TURUN
YLIOPISTO
UNIVERSITY
OF TURKU

FACTORS AFFECTING THE DISTRIBUTION OF THE EURASIAN BEAVER AND THE NORTH AMERICAN BEAVER IN FINLAND

Riikka Alakoski

TURUN YLIOPISTON JULKAISUJA – ANNALES UNIVERSITATIS TURKUENSIS
SARJA – SER. AII OSA – TOM. 383 | BIOLOGICA – GEOGRAPHICA – GEOLOGICA | TURKU 2021

TURUN
YLIOPISTO
UNIVERSITY
OF TURKU

FACTORS AFFECTING THE DISTRIBUTION OF THE EURASIAN BEAVER AND THE NORTH AMERICAN BEAVER IN FINLAND

Riikka Alakoski

TURUN YLIOPISTON JULKAISUJA – ANNALES UNIVERSITATIS TURKUENSIS
SARJA – SER. AII OSA – TOM. 383 | BIOLOGICA – GEOGRAPHICA – GEOLOGICA | TURKU 2021

University of Turku

Faculty of Science
Department of Biology
Section of Ecology
Doctoral programme in Biology, Geography and Geology (BGG)

Supervised by

Docent, Vesa Selonen
University of Turku
Finland

Docent, Kaarina Kauhala
University of Helsinki
Finland

Reviewed by

Associate Professor, Göran Hartman
Swedish University of Agricultural Sciences
Sweden

Docent, Janne Sundell
University of Helsinki
Finland

Opponent

Docent, Petri Nummi
University of Helsinki
Finland

The originality of this publication has been checked in accordance with the University of Turku quality assurance system using the Turnitin Originality Check service.

ISBN 978-951-29-8544-9 (PRINT)
ISBN 978-951-29-8545-6 (PDF)
ISSN 0082-6979 (Print)
ISSN 2343-3183 (Online)
Painosalama, Turku, Finland 2021

To all beavers

UNIVERSITY OF TURKU
Faculty of Science
Department of Biology
Section of Ecology
RIIKKA ALAKOSKI: Factors Affecting the Distribution of the Eurasian Beaver and the North American Beaver in Finland
Doctoral Dissertation, 134 pp.
Doctoral Programme in Biology, Geography and Geology (BGG)
August 2021

ABSTRACT

Understanding the factors affecting the distribution of species lies at the core of ecology and is becoming increasingly important in the field of applied ecology, such as conservation biology and wildlife management. Distribution patterns of species are largely affected by climate, resource availability, dispersal, disturbance and population dynamics. In my thesis, I studied the factors affecting the distribution of two beaver species in Finland, the Eurasian (*Castor fiber*) and the North American beaver (*Castor canadensis*). These species were simultaneously introduced in the 1930s but show a strikingly different distribution and population size at present. I determined the population dynamics, habitat use and availability, and patterns of distribution for both beaver species utilizing data gathered by hunters in beaver monitoring counts and landscape data from a geographic information system (GIS). The results of this thesis indicate that the dynamics of both species is density dependent and migration is an important aspect. In addition, population growth rates have not differed considerably between the species. Beavers seem to disperse slowly from the source populations and a comprehensive water system may enable them to locate habitats close to their natal sites. In addition, habitat use, and thus, available suitable habitats of the two beaver species seem to be similar in Finland, indicating a competition for resources. However, the present environments might affect the different observed patterns, most noticeably that the Eurasian beaver occurs closer to agricultural areas, which may also provide highly suitable habitats for beavers. The importance of deciduous trees and aquatic habitat to beavers was also apparent in my studies. Moreover, I found that the North American beaver has spread longer distances from the introduction sites. The reason for the smaller range of the Eurasian beaver was not, however, completely clear as lack of suitable habitats and barriers to movement do not seem to restrict the spread of the native species. The results of this thesis show that the reasons for the different distribution patterns of the two species are likely complex, and the patterns can be caused by several intrinsic and extrinsic factors. This highlights that it is hard to predict how an introduced species will succeed in new areas. These results can be utilized when planning species introductions, and in wildlife management and the conservation of species.

KEYWORDS: *Castor fiber*, *Castor canadensis*, distribution, monitoring counts, population dynamics, habitat use

TURUN YLIOPISTO
Matemaattis-luonnontieteellinen tiedekunta
Biologian laitos
Ekologia
Riikka Alakoski: Euroopanmajavan ja amerikanmajavan levinneisyyteen vaikuttavat tekijät Suomessa
Väitöskirja, 134 s.
Biologian, maantieteen ja geologian tohtoriohjelma (BGG)
Elokuu 2021

TIIVISTELMÄ

Lajien levinneisyyteen vaikuttavien tekijöiden ymmärtäminen on keskeisessä osassa ekologiassa, ja on yhä enemmän tärkeää myös sovelletun ekologian aloilla, kuten suojelubiologiassa ja riistanhoidossa. Lajien levinneisyyteen vaikuttavat suuresti ilmasto, resurssien saatavuus, dispersaali, häirintä ja populaatiodynamiikka. Väitöstyössäni tutkin kahden majavalajin, euroopanmajavan (*Castor fiber*) ja amerikanmajavan (*Castor canadensis*), levinneisyyteen vaikuttavia tekijöitä Suomessa. Nämä lajit istutettiin Suomeen samanaikaisesti 1930-luvulla, mutta lajien levinneisyys ja populaatiokoot ovat silmiinpistävän erilaisia tällä hetkellä. Tutkin molempien lajien populaatiodynamiikkaa, habitaatinkäyttöä ja -saatavuutta, sekä alueellista sijoittumista, majavalaskennoista saadun datan ja paikkatietoaineistojen avulla. Tulokseni viittaavat siihen, että molempien lajien populaatiodynamiikka on tiheydestä riippuvaista ja migraatio on tärkeä tekijä. Lisäksi populaatioiden kasvukertoimet eivät ole paljoakaan eronneet lajien välillä. Majavat näyttäisivät leviävän hitaasti lähdepopulaatioistaan ja kattava vesistöverkosto saattaa auttaa niitä sopivan habitaatin löytämisessä synnyinalueen läheltä. Myös lajien habitaatinkäyttö, ja näin ollen sopivien habitaattien saatavuus, näyttäisivät olevan samankaltaisia, mikä merkitsisi lajien välistä kilpailua resursseista. Lajien nykyiset elinympäristöt saattavat kuitenkin vaikuttaa havaittuihin eroihin alueellisessa sijoittumisessa, mistä huomattavin on euroopanmajavan esiintyminen maatalousalueiden läheisyydessä. Maatalousalueet voivat näin ollen tarjota sopivia habitaatteja majaville. Lehtipuiden ja vesistöjen tärkeys majaville oli myös nähtävillä tutkimuksissani. Lisäksi havaitsin, että amerikanmajava on levinnyt pidemmälle istutuspaikoiltaan. Euroopanmajavan pienempään levinneisyyteen ei kuitenkaan löytynyt täysin selkeää syytä, sillä sopivien habitaattien saatavuus ja ympäristön esteet leviämiselle eivät näyttäisi estävän lajin levittäytymistä. Tämän tutkimuksen perusteella syyt lajien erilaisiin levinneisyyksiin ovat todennäköisesti monimutkaiset, ja useat lajien sisäiset ja ulkoiset tekijät voivat vaikuttaa levinneisyyteen. Tämä korostaa, että siirrettyjen eläinten menestymistä uusilla alueilla on vaikea ennustaa. Tuloksia voidaan hyödyntää lajien siirtoistutusten suunnittelussa, sekä populaatioiden kannanhoidon ja lajien suojelun suunnittelussa.

ASIASANAT: *Castor fiber*, *Castor canadensis*, levinneisyys, kannanseuranta, populaatiodynamiikka, elinympäristönkäyttö

Table of Contents

List of Original Publications

This dissertation is based on the following original publications, which are referred to in the text by their Roman numerals:

I Brommer J.E., **Alakoski R**, Selonen V, Kauhala K. Population dynamics of two beaver species in Finland inferred from citizen-science census data. *Ecosphere*, 2017; 8(9):e01947.

II **Alakoski R**, Kauhala K, Selonen V. Differences in habitat use between the native Eurasian beaver and the invasive North American beaver in Finland. *Biological Invasions*, 2019; 21:1601–1613.

III **Alakoski R**, Kauhala K, Tuominen S, Selonen V. Environmental factors affecting the distribution of the native Eurasian beaver and the invasive North American beaver in Finland. *Biological Conservation*, 2020; 248: 108680.

IV **Alakoski R**, Kauhala K, Selonen V. Distribution patterns of the native Eurasian and the non-native North American beaver in Finland – possible factors affecting the slow range expansion of the native species. *Mammalian Biology*, 2021; https://doi.org/10.1007/s42991-021-00148-9

The original publications have been reproduced with the permission of the copyright holders.

1 Introduction

1.1 Distribution of animals

Understanding the factors affecting the distribution of species is the essence of ecology and is becoming increasingly important in the field of applied ecology, such as conservation biology and wildlife management. Distribution patterns of species are largely affected by climate, resource availability, dispersal, disturbance and population dynamics (Guisan & Thuiller, 2005). More specifically, habitat requirements usually determine where a species can occur, but e.g. anthropogenic disturbance and both intra- and interspecific competition may exclude individuals from otherwise suitable habitats. This relates to the concept of fundamental and realized niches, where the fundamental niche encompasses the total range of environmental conditions where a species can survive, whereas the realized niche is typically smaller and is influenced by factors such as species interactions (Hutchinson, 1958; Mott, 2010).

Habitat fragmentation and low proportion of suitable habitats due to e.g. anthropogenic landscape, and lack of connectivity between habitat patches can constrain the range expansion of species (Wilson et al., 2009; Barros et al., 2016). In addition, natural and anthropogenic barriers, e.g. mountains, large bodies of water, dams and roads, may prevent the dispersal of animal species (Shephard et al., 2008; Hapeman et al., 2011; Bracken et al., 2015; Machado et al., 2018). Furthermore, populations can become clumped due to aggregation of resources and high-quality habitats or due to conspecific attraction (Stephens & Sutherland, 1999).

For a species introduced into a new area, the location of the introduction site and the size of the founder population largely determine the present distribution and population size (Stephens & Sutherland, 1999). In newly formed populations, and at range edges, the rate of spread may also decrease due to problems related to a small population size, such as difficulty in finding mates at low densities (Allee, 1931; Stephens & Sutherland, 1999; Mott, 2010).

1.2 Competitive exclusion

According to the Volterra-Gause principle, also known as Gause's law, two species utilizing and limited by a common resource cannot coexist in a limited system;

thereby in an undiversified environment one species becomes extinct due to competition (Volterra, 1926; Lotka, 1932; Gause, 1934, 1935). That is, two very similar species, which share the same ecological niche, seldom coexist in the same area for a long time (Krebs, 1972; Ehrlén & Morris, 2015). A serious problem can develop when an alien species is introduced into an area where a very similar native species already exists (Ebenhard, 1988). In the worst case, the invasive species may outcompete the native one.

1.2.1 Interspecific competition between two beaver species

There are two beaver species in Finland, the native, reintroduced, Eurasian beaver (*Castor fiber*) and the non-native North American beaver (*C. canadensis*). The native beaver occupies a smaller range and has a smaller population size than the non-native one. It has been assumed that the North American beaver outcompeted the Eurasian beaver in areas where both species were introduced, since only the North American beaver survived (Lahti & Helminen, 1974). Lately, the dominance of the North American species has been questioned, as in Russian Karelia and central Europe it seems that the Eurasian beaver has replaced the North American beaver in sympatric areas (Danilov & Fyodorov, 2015, 2016; Halley et al., 2021).

Lahti and Helminen (1974) suggested that the North American beaver population increased faster than that of the Eurasian beaver in Finland because of differences in life history, more specifically, due to a larger litter size. Their data had ca 4.7 embryos for the North American beaver, whereas Ruusila et al. (2000) reported a mean foetus number of 3.7 for the North American beaver, and 72.7% of females were pregnant in one year. However, the difference between the two species in Finland remains unclear because, to my knowledge, no comparative data exists for the Eurasian beaver nor for the actual litter size and survival rate of beavers. In Russia, where the two species coexist, the Eurasian beaver has been reported to have 1.9 or 2.2 kits, and the North American beaver 3.2 or 4.0 kits per litter (Danilov, 1995; Danilov et al., 2011, respectively), indicating a competitive advantage for the North American beaver. In other countries, the Eurasian beaver has been reported to usually have 2–3 kits in a litter (Hinze, 1950; Wilsson, 1971; Zurowski & Kasperczyk, 1986) and the North American beaver approximately 2.4 (computed from Pietrek et al., 2017). Rosell and Parker (1995; in Parker et al., 2012) found in an extensive review on both continents a mean colony/family group size (including reproducing adults, kits of the year, and subordinate beavers) of 3.8 ± 1.0 for the Eurasian beaver (N = 13 studies; range: 2.4–5.5) and 5.2 ± 1.4 for the North American beaver (N = 51 studies; range: 2.7–9.2). However, as mentioned above, information on litter and family group sizes in Finland is not adequate, and there is variation in the data obtained from other countries.

Fecundity, fertility, and primiparity are known to vary in beavers between years and areas, and females do not commonly reproduce every year (e.g. Parker et al., 2017). Factors causing the variability include body size, fat and age of the female (Parker et al., 2017), population density (Bergerud & Miller, 1977; Payne, 1984; Pietrek et al., 2017), occurrence of a dominant breeder (Wilsson, 1971; Brooks et al., 1980), severity of climate (Boyce, 1974), and habitat quality or availability of resources (Bergerud & Miller, 1977; Payne, 1984; Pietrek et al., 2017), as well as variation in detection probability (Pietrek et al., 2017). In addition, mortality rates vary, being usually highest in kits and lowest in adult territory holders (Payne, 1984; Bloomquist & Nielsen, 2010; Pietrek et al., 2017), and are affected by e.g. hunting (Parker et al., 2007; Havens et al., 2013), predators (Müller-Schwarze, 2011), diseases (Novak, 1987; Nolet et al., 1997), available resources (Bergerud & Miller), and climate (Campbell et al., 2012).

According to Halley et al. (2021; cf. Danilov & Fyodorov, 2016), factors that can tip the balance between the Eurasian and the North American beaver are likely to be complex and may include local biotic conditions and the provenance and genetic diversity of founder populations. Furthermore, relative sizes of populations, and thus, the number of dispersers likely influence the results of the interspecific competition (Parker et al., 2012). Therefore, it is critical to gain knowledge on the habitat use and population dynamics of both the native and the non-native species possibly competing for the same resources.

1.3 History of beavers in Finland

The native Eurasian beaver was hunted to near extinction in Europe in the late 1800s, and only eight populations and a total of 1200 individuals survived in small refuges (Nolet & Rosell, 1998). In recent decades, the species has been reintroduced into several countries in Europe (e.g. Halley et al., 2021). In Finland, the original Eurasian beavers were hunted to extinction in the late 19th century, the last report of a hunted beaver being from 1868 (Granit, 1900; Lahti, 1972; Lahti & Helminen, 1974). During the 1930s, beavers were reintroduced to Finland: 17–19 Eurasian beavers were brought to Finland from Norway in 1935–1936 (Linnamies, 1956; Lahti & Helminen, 1974; Härkönen, 1999) and 7–11 North American beavers from the United States were introduced in 1933 and 1937 (Linnamies, 1956; Lahti & Helminen, 1969, 1974, 1980; Moilanen, 1980; Ermala et al., 1989), because at the time, their species status was not known (Lahti & Helminen, 1974). Both species were introduced to several places in Finland (Fig.1, Table 1). However, reportedly only three individuals (one female and two males) of the Eurasian beavers survived and reproduced (Lahti & Helminen, 1980).

