., 2016; Melis et al., 2013).

We used conditional logistic regression to estimate resource selection functions (RSFs) by sex, study area, and dispersal status (Chetkiewicz and Boyce, 2009). RSFs rely on a use-availability design, wherein locations used by the animal (hereafter "used points") are compared to the available surrounding landscape (Boyce and McDonald, 1999; Johnson et al., 2006; Manly et al., 2007). For availability data, we generated circular buffers around each VHF or GPS location using a radius of 16 km for established lynx (approximate home range size based on our data and published studies) (Aronsson et al., 2016; Herfindal et al., 2005) and 5 km for dispersers (approximate daily step length for dispersers; our data). Five random points were generated within each buffer to represent available locations (hereafter "available points") (Boyce et al., 2003). We also tested three other buffer radii (one, five, and 22 km for established lynx and one, 16, and 22 for dispersers) to validate our buffer size choice. The one kilometer buffers were uninformative and completely overlapped zero, and the direction of selection was the same for all variables using five, 16, and 22 kilometer buffers. We used binomial generalized linear mixed effects models with logit links in the lme4 package (Bates et al., 2014) for R Studio 1.0.40 (R Core Team, 2018) to model RSFs. Individual identity was included as a random effect to account for correlation between used points. Initially we included the point cluster identity of used and corresponding available points as a nested random effect within individual (Fieberg et al., 2010; Gillies et al., 2006), but removed point cluster identity after finding that the variance explained was not significant. All predictor variables were checked for collinearity using Pearson's correlation coefficient (Crawley, 2014) and variables with $r > 0.3$ were not included in the same model. Therefore, "distance to agricultural land" was removed in favor of "distance to forest." All continuous variables were standardized to a mean of zero and a standard deviation of one. Determinants of resource selection were grouped into the categories of prey, human disturbance, land cover, and terrain (Table 1). A set of candidate models were identified based on these groups, which include all variables, each category separately, one model with all variables except prey, and one with land cover and terrain variables. Models were selected based on Akaike information criterion (AIC) values (Burnham and Anderson, 2003) (Table A2).

2.3. Model validation and prediction

To test the predictive ability of our RSF models, we generated predictive surfaces (raster maps) wherein every pixel is assigned a resource value according to the coefficients for the model with the best fit (Chetkiewicz and Boyce, 2009; Hebblewhite et al., 2011; Inman et al., 2013). Because we oversampled availability points at a ratio of 5:1, an approximate value for neutral selection in this case is 1/6, or 0.167. We removed random effects from the models that were used to inform predictive surfaces due to limitations in generating predictive maps using mixed effects models, which did not change the direction of selection in any model.

We validated the predictive power of these surfaces by calculating the mean predicted habitat quality score of the lynx monitoring data that was not used in training each model, and comparing it to the predicted values from the training data using Welch two-sample *t*-tests. To verify whether lynx actually used areas of higher habitat suitability compared to the available landscape, we ran two-way repeated ANOVAs by individual, comparing the mean habitat suitability scores of each lynx's used and available points. We also used Tukey HSD tests to make pairwise comparisons between groups, based on study area and dispersal stage.

2.4. Core habitat patches and connectivity

To test whether core habitat patches supporting lynx establishment in southern Sweden were identifiable based on data from central Sweden, we used the results of the central area RSF to identify patches of contiguous habitat large enough to encompass one, two, and three female home ranges or more (i.e. 315, 630, and 945 km^2; (Aronsson et al., 2016; Herfindal et al., 2005), with habitat quality scores >0.15 (0.167 being an approximate value for neutral selection). This value was chosen because lynx can tolerate some non-optimal habitat in their home ranges, as mean habitat values for 95% kernels and 95% minimum convex polygons for established individuals are 0.170 (± 0.018 SD) and 0.174 (± 0.019 SD), respectively. The results for the threshold of two female home ranges were identical to using a threshold value of three female home ranges (Fig. A2). The single home range size resulted in the identification of five additional smaller patches, two of which were in the matrix habitat between the large lakes (Fig. A2).

To evaluate connectivity between the core habitat patches, we used cost distance analysis to assess the resistance of the landscape (Sawyer et al., 2011). We calculated cost-weighted distances based on the habitat values assigned to each map pixel, based on the RSF model results using Linkage Mapper 1.1.1. (McRae and Kavanagh, 2011). This was done separately for dispersing and established lynx RSF models, resulting in two raster maps, wherein pixel values provided the cost-weighted distance to the nearest core habitat patch (McRae and Kavanagh, 2011). We calculated the ratio between these rasters to test whether predictions made based on established or dispersing animals are sufficient to identify landscape that can facilitate dispersal. We focused on the permeability of the overall landscape between core habitat patches and did not use least cost paths (LCPs) or corridors because these methods are restrictive in that they identify single pixel-wide paths (LCPs) and rely on arbitrary cut-off thresholds in their cost-weighted distances (corridors), which can lead to loss of information and conclusions that are not biologically meaningful (Moilanen, 2011).

3. Results

3.1. Resource selection

The full models, including all variables, were the top RSF models for both male and female established lynx in both study areas. In contrast, dispersers were less selective, as both anthropogenic effects and prey were absent in the top RSF models based on dispersers (Table A3, A4). For variables that were in both top models, dispersers tended to select in accordance with established lynx (Table A3, A4). All groups selected for forest and against semi-natural areas, marshland, human infrastructure, and waterways (Table A3, A4). Where selection differed, the two sexes tended to be in alignment within each area for all variables except prey (Table A3, A4). Southern established lynx of both sexes and central males selected against areas of higher roe deer availability, whereas central females selected for roe deer availability. Both groups of established lynx selected for longer distance to large roads. Central established lynx of both sexes selected for proximity to small roads, whereas southern males selected against road proximity (Table A3). Established lynx of both sexes selected for grassland and agricultural land in the south and against these land cover types in the central area.

3.2. Model validation and prediction

We identified areas of high quality habitat based on models informed by central established lynx (Fig. 2a), southern established lynx (Fig. 2b), and dispersers (Fig. 2c). According to all three models, all groups of lynx selected for higher habitat quality scores than the surrounding available landscape (Fig. 2d–f). Southern established lynx selected higher quality habitat compared to central established lynx and dispersers, irrespective of the predictive surface used ($p < 0.001$ in all cases) (Fig. 2d–f). Dispersers and central established lynx did not differ as much in the quality of habitat they selected. The mean used habitat quality score for dispersers, although slightly lower than scores for central established lynx in all three cases, did not differ significantly from central established lynx ($p = 0.284, 0.057, 0.281$ for the northern, southern, and disperser models respectively) (Fig. 2d–f). According to the model based on central established lynx which informed our subsequent analysis, mean habitat quality score did not differ between animals that were used to train the model and government monitoring locations in the same area ($p = 0.97$).

3.3. Core habitat patches and connectivity

Eight large core patches of potential lynx establishment ranging between 1388 and 26,720 km^2 were identified across both study areas, covering 49% of the landscape (46% in central and 52% in the south; Fig. 3a). Two of these patches were fully within the southern study area and two were primarily in the central study area, with small portions extending into the south (Fig. 3a). Lynx monitoring locations were found more often within these patches in both areas (73%, $n = 645$, $G = 99$, $df = 1$, $p < 0.001$ in central and 77%, $n = 441$, $G = 62$, $df = 1$, $p < 0.001$ in southern). The two large core habitat patches identified in southern Sweden were 10,220 and 26,720 km^2, and therefore could contain 31 and 82 non-overlapping female home ranges, respectively (Fig. 3a). Additionally, five core habitat patches the size of a single female home range or smaller were identified, four in the central study area and one spanning the border between the two.

Cost-weighted distances between the large core habitat patches based on established lynx (Fig. 3b) and dispersers (Fig. 3c) identified very similar areas of permeability, although the resistance of the landscape was estimated to be higher for surfaces based on established lynx models. The median cost distance value based on established lynx was 26% higher than for dispersing lynx, with minimum, first quartile, third quartile, and maximum of 0%, 22%, 31%, and 94% higher values respectively for established lynx.

4. Discussion

The ability of large carnivores to recolonize their former ranges is a central conservation issue in many parts of the world (Chapron et al., 2014; Gantchoff and Belant, 2017; LaRue and Nielsen, 2016; Mattson and Clark, 2010). Therefore, in this study we predicted areas of lynx recolonization based on resource selection functions (RSFs) from the source area, and successfully validated these predictions with data from individuals in the settlement area and with independent monitoring data (Fig. 2). We also found that landscape permeability was predicted to be lower when using data from established individuals compared to dispersers, showing that dispersers were less selective and more likely to move through suboptimal habitat (Fig. 3). Consequently, we provide support for the feasibility of an essential management action, namely predicting core habitat patches and connectivity to facilitate recolonization, even when presence data are limited. Such extrapolation is possible when the source and recolonization areas are similar in terms of habitat composition (Guisan et al., 2017) as in this case, while we still caution that the predictive ability of these models could deteriorate as recolonization areas diverge structurally from those in which the source population originates (Boyce, 2006).

4.1. Resource selection

The resource selection of lynx in this study aligned with previous studies, as both established and dispersing individuals selected for forests (Müller et al., 2014; Niedziałkowska et al., 2006; Schadt et al., 2002b) and rugged terrain (Basille et al., 2009; Bouyer et al., 2015b; Rauset et al., 2013), both of which provide essential cover, while avoiding large roads (Basille et al., 2009). We found that lynx selected for proximity to small roads, which they use for movement and scent-marking (Krofel et al., 2017). The unexpected selection away from high roe deer density by females in the south and by males could be explained by lynx selecting for other factors related to prey catchability, e.g. proximity to forest edges, rather than for high prey density (Balme et al., 2007; Basille et al., 2009; Hebblewhite et al., 2005; Hopcraft

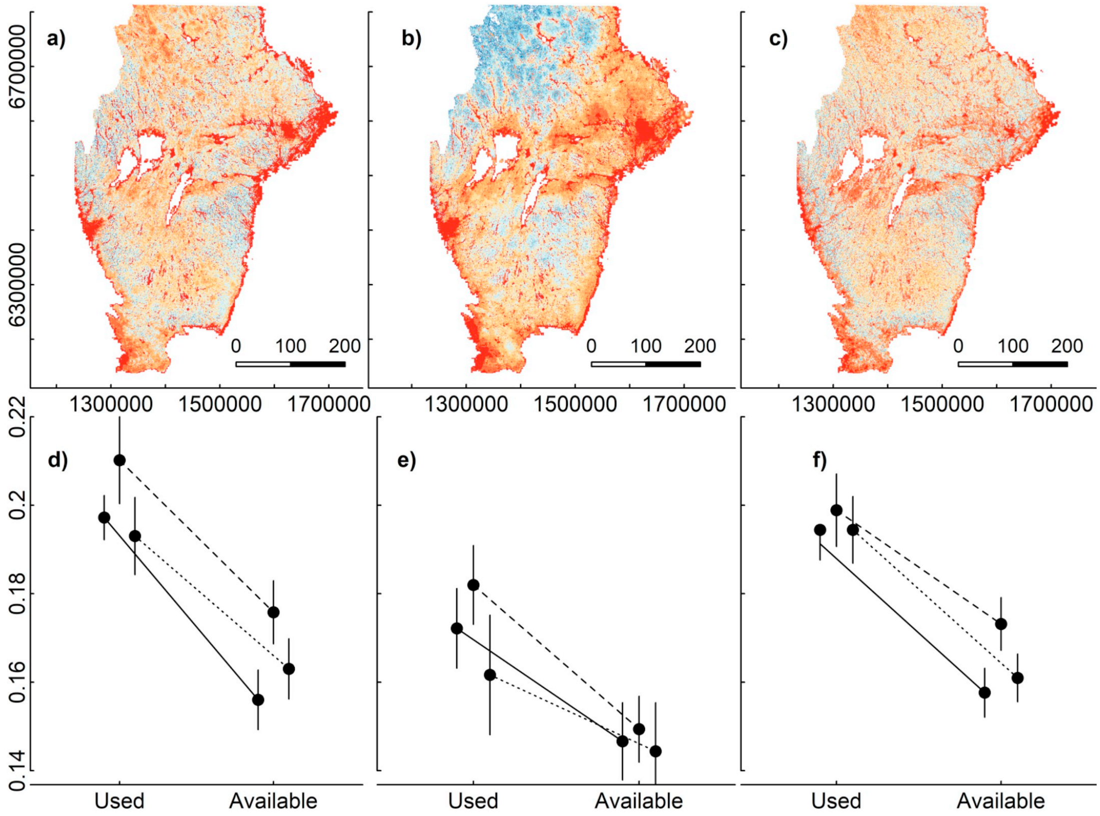

Fig. 2. a–c) Predictive surfaces identifying habitat quality with a theoretical range from 0 (red) indicating total avoidance to 1 (blue) indicating selection, with 0.1667 indicating approximate neutral selection. a) Predictions based on central established lynx models ($n = 66$ individuals), b) Predictions based on southern established lynx ($n = 43$ individuals), c) Predictions based on dispersing lynx (n = 35 individuals); d-f) Difference in habitat quality score between used and available points, based on each of the three models; solid line, dashed line, and dotted lines indicates values for central established lynx, southern established lynx, and dispersers respectively. Scale bar distances are in kilometers. (For interpretation of the references to color in this figure legend, the reader is referred to the web version of this article.)

et al., 2005), especially as roe deer density in our study areas was high enough to minimally affect the lynx kill rate (Andrén and Liberg, 2015; Nilsen et al., 2009).

While lynx neither selected for nor avoided coniferous forest (Table A3, A4), they selected for all other forest types, and every individual had ≥50% forest cover in their home range (mean 78% ± 9 SD), which aligns with other studies showing that lynx need forest (Niedziałkowska et al., 2006; Schadt et al., 2002a; Schmidt-Posthaus et al., 2002). Although southern lynx selected for agricultural patches, they remained near forest edges, with median distance of 25 m from forest while in agricultural land. This aligns with previous findings that lynx utilize fields to hunt in proximity to forest (Filla et al., 2017; Gehr et al., 2017).

4.2. Core habitat patches and connectivity

We validated that lynx in the southern area surrounded themselves with higher quality habitat than those in central Sweden (Fig. 2d–f). This indicates that when high-quality habitat is available for a recolonizing population, individuals settle in these areas to a greater extent than in lower quality habitat. This highlights the importance of taking the extent of the recolonized area, as well as the stage of recolonization, into account in RSF modelling, where the analysis of a population at an early stage of a recolonization event may suggest selection for higher quality habitat than would ultimately be used at later stages of recolonization and thus underestimate habitat availability.

Models based on established lynx estimated the landscape to be slightly less permeable than those based on dispersers, although the areas of highest permeability were similar (Fig. 3b–c). This suggests that it was easier for dispersers to move through the landscape than models based on established individuals would indicate. This is consistent with other studies of wide-ranging carnivores showing that dispersers select similar habitat but are less selective than established adults, and are therefore more prone to move through less-optimal habitat (Abrahms et al., 2017; Blazquez-Cabrera et al., 2016; Gastón et al., 2016; Jackson et al., 2016; Mateo-Sánchez et al., 2015; Vanbianchi et al., 2018). Therefore, even when data on dispersing individuals is unavailable, dispersal habitat can be identified based on data from resident individuals, although some lower quality dispersal habitat may be missed.

Although there were gaps between core habitat patches, matrix habitat was available, which can facilitate dispersal. Possible dispersal routes for lynx in south-central Sweden are narrowed by four large lakes and crossed by major fenced highways (Fig. 1d), which were avoided by lynx in this study and can act as barriers to lynx dispersal

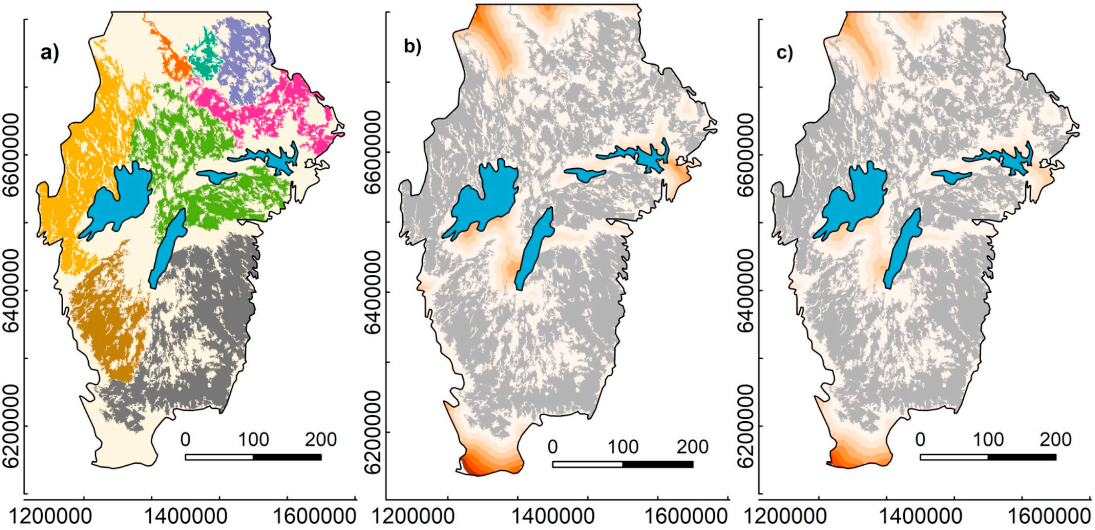

Fig. 3. a) Core habitat patches larger than a single female home range as identified by the model based on established lynx in the central study area; b) cost distance to nearest habitat patch based on established lynx (dark colors indicate higher cost distance); c) cost distance to nearest habitat patch based on dispersers (dark colors indicate higher cost distance). Scale bar distances are in kilometers. (For interpretation of the references to color in this figure legend, the reader is referred to the web version of this article.)

(Zimmermann et al., 2007). Moreover, the agricultural belt between the two study areas could also discourage dispersal (Magg et al., 2016; Niedziałkowska et al., 2006) (Fig. 1b), as agricultural land was avoided by central established lynx and by dispersers. Although agricultural land was slightly selected by southern established lynx (Table A3, A4), they stayed close to the forest edge and were therefore unlikely to use large patches of agricultural land.

Lynx broad use of dispersal habitat indicates that seeking to identify and protect narrow movement corridors should not be over-emphasized when planning for recolonization by habitat generalists and in areas dominated by permeable habitat (Woodroffe, 2003). In such cases, we would instead recommend using a whole-landscape approach to assess where the population is likely to establish, and to assess their potential use of matrix habitat during dispersal.

4.3. Conclusion

The successful recolonization of lynx in southern Sweden demonstrates that the management goal to increase the population in the southern management region was realistic. Lynx have recolonized southern Sweden, despite passing through areas of high human disturbance without access to protected areas (Linnell et al., 2001). Although lynx in this study generally avoided areas of high human density, they selected for proximity to small roads and agricultural land, in line with previous studies showing that lynx select for areas of moderate levels of human activity (Basille et al., 2009; Bouyer et al., 2015a; Bouyer et al., 2015b). Although recolonization success is clear from monitoring data, we validated the management assumption that enough core habitat is available to support lynx. Additionally, our identification of two large patches of core lynx habitat in the south, together the size of 113 non-overlapping female home ranges, as well as a patch the size of a single home range between them (Fig. A2b) suggests that the current population target for southern Sweden of 40 family groups is conservative.

The ability to predict establishment based on existing populations, as we demonstrate here, is a useful tool in planning for reintroductions or natural recolonizations (Bleyhl et al., 2015; D'Elia et al., 2015; Gehring and Potter, 2005; Inman et al., 2013), and in promoting connectivity between isolated sub-populations (Marini et al., 2010; Peters et al., 2015). It would also be useful to complement or validate other modelling approaches that require more data or do not rely on source population information like those used to predict suitable reintroduction sites, such as for proposed lynx reintroduction in Scotland (e.g. Ovenden et al., 2019; Philips, 2019).

Although RSFs and similar models are widely used in conservation planning, core habitat patches and connectivity between them are often not validated after management actions are implemented. We show that independent data sources, such as monitoring data, can be used to validate models. Therefore, as recolonizations progress, regular validation and updates associated with new findings could inform management and conservation actions by identifying areas of potential recolonization (Eriksson and Dalerum, 2018; Recio et al., 2018), and to plan for successful reintroductions or expansions by identifying overlaps between areas of high human activity and high quality recolonization habitat, so as to proactively mitigate human conflicts that are often associated with large carnivores (Bleyhl et al., 2015; Eriksson and Dalerum, 2018; Recio et al., 2018). Today, much work seeks to extrapolate the predictive ability of RSFs from small study areas to scales at the national or even continental level (e.g. Bleyhl et al., 2015; D'Elia et al., 2015; Inman et al., 2013; Kuemmerle et al., 2011), and the implications of these broad extrapolations should be further explored. We hope that this study will help to inform the ongoing recolonization of lynx in southern Sweden, and inspire others to validate modelling efforts concerning reintroductions and natural recolonizations around the world.