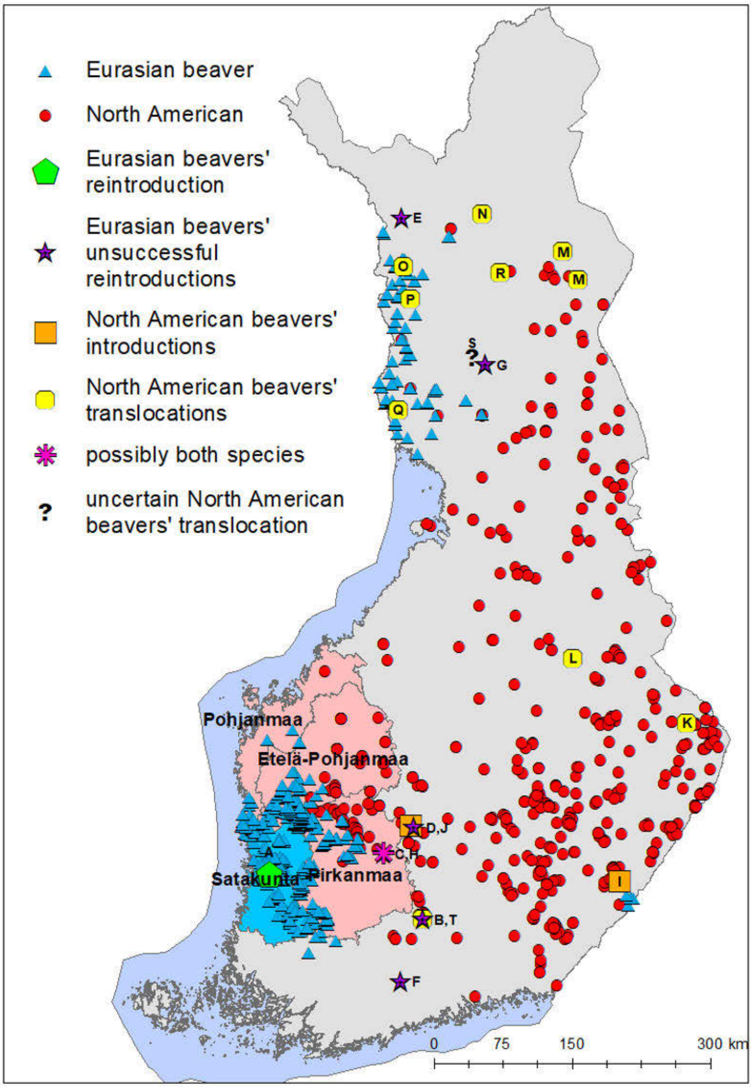

Figure 1. Distribution of the Eurasian and the North American beaver in Finland. Introduction and translocation sites of the two species in the 1930s and field observations from the 2017 beaver monitoring counts. Only observations where coordinates were reported are shown. The species is identified based on DNA-analysis in Lapland and in parts of southern Finland. Detailed description in Table 1.

The number of North American beavers was not much greater and possibly 4–9 beavers survived. The introduction history of both beaver species is partly unclear as no systematic records were kept of beavers imported and released during the 1930s (Moilanen, 1980). Härkönen (1999) suggested that the present North American beaver population in Finland composes of the descendants of two pairs introduced in Sääminki, in the present region of Etelä-Savo in southeastern Finland, and Lahti and Helminen (1975) also mention two pairs introduced in Sääminki. However, Linnamies (1956) reported that only one pair was introduced in the area. Moilanen (1980) reported that the first North American beaver introductions had already taken place in 1933 with one female and two males in Korkeakoski in Ruovesi, in the region of Pirkanmaa; however, this introduction has not always been mentioned in the literature (e.g. Halley & Rosell, 2002) and information on their reproduction is not clear as Eurasian beavers were also introduced in the area (Linnamies, 1956; Moilanen, 1980). In 1970, in addition to the North American beaver population in eastern Finland and the Eurasian beaver population in Satakunta, both species were still assumed to occur in central/western Finland, as well as in Evo, in the region of Kanta-Häme, and in Lapland. Nevertheless, in 1975, the only certain Eurasian beaver area was reported to be in Satakunta (Lahti & Helminen, 1980).

Therefore, the Eurasian beaver population apparently survived and started to increase slowly although only in Satakunta where no North American beavers were released. The majority of the Finnish Eurasian beavers still occur within this area in southwestern Finland (in and around Satakunta; Fig.1). Smaller populations are found in western Lapland where the species has probably spread from Sweden (Kauhala & Timonen, 2016; Iso-Touru et al., 2021) and close to the southeastern border of Finland where it likely dispersed from Russia (only seven observations; Iso-Touru, et al., 2021). At present, the population size of the Eurasian beaver is estimated to 3700–5000 individuals (Luke, 2021). The Eurasian beaver is classified as near threatened in Finland (Hyvärinen et al., 2019), but in 2019–2020 up to 400 hunting licenses could be permitted (Suomen Riistakeskus, 2020), and a total of 334 Eurasian beavers were hunted during the hunting season from 20 August to 30 April (A. Impola, pers. comm.).

North American beavers flourished especially well in Sääminki, where the population size was already estimated to be 130–140 in 1945 (Linnamies, 1956). In 1945–1957, North American beavers were further translocated to the north and west of this population (Fig. 1; Table 1; Linnamies, 1956; Lahti & Helminen, 1980; Ermala, 1996; Nummi, 2015). Beavers also dispersed naturally to the Russian side of the border (e.g. Danilov & Fyodorov, 2016). As stated above, the introduction history of beavers is partly unclear, and possibly up to five North American beavers were also introduced to western Finland (e.g. Linnamies, 1956; Moilanen, 1999), and part of the western North American beaver population possibly originates from these individuals. Nonetheless, Lahti and Helminen (1980) estimated that in 1975, the North American beavers in eastern Finland composed 80–90% (3500–5300 animals) of the beaver population in Finland (both species included), whereas the

Table 1. Year, area, and number of beavers released in Finland (Fig.1).

	Year	Area	Eurasian beaver
A	1935	Kortejärvi, Noormarkku, Satakunta	4 (two pairs, but one female soon died)
B	1935	Majajärvi, Evo, Kanta-Häme	4 (two pairs)
C	1935, 1937	Karhujärvi and Kuivajärvi, Ruovesi, Pirkanmaa	2 (one male and female separately)
D	1935, 1940	Kalajärvet and Vasikkalampi, Keuruu, Keski-Suomi	5 (two pairs, one female translocated from Noormarkku)
E	1935	Killinpoikainjärvet, Muonio, Lapland	4 (two pairs)
F	1936	Pienviljelijäopisto, Hyvinkää, Uusimaa	4 (one pair and two females, the pair may have been Cc)
G	1945	Vikajoki, Rovaniemi, Lapland	3 (translocation from Keuruu)

	Year	Area	North American beaver
H	1933	Hyytiälä beaver enclosure or a river, Ruovesi, Pirkanmaa	3 (one pair and one male)
I	1937	Pihlajavesi, Sääminki, Etelä-Savo	2–4 (one or two pairs)
J	1937/38	Vasikkalampi, Keuruu, Keski-Suomi	2 (one pair)
K	1945	Nälämänjoki, Ilomantsi-Pielisjärvi, Pohjois-Karjala	4 (two pairs)
L	1945	Tuohenlampi, Sotkamo, Kainuu	2 (pregnant female, male died next year)
M	1949–50	Kouterojoki and Kairijoki, Savukoski, Lapland (two sites)	7
N	1950–51	Ätsärinjoki and Kitisenjoki, Sodankylä, Lapland (two sites)	6 (two and one pair(s), respectively)
O	1954	Tunturijärvi, Kolari, Lapland	2 (one pair)
P	1954	Majavalantat, Venejärvi, Lapland	4 (two pairs)
Q	1954–55	Vinsajärvi, Alatornio (Tornio), Lapland	6 (two were soon killed)
R	1955	Sattanen, Sodankylä, Lapland	4 (one female with three kits)
S	1955	Haarainlampi, Rovaniemi, Lapland	4 (two pairs; no further mention of beaver signs)
T	1957	Ylinen Rautjärvi, Evo, Kanta-Häme	2 (one pair)

North American beaver population in western Finland was approximately 100–200 animals. The number of North American beavers reached 10 000 in the late 1990s, but the numbers reported by hunters during monitoring counts decreased in the early 21st century (Ermala et al., 1999; Kauhala & Turkia, 2013), because since 2001 no hunting license for the North American beaver was required. The range of the North American beaver has continuously increased, and it has spread westwards close to the range of the Eurasian beaver (Kauhala & Turkia, 2013). At present, the estimated number of North American beavers is 10 000–19 000 individuals (Luke, 2021). Annually, approximately 2000–7000 North American beavers were hunted in Finland between 2010 and 2019 (Luke, 2020). The North American beaver's range covers most of eastern and central Finland as well as parts of Lapland, and both species occur in the regions of Pirkanmaa, Pohjanmaa and Etelä-Pohjanmaa, as well as in western Lapland (Fig.1).

1.4 Aims of the thesis

The main aim of my thesis is to study why the Eurasian beaver has a smaller distribution and population size than the North American beaver in Finland. Furthermore, I set out to determine whether the two species would compete for the same habitats if they lived in the same area. From the factors affecting the distribution of animals, I especially focused on the population dynamics, habitat use, and patterns in distribution due to e.g. barriers to movement. I utilized data gathered by hunters in the beaver monitoring counts, and mostly freely available landscape data (Materials and Methods 2.3 and 2.4, respectively).

Distribution, abundance, and density of populations vary in space and time (Andrewartha & Birch, 1954). In Chapter **I**, the population dynamics of beavers is examined to discover the spatial and temporal trends in local abundances.

Habitat requirements largely determine the distribution and abundance of species. In Chapters **II** and **III**, I study the habitat use of beavers and map the predicted distribution based on suitable habitats for both species.

Barriers to movement can inhibit the range expansion of species. In Chapter **IV**, I determine the distribution patterns of beavers and investigate possible factors that could inhibit the spread of the Eurasian beaver in southwestern Finland.

I address the following main research questions:

1) Which factors explain the local population size of beavers? What is the present trend in abundances? (Chapter **I**)
2) Does the habitat use of the two beaver species differ? (Chapter **II**)
3) Which environmental factors contribute to the present distribution of the two species? Where do suitable habitats occur in Finland? (Chapter **III**)
4) Why has the range of the Eurasian beaver not shown similar expansion to the North American beaver? (Chapter **IV**)

In Chapter **I**, my prediction was that beavers would be more abundant close to their introduction site and in areas with a large number of water areas and waterways, and a high proportion of deciduous forest. Furthermore, the effect of hunting and climate were considered. In Chapter **II**, my expectation was that the habitat use may differ between the core areas and territories of the two species in terms of vicinity to agriculture and urban area, and in abundance of deciduous trees. In Chapter **III**, I expected to observe that the aquatic habitat type, available forage, anthropogenic environment and climate would affect the habitat suitability, and thus, would be the environmental factors determining the distribution of beavers in Finland. In Chapter **IV**, my anticipation was that the North American beaver has spread longer distances from the introduction sites, and this could be due to faster population growth of the non-native species, and barriers to movement, such as watershed divides and lack of available habitats, in the environment of the Eurasian beaver.

2 Materials and Methods

2.1 Study species

The Eurasian beaver and the North American beaver are morphologically and ecologically similar species. They are semiaquatic, monogamous, herbivorous, crepuscular, and nocturnal rodents that defend a territory by marking it with anal gland secretion and castoreum (Willson, 1971; Nolet & Rosell, 1994). Both species feed on broadleaved trees, which they depend on during winter, and aspen (*Populus tremula*) and birch (*Betula* spp.) are often the most favored (Lahti & Helminen, 1974; Danilov et al., 2011). Sometimes though, also coniferous species are consumed (Danilov et al., 2011; Kauhala & Karvinen, 2018), and mixed forests can be used as habitats (Kauhala & Turkia, 2013; Kauhala & Karvinen, 2018). Young trees with a diameter of < 20 cm are often preferred as forage (e.g. Dvořák, 2013). In summer, aquatic and terrestrial herbs are also included in the diet (Wilsson, 1971; Lahti & Helminen, 1974; Danilov et al., 2011).

Beavers require an aquatic habitat where they build a lodge (either a free-standing lodge, a bank burrow, or a combination of these) with an underwater entrance, and in addition to foraging, trees are also used for lodge and dam building (Willson, 1971; Lahti & Helminen, 1974; Allen, 1982; Müller-Schwarze, 2011). Beavers are known to build dams in order to regulate the water level at the site of the lodge, but lodges can also be built in stream, river, and lake shores without dams. The critical water depth needed for a lodge may be about 50 cm (Rosell & Parker, 1996; Hartman & Törnlöv, 2006; Baskin, 2011); thus, the lodges of beavers are always by an area of water.

Beavers live in family groups consisting of the reproducing female and male, the offspring of that year and, often, subordinate beavers that usually disperse at the age of two years (e.g. Müller-Schwarze, 2011). However, natal dispersal age is density dependent and beavers in sparse populations may disperse earlier, and in high densities can stay in their natal territories for several years (Parsons & Brown, 1979; Hartman, 1997; Sun et al., 2000; McNew & Woolf, 2005; Mayer et al., 2017). A beaver family can occupy several lodges during the summer, but only one lodge is used during the winter (Lahti & Helminen, 1974). Beavers are central-place foragers (e.g. Haarberg & Rosell, 2006), and they commonly forage within a 50-meter radius from the lodge, which can be defined as their core area. Beavers can, however, move up to 250 m from water in search of good foraging trees (Smith et al. 1994; Müller-Schwarze, 2011). A territory of a family group can vary from <1 to >10 km of shoreline (Hartman, 1994a; Campbell et al., 2005; Havens et al., 2013; Graf et al., 2016).

Subordinate beavers have been reported to disperse on average 2–13 km a year (Hodgdon, 1978; VanDeelen & Pletscher, 1996; Sun et al., 2000; McNew & Woolf, 2005; Mayer et al., 2017) but often stay close to the natal territory if there is suitable habitat available (Hartman, 1994a). Adult beavers may also abandon the lodge and move to a new area when food resources become scarce (i.e. when they have consumed most of the suitable trees). Although beavers can move on land, they mainly disperse along watercourses (e.g. Leege, 1968; Novak, 1987; Hartman, 1994b; Müller-Schwarze, 2011), and watershed divides are expected to decrease the expansion rate of beavers (Hartman, 1995). Beavers usually inhabit forested areas, but may also use agricultural areas, especially areas that are mosaics of fields and forest patches along a river system. In addition, they have been found even in parks close to city centers (J. Raitaniemi, pers. com.) and within highly urbanized regions (Dewas et al., 2012).

2.2 Study areas

The landscape in Finland is dominated by bodies of water and industrial coniferous and mixed forests, where scots pine (*Pinus sylvestris*) is the most dominant species, along with Norway spruce (*Picea abies*), downy birch (*Betula pubescens*) and silver birch (*B. pendula*) as common species. Agricultural areas and denser human populations are found mainly in southwestern (SW) and southern Finland. Data for the Eurasian and North American beaver observations in the whole country (excluding the archipelago) were used in Chapters **III** and **IV**, but in Chapters **I** and **II**, Lapland was not included due to a lack of continuous and/or comprehensive data. In addition, in Chapter **II**, the sympatric area in Pirkanmaa, and, in Chapter **IV**, the SW range of the Eurasian beaver were of special interest. The Eurasian beaver's original area was defined as the region of Satakunta in SW Finland which was the original reintroduction site, and the novel areas as the adjacent regions of Pirkanmaa, Etelä-Pohjanmaa and Pohjanmaa in SW Finland (Fig.1). Furthermore, when studying habitat use in Chapters **II**, **III** and **IV**, the environment was restricted to the immediate proximity of watercourses (at two scales: 50 and 250 m from shoreline).