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Appendix A. Supplementary data

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Appendix 1

Table A1: Land cover class details, consolidated from the categories provided in the 2000 Swedish Land Cover (SMD) National Land Survey of Sweden

Land cover category	SMD land cover classes	Description	Land cover central (%)	Land cover south (%)	Used points (%)	Available points (%)
Coniferous forest	43-50, 56	Coniferous forest above 5 meter tree height	45	39	51	47
Mixed forest	56	Mixed forest above 5 meter tree height	6	5	7	5
Deciduous forest	40-42	All broad-leafed forest	4	9	19	14
Early forest and thickets	53-55, 61	Thickets, clear-felled and burnt areas, regrowth.	15	10	7	6
Grasslands and meadows	4, 16-18, 32, 51, 52 63-64	Natural and human-made grassy areas	2	5	3	3
Rural and semi-natural	12, 14, 15, 19, 20	Recreational areas that are sparsely used at certain times	.77	.62	.14	.38
Bare rock, glacier, sand	6, 10, 11, 58, 59, 60, 62	Natural and human-made bare areas	.33	.12	.12	.08
Agricultural	30, 31	Arable land and orchards	12	19	7	10
Human infrastructure	1-3, 7- 9, 13	Urban and suburban built-up areas, road and rail network	2	3	1	2
Bogs, marshes, water	70-74, 80-86	Mires, salt marshes, peat extraction sites, open water and wetlands	13	9	4	13

Table A2: Model selection by AIC weight. The best model for each category is shown in bold. The variables in each category are given in Table 1.

	Established Central All		**Established Central Male**		**Established Central Female**		**Established South All**		**Established South Male**		**Established South Female**		**Disperser All**		**Disperser Male**		**Disperser Female**	
Variable Category/ Model	**ΔAIC**	**AIC Weight**	**ΔAIC**	**AIC Weight**	**ΔAIC**	**AIC Weight**	**ΔAIC**	**AIC Weight**	**ΔAIC**	**AIC Weight**	**ΔAIC**	**AIC Weight**	**ΔAIC**	**AIC Weight**	**ΔAIC**	**AIC Weight**	**ΔAIC**	**AIC Weight**
All Variables	**0**	**1**	**0**	**.62**	**0**	**1**	0	1	0	.8	0	1	6.3	.04	6.2	.04	6.0	.04
Land cover, human dist, terrain	16.4	0	1	.38	33.1	0	13.6	0	2.8	.2	19.5	0	4.9	.08	4.3	.10	4.8	.08
Land cover and terrain	266.6	0	127.4	0	188.9	0	190.4	0	160.5	0	50.0	0	**0**	**.88**	**0**	**.86**	**0**	**.87**
Terrain only	1552.2	0	376.7	0	1223.0	0	814.4	0	568.8	0	267.2	0	67.5	0	32.5	0	22.7	0
Land cover only	1476.9	0	277.1	0	1254.0	0	893.4	0	596.8	0	281.2	0	25.5	0	14.7	0	9.2	.01
Human disturbance	3147.8	0	497.3	0	2671.9	0	1719.9	0	1140.9	0	569.4	0	126.8	0	67.2	0	50.1	0
Prey only	3395.0	0	628.3	0	2797.6	0	1903.3	0	1290.8	0	589.5	0	123.2	0	64.3	0	46.2	0
Null model	3408.0	0	637.4	0	2829.8	0	1920.1	0	1289.9		604.6	0	121.2	0	62.3	0	44.3	0

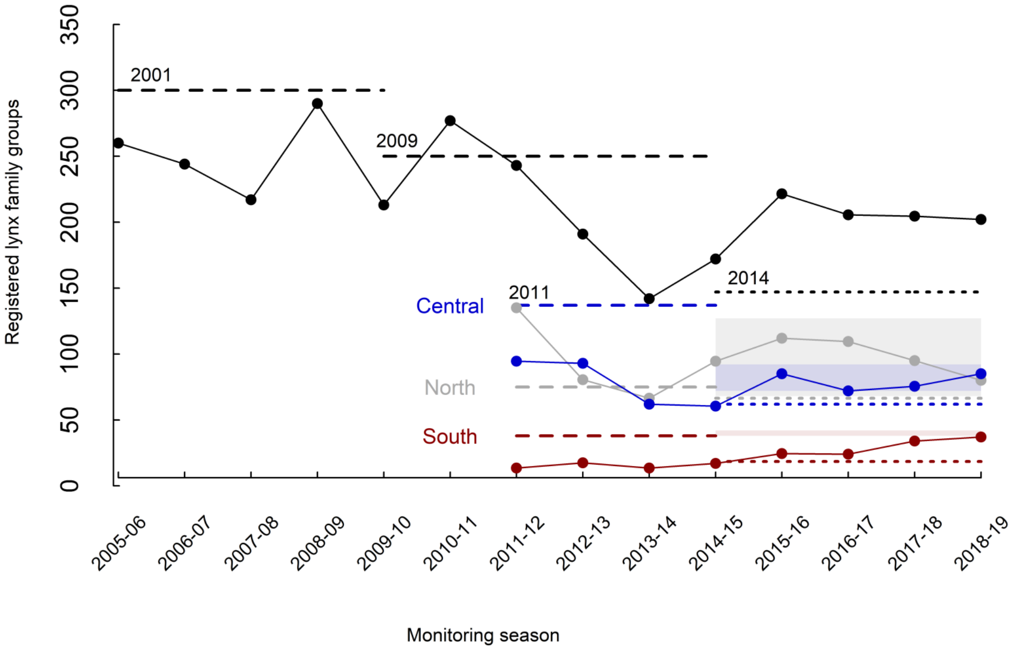

Figure A1: Dashed lines denote population targets for lynx (pre-2014) labeled with the year the target was set; dotted lines denote minimum population thresholds (post-2014); dots connected by solid lines denote yearly monitoring results. Shaded boxes (post-2014) denote population target intervals.

Table A3: RSF model outputs, established lynx. Coefficients are on a log-odds scale with a 5:1 inflation of zeroes to ones, i.e. there are five available points per presence point. Therefore, neutral selection is at a value of -1.609, which is the logit-transformed value of 1/6, or .167. Categorical variables (marked with *) are selected if the coefficient value plus the intercept value is above -1.609, and avoided if this value is below -1.609.

	Established Central All			**Established Central Male**			**Established Central Female**			**Established South All**			**Established South Male**			**Established South Female**		
Predictors	*Log-Odds*	*CI*	*p*	*Log-Odds*	*CI*	*p*	*Log-Odds*	*CI*	*p*	*Log-Odds*	*CI*	*p*	*Log-Odds*	*CI*	*p*	*Log-Odds*	*CI*	*p*
Coniferous Forest* (Intercept)	-1.601	-1.657 – -1.546	**<0.001**	-1.482	-1.600 – -1.365	**<0.001**	-1.643	-1.709 – -1.578	**<0.001**	-1.597	-1.702 – -1.492	**<0.001**	-1.611	-1.718 – -1.503	**<0.001**	-1.489	-1.709 – -1.269	**<0.001**
Deciduous Forest*	0.256	0.175 – 0.338	**<0.001**	0.198	0.018 – 0.378	**0.031**	0.269	0.178 – 0.361	**<0.001**	0.275	0.193 – 0.357	**<0.001**	0.285	0.186 – 0.384	**<0.001**	0.243	0.095 – 0.392	**0.001**
Young Forest and Thicket*	0.196	0.151 – 0.240	**<0.001**	0.161	0.057 – 0.264	**0.002**	0.203	0.153 – 0.253	**<0.001**	0.235	0.169 – 0.300	**<0.001**	0.165	0.085 – 0.244	**<0.001**	0.379	0.266 – 0.493	**<0.001**
Mixed Forest*	0.175	0.109 – 0.242	**<0.001**	0.105	-0.051 – 0.261	0.189	0.190	0.116 – 0.263	**<0.001**	0.190	0.090 – 0.289	**<0.001**	0.203	0.082 – 0.324	**0.001**	0.159	-0.013 – 0.331	0.070
Grassland*	-0.352	-0.474 – -0.229	**<0.001**	-0.248	-0.521 – 0.025	0.075	-0.377	-0.515 – -0.240	**<0.001**	0.389	0.283 – 0.496	**<0.001**	0.318	0.187 – 0.449	**<0.001**	0.536	0.353 – 0.718	**<0.001**
Semi-Natural*	-1.149	-1.537 – -0.761	**<0.001**	-0.818	-1.668 – 0.031	0.059	-1.230	-1.667 – -0.793	**<0.001**	-0.757	-1.439 – -0.075	**0.030**	-0.618	-1.346 – 0.111	0.096	-1.438	-3.438 – 0.563	0.159
Bare Ground, Rock*	-0.096	-0.641 – 0.450	0.731	0.654	-0.315 – 1.623	0.186	-0.374	-1.040 – 0.293	0.272	0.998	0.275 – 1.720	**0.007**	1.417	0.533 – 2.301	**0.002**	0.197	-1.126 – 1.521	0.770
Agricultural Land*	-0.536	-0.606 – -0.466	**<0.001**	-0.614	-0.788 – -0.440	**<0.001**	-0.520	-0.596 – -0.443	**<0.001**	0.173	0.077 – 0.268	**<0.001**	0.119	0.004 – 0.234	**0.042**	0.291	0.121 – 0.461	**0.001**
Human Infrastructure*	-0.820	-0.990 – -0.651	**<0.001**	-1.558	-2.201 – -0.916	**<0.001**	-0.760	-0.939 – -0.581	**<0.001**	-1.834	-2.409 – -1.259	**<0.001**	-2.266	-3.151 – -1.380	**<0.001**	-1.329	-2.089 – -0.569	**0.001**
Bog and Water*	-0.896	-0.973 – -0.818	**<0.001**	-1.005	-1.189 – -0.822	**<0.001**	-0.872	-0.958 – -0.786	**<0.001**	-1.125	-1.259 – -0.990	**<0.001**	-1.156	-1.319 – -0.994	**<0.001**	-1.044	-1.282 – -0.805	**<0.001**
Altitude	-0.089	-0.111 – -0.066	**<0.001**	-0.098	-0.138 – -0.058	**<0.001**	-0.089	-0.117 – -0.061	**<0.001**	0.160	0.122 – 0.198	**<0.001**	0.133	0.091 – 0.175	**<0.001**	0.193	0.124 – 0.262	**<0.001**
Distance to Forest Edge	-0.098	-0.123 – -0.073	**<0.001**	-0.077	-0.133 – -0.021	**0.007**	-0.103	-0.130 – -0.075	**<0.001**	-0.074	-0.109 – -0.039	**<0.001**	-0.072	-0.115 – -0.030	**0.001**	-0.068	-0.128 – -0.008	**0.027**
Log Human Population Density	-0.081	-0.104 – -0.058	**<0.001**	-0.191	-0.260 – -0.122	**<0.001**	-0.077	-0.103 – -0.052	**<0.001**	-0.115	-0.145 – -0.086	**<0.001**	-0.096	-0.128 – -0.064	**<0.001**	-0.132	-0.195 – -0.068	**<0.001**
Distance to Large Road	0.072	0.052 – 0.091	**<0.001**	0.120	0.086 – 0.154	**<0.001**	0.054	0.031 – 0.077	**<0.001**	0.119	0.097 – 0.140	**<0.001**	0.126	0.101 – 0.151	**<0.001**	0.093	0.049 – 0.137	**<0.001**
Distance to Small Road	-0.115	-0.133 – -0.097	**<0.001**	-0.123	-0.161 – -0.084	**<0.001**	-0.114	-0.134 – -0.094	**<0.001**	0.099	0.067 – 0.132	**<0.001**	0.150	0.112 – 0.188	**<0.001**	-0.017	-0.076 – 0.043	0.584
Terrain Ruggedness Index	0.328	0.309 – 0.346	**<0.001**	0.254	0.214 – 0.294	**<0.001**	0.345	0.325 – 0.366	**<0.001**	0.231	0.212 – 0.250	**<0.001**	0.222	0.200 – 0.244	**<0.001**	0.255	0.219 – 0.290	**<0.001**
Roe Deer Hunting Bag	0.002	0.001 – 0.003	**<0.001**	-0.002	-0.004 – 0.000	0.052	0.003	0.002 – 0.004	**<0.001**	-0.002	-0.003 – -0.001	**<0.001**	-0.001	-0.002 – -0.000	**0.026**	-0.005	-0.007 – -0.003	**<0.001**
Random Effects																		
Between-Individual Variance (τ_{00})	$0.01_{\text{individual}}$			$0.00_{\text{individual}}$			$0.01_{\text{individual}}$			$0.03_{\text{individual}}$			$0.01_{\text{individual}}$			$0.05_{\text{individual}}$		
Intraclass Correlation Coefficient	$0.00_{\text{individual}}$			$0.00_{\text{individual}}$			$0.00_{\text{individual}}$			$0.01_{\text{individual}}$			$0.00_{\text{individual}}$			$0.01_{\text{individual}}$		
Observations	99442			18959			80483			54718			36719			17999		
Individuals	66			30			36			43			29			14		

Table A4: RSF model outputs, dispersing lynx. Coefficients are on a log-odds scale with a 5:1 inflation of zeroes to ones, i.e. there are five available points per presence point. Therefore, neutral selection is at a value of -1.609, which is the logit-transformed value of 1/6, or .167. Categorical variables (marked with *) are selected if the coefficient value plus the intercept value is above -1.609, and avoided if this value is below -1.609.

	Disperser All			**Disperser Male**			**Disperser Female**		
Predictors	*Log-Odds*	*CI*	*p*	*Log-Odds*	*CI*	*p*	*Log-Odds*	*CI*	*p*
Coniferous Forest* (Intercept)	-1.577	-1.708 – -1.446	**<0.001**	-1.622	-1.795 – -1.450	**<0.001**	-1.507	-1.709 – -1.306	**<0.001**
Deciduous Forest*	0.460	0.151 – 0.770	**0.004**	0.576	0.189 – 0.963	**0.004**	0.224	-0.303 – 0.751	0.405
Young Forest and Thicket*	0.359	0.120 – 0.598	**0.003**	0.453	0.132 – 0.774	**0.006**	0.254	-0.107 – 0.615	0.168
Mixed Forest*	0.203	-0.113 – 0.518	0.208	0.039	-0.390 – 0.468	0.858	0.434	-0.037 – 0.904	0.071
Grassland*	-0.311	-0.799 – 0.178	0.213	-0.267	-0.869 – 0.335	0.384	-0.378	-1.229 – 0.472	0.383
Semi-Natural*	-0.450	-1.941 – 1.042	0.555	-0.638	-2.716 – 1.441	0.548	-0.190	-2.357 – 1.976	0.863
Bare Ground, Rock*	-13.355	-869.989 – 843.278	0.976	-13.285	-872.304 – 845.734	0.976			
Agricultural Land*	-0.812	-1.163 – -0.461	**<0.001**	-0.712	-1.182 – -0.241	**0.003**	-0.957	-1.486 – -0.427	**<0.001**
Human Infrastructure*	-1.655	-2.820 – -0.491	**0.005**	-1.877	-3.879 – 0.125	0.066	-1.567	-3.004 – -0.130	**0.033**
Bog and Water*	-0.725	-1.131 – -0.319	**<0.001**	-0.860	-1.484 – -0.237	**0.007**	-0.663	-1.209 – -0.118	**0.017**
Altitude	-0.091	-0.183 – 0.002	0.055	-0.052	-0.165 – 0.061	0.369	-0.182	-0.349 – -0.014	**0.033**
Distance to Forest Edge	-0.132	-0.234 – -0.029	**0.012**	-0.105	-0.242 – 0.032	0.132	-0.161	-0.316 – -0.005	**0.043**
Terrain Ruggedness Index	0.223	0.143 – 0.303	**<0.001**	0.226	0.126 – 0.326	**<0.001**	0.239	0.103 – 0.375	**0.001**
Random Effects									
Between-Individual Variance (τ_{00})	$0.00_{\text{individual}}$			$0.00_{\text{individual}}$			$0.00_{\text{individual}}$		
Intraclass Correlation Coefficient	$0.00_{\text{individual}}$			$0.00_{\text{individual}}$			$0.00_{\text{individual}}$		
Observations	3888			2226			1662		
Individuals	35			19			16		

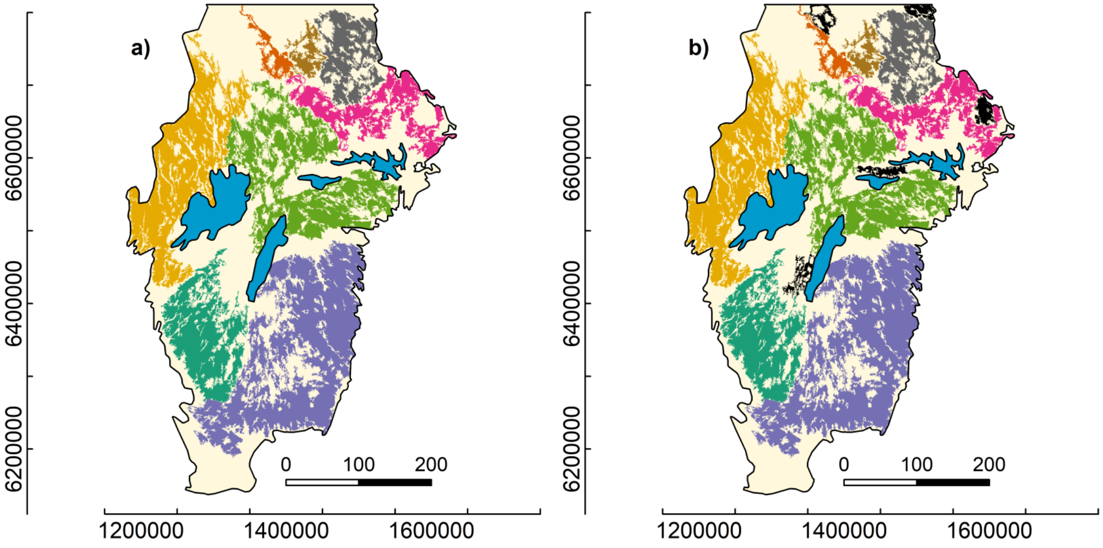

Figure A2: a) Core habitat patches identified based on a size threshold of more than two female home ranges. b) Core habitat patches based on a size threshold of more than one female home range. Patches that are smaller than two female home ranges are shown in black. Scale bar distances are in kilometers.

Appendix 2

Evaluating habitat suitability and connectivity for a recolonizing large carnivore

Supplementary Material: Swedish Lynx Population Estimation and Management

Population Estimation

Sweden and Norway use a common lynx monitoring methodology based on un-replicated counts of family groups (Knight et al. 1995, Linnell et al. 2007a, 2007b, Gervasi et al. 2013). Monitoring is primarily based on the snow-tracking of lynx tracks from two or more individuals moving together outside the mating season, which are assumed to be a family group consisting of an adult female and her kittens from the same year (Linnell et al. 2007a). Other “proof of reproduction” can contribute to the family group count, including camera-trap images of kittens, any kittens shot in the early part of the hunting season, or those killed in traffic accidents. In Sweden, certified personnel from the regional government administrations (called County Administration Boards or CABS) perform lynx monitoring in their respective counties. The monitoring is conducted from October until the end of February, but most observations are recorded from December to February. Hunters, game wardens, and the public can also report records of lynx tracks, but all observations of lynx tracks from two or more individuals have to be verified by authorized personnel from the CABs before entry into the monitoring database (Rovbase; www.rovbase.se).

To distinguish between family groups identified during snow-tracking, distance criteria based on home-range sizes and movement patterns from radio-marked female lynx are used to distinguish observations of separate family groups (Linnell et al. 2007a, Gervasi et al. 2013). Nilsen et al. (2011) found a good fit (r = 0.84) between the estimated population size based on this monitoring technique, and a reconstructed population size for Norway.

The number of monitored family groups is multiplied by a conversion factor to estimate the number of lynx in the population to include males and non-reproductive females. This conversion factor varies by region, with the average being 5.48 (± 0.40 SD) to get the total number of lynx in the population in central and southern Sweden (Andrén et al. 2002). The conversion factor is based on the estimated population structure in January-February, which is based on age-specific and sex-specific survival rates, as well as age-specific reproduction rates. Thus, this method provides an index of the total lynx population in an area, and not just the females with kittens.

Lynx Management

Lynx management in Sweden is governed centrally by the Swedish Environmental Protection Agency (SEPA) and administered by 20 County Administration Boards that are grouped into three management regions. A nationwide lynx population target of 300 family groups was set in 2001 (Swedish Government 2000) and reduced to 250 family groups in 2011 (SEPA 2011). In 2011, lynx management was also decentralized to three geographical management regions, each with a specified minimum number of yearly lynx family groups summing to the national population goal. Hunting quotas are set annually at the county level. Hunting is allowed if the previous year's lynx population estimate exceeds the regional target, and a moratorium is set on quota hunting for the year if the regional population estimate is lower than the target (Andrén et. al, In press). During years when quota hunting is permitted (e.g. when the lynx population exceeds the target), the hunting season takes place in the month of March. Regional population management goals were initially set to 75, 137 and 38 family groups in the northern, central and southern management region, respectively (SEPA 2013). In 2011, the monitoring results showed that there were 245 family groups in Sweden, of which 135 were in the northern region (Zetterberg and Svensson 2012). This led to high harvest rates of lynx in the northern region to reduce predation on semi-domestic reindeer herded by indigenous Samí (SEPA 2014). Reindeer are the main prey for lynx in the northern region, and lynx abundance negatively influence reindeer harvest (Mattisson et al. 2011, Hobbs et al. 2012). At the same time, the lynx population decreased in the central region, while there was a small increase in the southern region.