2.3 Data on beavers

Monitoring counts of beavers have been carried out approximately every third year since 1995. Local hunters have counted the number of active winter lodges in the autumn (September–November), usually in connection with moose (*Alces alces*) hunting, in their hunting association area. There are approximately 300 000 hunters in Finland (5.4% of the population), and hunting is legal, with permission, on both private and state-owned land (Finnish Wildlife Agency, 2020). Food storage or other signs of beaver activity should be seen in the vicinity of an inhabited winter lodge. Hunters return the report to the Natural Resources Institute Finland (Luke; formerly the Finnish Game and Fisheries Research Institute) via the Finnish Wildlife Agency (Suomen riistakeskus). The population size estimates of Luke are based on the number of wintering lodges, which is multiplied by the estimated family group size, 2.8 and 3.8 or 5.2, to obtain the minimum and maximum estimated number of individuals for the Eurasian beaver (E) and the North American beaver (NA), respectively (Luke, 2021). The smaller value, 2.8, is based on a preliminary research on the family group size of the North American beaver in Finland (Ermala et al., 1999), and the maximum sizes are the mean family group sizes in a review by Rosell and Parker (1995). From 2013, hunters have also been asked to report the coordinates of lodges, and from 2017, a mobile app OmaRiista became available for citizens enabling the reporting of exact location of all beaver observations, including lodges, dams, feeding sites, other sightings and sounds. The app is also used for the monitoring counts for the collection of beaver lodge abundances in the areas of hunting clubs, with information on the coordinates of each hunting club (this data has been available just since 2021).

The two beaver species cannot be distinguished in the field. The lodges and other observations are considered to belong either to Eurasian or North American beavers on the basis of the history of beavers in Finland, from DNA analyses and skull morphometry from hunted beavers in the area of sympatry, as well as from DNA analyses from wood chips collected at the base of trees felled by beavers (Kauhala & Timonen, 2016; Iso-Touru et al., 2020, 2021). In practice, most of the data lacked a verified species identification. However, available data for individuals identified by their species (259 DNA samples and 129 skulls) indicate that the Eurasian and North American beavers mainly live in separate areas in Finland, but there are also areas of sympatry in Pirkanmaa, Etelä-Pohjanmaa and western Lapland (Fig.1; Kauhala & Karvinen, 2018, Iso-Touru et al., 2020, Sjöberg & Belova, 2020).

In Chapter **I**, the abundance of beavers per municipality in different monitoring counts from 1995 to 2013 (seven monitoring counts) was computed. Municipalities were defined according to the borders in 2013 (National Land Survey of Finland 2/2015), and some older monitoring counts in originally separate municipalities were thus combined according to the municipalities' borders in 2013. For the period considered in Chapter **I**, the municipalities with occurrences of Eurasian and North American beavers were considered as distinct sets of local populations, i.e. the two species occurred in different municipalities. There were 168 and 29 municipalities where the North American and the Eurasian beaver occurred, respectively. In Chapters **II**, **III** and **IV**, I used the location data on beaver occurrences from the most recent beaver monitoring count. In Chapter **II**, coordinates of 428 Eurasian and 466 North American beaver lodges from the fall of 2013 and 2014, and the spring of 2015 were used. In addition, 50 beaver observations were used from the sympatric area in Pirkanmaa, including beaver lodges (15 E; 7 NA), feeding sites (4 NA), sites where droppings were found (1 NA) and sites where beavers were shot (13 E; 10 NA). In Chapters **III** and **IV**, the data on 367 Eurasian and 488 North American beaver observations with coordinates, from August 2017 to August 2018, including beaver lodges (E 169; NA 179), dams (E 41; NA 53), feeding sites (E 50; NA 59) and other sightings and sounds (E 107; NA 197) were used. In addition, in Chapter **IV**, 194 and 73 locations of DNA-samples (Iso-Touru et al. 2020, 2021), and 62 and 28 locations of hunted beavers (species identified from skull morphometry; Kauhala & Timonen, 2016) were included for the Eurasian beaver and the North American beaver data, respectively. Data for the estimated population sizes of the two species were collected from the literature (Linnamies, 1956; Lahti & Helminen, 1980; Ermala et al., 1989; Ermala, 1996), and for the Eurasian beaver, only the information on the Satakunta population was utilized. The first national beaver census based on an inquiry was organized in 1965 by the Game Research Institute (Lahti & Helminen, 1974). Before 1995, the minimum and maximum population sizes were based on citizens' estimates on beaver numbers in their area, i.e. estimates were not made by multiplying lodge numbers with mean family group sizes. Monitoring counts of the Natural Resources Institute Finland were also used, starting from 1995 (described above). With these data, I computed the annual growth rate (r) relative to the previous population size of both species in different years (Table 2; Fig.2) with the equation:

$$r = \exp\,(\ln Nt_2 - \ln Nt_1) / (t_2 - t_1)$$

where Nt_1 and Nt_2 are population sizes in consecutive estimation times t_1 and t_2, respectively. Because the reporting activity for the North American beaver lodges was low in 2004–2013, and therefore, the decline in the number of North American beavers was probably not real, the annual growth rate for 2017 was computed from the 2001 population size.

Table 2. Estimated population sizes, annual growth rates relative to the previous population size estimates and the number of hunting clubs that reported beaver observations in their area for a) the Eurasian and b) the North American beaver. The population size estimates for years 1935–1985 have been collected from literature, and from 1995 they are from the beaver monitoring counts of Luke (formerly the Finnish Game and Fisheries Research Institute; population size estimate from the number of lodges × 2.8 (min) or 3.8 (max for the Eurasian beaver) and 5.2 (max for the North American beaver); Luke, 2021).

a) the Eurasian beaver

Year	Pop. Size (min)	Pop. Size (max)	Growth rate (min)	Growth rate (max)	Areas
1935	2*	3			
1955	20	20	1.122	1.100	
1956	30	80	1.500	4.000	
1970	40	75	1.021	0.995	
1975	150	200	1.303	1.217	
1985	500	500	1.128	1.096	
1995	1100	1400	1.082	1.108	50
1998	1400	1800	1.084	1.087	86
2001	1700	2300	1.067	1.085	70
2004	2100	2900	1.073	1.080	56
2007	1800	2400	0.950	0.939	60
2010	2000	2800	1.036	1.053	76
2013	2400	3000	1.063	1.023	96
2017	3300	4500	1.083	1.107	173
2020	3700	5000	1.038	1.036	203

* assumed that only one male and one female have reproduced

b) the North American beaver

Year	Pop. Size (min)	Pop. Size (max)	Growth rate (min)	Growth rate (max)	Areas
1937	4	9			
1955	450	500	1.300	1.250	
1960	500	600	1.021	1.037	
1965	1800	3000	1.292	1.380	
1970	1800	3200	1.000	1.013	
1975	3800	5800	1.161	1.126	
1995	7500	13 900	1.035	1.045	720
1998	10 400	19 400	1.115	1.118	887
2001	10 800	20 100	1.013	1.012	896
2004	6600	12 300	0.849	0.849	213
2007	5500	10 300	0.941	0.943	549
2010	3800	7000	0.884	0.879	325
2013	3900	7200	1.009	1.009	389
2017	10 300	19 100	0.997*	0.997*	1264
2020	10 400	19 400	1.003	1.005	1281

* computed from the 2001 population size estimates, because the low reporting activity after 2001 decreased the population size estimates in 2004–2013

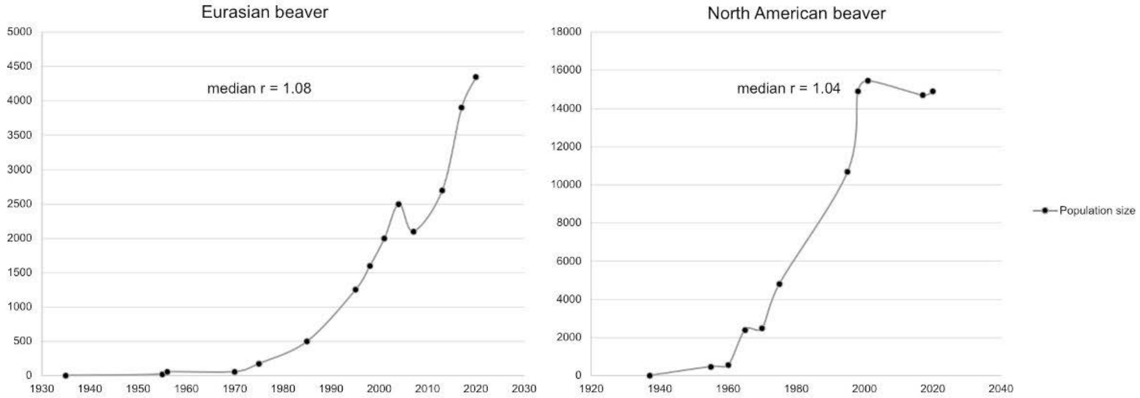

Figure 2. Population growth of the Eurasian and the North American beaver based on the mean population size estimates, and median growth rates for the study period. Data for years 2004–2013 have been excluded for the North American beaver because of low reporting activity. Population size in y-axis and year in x-axis. Median growth rate before the year 2000 was 1.10 and 1.12, and after, 1.06 and 1.00, for the Eurasian and the North American beaver, respectively.

I compared the relative population sizes (population size in year_t /population size in a year with the highest population size) to the relative number of occupied areas (hunting clubs reporting beaver observations/the highest number of reporting hunting clubs) in different years (Table 2) visually. This was done to see if the population sizes have increased faster than the number of occupied areas or vice versa (Hartman, 1995). The number of hunting clubs that reported beaver observations in their area was collected from the data of the monitoring counts. The hunting area of a hunting club is usually 20–100 km^2 (Finnish Wildlife Agency, 2020).

2.4 Explanatory variables

Because beavers are semiaquatic, I took aquatic habitat into account in all of the chapters, in order to either describe the habitat quality or to restrict the coverage of other variables and analyses. All landscape variables were computed in ArcMap 10.2 (ESRI, 2011). Watercourses (as polylines) and water areas (as polygons) were computed using the large-scale topographical map (1:100 000) in the open digital data of the National Land Survey of Finland (2/2015). In Chapter **I**, I used the total length of watercourses (streams with width <20 meters, in units of 10 kilometers) and total area of water areas (lakes and large rivers, in units of hectares) in a municipality. In Chapters **II**, **III** and **IV**, the watercourses and water areas were merged together as polylines, i.e. shorelines from water areas (hereafter called shoreline). Therefore, the “shoreline” for watercourses includes only one line. In

Chapter **II**, the territory was computed as maximum 500 m of shoreline from the lodge to all possible directions, and the territory and landscape scale variables were restricted to 250 m from the shoreline. In Chapters **III** and **IV**, all landscape variables were restricted to 50 m from the shoreline, and the aquatic habitat type was also used as an explanatory variable. The classification of the National Land Survey of Finland was used to describe the aquatic habitat type (excluding sea water, which did not occur in the data) occurring in a 16 m × 16 m grid cell. In Chapter **III**, lakes were divided into four classes according to their size. Therefore, there were ten aquatic habitat type classes: 1) streams < 2 m, 2) streams 2–5 m, 3) streams 5–20 m, 4) streams > 20 m, 5) canals, 6) reservoirs, 7) lakes ≤1 ha, 8) lakes ≤10 ha, 9) lakes ≤100 ha, and 10) lakes > 100 ha. In Chapter **IV**, the aquatic habitat type composition was computed from a raster data (pixel size 20 m × 20 m). Canals and reservoirs did not occur in the beaver habitats and they were also rare in the environment, so they were excluded from the analyses. Therefore, there were five aquatic habitat type classes: 1) lakes 2) streams <2 m, 3) streams 2−5 m, 4) streams 5−20 m, and 5) streams >20 m. In addition, in Chapter **III**, the length of shoreline in meters was computed with the merged polylines of waterways and water areas in a grid cell of 20 km × 20 km covering the whole area of Finland. The original beaver observations could occur anywhere inside the grid cell. Twenty km was selected as the axis length, because it is a reported maximum dispersal distance of beavers in one year (Hartman, 1995). In Chapter **IV**, data for dams and sluices (National Land Survey of Finland 2/2015; topographical map 1:100 000), and watershed areas, i.e. an area where water flows to e.g. one lake, and main drainage basins, i.e. a larger watershed area system (SYKE 12/2019) were also used.

Because beavers forage mainly on deciduous trees, I also used forest composition or volume of trees as explanatory variables. In Chapter **I**, the pooled percentage (%) of deciduous and mixed forests covering the landscape in a municipality was computed using the Corine land cover maps of Finland in 2000 released by the Finnish Environment Institute (SYKE 2/2015). In Chapters **II**, **III** and **IV** the volumes of birches and other deciduous trees (m^3/ha) were computed using the tree volume data from the forest inventory data of the Finnish Forest Research Institute in 2013 and 2015 (2013 for Chapter **II** and 2015 for Chapters **III** and **IV**; http://kartta.luke.fi/). The data gives the volume of birches (*Betula pendula*, *B. pubescens* and *B. nana*), and other deciduous trees as one group, including the Eurasian aspen (*Populus tremula*), grey alder and black alder (*Alnus incana* and *A. glutinosa*), European mountain ash or rowan (*Sorbus aucuparia*), and the goat willow (*Salix caprea*) (Ylitalo, 2013) within 16 m × 16 m squares. In Chapters **II** and **III**, birches and other deciduous trees were treated separately, and in Chapters **III** and **IV**, a combined variable of “deciduous trees” was (also) computed as the sum of the birch and other deciduous trees. In Chapter **III**, volume of spruce and pine (m^3/ha), forest age, and site fertility were also used (Tomppo et al., 2008). In addition, the abundances of aspen, willow trees, grey alder and black alder (m^3/ha) were computed by dividing the volume of other deciduous trees into species-specific proportions on the basis of geostatistical interpolation of the National Forest Inventory sample plot tree data. The abundance data of species-specific volumes of other deciduous species were computed with a resolution of 1 km × 1 km, representing a relative abundance of these species at the landscape level. Forest age is the weighted average age of the growing stock in a forest stand in classes of one year. Site fertility is based on classification of the forests by vegetation zones into ten classes according to their fertility and wood production capacity (site fertility index: rank of 1: high to 8–10: low fertility). These classes are: 1) herb rich forest, 2) herb rich heath forest, 3) mesic forest, 4) sub-xeric forest, 5) xeric forest, 6) barren forest, 7) rocky and sandy soils/alluvial land, 8) summit and fjeld land with single coniferous trees, 9) mountain birch dominated fjelds and 10) open fjelds. Classes 1–6 are classified as forest, class 7 can be forest land, poorly productive forest land or unproductive land. Classes 8–10 occur in Northern Finland and are either poorly productive forest land or unproductive land. In Chapter **IV**, the 2018 Corine land cover data was used to obtain the composition of broadleaved, mixed, coniferous and transitional forest (classes 3.1.1–3.1.3, and 3.2.4; resolution 20 m × 20 m; SYKE 1/2020). In addition, a variable “forage” was computed from the added percentage of broadleaved forest and mixed, coniferous, and transitional forest that may include suitable forage (mainly on mineral soil, i.e. excluding mixed, coniferous and transitional forest on peatland and rocky soil).

Anthropogenic disturbance, climate and distance to the introduction site were also used as explanatory variables. In Chapter **I**, the hunting pressure of beavers was computed by dividing the number of hunted beavers with the total area covered by all municipalities where beavers were counted in the hunting district. The hunting pressure for all municipalities belonging to a hunting district was assumed to be equal. In Chapters **II**, **III** and **IV**, the distance to agricultural and urban areas were computed from the Corine land cover data for Finland for years 2012 and 2018 (20 m × 20 m per grid cell; 2012 for Chapters **II** and **III**, and 2018 for Chapter **IV**; SYKE 2/2015 and 1/2020, respectively). In addition, in Chapter **III** the local human population size was computed with the 2017 population size in each municipality (Statistics Finland, 2018).