In 2014, favorable conservation status (a requirement for species listed in Appendix 2, EU Habitat Directive 92/43/EEG) for lynx in Sweden was reassessed and the national population absolute minimum was set to 870 individuals, which corresponds to 147 family groups (SEPA 2014). Regional absolute minimum numbers of family groups were reduced accordingly (i.e. 66.5, 62 and 18.5 family groups in the northern, central and southern management region, respectively). However, these numbers are considered the absolute minimum population level, as opposed to the population targets that were set previously. Therefore, to minimize the risk of coming below this threshold, the three management regions set up population target intervals that were higher than the absolute minimum levels dictated by SEPA (northern region, management interval to 68 – 127 family groups; central region, management interval to 72 – 92 family groups; southern region, a target of 40 family groups). In 2018, monitoring data showed that the lynx population was within the management intervals for the northern and central regions, while it had not reach the target of 40 family groups in the southern region (Tovmo and Zetterberg 2018). In 2019, the regional absolute minimum levels were reassessed to 58, 62 and 27 family groups in the northern, central and southern management region, respectively (SEPA 2019) and the management intervals will be reassessed accordingly. The purpose of the reduction in the northern region was to further reduce predation on semi-domestic reindeer, while the higher targets in southern Sweden were implemented to encourage growth in southern Sweden relative to the other two management regions. This management plan is only possible if lynx expand and increase in number in southern Sweden. Thus, to meet the national management goal, the situation for lynx in southern Sweden is very important.

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ARTICLE

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No Allee effect detected during the natural recolonization by a large carnivore despite low growth rate

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Abstract

Eurasian lynx (*Lynx lynx*) have recently naturally recolonized southern Sweden. The first documented reproduction of lynx in recent times occurred in 2003, and the population increased from 2 to 48 family groups (the unit of measurement in Swedish monitoring) during its first 18 years (2003/2004–2020/2021). We did not detect any Allee effect, that is, lower growth rate at low population density, during the recolonization of southern Sweden, although our population simulations revealed a non-negligible (30%) chance that population observed development could include an Allee effect. The probable absence of an Allee effect was likely because colonizing females did not lack mating partners, as a larger number of wide-ranging males were established in the area before documented reproduction took place. Despite the absence of an Allee effect, the growth rate during recolonization was lower in southern Sweden ($\lambda = 1.20$) than in central Sweden ($\lambda = 1.29$). We have no evidence of higher mortality, including that from poaching, or lower reproduction in southern Sweden could explain the lower growth rate. Instead, we suggest that the lower growth rate during the recolonization of southern Sweden was explained by fewer immigrants arriving from central Sweden due to areas of less suitable habitat between central and southern Sweden, partially preventing immigration southward. From a conservation point of view, it is positive that this small population could recover without being negatively influenced by an Allee effect, as small populations with an Allee effect experience lower viability than those without.

KEYWORDS
Allee effect, barrier, colonization, growth rate, habitat suitability, inverse density dependence, lynx

INTRODUCTION

For populations to successfully recolonize areas where they were previously extirpated, several requirements should be met during the colonization process (Ferriere et al., 2000; Sutherland et al., 2000; Whitmee & Orme, 2013). First, there must be a source population from which individuals can disperse. Second, there needs to be suitable habitat where dispersing individuals can establish. Third, dispersing individuals should be able to move through the interim landscape, thus enabling connectivity between suitable areas that are not too far apart and not separated by dispersal barriers (With et al., 1997). However, anthropogenic barriers, such as roads, can reduce connectivity between suitable areas, or landscape permeability, when individuals are killed in vehicle collisions (Kramer-Schadt et al., 2004; Stoner et al., 2013). Finally, even though immigration enables successful colonization, it is vital that the population growth rate remains positive, to maintain itself and to expand. During the early phase of colonization, population sizes are naturally small. The Allee effect (i.e., inverse or positive density dependence) is a situation in which the density and growth rate of a small population are positively correlated; that is, the population growth rate increases as the population density increases (Courchamp et al., 1999). The Allee effect can have a strong influence on the probability of successful colonization, as there could be a threshold in population size below which a population has a very slow or even negative growth rate, known as the Allee threshold. Three main factors that may cause Allee effects are inbreeding, demographic stochasticity, and cooperative interactions (Courchamp et al., 1999; Lande, 1998). Within the last category, a key factor is the ability to find mates, which can be difficult at low population densities when animals are far apart, even for nonsocial species (Gascoigne et al., 2009; Wells et al., 1998). There are few documentations of Allee effects in large solitary carnivores (Gregory et al., 2010), probably because it is very difficult to detect an Allee effect in decreasing populations (Gilroy et al., 2012; Molnar et al., 2008). Therefore, predictive process-based models are often used to forecast potential risks of Allee effects (Molnar et al., 2014). Courchamp et al. (2000) showed using mechanistic models that pack formation, that is, the probability to colonize new territories, could lead to Allee effect in African wild dogs (*Lycaon pictus*), which are obligate cooperative breeders. For a solitary predator, polar bears (*Ursus maritimus*), Molnar et al. (2014) used process-based models and showed the mate finding at low density could cause an Allee effect. In an increasing wolf (*Canis lupus*) population in southern Scandinavia, Wikenros et al. (2021) found that the age of first reproduction in females decreased with increasing population size, which indicates an Allee effect. In this study, we explored whether an Allee effect influenced a recent increase in the population of a solitary predator, the Eurasian lynx (*Lynx lynx*), recolonizing southern Sweden.

The Eurasian lynx population in Sweden was severely reduced during the 19th and early 20th centuries due to human persecution, encouraged by government bounties up until 1928. At that time, possibly less than 100 lynx remained in the country, in one or two isolated populations in central Sweden. Since then, lynx have naturally spread southward and have now recolonized almost all of Sweden. In the winter 2021, the national population was estimated to be about 1000–1400 individuals (Frank & Tovmo, 2021) with limited hunting of lynx permitted based on yearly regional population estimates (Andrén et al., 2020). Southern Sweden was the last area to be recolonized, and the first documented reproduction of lynx in this area in modern times occurred in 2003 (Wildlife Damage Center, 2005). Since then, the lynx population in this area has continued to increase (Frank & Tovmo, 2021; Liberg & Andrén, 2006, and Figure 1).

There are large areas of suitable habitat for lynx in southern Sweden (Hemmingmoore et al., 2020). However, areas between central and southern Sweden are of lower habitat suitability, with highways, railways, agricultural land, three large lakes, and densely human-populated areas, which may partially isolate southern from central Sweden (Hemmingmoore et al., 2020). To what extent this area acts as a barrier is still unknown. Although it has a lower habitat suitability, the area spans a relatively short distance in terms of lynx movement capability and there are several documented cases of lynx dispersing between central and southern Sweden (Samelius et al., 2012).

The recolonization of Sweden occurred in phases, with the lynx population establishing in central Sweden in progressively southward waves prior to the recolonization of southern Sweden at a later time (Liberg & Andrén, 2006, Figures 1 and 2). It can therefore be considered as two separate colonization events. Thus, our aims are (1) to test whether lynx recolonization in southern Sweden (18-year-long data set) was affected by an Allee effect (i.e., inverse or positive density-dependent growth rate) and (2) to compare the lynx population growth rate during the recolonization of southern Sweden with that of central Sweden. In the comparison between southern and central Sweden, we also explored the effects of traffic mortality by adding lynx killed in vehicle collisions to the models together with the legal harvest.

STUDY AREA

The main study area was southern Sweden (approximately 73,000 km^2) south of the large agricultural areas in the counties of Västra Götaland and Östergötland (Figure 1). It is dominated by forest (63%), most of which is intensively managed with the primary tree species being not only Norway spruce (*Picea abies*) and Scots pine (*Pinus sylvestris*) but also birch (*Betula pubescens*

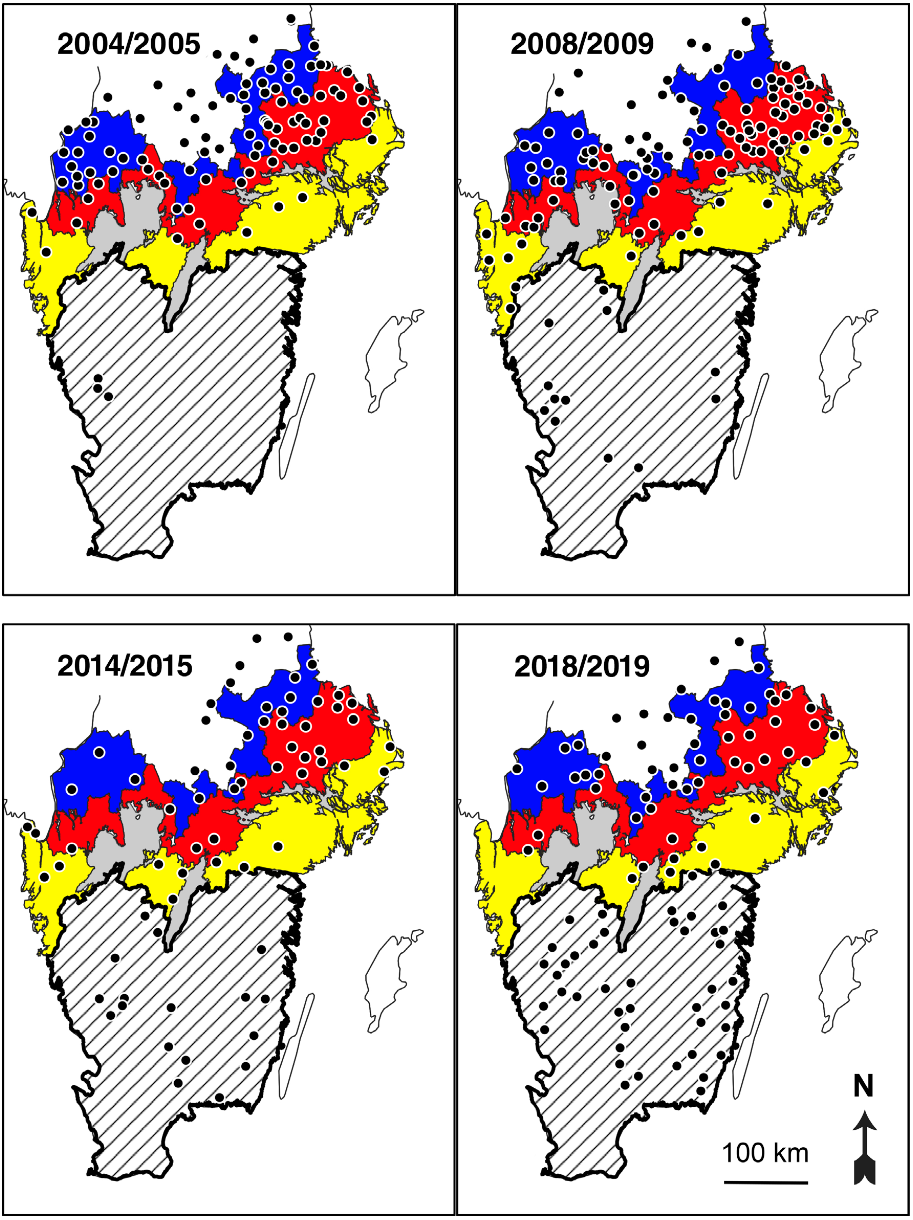

FIGURE 1 Distribution of lynx family groups (black dots) documented in central Sweden (Region A [blue], Region B [red], and Region C [yellow]) and southern Sweden (striped) in winter 2004/2005, 2008/2009, 2014/2015, and 2018/2019. The area north of Region A (white) was not included in the study

and *Betula pendula*), and interspersed with other broad-leaved species such as aspen (*Populus tremula*), ash (*Fraxinus excelsior*), elm (*Ulmus glabra*), lime (*Tilia cordata*), oak (*Quercus robur*), and beech (*Fagus sylvatica*) (Esseen et al., 1997). Agricultural and grasslands cover about 24% of the region. Southern Sweden is partly isolated from central Sweden by highways, railways, agricultural land, three large lakes, and densely human-