In Chapters **I** and **IV**, weather information was extracted from the Finnish Meteorological Institute (FMI). In Chapter **I**, all weather stations were considered that were situated up to 200 km from the outer municipalities where North American and Eurasian beavers occurred, respectively. For each of these weather stations, the arithmetic average temperature and snow cover recorded in the winter months (December–February) were computed. For each three-year census period, the geometric mean of three winters relevant to the time period was computed. For example, to explain the dynamics between 1995 and 1998, the winters of 1995/1996, 1996/1997, and 1997/1998 were included. In order to arrive at a measure for the winter weather of each municipality, ordinary kriging (Cressie, 1993) was used to obtain the geometric mean winter weather for all weather stations with the data for a particular census period. Ordinary kriging assumes a spatial autocorrelation in the data, where the correlation between two sites reduces following an exponential function of the distance between the two sites. Based on the kriging parameters, geometric mean winter weather was predicted for the center coordinate of each municipality. The ordinary kriging and predictions were performed using the R package "gstat" (Pebesma, 2004) in R (R Core Team, 2015). In Chapter **IV**, to describe the areal climatic conditions, the average monthly air temperatures for the ten previous years from October 2007 to April 2017 were derived: the average temperatures from October to November (late autumn), December to February (winter) and March to April (early spring) were computed. Twenty-two observation stations distributed evenly in Finland that offered continual weather data were used to measure the weather variables. The average temperatures were extrapolated with the spline tool in GIS from the selected measurement points to describe areal temperature variation in Finland.

In Chapters **I** and **IV**, the distance to the introduction site was also considered. The introduction and translocation sites (from now on called introduction sites) were collected from the literature (Linnamies, 1956; Lahti & Helminen, 1980), and only sites where the species were presumed to have been present since the introductions were selected. In Chapter **I,** without data for Lapland, there was one introduction site for the Eurasian beaver and four for the North American beaver. In this study, the introduction site in Sotkamo was excluded because of uncertainty about the successfulness of the introduction (Fig.1, Table 1); two adults were introduced and although one was soon hunted there were kits. This site did not appear on the map of beaver introductions and translocations in Lahti and Helminen (1975, 1980). A weighted mean proximity was computed based on the distance of the municipality to the introduction sites (in units of 100 km). In Chapter **IV**, there was one introduction site for the Eurasian beaver and twelve for the North American beaver. In this study, it was decided that all introduction and translocation sites of the North American beaver were to be included if beavers were reported to have had offspring and/or surrounding areas had been occupied by beavers (Ruovesi and Rovaniemi were left out because of uncertainty; Fig.1, Table 1). Therefore, these represent a possible maximum number of successful introduction sites. A straight-line distance and distance along watercourse were computed from the present beaver observations to the nearest introduction site (only the SW range for the Eurasian beaver).

In Chapters **II** and **IV**, I studied the habitat use of beavers by creating buffers around the locations of beaver observations (Fig.3). I created territories with approximately two kilometers of shoreline (**II**). Lodges that were closer than one km to another lodge along a watercourse were counted as the same family group's lodges (Hartman, 1994a), because family groups' home ranges do not usually overlap (Korbelová et al., 2016). Only the centermost lodge in a family group's area was included in the analysis. The territory extended a maximum of 500 m from the core area along all watercourses connected to the core area and 250 m from the shoreline of the lake or from the middle of the stream. Core areas were created by computing buffers with 50 m radius around lodges (**II**) or all observations (**IV**). In Chapter **IV**, if the buffers intersected with each other, they were dissolved together and treated as one buffer. In addition, $r = 250$ m buffers for the activity sites of beavers were created for the sympatric area in Pirkanmaa (**II**).

To compare habitat variables within core areas and territories with those available in the landscape in habitats close to riparian zone, I laid random points in the proximity of all watercourses in the landscape. I used random points that were a maximum of 250 m from a watercourse (from now on called a watercourse area), and, in Chapter **II**, that did not overlap with a beaver territory. Random points were laid within each municipality in Finland with beaver lodge coordinates using the 2013 municipality division from the data of the National Land Survey of Finland (2/2015). Municipalities were selected as the available landscape areas because the municipalities are of suitable size for the beavers to potentially disperse (the median size of a municipality in Finland is 750 km^2). In Chapter **II**, the number of random points for each municipality was computed by multiplying the watercourse area as hectares (excluding beaver territories) in a municipality with the highest number of lodges (two species separately) per watercourse area found in all municipalities. The number of random points was then multiplied so that their total numbers were approximately tenfold compared to the number of lodges: 4452 for the Eurasian and 4874 for the North American beaver. The habitat variables were computed from the pixels intersecting the random points. In Chapter **IV**, a total of 1939 and 3528 random points were computed along the shoreline in the municipalities with observations in the original area and the novel areas of the Eurasian beaver, respectively, so that there was approximately one point per 10 km of total shoreline in a municipality. To avoid overlapping buffers, the minimum distance between random points was set to 500 m. Buffers of $r = 50$ m were then computed around the random points in the same way as around the beaver observations and the habitat variables were computed.

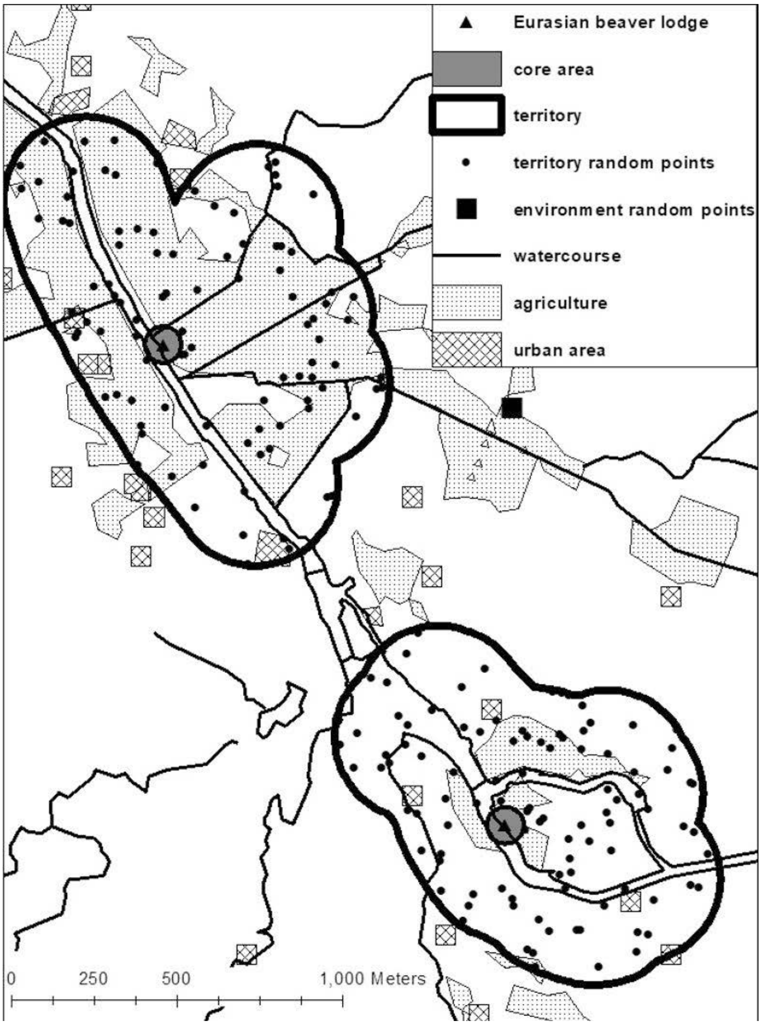

Figure 3. An example of the Eurasian beaver lodge site, the core area and the territory computed along the watercourses in Chapter II.

2.5 Statistical analyses

In Chapter **I**, I studied the factors affecting the present population growth and the initial abundance in the municipalities. The data were fitted to single-census open population N-mixture models (Dail & Madsen, 2011; Hostetler & Chandler, 2015) that have been developed to estimate population size with presence-only data. The open population N-mixture models assume that a consensus of several local populations (sites) were conducted at some time interval, and the models estimate the population size and population dynamics by taking detection probability into account. Detection probability was estimated based on the number of reports returned per municipality. Covariates were added to explain the initial population size and intrinsic population growth rate. The most parsimonious models for both species were first selected using Akaike's information criteria (AIC) and likelihood-based approach, and then, a Bayesian version of the model was constructed (more details in the original Paper **I**).

In Chapter **II**, I studied the habitat use of both beaver species. Johnson (1980) proposed a multi-scale, hierarchical approach for studying habitat selection by selecting four levels: first, the physiological or geographical range of the species; second, the home range or an individual social group; third, various habitat patches within the home range; and forth, resources within a habitat patch. Statistical methods utilized in studying habitat selection include generalized linear modelling and maximum entropy (McGarigal et al., 2016). The selection can be further analyzed as conditional with e.g. (conditional or paired) logistic regressions. I compared the core areas and the territory buffers using conditional logistic regression analyses separately for the two beaver species (Duchesne et al., 2010). For a comparison of core area/territory versus random points in the landscape, matched pairs could not be formed (conditional model). Instead, I built two logistic regression models, where the binomial response variable was the used habitat (1) of the core area or territory versus available habitat (0) in the landscape, represented by random points along the shore of all watercourses in the municipality. To analyze whether the habitat use differed between the species, I combined the data of both beavers and performed models similar to those described above (core vs. territory, core vs. landscape, territory vs. landscape). Conditional logistic regression was used when comparing the core area to the territory, and binomial logistic regression when comparing the core area and territory to the environment. In addition, I included the interaction terms between the class variable 'species' (1 E, 2 NA) and the habitat variables in the models. The interaction terms were included separately for each habitat variable. Thus, I could test if habitat use differed between the Eurasian and the North American beaver. For the comparison of habitat use of the native and non-native beavers in an area where they are sympatric (Pirkanmaa), I built a model were species (1 E, 2 NA) was the response variable.

In Chapter **III**, in order to predict the possible distribution of beavers based on suitable habitats in Finland, I utilized the Maximum entropy modelling software, Maxent (Phillips et al., 2006, 2017, 2019); this models species distributions using presence-only records and compares the environmental data at the species locations to that of background samples in the environment (e.g. Phillips et al., 2006, 2017; Elith et al., 2011; Merow et al., 2013). Maxent uses a machine learning method and aims to find the distribution that is most widely spread, or closest to uniform, while taking into account the most contributing environmental variables at known species locations. Maxent chooses the distribution that maximizes the similarity between the environmental characteristics at the species locations and that of the whole environment. Model performance is estimated with the area under the receiving operating character (ROC) curve (AUC). The maps of suitable habitats can be visualized in GIS and edited to find potential patterns of interest. I built (i) a model with seventeen possible environmental variables affecting the habitat suitability, (ii) a more parsimonious model with only the five most important variables, and (iii) a model with seven resource factors (more details in the original Paper **III**).

In Chapter **IV**, I studied the possible internal and external reasons for the vaster distribution of the North American beaver occurring between the species or within the Eurasian beaver's environment. For comparisons between the beaver species or between the original and novel areas of the Eurasian beaver, I used the Mann–Whitney two-sample test. To study whether the watershed divides affect the occurrence of the Eurasian beavers, I used a generalized linear model with negative binomial distribution. To study if the habitat use of the Eurasian beaver differs between the original and novel areas, I used binomial logistic regressions.

In Chapter **I**, the N-mixture models were analyzed in R (R Core Team, 2015). In Chapter **II**, (conditional) logistic regressions were made in SAS software (SAS Enterprise 6.1. SAS Institute Inc., Cary, NC, USA). In Chapter **III**, Maxent software (Phillips et al., 2019) was utilized. In Chapter **IV**, statistical analyses were computed in XLSTAT Free (Addinsoft SARL 2018) and JMP (JMP®, Version Pro 15. SAS Institute Inc., Cary, NC, USA).

3 Results and Discussion

3.1 Abundance of beavers

The modeling results in Chapter **I** underline the similarity of the two beaver species, with respect to their population dynamics. The dynamics of both species are density dependent following the Gompertz (1825) formulation, and immigration is an important aspect. Another apparent feature is that as regards the North American beaver the initial abundance (i.e. abundance in 1995) was higher in municipalities, which were closer to the original introduction site(s). Hence, a spatial signature of the introduction is still observable six decades after the beaver species were introduced. This might indicate limits in dispersal capacity or that there are still suitable habitats near introduction sites, and therefore, the ranges have not expanded further (Nolet & Rosell, 1994). In this study, the translocation site in Sotkamo was excluded from the analysis because of the lack of clarity on whether this introduction was successful. Nonetheless, including this site would unlikely decrease the importance of the proximity of the original introduction site because the number of beavers is also high close to this site.

The findings demonstrate that Eurasian beavers were numerically increasing in Finland, while North American beavers, although more widespread, were declining in numbers based on the data available in 2013 (Fig.4). However, the reporting activity for North American beaver lodges was low 2004–2013. Since then the reported number of North American beaver lodges has increased and although it is now close to the levels in 2001 it has remained at the same level, contrary to the Eurasian beaver population which has increased (Table 2; Fig.2). The carrying capacity for North American beaver lodges was estimated to be low, indicating a low density of lodges per watercourse area and length. In addition, a low intrinsic rate of population increase in the Gompertz dynamics for this species was detected. The Gompertz curve or function describes growth being slowest at the start and end of a given time period, suggesting that the North American beaver population would have reached the carrying capacity of the environment. However, it is currently not clear what the reasons are for the low values of these estimated parameters. In particular, North American beavers are reported to have a larger litter size than Eurasian beavers

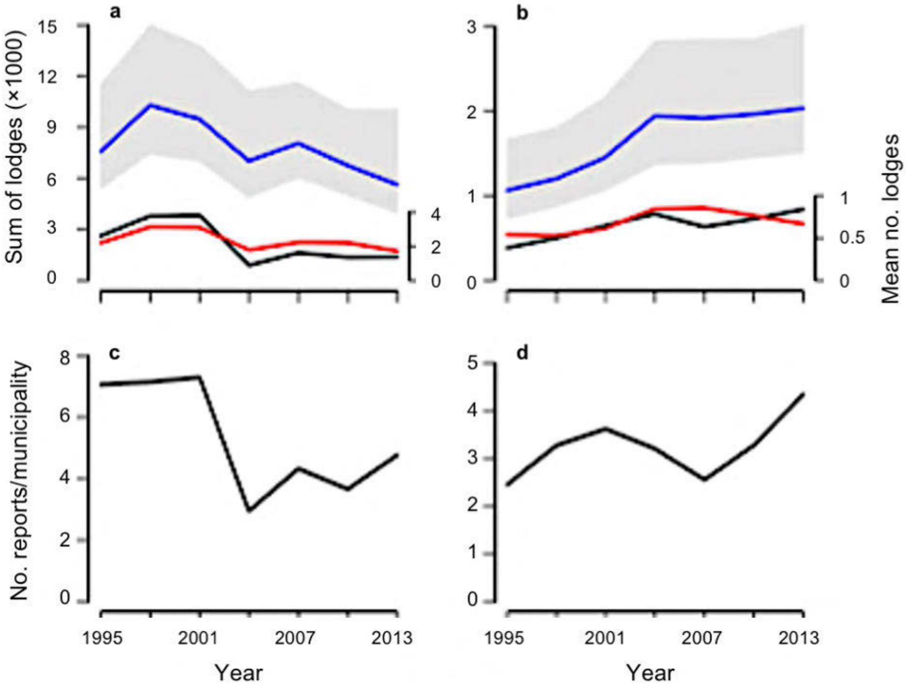

Figure 4. Population dynamics of the number of lodges of (a) North American and (b) Eurasian beavers in Finland during 1995–2013 based on monitoring every third year. For each species, the model prediction (blue line with 95% credible interval) and sum of all reported lodges (black line) are shown as well as the mean number of lodges reported by hunting clubs (red line; scale on right-hand side). The lower panels show the average number of reports per municipality of (c) North American and (d) Eurasian beaver lodges filed during the study period. Figure modified from Brommer, J.E., Alakoski, R, Selonen, V, Kauhala, K, 2017. Population dynamics of two beaver species inferred from citizen-science census data. *Ecosphere* 8(9):e01947. 10.1002/ecs2.1947.

(Danilov, 1995; Danilov et al., 2011). It is likely that these parameters are strongly affected by the hunting pressure on this species. Although the models suggest that inclusion of hunting pressure is not very important, it should be noted that the estimates of hunted North American beavers are rough, both spatially (hunting statistics on the level of municipality are not available), and in terms of accuracy because hunting statistics are generated by sending an inquiry to only a fraction (about 2%) of hunters.

It is difficult to evaluate the effect of habitat parameters on North American beaver numbers, because hunting likely affects key population parameters of the North American beaver population and thus their local abundance in different habitats in a manner which cannot be fully addressed within this model. Nevertheless, the findings in this respect are intuitive; North American beavers show a high mean initial abundance in municipalities with more water areas and watercourses. A comprehensive water system could enable beavers to move more broadly in search of food. Moreover, the range expansion of beavers usually occurs within drainage basins (e.g. Hartman, 1995). Winter temperature, which AIC-selected modeling suggested to be a covariate affecting intrinsic population growth rate in North American beavers, was not significant in the Bayesian implementation of the model. Likewise, all AIC-selected covariates for initial abundance for the Eurasian beaver were not significant in the final Bayesian implementation of the model. Therefore, the list of covariates used in Chapter **I** clearly does not cover all aspects relevant to beavers, e.g. aquatic habitat quality.

These results do not fully support the view that differences in population dynamics would be the reason for the larger distribution and population size of the North American beaver in Finland. However, the limitations of the data are likely to have some effect on the model estimates concerning the population dynamics of these species. Furthermore, the environmental factors used in this study did not explain the local population sizes very well, especially that of the Eurasian beaver, which suggests that the local abundance of the species might not be limited by environment. However, the variables used here do not necessarily capture the effect of the environment on the local abundance; for example, forests were measured within the whole municipality as a percentage of the whole available environment, instead of computing the abundance of trees in the riparian environment.

Density dependence has been reported to result in lower fecundity in high densities in the North American beaver possibly due to lack of available resources (Bergerud & Miller, 1977; Payne, 1984; Pietrek et al., 2017), and can generate fluctuating rates of spread by increasing dispersal distance in areas where resources have been depleted (Dwyer & Morris, 2006). Dense local populations can also relate to aggregated distribution patterns where sink populations are colonized with emigrating individuals from source populations (Hanski & Gilpin, 1991). The population sizes of metapopulations are often determined by the size or quality of the habitat patch (Harrison, 1991). For beavers, colonization is often first found to occur within drainage basins (Hartman, 1995; Halley et al. 2012, 2021); thus, the size and available resources of the watersheds may determine the local population sizes.

3.2 Habitat use and suitable habitats in Finland

An important difference between the Eurasian beaver and the North American beaver was related to their distance from agricultural areas. In Chapter **II**, for the North American beaver, the average distance from lodges to the nearest agricultural area was more than 1200 m, whereas it was approximately 300 m for the Eurasian beaver. Agriculture also explained the present distribution of the Eurasian beaver in

Chapter **III** where habitat suitability was highest immediately next to agriculture. Agriculture is more dominant in the range of the Eurasian beaver, as the beavers seemed to select sites closer to agriculture than could be expected at random. Additional forage might attract the beavers close to agriculture because they might also forage in fields (Danilov et al., 2011). The preference for agriculture may also be due to avoidance of less fertile areas, such as coniferous forests, as seen in Chapter **IV**. Contrary to prediction, neither species avoided urban areas (**II**), but neither did they favor them. However, a very small human population size explained the distribution of the Eurasian beaver (**III**). It might be that the urban fabric close to beavers in Finland is mostly sporadic and consists mainly of recreational cottages that neither disturb nor attract the beavers. Earlier studies indicate that even highly used built up areas are not necessarily unfavorable to beavers, as they are known to adapt to the vicinity of humans (Korbelová et al., 2016), even in highly urbanized regions (Dewas et al., 2012).

The results of the habitat use models (**II)** indicated that for both species, birch is important in the vicinity of lodges. However, I found that birch was less abundant in the territories compared to the core areas of the Eurasian beaver, whereas with the North American beaver, the territories had a similar amount of birch to the core areas, and on average ~100 m^3/ha more birch than in the Eurasian beaver territories. This might suggest smaller territories for the native species or that their forage is more scattered, because the average amount of birch was similar in the riparian environments of the two species. It is possible that Eurasian beavers need a smaller area for foraging than North American beavers due to smaller family groups (Parker et al., 2012). However, in Norway, territory size and family group size did not correlate, although territory size and proportion of deciduous trees correlated positively (Campbell et al., 2005). Furthermore, the density of Eurasian beaver lodges was much higher than that of North American beaver lodges in the data of the study, which suggests smaller territories for the Eurasian beaver because territory size and population density are often negatively correlated (e.g. Morse, 1976). In another study (Kauhala & Karvinen, 2018), the mean size of home ranges of the Eurasian beaver indeed seemed to be smaller than that of the North American beaver in Finland (6.42 ± 4.95 ha vs. 10.87 ± 10.26 ha, N = 19 and 16, respectively), but the difference was not significant.

In addition, similar to previous studies (e.g. Danilov et al., 2011), aspen was the tree species most favored by both species (**III**). Birch contributed from the resource factors as the second most important to the habitat suitability of the Eurasian beaver, whereas for the North American beaver, grey alder was important. In line with my results, Danilov and Kanshiev (1983) found that the North American beaver utilized grey alder more often than the Eurasian beaver when the two species lived in the same area, although not in a similar habitat. Furthermore, in the sympatric area in

Pirkanmaa, more birch and fewer other deciduous trees were located at the activity sites of the Eurasian beaver than at those of the North American beaver (**II**). Unfortunately, aspen and grey alder were not separated from other deciduous trees in this analysis. However, both beaver species appear quite flexible in their habitat use as the preference for deciduous trees was not apparent when compared to what was available in the environment (**II**) and did not explain the present distribution very well (**III**). This may partly relate to the scale and accuracy of the data used in these studies, as information on the actual territory sizes was not available. Furthermore, Nolet and Rosell (1994) found that forage may not need to be abundant in a small area in the riparian zone but could be more scattered in a larger area. Probably all deciduous species can increase the habitat suitability for beavers, but their importance mostly depends on the local abundance and composition of the tree species.

I observed that aquatic habitat type best explained the riparian habitat suitability for beavers (**III**). Both species preferred medium sized lakes and medium to large streams and rivers. The suitability of medium to large streams is in accordance with earlier studies of the Eurasian beaver. Ruys et al. (2011) reported that colonizing beavers selected the widest possible waterways in France, with a mean width of 59 m. These rivers offer a constant water level and a water depth of >50 cm, which may be required for a lodge site (Rosell & Parker, 1996; Hartman & Törnlöv, 2006; Baskin, 2011; Müller-Schwarze, 2011). Furthermore, climate, indicated here by the winter or autumn temperature, was an important factor explaining habitat suitability and the distribution of beavers. The mean winter temperature for the Eurasian beaver was between −3 and − 2 °C and for the North American beaver approximately −6 °C. The observed difference between the species may, at least partly, result from difference in distribution due to different introduction histories. Indeed, in the model for both species together, the response to mean winter temperature was more linear, indicating a preference for areas with a warmer winter temperature. A warm winter temperature likely reflects a generally warmer climate and better food resources for beavers.

Based on the species distribution models conducted with Maxent (**III**), both beaver species presently occupy a large proportion of areas that are most suitable for them (Fig.5). However, these results partly depend on the background area used in the species-specific models, i.e. the present distribution of each species. Thus, the models with both species combined might best predict the potential location of suitable habitats for beavers in Finland: when aquatic habitat and climate were included in the model, mostly northern Finland had habitats of low suitability. When taking into account only the resource factors, suitable habitats occur in most of Finland, except in a small area in northeastern Finland. This corresponds better to

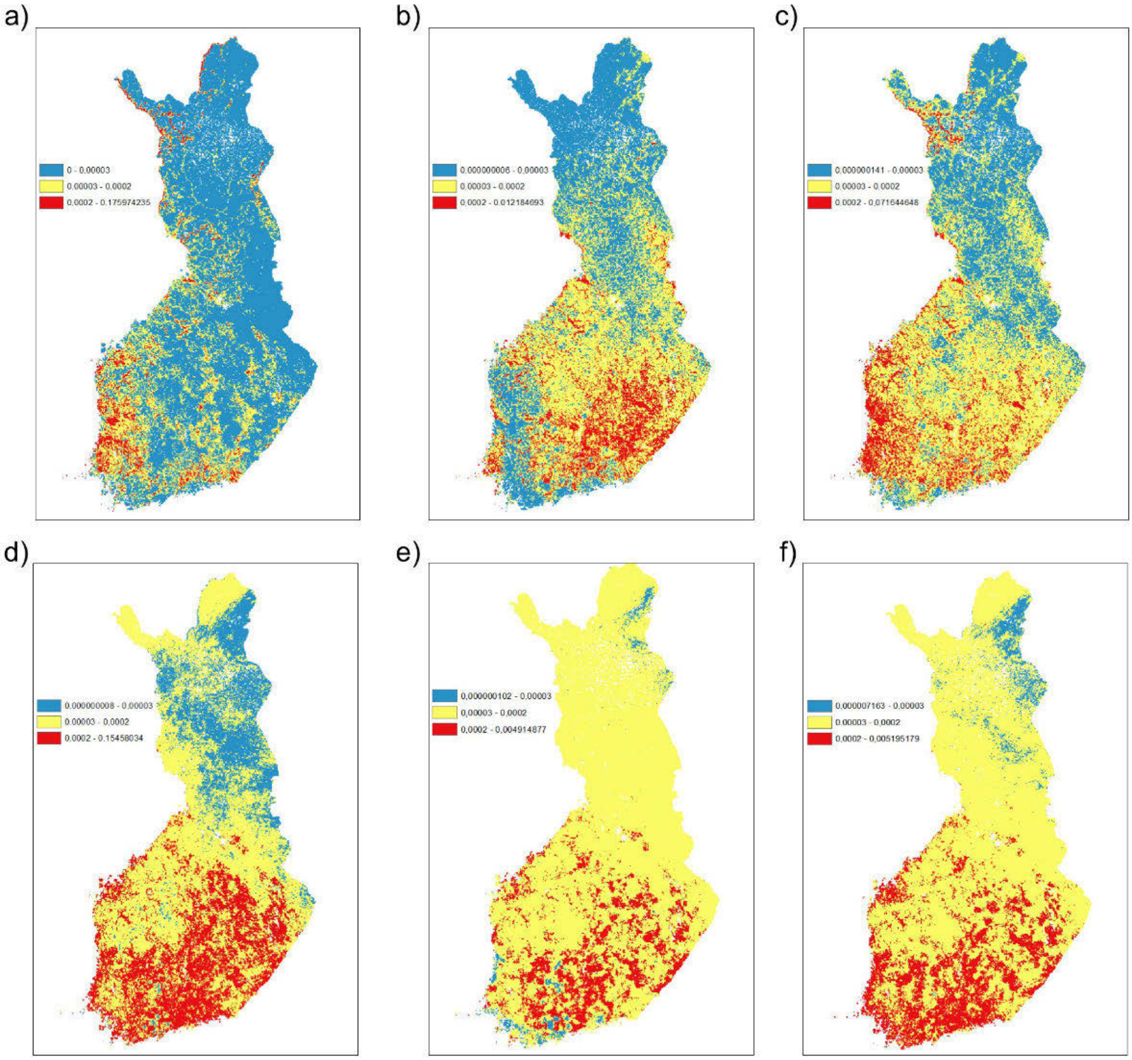

Figure 5. Maps of potential suitable habitats for the Eurasian beaver (a, d), the North American beaver (b, e) and both species modelled together (c, f). Red = most suitable habitat, yellow = medium habitat and blue = least suitable habitat. Maps produced using the averages of raw output of the full model (a–c), and the resource model (d–f), i.e. with tree species, site fertility and forest age.

the present knowledge of multiple beaver occurrences in Northern Finland than the full model. However, it is possible that the habitats and climate in Southern Finland are more suitable for beavers. In this study, the model performance was better for the Eurasian beaver. However, AUC values tend to be higher in Maxent models for species with narrow ranges, but this does not necessarily mean that the models are better (Phillips, 2017). In addition, when using background data instead of true absences, AUC-values are not recommended for comparing model fit, and a model with a lower AUC-value could predict a potential distribution, or fundamental niche, better than a model with a higher value, which could approximate the realized distribution, or realized niche better (Jiménez-Valverde, 2012). This might partly explain the low number of suitable habitats in the full model for the Eurasian beaver that were also approximating the present range. Therefore, based on available resources, most of Finland seems to have suitable habitats for beavers.

These results indicate that habitat use, and thus, available suitable habitats for the Eurasian and the North American beaver are similar in Finland. Both species naturally need deciduous trees in their habitat, and the differences in habitat use are likely explained by differences in the present environments. This is in accordance with other studies that have also shown that beavers are flexible in their habitat use, and selection of forage largely depends on the local abundance of tree species (Gorshkov & Gorskhov, 2011). Because deciduous trees, especially birches, occur in the whole country, resource availability is unlikely to limit the distribution of the two species. Indeed, available recourses mostly determine the fundamental niche of the species, but other factors limit the distribution. In beavers, disturbance such as an anthropogenic environment does not seem to have a negative effect. This is not surprising if there are suitable habitats available and the beavers are not hunted. Species distribution modelling software, such as Maxent, are built onto the resource selection functions and specifically model the habitat suitability, but, for example, intrinsic factors contributing to distribution cannot be included.

Because of the similar habitat use, the two species would compete for the same habitats if living in the same area. Hypothetically, North American beavers could exclude Eurasian beavers at least locally (Parker et al., 2012), although the contrary has been observed in Russia (Danilov et al., 2011). Beavers patrol and defend their territories sometimes aggressively (Mayer et al., 2020), although few cases of beavers dying from (infected) wounds caused by another beaver have been reported (Svendsen, 1980; DeStefano et al., 2006). However, beavers also mark their territories with scent mounds containing anal gland secretion and/or castoreum, which could be expected to reduce deliberate contact between dispersing beavers and territory holders (Rosell, 2001; Rosell & Bjørkøyli, 2002). Thus, colonization of available habitats may be more affected by timing, i.e. the first beaver to arrive occupies the territory.

3.3 Possible reasons for the differences in range sizes

I found that the North American beaver has spread significantly farther from the introduction sites than the Eurasian beaver (**IV**), the maximum yearly spread being ca 7 km vs 3 km, respectively, suggesting that there might be differences in dispersal behavior. It should be noted that these values represent the shortest route between the closest introduction site and current beaver sites, and also that the number of successful introduction sites of the North American beaver may be an overestimation. In addition, translocations for the North American beaver were also made in 1945–1955. Thus, these are conservative estimates of the (annual) spread rate especially for the North American beaver. Nonetheless, the North American beaver has spread farther from the introduction sites and this could relate to e.g. possibly higher fecundity and to longer dispersal distances of the species. However, reported differences in dispersal distances and spread rates of both species in different areas (e.g. Hodgdon, 1978; Hartman, 1995; Cleere, 2005; McNew & Woolf, 2005; Skewes et al., 2006; Mayer et al., 2017; Bartak, 2013) suggest that environmental factors and population density have an influence on the dispersal of beavers. Therefore, the differences between the two species' spread rates in Finland may not be only due to differences between the species but might be related e.g. to the environment. For example, watershed divides that may decrease dispersal efficiency (Hartman, 1995) are more abundant in the Eurasian beaver's SW range than in the North American beaver's range in Finland. However, considering the whole ranges of the two species, the sizes of the main drainage basins did not differ between the ranges of the two species.