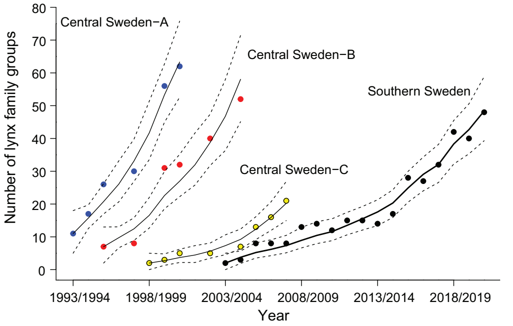

FIGURE 2 Number of lynx family groups in relation to year in central Sweden (Region A [blue dots], Region B [red dots], and Region C [yellow dots]) and southern Sweden (black dots). Medians of posterior distributions of the estimated number of lynx family groups (solid line) and 95% Bayesian credible intervals (dashed lines). See Appendix S1: Figure S7 for log(number of lynx family groups) in relation to year

populated areas (Hemmingmoore et al., 2020). The mean primary paved road density is 0.47 km/km^2, and the mean secondary gravel road density is 1.52 km/km^2.

We divided central Sweden (north of the main study area) into three regions (A, B, and C, total area approximately 65,000 km^2) to describe the frontiers of recolonization as the population progressed southward (Figure 1). These three areas are parts of the southern continuous boreal forest. Forest covers 69%, and most of it is intensively managed and dominated by Norway spruce and Scots pine. Agricultural land covers 24% of the land and increases toward the south. The mean primary road density is 0.39 km/km^2, and the mean secondary road density is 1.18 km/km^2.

MATERIALS AND METHODS

Lynx monitoring

We used data from the Swedish lynx monitoring system, available in the official carnivore database (Rovbase; rovbase30.miljodirektoratet.no). Lynx monitoring in Sweden is based on non-replicated counts of family groups (Gervasi et al., 2013; Linnell, Fiske, et al., 2007; Linnell, Odden, et al., 2007). The monitoring is primarily conducted from December to the end of February and largely based on snow-tracking and identifying lynx tracks from two or more individuals, which are then assessed as a family group consisting of an adult female and young of the year (Linnell, Odden, et al., 2007). Simultaneous snow tracking or a distance criterion based on home-range sizes and movement patterns from radiomarked female lynx with kittens is used to separate observations of different family groups, to assure that counts of family groups are distinct (Gervasi et al., 2013; Linnell, Odden, et al., 2007). Additional observations that are used to confirm reproduction include camera-trap images of kittens, and any kittens shot in the early part of the hunting season (February) or killed in traffic accidents. Trained and authorized personnel from the Swedish County Administration Boards perform the lynx monitoring. Game wardens, hunters, and the public can report records of lynx tracks, but all observations need to be verified by the authorized personnel before being confirmed and entered into the carnivore database and thus used in the national count of family groups. The family group counts are multiplied by a conversion factor to encompass the entire lynx population, including males and nonreproducing females. The conversion factor is on average 5.48 (±0.40 SD) in central and southern Sweden (Andrén et al., 2002). There was a good fit between the monitored number of lynx family groups and the reconstructed population size (Nilsen et al., 2011). Thus, the lynx monitoring provides a proxy of all lynx in an area. In the population models, we included dead lynx. Data on dead lynx were downloaded from the carnivore database (Rovbase; rovbase30.miljodirektoratet.no).

Population model

We used the Bayesian hierarchical population models to estimate the posterior distribution of the unobserved lynx population size, using four different process equations to assess the presence of an Allee effect during lynx colonization of southern Sweden. In all process models, μ_t is the deterministic prediction of the lynx population at time t, N_t is the unobserved population size at time t, $H_{(t-1)}$ is the observed legal harvest of lynx at time $t-1$ (i.e., legal harvest from the previous hunting season in February and March), and σ_{proc} is the SD of the unobserved population size.

Process model 1—Linear density-dependent growth rate

$$\mu_t = \log\left[\left(N_{(t-1)} - H_{(t-1)}\right) \times \exp\left(a_0 + a_1 \times N_{(t-1)}\right)\right]$$

$$N_t \sim \text{lognormal}\left(\mu_t, \sigma_{\text{proc}}\right)$$

Here, a_0 represents the growth rate ($\log(\lambda)$) at zero density, and a_1, the per capita change in growth rate. An

Allee effect would result in a positive a_1 estimate ($a_1 > 0$), while for classic density dependence, the a_1 estimate would be negative ($a_1 < 0$). This model describes the same linear relationship between growth rate and population density over the entire range of the data. If $a_1 > 0$, the growth rate increases continuously with population density; that is, population density never reaches the point where the relationship between growth rate and population density changes from being positive to negative (Appendix S2: Figure S2).

Process model 2—Quadratic density-dependent growth rate

$$\mu_t = \log\left[\left(N_{(t-1)} - H_{(t-1)}\right) \times \exp\left(b_0 + b_1 \times N_{(t-1)} + b_2 \times {N_{(t-1)}}^2\right)\right]$$

$$N_t \sim \text{lognormal}\left(\mu_t, \sigma_{\text{proc}}\right)$$

Here, b_0 represents the growth rate ($\log(\lambda)$) at zero density, and b_1 and b_2 describe the shape of the quadratic curve. We added the quadratic term to test whether the growth rate was first positive at low densities (i.e., Allee effect), and then changes to negative when density increases (i.e., classic density dependence), resulting in a hump-shaped or concave growth rate curve, resulting in a negative b_2 estimate ($b_2 < 0$). This hump-shaped relationship between growth rate and population density means that the population density reaches the point where the relationship between growth rate and population density changes from being positive to negative (Appendix S2: Figure S2).

Process model 3—Density-independent growth rate and comparing between southern and central Sweden

$$\mu_t = \log\left[\left(N_{(t-1)} - H_{(t-1)}\right) \times \exp(c_0)\right]$$

$$N_t \sim \text{lognormal}\left(\mu_t, \sigma_{\text{proc}}\right)$$

Here, c_0 represents the estimated constant density-independent growth rate ($\log(\lambda)$). We used one model to estimate the density-independent growth rate and included two region-specific growth rates in the model: $c_{0-\text{southern}}$ (for southern Sweden) and $c_{0-\text{central}}$ (one common for regions A, B, and C in central Sweden), which is expected to decrease uncertainty due to borrowing strength between data sets (Hobbs & Hooten, 2015; see also Appendix S1: Table S1 and Figure S1). We estimated one common growth rate across the three regions of central Sweden because the data show a similar rate during each wave of recolonization, and also due to small sample sizes within each region and because the recolonization of central Sweden occurred within continuous suitable lynx habitat (Hemmingmoore et al., 2020).

Process model 4—Density-independent growth rate, including lynx killed in vehicle collisions and comparing between southern and central Sweden

$$\mu_t = \log\left[\left(N_{(t-1)} - H_{(t-1)} - T1_{(t-1)}\right) \times \exp(d_0) - T2_{(t-1)}\right]$$

$$N_t \sim \text{lognormal}\left(\mu_t, \sigma_{\text{proc}}\right)$$

Here, d_0 represents the estimated constant density-independent growth rate when lynx killed in vehicle collisions (T) are included in the yearly mortality estimate, along with legal harvest. We used one model to estimate the density-independent growth rate, including lynx killed in vehicle collisions, and included two region-specific growth rates in the model: $d_{0-\text{southern}}$ (for southern Sweden) and $d_{0-\text{central}}$ (one common for regions A, B, and C in central Sweden). $T1_{(t-1)}$ is the observed number of lynx killed in vehicle collisions after the census in February but before the birth pulse in late May at time $t - 1$, and $T2_{(t-1)}$ is the observed number of lynx killed in vehicle collisions after the birth pulse in late May but before the census in February at time t.

Observation model

All four process equations were linked to data using the same observation equation:

$$\text{alpha}_t = {N_t}^2 / \sigma^2_{\text{Nobs}}$$

$$\text{beta}_t = N_t / \sigma^2_{\text{Nobs}}$$

$$\varphi_t \sim \text{gamma}(\text{alpha}_t, \text{beta}_t)$$

$$Fgobs_t \sim \text{Poisson}(p \times \varphi_t)$$

where $Fgobs_t$ is the observed number of family groups at time t, p is the number of family groups per total number of lynx, and σ^2_{Nobs} is the estimated observation error of the population size. This formulation views the count data hierarchically, where the mean observed count of lynx family groups at time t is Poisson-distributed with mean φ_t multiplied by p, and this mean (φ_t) is drawn from a gamma distribution with a mean equal to the prediction of the process model (N_t) and a SD for observation error (σ_{Nobs}). The shape parameters for the gamma distribution (alpha_t and beta_t) were derived from N_t and σ^2_{Nobs} using moment matching. We chose this approach because it allows the uncertainty in the data model to be larger than the variance of the Poisson parameter φ_t. This gamma–Poisson mixture for count data is the same as using a negative binomial distribution, but has computational advantages (McCarthy, 2007).