Because the present Eurasian beaver population started to expand from only one introduction site, and one female, it was probably difficult for a dispersing beaver to find a mate, and the population started to grow very slowly (Fig.2). Problems of small populations and stochasticity in deaths and births, in addition to competition with North American beavers, may partially explain the failure of the other Eurasian beaver introductions in Finland. In the available data on population size estimates (Table 2; Fig.2), the median population growth rate has been higher for the Eurasian beaver population that has continuously grown throughout the whole study period, whereas the North American beaver population first increased to a large size, but during the last decades has not increased continuously possibly due to a higher hunting pressure compared to that of the Eurasian beaver. This suggests that lower fecundity alone might not explain the smaller range of the Eurasian beaver. However, during the first decades, the North American beaver population grew substantially faster (growth rate 1.24 from 1937 to 1965) than the Eurasian beaver population (growth rate 1.12 from 1935 to 1975) and reached approximately 2000 individuals in 30 years whereas for the Eurasian beaver this took 65 years. Eurasian beavers were illegally hunted in Satakunta at least during the first decades, and their population was only twenty beavers in 1955, twenty years after the reintroduction (Linnamies, 1956). Thus, the slow growth of the population may have been partly caused by humans. Nevertheless, the faster population growth and larger population size of the North American beaver already during the first decades may have greatly affected the faster increase in population size and distribution of the species because of the higher number of reproducing and dispersing animals (Parker et al., 2012). It should also be noted that the reporting activity of hunters affects the population size estimates and it may have been smaller for the North American beaver than for the Eurasian beaver. In any case, and against my prediction, there was no clear difference in the comparison of the relative population size versus the relative number of colonized areas between the two species (Fig.6). I expected that for the Eurasian beaver with a smaller range the population size would have increased faster than the number of colonized areas.

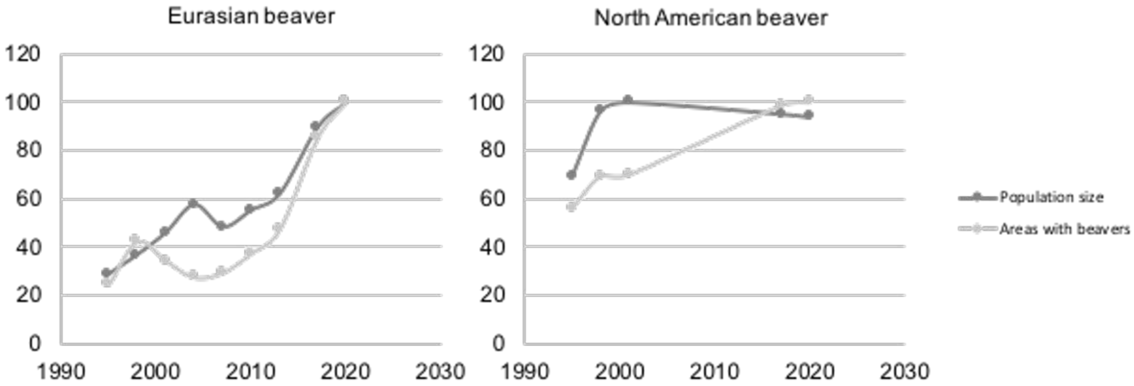

Figure 6. Relative increase (relative to the largest value, which gets 100%) in the number of hunting clubs that reported beaver observations in their area (100% = 203 (E) and 1281 (NA)) and mean population size estimate (100% = 4350 (E) and 15 450 (NA); data in Table 2). Data for years 2004–2013 have been excluded for the North American beaver because of low reporting activity. Percentage in y-axel and year in x-axel.

Nevertheless, the density of North American beavers is lower than that of Eurasian beavers in the hunting club areas (approximately 5 vs 9 lodges per area, respectively; Table 2). In addition, a higher number of introduction and translocation sites for the North American beaver has expanded the distribution of the species more rapidly. However, the number of occupied areas per release site in southern Finland (i.e. excluding Lapland; Luke, 2021), where majority of beavers occur, is larger for the North American beaver. There are at present approximately 246 occupied areas per introduction site (N=5), which is more than the present 156 occupied Eurasian beaver areas in SW Finland. This emphasizes the faster spread of the North American beaver.

In SW Finland, the numbers of Eurasian beavers correlated negatively with the number of watershed divides created by the main drainage basins (**IV**). However, this relationship was not very strong, and it seems likely that watershed divides do not much restrict the dispersal of beavers in the environments where watershed areas are small and closely located, and drainage basins are not separated by e.g. mountains. However, in the data for 2015, the distribution of the Eurasian beaver lodges seems to be more concentrated within one main drainage basin, and along larger rivers, as opposed to the 2018 data used in this study where observations were more evenly distributed, possibly due to lack of data (Fig.7). In the data for 2018, the distance from the introduction site explained the numbers of beavers better than the number of watershed divides. In addition, artificial barriers, dams and sluices, did not lengthen the distances between beaver locations considerably, possibly because there are many alternative aquatic routes available. Therefore, it seems unlikely that natural or artificial barriers could constrain the range expansion of Eurasian beavers in SW Finland. Nevertheless, drainage basins and larger watercourses may have some effect on the expansion direction of beavers also in Finland.

Agricultural areas and wider streams and rivers were used more, whereas less small streams and coniferous forest were found in the beaver habitats in the novel areas than in the original area in SW Finland (**IV**), indicating a use of higher quality habitats in the novel areas based on my earlier studies. Perhaps these preferred habitats were more available in the novel areas because of lower overall beaver densities compared to the areas near the introduction site with a high density of beavers. Thus, these results indicate that lack of high-quality habitats in the novel areas has not restricted the spread of Eurasian beavers from the original area.

These findings indicate that lack of suitable habitats or barriers for movement do not restrict the range expansion of the Eurasian beaver in Finland. Instead, the environment in the original area may have offered enough suitable habitat patches for the Eurasian beaver, enabling the increase in the population density within this area. Perhaps only recently the population has increased close to saturation level, which may explain the recent spread of Eurasian beavers to the novel areas. However, the reason for the higher spread rate of the North American beaver could not be determined based on these data. Higher fertility of the non-native species was not supported based on the growth rates of the populations (**I** and **IV**), although it should be noted that the North American beaver is hunted more. In addition, the estimated population sizes of the two species are based on the number of reported lodges and family group sizes from the literature, thus, these data may not accurately describe the population growth for either species. Nevertheless, even if the North American beaver had larger litters, the higher mortality rate in the population due to hunting may restrain the population growth at present. In addition, it cannot be ruled out that Eurasian beavers are hunted when colonizing new areas outside the areas where the hunting of beavers is restricted. However, this does not explain the high density of the species close to the reintroduction site.

Beaver populations are reported to follow a sigmoid growth pattern with a slow population increase during the first decades, followed by an almost exponential growth, and then a decline in growth rate in high densities (Hartman, 1992; Busher & Lyons, 1999; Wróbel & Krysztofiak-Kaniewska, 2020). Because the number of founding animals was very small in Finland, the Eurasian beaver population grew slowly but the growth pattern seems similar to other European populations of the species (Hartman, 1992; Wróbel & Krysztofiak-Kaniewska, 2020). However, the Finnish North American beaver population grew substantially faster in the beginning than the Swedish and Polish Eurasian beaver populations with more founding animals. In contrast, the North American beaver population in Tierra del Fuego, Chile, grew from 50 beavers to an estimated 41 000–49 000 in only fifty years (Skewes et al., 2006).

Growth rates of beaver populations vary greatly between years and, although high during the first decades, the maximum population growth rate of the Finnish North American beaver population does not seem greater than that of local populations in the USA (maximum growth rate during first decades in two populations 1.35 and 1.23; computed from Busher & Lyons, 1999; Table 2). In comparison, the North American beaver population seemed to grow exceptionally fast in the lake district in eastern Finland. If the number of founding animals is correct, the Sääminki population increased from two or four to 130–140 animals in only eight years (Linnamies, 1956), meaning an annual population growth rate of 1.56–1.69. In contrast, the western population of the North American beaver was estimated at only 100–200 animals in 1975, approximately forty years after introductions (growth rate 1.08–1.11; Lahti & Helminen, 1980). In addition, the number of beavers in Lapland was estimated to be between 100–150 animals both in the 1950s and the 1970s.

Therefore, there have been differences in growth rates also between the North American beaver populations in Finland. The beavers brought to Sääminki were from the state of New York, USA (Linnamies, 1956), whereas the beavers introduced in central/western Finland were from both New York (in Keuruu; Linnamies, 1956) and Minnesota (in Ruovesi; Moilanen, 1980). Indeed, intrinsic difference in fecundity between populations and species is possible. However, spatial and temporal variation in reproductive rate, e.g. due to habitat quality and population density, is common in beavers (e.g. Bergerud & Miller, 1977; Payne, 1984; Rosell & Parker, 1995; Pietrek et al., 2017). The survival rate and/or fecundity of North American beavers in eastern Finland seem to have been continuously high during the first decades after introduction. Fecundity and survival greatly affect the viability of beaver populations (South et al., 1999), but population growth and expansion are also dependent on the possibility of finding mates and available habitats (South & Kenward, 2001). Population growth can be expected to be highest when dispersal distances and mate finding possibilities are in a balance (South & Kenward, 2001). Perhaps population density and habitat availability have not limited the reproductive rate of beavers in the lake district of Finland.

Possibly larger territories (**II**) and longer dispersal distances could also result in the lower density and faster spread of the North American beaver. Other studies have shown that beavers usually occupy the most optimal habitats first (Halley & Rosell, 2002; John et al., 2010; Halley et al., 2013), resulting in distant and irregular colonization patterns (Fustec et al., 2001), but often stay close to their natal territory if there is a suitable habitat available (Hartman, 1994a). In Norway, the expansion rate of Eurasian beavers was reported to be slow in high densities, and subordinate beavers could stay in their natal territory up to seven years, possibly replacing their parents as breeding adults (Mayer et al., 2017). Furthermore, a beaver family can occupy a site from a few years to several decades, and less suitable sites may be abandoned more quickly than productive sites (Johnston & Naiman, 1990; Fustec et al., 2001; Hyvönen & Nummi, 2008). My work did not indicate that there would be less available resources, i.e. deciduous trees, in the environment of the North American beaver, and there was more birch within their estimated territory area (**II** and **III**). However, habitat fragmentation and distance between habitat patches, which were not studied here, often constrain the range expansion of species, but may also increase dispersal distances if the habitat patches are connected (Matthysen et al., 1995; Trenham et al., 2001; Bocedi et al., 2014). Furthermore, beavers have been reported to often occur sporadically around the most suitable habitats, and territories usually become larger if forage is scarce (Fustec et al., 2001). For example, the colony densities of the North American beaver have been observed to vary substantially in South America, where beavers were not hunted extensively and have no natural predators, as depending on the vegetation coverage and geomorphology: colony densities were highest (up to 5.6 colonies per km) in areas with wetland, continuous riparian forest (*Nothofagus* ecosystem) at least on one shore, and medium steepness in bank height (Lizarralde, 1993; cf. Henn et al., 2016). That is, abundant suitable habitat can support a higher density of beaver colonies than sparsely located or less optimal habitats.

Whether the environment has a larger carrying capacity in the Eurasian beaver's range, or whether habitat fragmentation affects the expansion rate in either of the species in Finland, remains a matter for speculation. In that sense, my results in Chapter **IV** were inconclusive on whether the environment might affect the distribution patterns of beavers in Finland; there may be differences in the habitats of the two species that were not yet taken into account, and some, that were already identified in the previous chapters. There are undeniably differences in the environments in the present ranges of the two species. The agricultural areas in SW Finland may provide high-quality habitats for the Eurasian beaver (**II**, **III** and **IV**), with suitable geomorphology and aquatic and terrestrial vegetation, resulting in a concentrated distribution pattern. On the other hand, large and abundant water areas (**I**) in the lake district in eastern Finland may have increased the speed of the range expansion in the North American beaver (Fig.7).

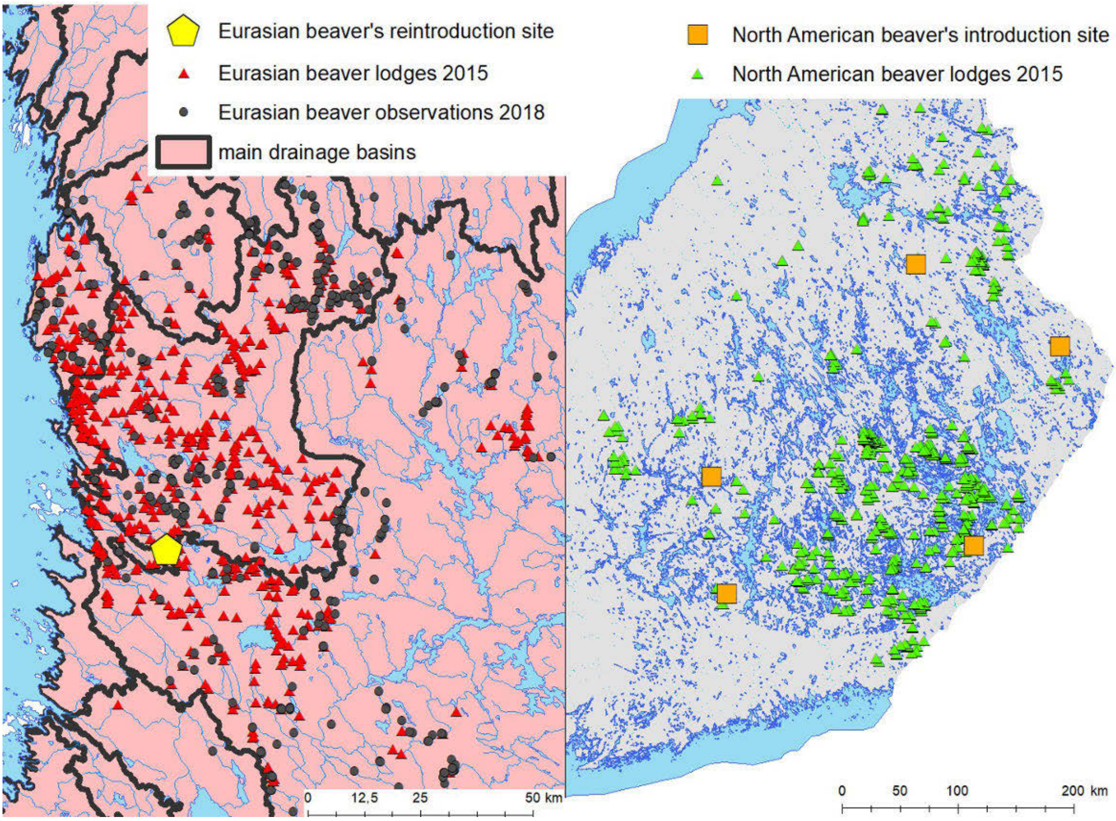

Figure 7. Distribution of Eurasian beaver observations over the main drainage basins (on the left), and the distribution of North American beaver observations in respect to large water areas in Finland (on the right).

4 Conclusions

In my thesis I have studied the factors affecting the distribution of the Eurasian and the North American beaver in Finland. These species were simultaneously introduced in the 1930s but show a strikingly different distribution and population size at present. I determined the population dynamics, habitat use and availability, and distribution patterns for both beaver species. The results of this thesis show that the dynamics of both species are density dependent and migration is an important factor (**I**). Beavers also seem to disperse slowly from the source populations and a comprehensive water system may enable them to locate habitats close to their natal sites, as the North American beaver occurs more abundantly close to the introduction sites and in areas abundant in water areas and watercourses (**I**). The Eurasian beaver also occurs in high densities close to its original introduction site. In addition, habitat use (**II**), and thus, available suitable habitats (**III**) of the two beaver species seem to be similar in Finland, indicating a competition for habitats. However, the present environments might affect the slightly different observed patterns, most noticeably, the Eurasian beaver occurring in areas close to agriculture, which may also provide highly suitable habitats for beavers. Indeed, anthropogenic disturbance occurring close to beavers in Finland does not seem to affect the beavers negatively, but the effect of hunting (**I**) should be examined more. The importance of deciduous trees and aquatic habitat to beavers was apparent in my studies, and, although the scale and accuracy of the data, and selected variables affect the results, the contribution of these factors could be seen with the environmental data in GIS. Therefore, these results and methods can also be easily utilized when planning the management of the species and securing a future for the Eurasian beaver.

In a world where anthropogenic influence is increasingly affecting wildlife through climate change, invasive species, and the degrading and destroying of habitats, securing the present habitats and their connectivity including those close to anthropogenic areas is of paramount importance (Fahrig, 1997; Mawdsley et al., 2009; Cross et al., 2012; Kaushik & Mungi, 2015). For the native Eurasian beaver, in order to ensure the possibility of spreading to new areas, forested riparian areas and aquatic habitats in agricultural areas are especially important, and deciduous trees should be available in these environments. Active preference for native species over non-native species has been suggested as a management policy to control the North American beaver in Europe (Halley et al., 2021). This usually means excluding the North American beaver from areas of contact by hunting. However, battling to keep the North American beaver from spreading into available habitats seems arduous. Although beaver populations have been hunted to extinction before, politically or even ecologically it may be hard to justify an eradication of the North American beaver in Finland. Therefore, the range of the Eurasian beaver will hopefully expand, thus, sustaining the viability of the species in Finland.

The reason for the smaller range of the Eurasian beaver was not, however, completely clear as lack of suitable habitats and barriers to movement do not seem to restrict the spread of the species (**IV**). Naturally, dispersal from only one introduction site possibly retards the expansion rate of the native species, suggesting that translocations of beavers would enlarge the range of the Eurasian beaver substantially faster than natural dispersion. Furthermore, the genetic diversity of the Eurasian beaver population in SW Finland, originating from only one female, is extremely low (Iso-Touru et al., 2020). However, this may not affect the viability of the population as the Swedish Eurasian beaver population also possesses extremely low genetic diversity. This was due to a bottleneck in the Norwegian population used for reintroductions, however, the population has still grown large (Ellegren et al., 1993). Eurasian beavers have now, apparently quite recently, dispersed to Finland from Sweden and Russia, and this also increases the distribution of the Finnish population. Optimally, these immigrants would at some point reproduce with individuals of the original population and increase the genetic diversity.

The minor difference in the number of successfully introduced and reproducing animals may have contributed to the major differences in the distribution and population sizes visible today, in addition to the translocations of the North American beaver. However, the North American beaver has evidently spread longer distances from the introduction sites than the Eurasian beaver (**IV**). Differences between the species regarding fecundity, colony and territory sizes, and dispersal distances, might all affect the expansion rate of the populations and need further studies. However, although sometimes a single factor can limit the distribution of a species, it is more likely that combinations of several factors, such as distance between habitat patches, population density, and reproductive fitness, act synergistically, antagonistically, or independently from one another in determining the range expansion of species (Mott, 2010).

To conclude, the results of this thesis advance the knowledge on what determines the distribution and population sizes of introduced species. The North American beaver was translocated to several areas, thus, increasing its distribution more rapidly, and this non-native species has also been more effective in spreading from the introduction sites, even compared to an ecologically seemingly similar species, the Eurasian beaver. The results of this thesis show that the reasons for the different distribution patterns of the two species are likely complex, and the patterns can be caused by several intrinsic and extrinsic factors. This highlights that it is hard to predict how introduced species succeed in new areas. These results can be utilized when planning species introductions, and in wildlife management and the conservation of species.

Acknowledgements

I am grateful to my supervisors, Kaarina Kauhala and Vesa Selonen, for their support during this project. This thesis would not exist without Kaarina and the need to study the Finnish beavers utilizing the data curated by the Natural Resources Institute Finland. Thank you Kaarina for introducing me to beaver management. I am also thankful that you accompanied me in the field when I first saw beaver habitats. I want to thank Vesa for your expertise in statistical analyses, and, without your ideas, the Papers I–III would not be what they are. I am especially thankful that you always replied to my emails quickly and gave me good and concise advice. This PhD project started slowly but increased to an almost exponential speed when it comes to publishing articles. You both were my toughest reviewers, and with your contribution, I think we wrote pretty good papers. With your supervision, I have become an independent researcher, and most importantly, I managed to finalize this project.

I am grateful to all the volunteers that have reported beaver observations over the years. These are truly exceptionally comprehensive data that you have gathered. Thank you also to everyone that have organized the beaver counts and filed and saved the data.

I wish to thank my co-authors Jon Brommer and Sakari Tuominen for your contribution to this thesis. I would like to thank my pre-examiners Göran Hartman and Janne Sundell for your valuable advice on improving this thesis. You made the pre-examination process much less intimidating than what I expected it to be. Thank you for your kind words.

I wish to thank my research director Veijo Jormalainen for your guidance especially at the last stages of this project. I also want to thank all the people at the Department of Biology. Although I have been working remotely already before the pandemic, and many of the familiar PhD students have already graduated, there have always been friendly faces when I have visited Turku or, more recently, on the computer screen. I am especially thankful to Tiia Kärkkäinen for your peer-support during the writing of the synopsis. I also wish to thank Elizabeth Nyman for proofreading the synopsis. I have nothing but warm feelings about everyone I have encountered over the years while working with beavers; either in congresses, beaver workshops, beaver meetings, or in the field. Special thanks to Jessika Karvinen, I had fun when surveying beaver habitats with you.

I am grateful for my fellow ecologist, and most importantly, my dear friends Tuuli, Tytti and Suvi. You have been, respectively, my most valuable example and inspiration for finishing a PhD.

I wish to acknowledge all the funders that have made it possible for me to work on this thesis: Maj and Tor Nessling Foundation, the Department of Biology at the University of Turku, Finnish Cultural Foundation, and the Doctoral Programme in Biology, Geography and Geology.

Finally, I am most grateful for my furry son, Hannibal the Cat. You have been the light of my life, my precious, for already fourteen years. I also wish to thank Jussi for being the greatest cat dad ever! You two have been my most important mental support for finishing this thesis.

6.8.2021
Riikka Alakoski

References

Allee, W.C., 1931. Animal aggregations: a study in general sociology. University of Chicago Press.

Allen, A.W., 1982. Habitat suitability index models: beaver. Washington, DC. US Department of the Interior, Fish and Wildlife Service FWS/OBS-82. 20 pp.

Andrewartha, H.G., Birch, L.C., 1954. Distribution and abundance of animals. University of Chicago Press, Chicago, Illinois, USA.

Barros, C., Palmer, S.C.F., Bocedi, G., Travis, J.M.J., 2016. Spread rates on fragmented landscapes: the interacting roles of demography, dispersal and habitat availability. Diversity and Distributions 22:1266–1275. https://doi:10.1111/ddi.12487

Barták, V., Vorel, A., Šímová, P., Puš, V., 2013. Spatial spread of Eurasian beavers in river networks: a comparison of range expansion rates. *Journal of Animal Ecology*, 82:587–597. https://doi:10.1111/1365-2656.12040

Baskin, L.M., 2011. Predators as determinants of beaver alertness and shelter-making behaviour. In: Sjöberg, G., Ball, J.P. (Eds.). Restoring the Eurasian beaver: 50 years of experience. Pensoft Publishers, Sofia. pp. 271–280.

Bergerud, A. T., Miller, D. R., 1977. Population dynamics of Newfoundland beaver. *Canadian Journal of Zoology*, 55(9):1480–1492.

Bloomquist, C.K., Nielsen, C.K., 2010. Demography of unexploited beavers in Southern Illinois. *The Journal of Wildlife Management*, 74:228–235.

Bocedi, G., Zurell, D., Reineking, B., Travis, J.M.J., 2014. Mechanistic modelling of animal dispersal offers new insights into range expansion dynamics across fragmented landscapes. *Ecography*, 37: 1240-1253. https://doi.org/10.1111/ecog.01041

Boyce, M.S., 1974. Beaver population ecology in interior Alaska. M.Sc. thesis, University of Alaska, Fairbanks. 161 pp.

Bracken, F.S.A., Hoelzel, A.R., Hume, J.B., Lucas, M.C., 2015. Contrasting population genetic structure among freshwater-resident and anadromous lampreys: the role of demographic history, differential dispersal and anthropogenic barriers to movement. *Molecular Ecology*, 24:1188–1204. https://doi:10.1111/mec.13112

Brooks, R.P., Fleming, M.W., Kennelly, J.J., 1980. Beaver colony response to fertility control: evaluating a concept. *The Journal of Wildlife Management*, 44(3):568–575.

Campbell, R.D., Nouvellet, P., Newman, C., Macdonald, D.W., Rosell, F., 2012. The influence of mean climate trends and climate variance on beaver survival and recruitment dynamics. Global change biology, 18(9), 2730-2742.

Campbell, R.D., Rosell F., Nolet, B.A., Dijkstra, V.A., 2005. Territory and group sizes in Eurasian beavers (*Castor fiber*): echoes of settlement and reproduction?. *Behavioral Ecology and Sociobiology*, 58(6):597–607.

Cressie, N.A.C., 1993. Statistics for spatial data. Wiley Blackwell, London, UK.

Cross, M.S., Hilty, J.A., Tabor, G.M., Lawler, J.J., Graumlich, L.J. & Berger J., 2012. From connect-the-dots to dynamic networks: maintaining and enhancing connectivity as a strategy to address climate change impacts on wildlife. In: Brodie, Jedediah F., Post, Eric S. and Doak, Daniel F.

(Eds.), Wildlife conservation in a changing climate. Chicago: The University of Chicago Press. p. 307–329.

Dail, D., Madsen, L., 2011. Models for estimating abundance from repeated counts of an open metapopulation. *Biometrics* 67:577–587.

Danilov, P.I., 1995. Canadian and European beavers in Russian northwest: distribution, number, comparative ecology. In: Ermala, A., Lahti, S. (Eds.). The 3rd Nordic Beaver Symposium. Finnish Game and Fisheries Institute, Finland. pp. 10–16.

Danilov, P.I., Fyodorov, F.V., 2015. Comparative characterization of the building activity of Canadian and European beavers in northern European Russia. Russian Journal of Ecology, 46:272–278.

Danilov, P.I., Fyodorov, F.V., 2016. The history and legacy of reintroduction of beavers in the European North of Russia. *Russian Journal of Theriology*, 15:43–48.

Danilov, P., Kanshiev, V., 1983. The state of population and ecological characteristics of European (*Castor fiber* L.) and Canadian (*Castor canadensis* Kuh.) beavers in the northwestern USSR. *Acta Zoologica Fennica*, 174:95–97.

Danilov, P.I. Kanshiev, V., Fyodorov, F.V., 2011. Characteristics of North American and Eurasian beaver ecology in Karelia. In: Sjöberg, G, Ball, J.P. (Eds.). Restoring the European Beaver: 50 years of experience. Pensoft Publishers, Sofia, Bulgaria, pp. 55–72.

Dewas, M., Herr, J., Schley, L., Angst, C., Manet, B., Landry, P., Catusse, M., 2012. Recovery and status of native and introduced beavers Castor fiber and Castor cana- densis in France and neighboring countries. *Mammal Review*, 42:144–165.

DeStefano, S., Koenen, K.K., Henner, C., Strules, J., 2006. Transition to independence by subadult beavers (*Castor canadensis*) in an unexploited, exponentially growing population. Journal of Zoology, 269, 434–441. https://doi.org/10.1111/j.1469-7998.2006.00160.x

Duchesne, T., Fortin, D., Courbin, N., 2010. Mixed conditional logistic regression for habitat selection studies. *Journal of Animal Ecolology*, 79:548–555.

Dvořák, J., 2013. Diet preference of Eurasian beaver (*Castor fiber* L., 1758) in the environment of Oderské vrchy and its influence on the tree species composition of river bank stands. *Acta Universitatis Agriculturae et Silviculturae Mendelianae Brunensis*, 61(6):1637-1643. https://doi.org/10.11118/ actaun201361061637.

Dwyer, G., & Morris, W. F. (2006). Resource-dependent dispersal and the speed of biological invasions. The American Naturalist, 167(2), 165-176.

Ebenhard, T., 1988. Introduced birds and mammals and their ecological effects. *Swedish Wildlife Research* (Viltrevy), 13:1–107.

Ehrlén, J., Morris, W.F., 2015. Predicting changes in the distribution and abundance of species under environmental change. *Ecology Letters*, 18:303–314.

Elith, J., Phillips, S.J., Hastie, T., Dudíc, M., Chee, Y.E., Yates, C.J., 2011. A statistical explanation of MaxEnt for ecologists. *Diversity and Distribution*, 17:43–57. https://doi.org/10. 1111/j.1472-4642.2010.00725.x.

Ellegren, H., Hartman, G., Johansson, M., Andersson, L., 1993. Major histocompatibility complex monomorphism and low levels of DNA fingerprinting variability in a reintroduced and rapidly expanding population of beavers. Proceedings of the National Academy of Sciences, 90(17):8150–8153.

Ermala, A., Helminen, M., Lahti, S., 1989. Majaviemme levinneisyyden ja runsauden vaihteluista sekä tulevaisuuden näkymistä. Summary: Some aspects of the occurrence, abundance and future of the Finnish beaver population. *Suomen Riista*, 35:108–118.

Ermala, A., 1996. Euroopanmajava, Kanadanmajava. In: Lindén H, Hario M, Wikman M (Eds.). Riistan jäljille. Riista- ja kalatalouden tutkimuslaitos and Edita, Helsinki. pp. 30–33.

Ermala, A., Lahti, S., Vikberg, P., 1999. Majavakanta edelleen kasvussa – saalismäärä jo lähes 2500 yksilöä. *Metsästäjä* 4:28–31.

ESRI, 2011. ArcGIS desktop. Release 10. Environmental Systems Research Institute, Redlands, California, USA.

Fahrig, L., 1997. Relative effects of habitat loss and fragmentation on population extinction. The Journal of Wildlife Management, 61(3):603–610.

Finnish Wildlife Agency, 2020. Hunting in Finland. https://riista.fi/wp-content/uploads/2020/08/suomi_-riistamaana_2020_eng.pdf

Fustec, J., Lode, T., Le Jacques, D., Cormier, J.P., 2001. Colonization, riparian habitat selection, and home range size in a reintroduced population of European beavers in the Loire. *Freshwater Biology*, 46:1361–1371.

Gause, G.F., 1934. The struggle for existence. Baltimore, Williams & Wilkins. 163 pp.

Gause, G.F., 1935. Vérifications expérimentales de la théorie mathématique de la lutte pour la vie. Actualités scientifiques, Vol 277. Hermann et Cie, Paris. 63 pp.

Gompertz, B. 1825. On the nature of the function expressive of the law of human mortality, and on a new mode of determining the value of life contingencies. *Philosophical Transactions of the Royal Society of London*, 115:513–583.

Gorshkov, D., Gorskhov, Y., 2011. Feeding strategy of beavers in Tatarstan Republic. In: Sjöberg, G., Ball, J.P. (Eds.), Restoring the European Beaver: 50 Years of Experience. Pensoft, Sofia-Moscow.

Granit, A.W., 1990. Bävern i Finland. *Tidskrift för Jägare och Fiskare* 8:45–55.

Guisan, A., Thuiller, W., 2005. Predicting species distribution: offering more than simple habitat models. *Ecology Letters*, 8:993–1009.

Haarberg, O., Rosell, F., 2006. Selective foraging on woody plant species by the Eurasian beaver (*Castor fiber*) in Telemark, Norway. *Journal of Zoology,* 270:201–208.

Halley, D., Rosell, F., 2002. The beaver's reconquest of Eurasia: Status, population development, and management of a conservation success. *Mammal Review*, 32:153–178.

Halley, D., Rosell, F., & Saveljev, A., 2012. Population and distribution of Eurasian beaver (*Castor fiber*). *Baltic Forestry*, 18(1):168-175.

Halley, D., Saveljev, A., Rosell, F., 2021. Population and distribution of beavers Castor fiber and Castor canadensis in Eurasia. *Mammal Review*, 51:1–24. https://doi-org.ezproxy.utu.fi/10.1111/mam.12216

Halley, D., Teurlings, I., Welsh, H., Taylor, C., 2013. Distribution and patterns of spread of recolonising Eurasian beavers (Castor fiber Linnaeus 1758) in fragmented habitat, Agdenes peninsula, Norway. *Fauna Norvegica*, 32:1–12.

Hanski, I., Gilpin, M., 1991. Metapopulation dynamics: brief history and conceptual domain. *Biological Journal of the Linnean Society*, 42(1-2):3-16.