Model fitting and evaluation

Vague prior distributions were assigned to: a_0, a_1, b_0, b_1, b_2, c_0, and d_0, $\sim$ normal(0, 100), $\sigma_{\text{proc}} \sim$ uniform(0, 10), and $\sigma_{\text{Nobs}} \sim$ uniform(0, 100). On average, one lynx family group represents 0.184 ± 0.013 SD of total number of lynx in the population (Andrén et al., 2002). The prior for the number of family groups per total number of lynx (p) was calculated from this using moment matching; $p \sim$ beta(152, 677). We approximated the marginal posterior distributions of parameters fitting the models to data using the Markov chain Monte Carlo algorithm implemented in *rjags* and *coda* packages (Plummer, 2003) in R (R Core Team, 2018). We ran three chains of 100,000 iterations following a 50,000 burn-in. Convergence was checked by visual inspection of trace plots and by the diagnostics of Heidelberger (Heidelberger & Welch, 1983) and Gelman (using the threshold value of <1.02 indicating very low variation between the three chains; Brooks & Gelman, 1997) implemented in the *coda* package (Plummer, 2003). We used posterior predictive checks to evaluate the lack of fit between models and data using the Bayesian p values (p value >0.1 or <0.9 suggests a good fit between the model and the data; Hobbs & Hooten, 2015). We present posterior means and SD with the associated 95% Bayesian credible intervals (BCIs).

We used leave-one-out cross-validation to compare the models and estimated the mean square prediction error (MSPE). Low values of MSPE indicate models with a greater predictive ability (Hobbs & Hooten, 2015).

Statistical power analyses

We performed statistical power analyses by comparing the posterior distributions for the coefficients estimated from the monitoring data with the coefficients estimated from simulated data of a population development with Allee effect (i.e., Model 1 with positive linear density-dependent growth rate; Model 2 with negative quadratic density-dependent growth rate), as well as density-independent growth rate (Model 3). First, we used deterministic models to generate expected parameter values. Second, we generated stochastic population development by randomly selecting values for the model parameters (i.e., a_0 and a_1 for Model 1; b_0, b_1, and b_2 for Model 2; and c_0 for Model 3). These parameter values were randomly drawn from a normal distribution (Appendix S2: Table S1). Finally, we made 1000 simulations of the population development for each model, using the Bayesian hierarchical population models (process and observation models) described above to estimate the posterior distribution of each parameter. The model parameters from these simulations were then compared with the parameters estimated from the monitoring data. These comparisons give an indication of the probability to detect a linear density-dependent growth rate (difference for a_1 estimates) or a negative quadratic density-dependent growth rate (difference for b_2 estimates), given the observed monitoring data. See Appendix S2 for a detailed description of the statistical power analyses.

RESULTS

Model 1—Linear density-dependent growth rate

The mean coefficient estimate for the density dependence of the growth rate was negative ($a_1 = -0.00082$; Table 1), and there was only a 14% probability that the coefficient would be positive ($a_1 > 0$), thus contributing positively to the population growth rate as predicted from an Allee effect. The estimates of a_0 and a_1 passed both the Heidelberger and Gelman diagnostics. The Bayesian p value was 0.27, suggesting a good fit between the model and the data. However, the results were sensitive to the initial condition (i.e., 2 lynx family groups observed in winter 2002/2004), probably because the increase from 2 (2003/2004) to 3 (2004/2005) lynx family groups in the data set results in a high deterministic growth rate ($\lambda = 1.5$ or $\log(\lambda) = 0.41$). When changing the initial condition to 3 or 4 family groups, the a_1 estimate was closer to zero (27% and 45% probability for a positive a_1, respectively; Appendix S1: Table S2). The Bayesian p values were 0.22 and 0.20 for these alternative models. Consequently, from the posterior distribution there is neither a support for a positive (Allee effect) nor a negative (classic density dependence) relationship between growth rate and population density, because a_1 (per capita change in

TABLE 1 Statistics summarizing posterior distributions (mean ± SD) of the population model parameters estimates, with the associated 95% Bayesian credible intervals (BCIs)

Parameter	Definition	Mean ± SD	95% BCI
Model 1—Linear density-dependent growth rate			
a_0	Growth rate at zero density on log scale	0.264 ± 0.101	0.0970 to 0.503
a_1	Density-dependent effect on growth rate on log scale	−0.00082 ± 0.00090	−0.0029 to 0.00070
p	Number of family groups per total number of lynx	0.183 ± 0.0132	0.158 to 0.210
σ_{proc}	Process SD on log scale	0.163 ± 0.094	0.0129 to 0.377
σ_{Nobs}	Estimated observation error of the population size	6.43 ± 5.08	0.263 to 19.0
Model 2—Quadratic density-dependent growth rate (priors ~ uniform(−4, 4))			
b_0	Growth rate at zero density on log scale	0.499 ± 0.241	0.119 to 1.085
b_1	Describes the shape of the quadratic curve	−0.00646 ± 0.00517	−0.0191 to 0.0020
b_2	Describes the shape of the quadratic curve	0.000026 ± 0.000024	−0.000012 to 0.000083
p	Number of family groups per total number of lynx	0.186 ± 0.0135	0.160 to 0.213
σ_{proc}	Process SD on log scale	0.163 ± 0.099	0.0121 to 0.390
σ_{Nobs}	Estimated observation error of the population size	6.45 ± 5.33	0.236 to 19.7
Model 3—Density-independent growth rate and comparing between southern and central Sweden			
$c_{0-\mathrm{southern}}$	Density-independent growth rate on log scale in southern Sweden	0.179 ± 0.0262	0.128 to 0.237
$c_{0-\mathit{central}}$	Density-independent growth rate on log scale central Sweden	0.253 ± 0.0241	0.205 to 0.304
p	Number of family groups per total number of lynx	0.185 ± 0.0134	0.159 to 0.211
σ_{proc}	Process SD on log scale	0.0771 ± 0.0557	0.00212 to 0.203
σ_{Nobs}	Estimated observation error of the population size	4.27 ± 3.43	0.093 to 12.7
Model 4—Density-independent growth rate, including lynx killed in vehicle collisions and comparing between southern and central Sweden			
$d_{0-\mathrm{southern}}$	Density-independent growth rate on log scale in southern Sweden	0.207 ± 0.0249	0.159 to 0.262
$d_{0-\mathrm{central}}$	Density-independent growth rate on log scale in central Sweden	0.269 ± 0.0231	0.223 to 0.317
p	Number of family groups per total number of lynx	0.184 ± 0.0137	0.157 to 0.211
σ_{proc}	Process SD on log scale	0.0716 ± 0.0516	0.00293 to 0.191
σ_{Nobs}	Estimated observation error of the population size	4.37 ± 3.40	0.157 to 12.7

Note: See Appendix S1: Figures S2–S6 for posterior and prior distributions of the parameters.

growth rate) largely overlapped zero and showed good convergence around zero.

From the statistical power analysis, parameter a_1 estimated from our monitoring data was closer to zero and had a negative mean value, compared with the positive mean a_1 from the simulated data (Appendix S2: Figure S4). There was a 71% probability that a_1 from the monitoring data would be smaller than a_1 from the simulations (Appendix S2: Figure S5). Thus, about 30% of the simulated population development with a known Allee effect could be similar to the observed population development in our study.

Model 2—Quadratic density-dependent growth rate

The posterior distributions for all three (b_0, b_1, and b_2) coefficients were centered around zero with large SDs (Appendix S1: Figure S3), and they did not pass Heidelberger diagnostics. As the posterior distributions for b_0, b_1, and b_2 were close to the priors (Appendix S1: Figure S3), we also tested more informative priors restricting their range to more biological relevant values (~uniform(−4, 4)). Using restricted priors, all coefficients converged (Table 1), with a 99% probability for b_0 to be positive, a 92% probability for b_1 to be negative, and an 89% probability for b_2 to be positive. However, the coefficients resulted in a convex relationship between growth rate and population density (i.e., first decreasing and then increasing growth rate with increasing density). The Bayesian p value was 0.32, and the coefficient estimates passed the Gelman diagnostics. However, b_2 did not pass the Heidelberg diagnostics. Also, these results were sensitive to the initial condition: Changing the initial condition to 3 or 4 lynx family groups increased the uncertainty around the b_2 estimate (79% and 63%

probability for a positive b_2; Appendix S1: Table S2). Consequently, from the posterior distribution there is limited support for both a concave (i.e., hump-shaped) and a convex (as indicated by the results) relationship between growth rate and population density.

From the statistical power analysis, the parameter b_2 estimated from the lynx monitoring data was larger and with a positive mean value, compared with a negative mean b_2 from simulated data with a known quadratic density-dependent growth rate (Appendix S2: Figure S6). There was an 89% probability that b_2 from the monitoring data would be larger than the b_2 from the simulated data (Appendix S2: Figure S7).

Model 3—Density-independent growth rate and comparing between southern and central Sweden

The model without density dependence estimated the growth rate ($c_{0-\text{southern}}$) in southern Sweden to be 0.179 (Table 1), which corresponds to a lambda ($\lambda = \exp(c_{0-\text{southern}})$) of 1.197 (±0.031 SD, 95% BCI: 1.137–1.269). The growth rate ($c_{0-\text{central}}$) in central Sweden during the recolonization (1994–2008) was 0.253 (Table 1), which corresponds to a lambda ($\lambda = \exp(c_{0-\text{central}})$) of 1.289 (±0.031 SD, 95% BCI: 1.227–1.354). There was a 97% probability that the growth rate in southern Sweden was lower than in central Sweden. The Bayesian p values were >0.18. The coefficients $c_{0-\text{south}}$ and $c_{0-\text{central}}$ passed both the Heidelberger and Gelman diagnostics.

From the statistical power analysis, the parameter c_0 estimated from the monitoring data was very similar to the estimate from the simulated data with density-independent growth rate, the two posterior distributions largely overlapped (Appendix S2: Figure S8), and there was a 49.5% probability that c_0 from the monitoring data would be smaller than c_0 from the simulated data (Appendix S2: Figure S9). Lastly, the population simulation of Model 3 showed the strongest correlation with the monitoring data compared with simulations from the other two models (Appendix S2: Figure S10).

Model 4—Density-independent growth rate including lynx killed in vehicle collisions comparing between southern and central Sweden

Including lynx killed in vehicle collisions did not change the difference in growth rate between central Sweden and southern Sweden (Table 1). The mean lambda ($\lambda = \exp(d_{0-\text{south}})$) for southern Sweden was 1.229 (±0.029 SD, 95% BCI: 1.175–1.296) and for central Sweden was 1.308 (±0.030 SD, 95% BCI: 1.251–1.371) when including lynx killed in vehicle collisions. There was a 97% probability that the growth rate in southern Sweden was lower than in central Sweden when lynx killed in vehicle collisions were included. The Bayesian p values were >0.16. The coefficients $d_{0-\text{south}}$ and $d_{0-\text{central}}$ passed both the Heidelberger and Gelman diagnostics.

Model selection

We used leave-one-out cross-validation and estimated MSPE to evaluate the different models. Model 3 had the lowest MSPE (24.21), while Model 1 (33.43) and Model 2 (32.12) had similar MSPE, suggesting that Model 3 (density-independent growth rate) had the greatest predictive ability.

DISCUSSION

In this study, we aimed to assess whether the Allee effect was present during the early stage of population establishment during the natural recolonization of a species' previous range. We also assessed whether this recolonization of southern Sweden by lynx took place at a different rate than the previous recolonization of central Sweden. We found that the colonization of southern Sweden occurred more slowly than that of central Sweden, which raised the question as to whether this was due to an Allee effect (i.e., inverse or positive density dependence) in the south. Although only two reproductions were observed at the outset of the natural recolonization of southern Sweden, we did not detect any Allee effect while the population was initially establishing in this area (2004–2021). During this time period, the population increased from approximately 10 lynx (based on two family groups) to about 300 lynx (based on 48 family groups) (Figure 2). Considering that lynx colonized southern Sweden more slowly than central Sweden, it may be expected that there would be an Allee effect (i.e., inverse or positive density dependence) at low population levels, which we did not detect.

The population simulations indicate that there might be some difficulties to detect an Allee effect with an 18-year-long time series. There was a substantial overlap in the probability distributions for the coefficient describing the per capita increase in growth rate (a_1) in the Allee effect model (Model 1) between the monitoring and simulated data (Appendix S2: Figures S4 and S5). The similarity between the results from the monitoring data and the simulated data with a negative quadratic growth rate (Model 2) was weaker (Appendix S2: compare Figures S5 and S7). However, the estimates for the parameter describing density-independent growth rate (c_0) were most similar between the monitoring and simulated data (Appendix S2: Figures S8 and S9) and simulations from the density-independent growth rate model (Model 3) were very similar to the monitoring data (Appendix S2: Figure S10). Furthermore, the model evaluation (leave-one-out cross-validation) suggested that Model 3 (density-independent growth rate) had the greatest predictive ability. Therefore, we conclude that the density-independent growth rate model best described the lynx population development in southern Sweden, but we cannot completely rule out an Allee effect, as some of the simulated population development (about 30%) with a known Allee effect was similar to observed population development. The simulation is based on only one quantitative positive density-dependent growth rate ($a_0 = 0.12$ and $a_1 = 0.00095$, Allee effect; Appendix S2: Table S1, Figure S2). In this alternative, the growth rate at zero density (a_0) was positive. With a stronger Allee effect, for example, with a negative growth at very low densities ($a_0 < 0$), the difference between our monitoring data and simulated data had been larger. On the contrary, with a weaker Allee effect (a_0 larger than the chosen 0.12 and a_1 smaller than the chosen 0.00095), the difference between our monitoring data and simulated data had been smaller. A longer time series will of course increase statistical power to separate between an Allee effect (Model 1 or 2) and density-independent growth rate (Model 3).

There are several models for describing an Allee effect; for example, Courchamp et al. (2008, tab. 3.1) described 14 different models. Several of these models have one feature in common; they describe a concave or hump-shaped relationship between growth rate and population density, and assume a threshold for population density below which the growth rate is negative, known as the Allee threshold. Courchamp et al. (2008) suggested that our Model 2 (quadratic density-dependent growth rate) and our Model 1 (if b_2 in Model 2 is not significantly different from zero) are the most straightforward ways to test for the presence of an Allee effect using long-term monitoring data. Our Models 1 and 2 are very flexible, as they can describe both negative (i.e., include an Allee threshold; a_0 or $b_0 < 0$) and small positive growth rate (a_0 or $b_0 > 0$) at low population densities (Appendix S2: Figure S2).

A low mate encounter rate due to a shortage of mates at low population density is a commonly cited factor explaining an Allee effect (Deredec & Courchamp, 2007). Molnar et al. (2014) showed using process-based modeling that reduced mate finding at low population density can cause an Allee effect in another nonsocial predator, the polar bear. Early in the recolonization period with very low population density, it would be reasonable to expect that a low mate encounter rate could cause a lower growth rate. However, there are reasons to expect that female lynx do not necessarily experience a lack of mating partners when they colonize a new area. Lynx dispersal is male-biased, where most females (ca. 55%) but very few males settle in areas neighboring (within 30 km) their natal home range, and thus, males disperse further (mean 149 km, 32–428 km) than females (mean 46 km, 3–215 km; Samelius et al., 2012). It is thus likely that there is a male-biased sex ratio at the frontier of recolonization. Males also roam over larger home ranges, especially at low population density (Aronsson et al., 2016), increasing the likelihood that females will find a partner despite low density. Therefore, it is likely that the expansion of lynx is limited by female dispersal, which has been shown for other wide-ranging mammals with male-biased dispersal, for example, brown bears (*Ursus arctos*) (Jerina & Adamič, 2008; Swenson et al., 1998) and cougars (*Puma concolor*) (LaRue et al., 2012), rather than female access to mates. That this could have been the case in southern Sweden is supported by spontaneous observations of lynx prior to the first documented reproduction in 2003. In the official carnivore database (Rovbase), 179 observations of lynx were recorded between 1995 and 2002 in southern Sweden. Moreover, lynx have a polygynous mating system in which one male can mate with several females (Aronsson et al., 2016). This would suggest that females do not experience any difficulty in encountering mates during colonization even when population density is low and thus explaining why we did not detect any Allee effect.

Although we could not detect any Allee effect (i.e., inverse or positive density dependence) on the population growth rate, the growth rate during the recolonization of southern Sweden was lower than that during the recolonization of central Sweden (97% probability that the growth rate was lower). One explanation could be that the density of roads and traffic intensity are higher in southern Sweden than in central Sweden, and roads have been shown to be significant causes of mortality or barriers to lynx recolonization elsewhere in Europe (Basille et al., 2013; Schmidt-Posthaus et al., 2002; Zimmermann et al., 2007). Thus, the risk of mortality due to vehicle collisions could be higher in southern Sweden. However, reported traffic-killed lynx did not explain the difference in growth rate when included in our modeling (Table 1). This could be due to that road density and traffic intensity are still relatively low in southern Sweden compared with other parts of Europe, and therefore had less effect on lynx survival.

The lower growth rate could be explained by higher poaching. Andrén et al. (2006) found that poaching accounted for 46% of all adult mortality in Sweden, but with substantial regional variation driven by human–predator conflicts. Heurich et al. (2018) also suggested that increased poaching outside protected areas in central Europe lowered the growth rate and therefore slowed down the expansion of lynx. However, data from radiomarked lynx from southern and central Sweden showed no significant difference in poaching rate (p value = 0.33) between the two areas (Andrén, Aronsson, et al., 2022, but specific analyses done in this paper); 1 of 37 radiomarked lynx that were followed for 46 radioyears was assumed to be poached in southern Sweden, resulting in a mean poaching risk of 0.024 (0.00–0.071; 95% CI, Kaplan–Meier estimate). In central Sweden, 7 of 60 radiomarked lynx that were followed for 114 radioyears were confirmed or assumed to be poached lynx, resulting in a mean poaching rate of 0.060 (0.016–0.102; 95% CI, Kaplan-Meier estimate). Another potential explanation for the lower growth rate in southern Sweden could be lower reproduction. However, López-Bao et al. (2019) could not detect any spatial trend in the probability of reproduction, litter size, and kitten survival during the first 9 months from southern to central Sweden. One more explanation could be that source areas were not saturated and therefore provided relatively few female immigrants. Female lynx disperse shorter distances than males, and most young females settle very close to their natal area if possible (Samelius et al., 2012). Furthermore, the lynx population in Sweden is managed through licensed hunting, whereby adult individuals are removed from the population regularly, potentially creating a continuous availability of vacant areas for lynx settled in central Sweden. As a result, there was presumably an abundance of vacant areas suitable for lynx settlement in central Sweden, which may have limited the rate of dispersal of females to southern Sweden. Fewer emigrants from central Sweden likely result in lower connectivity with southern Sweden, which in turn result in a lower growth rate.

In addition to the potential influence of short female dispersal distance on recolonization, central Sweden and southern Sweden are separated by three large lakes, a network of highways, and large areas of agricultural landscape (Hemmingmoore et al., 2020). These areas of less suitable lynx habitat disrupt the mainly continuous distribution of high habitat suitability in central and southern Sweden. Lynx are able to cross these barriers, allowing colonization of southern Sweden. However, no such barrier exists between central Sweden and northern areas from which lynx originally recolonized (Samelius et al., 2012). The difficulty encountered by lynx crossing unsuitable habitat could be discouraging and thus slow down recolonization, as seen in other European populations (Magg et al., 2016; Niedziałkowska et al., 2006).

The ability to understand and assess the viability of small and recovering populations is very important in conservation and management. That an Allee effect was absent or unlikely to have occurred during the recolonization of lynx in southern Sweden is, despite a lower population growth rate, positive for conservation of this and other systems. Although this study was based on an 18-year-long series, more data would likely strengthen the conclusion. Some populations of large carnivores in North America (Smith et al., 2016) and Europe (Chapron et al., 2014) are recolonizing their former ranges, which can begin with a small population at the frontier of recolonization. If these species were to face an Allee effect in addition to other barriers to recovery, it would have a negative effect on the viability of small populations, as the growth rate would be even lower at low population sizes (Courchamp et al., 1999). The loss of continuous habitat is one of the most significant factors in contributing to lost resiliency and megafauna population decline worldwide (Courchamp et al., 2008; Tucker et al., 2018; Woodroffe, 2006). In Sweden, the potential barriers for lynx did not prevent recolonization of southern Sweden, although the lower growth rate illustrates the effect that even permeable barriers may have on the carnivore recovery.

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CONFLICT OF INTEREST

The authors declare no conflict of interest.

AUTHOR CONTRIBUTIONS

Henrik Andrén conceived the idea and designed the study, which was further developed in discussions with all the other coauthors. Henrik Andrén and Heather Hemmingmoore prepared the database. Henrik Andrén did most of the analyses with input from Malin Aronsson and Heather Hemmingmoore. Henrik Andrén wrote the first version of the manuscript with input from the other coauthors. All authors contributed to the writing of the manuscript and approved the final version for publication.

DATA AVAILABILITY STATEMENT

Data and statistical R codes for the Bayesian hierarchical population models (Andrén, Hemmingmoore, et al., 2022) are available from Dryad: https://doi.org/10.5061/dryad.8kprr4xqb.

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This thesis investigates the natural recolonization of the Scandinavian lynx in southern Sweden, following near-extinction a century ago. It identifies available habitat and explores whether the population faced an Allee effect during recolonization. It then assesses the genetic effects of this range expansion, emphasizing the genetic connectivity between source and newly established populations. The results highlight the importance of connectivity in enabling the recolonization of large carnivores in human-modified landscapes.

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