Hapeman, P., Latch, E.K., Fike, J.A., Rhodes, O.E., Kilpatrick, C.W., 2011. Landscape genetics of fishers (*Martes pennanti*) in the northeast: dispersal barriers and historical influences. *Journal of Heredity*, 102(3):251–259. https://doi-org.ezproxy.utu.fi/10.1093/jhered/esr001

Harrison, S. 1991. Local extinction in a metapopulation context: an empirical evaluation. *Biological Journal of the Linnean Society*, 42:73–88.

Hartman, G., 1994a. Ecological studies of a reintroduced beaver (*Castor fiber*) population. SLU/Repro Uppsala.

Hartman, G., 1994b. Long-term population development of a reintroduced beaver (*Castor fiber*) population in Sweden. *Conservation Biology*, 8:713–717.

Hartman, G., 1995. Patterns of spread of a reintroduced beaver Castor fiber population in Sweden. *Wildlife Biology*, 1:97–103. https://doi:10.2981/wlb.1995.0015

Havens, R.P., Crawford, J.C., Nelson, T.A., 2013. Survival, home range, and colony reproduction of beavers in east-central Illinois, an agricultural landscape. *The American Midland Naturali*st, 169(1):17–29.

Henn, J.J., Anderson, C.B., Pastur, G.M., 2016. Landscape-level impact and habitat factors associated with invasive beaver distribution in Tierra del Fuego. *Biological Invasions*, 18(6):1679–1688.

Hinze, G., 1950. Der Biber. Körperbau und Lebensweise, Verbreitung und Geschichte. Akademie Verlag, Berlin.

Hostetler, J. A., Chandler, R.B., 2015. Improved state-space models for inference about spatial and temporal variation in abundance from count data. *Ecology*, 96:1713–1723.

Hutchinson, G. E., 1958. Concluding remarks. Cold Spring Harbor Symposia on Quantitative Biology, 22:415–427.

Hyvärinen, E., Juslén, A., Kemppainen, E., Uddström, A., Liukko, U-M (Eds.), 2019. The 2019 Red List of Finnish Species. Ympäristöministeriö and Suomen ympäristökeskus. Helsinki. 704 pp.

Hyvönen, T., Nummi, P., 2008. Habitat dynamics of beaver Castor canadensis at two spatial scales *Wildlife Biology*, 14:302–8.

Härkönen, S., 1999. Management of the North American beaver (Castor canadensis) on the South-Savo game management district, Finland (1983–97). In: Busher PE, Dzięciołowski RM (Eds.) Beaver Protection, Management, and Utilization in Europe and North America. Springer, Boston, MA. https://doi.org/10.1007/978-1-4615-4781-5_2

Iso-Touru, T., Huitu, O., Tapio, M., Kučinskienė, J., Ulevičius, A., Bukelskis, E., Tirronen, K., Fyodorov, F., Panchenko, D., Saarma, U., Valdmann, H., Kauhala, K., 2020. Low genetic polymorphism in the re-introduced Eurasian beavers in Finland: implications for conservation. *Mammal Research*, 65:331–338.

Iso-Touru, T., Tabell, J., Virta, A., Kauhala, K., 2021. A non-invasive, DNA-based method for beaver species identification in Finland. *Wildlife Biology*, 2021: wlb.00808

Jiménez-Valverde, A., 2012. Insights into the area under the receiver operating char- acteristic curve (AUC) as a discrimination measure in species distribution modelling. *Global Ecology and Biogeography*, 21:498–507. https://doi.org/10.1111/j.1466-8238.2011.00683.x.

John, F., Baker, S., Kostkan, V., 2010. Habitat selection of an expanding beaver (*Castor fiber*) population in central and upper Morava River basin. *European Journal of Wildlife Research*, 56(4):663–671.

Johnston, C.A., Naiman, R.J., 1990. Aquatic patch creation in relation to beaver population trends *Ecology*, 71:1617–21.

Kauhala, K., Karvinen, J., 2018. Majavien elinympäristönkäyttö maastokartoitusten ja metsästäjien lähettämien pesäkoordinaattien perusteella (Summary: Habitat use of beavers based on mapping in the field and lodge coordinates from hunters). *Suomen Riista,* 64:21–34

Kauhala, K., Timonen, P., 2016. Mitä majavien kallot kertovat (Summary: What do beaver skulls reveal?). *Suomen Riista,* 62:7–18.

Kauhala, K., Turkia, T., 2013. Majavien elinympäristönkäyttö: alkuperäislajin ja vieraslajin alustavaa vertailua (Summary: Habitat use of beavers: preliminary comparison between a native and alien specis). *Suomen Riista,* 59:20–33.

Kaushik, M., Mungi, N., 2015. Meeting report: human-wildlife interactions and management of invasive alien species. *Current Science*, 108(6):1039–1040.

Korbelová, J., Hamšíková, L., Maloň, J., Válková, L., Vorel, A., 2016. Seasonal variation in the home range size of the Eurasian beaver: do patterns vary across habitats? *Mammal Research*, 61:243–253.

Krebs, C.J., 1972. Ecology: the experimental analysis of distribution and abundance. Harper and Row. New York.

Lahti, S., Helminen, M., 1969. Suomen majavien istutushistoriasta ja kannan levinneisyys 1960-luvulla (Summary: History of reintroductions and present population status of the beaver in Finland). *Suomen Riista,* 21:67–75.

Lahti, S., Helminen, M., 1974. The beaver Castor fiber (L.) and C. canadensis (Kuhl) in Finland. *Acta Theriologica*, 19:177–189.

Lahti, S., Helminen, M., 1980. Suomen majavien levinneisyyden muutokset vuosina 1965–1975 (Summary: The status of European and Canadian beavers in Finland in 1965–1975). *Suomen Riista*, 27:71–77.

Leege, T., 1968. Natural movements of beavers in southeastern Idaho. *Journal of Wildlife Management* 32(4):973–976. https://doi.org/10.2307/3799579

Linnamies, O., 1956. Majavien esiintymisestä ja niiden aiheuttamista vahingoista maastossamme. *Suomen Riista*, 10:63–86.

Lizarralde, M.S., 1993. Current status of the introduced beaver (*Castor canadensis*) population in Tierra del Fuego, Argentina. *Ambio*, 22(6), 351-358.

Lotka, A. J., 1932. The growth of mixed populations, two species competing for a common food supply. Journal of the Washington Academy of Sciences, 22:461–469.

Luke, 2020. statdb.luke.fi

Luke, 2021. https://www.luke.fi/tietoa-luonnonvaroista/riista/majavat/

Machado, A.P., Clément, L., Uva, V., Goudet, J., Roulin, A., 2018. The Rocky Mountains as a dispersal barrier between barn owl (Tyto alba) populations in North America. Journal of Biogeography, 45:1288–1300. https://doi-org.ezproxy.utu.fi/10.1111/jbi.13219

Matthysen, E., Adriaensen, F., Dhondt, A., 1995. Dispersal distances of nuthatches, *Sitta europaea*, in a highly fragmented forest habitat. *Oikos*, 72(3), 375–381. doi:10.2307/354612

Mawdsley, J.R., O'Malley, R. & Ojima, D.S., 2009. A review of climate-change adaptation

strategies for wildlife management and biodiversity conservation. *Conservation Biology*, 23: 1080-1089. https://doi.org/10.1111/j.1523-1739.2009.01264.x

Mayer, M., Zedrosser, A., Rosell, F., 2017. When to leave: the timing of natal dispersal in a large, monogamous rodent, the Eurasian beaver. *Animal Behaviour*, 123:375–382.

Mayer, M., Aparicio Estalella, C., Windels, S.K., Rosell, F.N., 2020. Landscape structure and population density affect intraspecific aggression in beavers. Ecology and Evolution, 10(24):13883–13894.

Merow, C., Smith, M.J., Silander, J.A., 2013. A practical guide to MaxEnt for modelling species' distributions: what it does, and why inputs and settings matter. *Ecography,* 36:1058–1069. https://doi.org/10.1111/j.1600-0587.2013.07872.x.

Moilanen, P., 1980. Täydentäviä tietoja Suomen majavien istutushistoriasta. (Summary: Additions to the history of beaver reintroduction in Finland). *Suomen Riista*, 27:78–80.

Morse, D.H., 1976. Variables affecting the density and territory size of breeding spruce-woods warblers. *Ecology*, 57:290–301.

Mott, C.L., 2010. Environmental constraints to the geographic expansion of plant and animal species. *Nature Education Knowledge*, 3(10):72.

Müller-Schwarze, D., 2011. The beaver. Its life and impact. Cornell University Press.

National Land Survey of Finland, 2/2015. https://tiedostopalvelu.maanmittauslaitos.fi/tp/kartta

Nolet, B., Rosell, F., 1994. Territoriality and time budgets in beavers during sequential settlement. *Canadian Journal of Zoology*, 72:1227–1237.

Nolet, B.A., Broekhuizen, S., Dorrestein, G.M., Rienks, K.M., 1997. Infectious diseases as main causes of mortality to beavers *Castor fiber* after translocation to the Netherlands. *Journal of Zoology*, 241(1):35–42.

Nolet, B., Rosell, F., 1998. Comeback of the beaver Castor fiber: an overview of old and new conservation problems. *Biological Conservation*, 83:165–173.

Novak, M., 1987. Beaver. Wild Furbearer Management and Conservation in North America (Eds. Novak, M., Baker, J.A., Obbard, M.E., Malloch, B.). Ontario Ministry of Natural Resources. Toronto. pp. 283–312.

Nummi, P. 2015. Majavan lammella. Metsäkustannus Oy. Jelgava Printing House, Latvia.

Parker, H., Rosell, F., Mysterud, A., 2007. Harvesting of males delays female breeding in a socially monogamous mammal; the beaver. *Biology Letters*, 3(1):107–109.

Parker, H., Nummi, P., Hartman, G., Rosell, F., 2012. Invasive North American beaver Castor canadensis in Eurasia: a review of potential consequences and a strategy for eradication. *Wildlife Biology*, 18(4):354–365.

Parker, H., Zedrosser, A., Rosell, F., 2017. Age-specific reproduction in relation to body size and condition in female Eurasian beavers. *Journal of Zoology*, 302(4):236–243.

Payne, N.F., 1984. Reproductive rates of beaver in Newfoundland. *The Journal of Wildlife Management*, 48(3): 912-917.

Pebesma, E. J. 2004. Multivariable geostatistics in S: the gstat package. *Computers and Geosciences* 30:683–691.

Phillips, S.J., Anderson, R.P., Schapire, R.E., 2006. Maximum entropy modelling of species geographic distributions. *Ecological Modelling*, 190(3-4):231–259. https://doi.org/10.1016/j.ecolmodel.2005.03.026.

Phillips, S.J., Anderson, R.P., Dudík, M., Schapire, R.E., Blair, M.E., 2017. Opening the black box: an open-source release of Maxent. *Ecography*, 40:887–893. https://doi.org/10.1111/ecog.03049.

Phillips, S.J., Dudík, M., Schapire, R.E. [Internet] Maxent software for modelling species niches and distributions (version 3.4.1). Available from url: http://biodiversityinformatics.amnh.org/open_source/maxent/. Accessed on 2019-9-5.

Pietrek, A. G., Escobar, J. M., Fasola, L., Roesler, I., Schiavini, A., 2017. Why invasive Patagonian beavers thrive in unlikely habitats: a demographic perspective. *Journal of Mammalogy*, 98(1):283–292.

R Core Team, 2015. R: a language and environment for statistical computing. R Foundation for Statistical Computing, Vienna, Austria.

Rosell, F., 2001. The function of scent marking in beaver (*Castor fiber*) territorial defence. Norwegian University of Science and Technology, Trondheim.

Rosell, F., Bjørkøyli, T., 2002. A test of the dear enemy phenomenon in the Eurasian beaver. Animal Behaviour, 63(6):1073–1078.

Rosell, F., Parker, H., 1995. Forvaltning av bever: dagens tilstand og fremtidig behov. (In Norwegian with an English summary: Beaver management: present practice and Norways future needs). Telemark University College. Bø i Telemark. Norway. pp. 52–55.

Rosell, F., Parker H., 1996. The beaver's (*Castor* spp.) role in forest ecology: a key species returns (in Norwegian with English summary). *Fauna,* 49:192–211.

Ruusila, V., Ermala, A., Hyvärinen, H., 2000. Costs of reproduction in introduced female Canadian beavers (*Castor canadensis*). *Journal of Zoology*, 252(1):79–82.

Ruys, T., Lorvelec, O., Marre, A., Bernez, I., 2011. River management and habitat characteristics of three sympatric aquatic rodents: common muskrat, coypu and European beaver. *European Journal of Wildlife Research*, 57(4):851–864. https://doi.org/10.1007/s10344-011-0497-y.

Shepard, D.B., Kuhns, A.R., Dreslik, M.J., Phillips, C.A., 2008. Roads as barriers to animal movement in fragmented landscapes. *Animal Conservation*, 11:288–296. https://doi:10.1111/j.1469-1795.2008.00183.x

Sjöberg, G., Belova, O., 2020. Beaver as a renewable resource. A beaver dam handbook for the Baltic Sea region. Interreg for Baltic Sea Region. WAMBAF. European Regional Development Fund.

Skewes, O., Gonzalez, F., Olave, R., Ávila, A., Vargas, V., Paulsen, P., König, H.E., 2006. Abundance and distribution of American beaver, *Castor canadensis* (Kuhl 1820), in Tierra del Fuego and Navarino islands, Chile. European Journal of Wildlife Research, 52(4):292–296.

Smith, D.W., Trauba, D.R., Anderson, R.K., Peterson, R.O., 1994. Black bear predation on beavers on an island in Lake Superior. *American Midland Naturalist*, 132:248–255.

Statistics Finland, 2018. www.stat.fi

Stephens, P.A., Sutherland, W.J., 1999. Consequences of the Allee effect for behaviour, ecology and conservation. *Trends in Ecology and Evolution*, 14(10):401–405. https://doi.org/10.1016/S0169-5347(99)01684-5

Suomen Riistakeskus, 2020. Hunting in Finland. https://riista.fi/wp-content/uploads/2020/08/suomi_-riistamaana_2020_eng.pdf

Svendsen, G.E., 1980. Population parameters and colony composition of beaver (*Castor canadensis*) in southeast Ohio. American Midland Naturalist, 104(1):47–56. https://doi.org/10.2307/2424957

SYKE, 12/2019. http://paikkatieto.ymparisto.fi/value

SYKE, 1/2020. https://www.syke.fi/fi-FI/Avoin_tieto/Paikkatietoaineistot/Ladattavat_paikkatietoaineistot

Tomppo, E., Haakana, M., Katila, M., Peräsaari, J., 2008. Multi-source national forest inventory – methods and applications. Managing Forest Ecosystems 18. Springer.

Trenham P.C., Koenig W.D., Shaffer H.B., 2001. Spatially autocorrelated demography and interpond dispersal in the salamander Ambystoma californiense. *Ecology*, 82:3519–3530.

Volterra, V., 1926. Variazioni e fluttuazioni del numero d'individui in specie animali conviventi. Memoria della Reale Accademia Nazionale dei Lincei, 2:31–113.

Wilsson, L., 1971. Observations and experiments on the ethology of the European beaver (Castor fiber L). *Viltrevy*, 8:115–266.

Wilson, R.J., Davies, Z.G., Thomas, C.D., 2009. Modelling the effect of habitat fragmentation on range expansion in a butterfly. Proceedings of the Royal Society B, 276:1421–1427. http://doi.org/10.1098/rspb.2008.0724

Ylitalo, E. (Ed.), 2013. Finnish Statistical Yearbook of Forestry 2013. Finnish Forest Research Institute, Vammalan Kirjapaino, Sastamala, Finland.

Żurowski, W., Kasperczyk, B., 1986. Characteristics of a European beaver population in the Suwałki Lakeland. *Acta Theriologica*, 31(24):311–325.

TURUN
YLIOPISTO
UNIVERSITY
OF TURKU

Painosalama, Turku, Finland 2021

ISBN 978-951-29-8544-9 (PRINT)
ISBN 978-951-29-8545-6 (PDF)
ISSN 0082-6979 (Print)
ISSN 2343-3183 (Online)