TURUN
YLIOPISTO
UNIVERSITY
OF TURKU

# THE RETURN OF THE WHITE-TAILED EAGLE

## Ecology of predator-prey relationships in the Baltic Sea and Arctic inland

Camilla Ekblad

TURUN YLIOPISTON JULKAISUJA – ANNALES UNIVERSITATIS TURKUENSIS
SARJA - SER. AII OSA - TOM. 391 | BIOLOGICA - GEOGRAPHICA - GEOLOGICA | TURKU 2022

TURUN YLIOPISTO
UNIVERSITY OF TURKU

# THE RETURN OF THE WHITE-TAILED EAGLE

## Ecology of predator-prey relationships in the Baltic Sea and Arctic inland

Camilla Ekblad

TURUN YLIOPISTON JULKAISUJA – ANNALES UNIVERSITATIS TURKUENSIS
SARJA – SER. AII OSA – TOM. 391 | BIOLOGICA – GEOGRAPHICA – GEOLOGICA | TURKU 2022

## University of Turku

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



## Supervised by

Professor Toni Laaksonen
Department of Biology
University of Turku, Finland

Professor emeritus Erkki Korpimäki
Department of Biology
University of Turku, Finland



## Reviewed by

Dr Rimgaudas Treinys
Laboratory of Avian Ecology
Nature Research Centre, Lithuania

Associate professor Johan Ekroos
Department of Agricultural Sciences
University of Helsinki, Finland



## Opponent

Dr Oliver Krone
Leibniz Institute for Zoo and Wildlife
Research,Germany



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

Cover photos: Olli Saksela (*adult eagle*), Olli-Pekka Karlin (*eaglets*), CE (*eiders*)

ISBN 978-951-29-9062-7 (PRINT)
ISBN 978-951-29-9063-4 (PDF)
ISSN 0082-6979 (Print)
ISSN 2343-3183 (Online)

Painosalama, Turku, Finland 2022

*To the Finnish white-tailed eagle working group*

UNIVERSITY OF TURKU
Faculty of Science
Department of Biology
Section of Ecology
CAMILLA EKBLAD: The return of the white-tailed eagle: Ecology of predator-prey relationships in the Baltic Sea and Arctic inland
Doctoral Dissertation, 120 pp.
Doctoral Programme in Biology, Geography and Geology (BGG)
November 2022

## ABSTRACT

Apex predators regulate ecosystems through top-down processes. In the last century many predator populations crashed due to anthropogenic impacts, but recently some have recovered and are re-colonizing old areas, as well as expanding to new suitable habitats. Rapid loss or return of apex predators can destabilize ecosystems and cause consequences for their prey species as well as for livestock. In the Baltic Sea area, the white-tailed eagle (*Haliaeetus albicilla*) was virtually absent due to persecution and pollutants during the mid-20th century. The rapid growth of the eagle population from the 1980s onward initiated by extensive conservation efforts has not only brought the species back from the brink of extinction, but also caused growing predation pressure on its prey species, in particular the common eider (*Somateria mollissima*), which is the major prey of the eagles in the Åland islands and especially in the outer archipelago. In Lapland in northern Finland, where husbandry of semi-domestic reindeer is a traditional livelihood, concerns are rising that the expanding white-tailed eagle population poses a threat to reindeer calves. As top predators, the white-tailed eagles are sensitive to bioaccumulating hazardous substances. Despite the decreased levels of pollutants, the Baltic Sea is still the world's most heavily polluted sea, while mercury levels in the major water bodies in Lapland, two artificial water reservoirs, are higher than in the Baltic.

For successful conservation of both the white-tailed eagle and its prey species research is needed regarding the diet of the eagles and the mechanisms shaping the diet. This system also provides an opportunity to study the predator-prey dynamics following the rapid return of an apex predator to a system from where it has been virtually absent. In this thesis I cover (i) the prey use and nesting habitat choice of white-tailed eagles nesting in the Finnish coast and Lapland, (ii) the connections between the prey use and the nesting habitat, (iii) the use of reindeer calves as prey, (iv) the association between nesting white-tailed eagles and the spatiotemporal population trends of the common eider, and (v) the consequences of prey use and nesting site choice on the mercury burden in white-tailed eagle nestlings in Lapland.

I found that the prey use of white-tailed eagles changed in time in the archipelago, and that it both in the archipelago and in the inland was influenced by the habitat in the nesting territories, which reflects the occurrence of prey species. In the inland, the white-tailed eagles preferred territories with higher proportions of lakes, peatbogs, and marshlands, which coincides with the higher occurrence of their preferred food source, fish. In the archipelago the main prey of the white-tailed eagles was common eider, which population in the Baltic has declined rapidly since a peak in 1997. The spatiotemporal changes in the core of the eider population distribution were influenced by the proximity of nesting white-tailed eagles. The eiders declined most in the outer archipelago and on unforested islands in the proximity of eagle nest. On the contrary, the population increased in the inner archipelago in areas with eagle nests. Finally, the prey use and nesting habitats influenced the eagles themselves. Elevated mercury burdens in white-tailed eagle nestlings in Lapland were linked with a diet on high trophic-level species and especially pike, the most important prey species in the area, as well as the proximity to a point source; the artificial reservoir of Porttipahta.

As flexible opportunists, the white-tailed eagles should not be food-deprived even though some prey species would decline. Likewise, the prey species should not be over-exploited, as the eagles use alternative prey species when a species decline. Population-level eagle-induced shifts has moved the core of the eider population towards safer nesting environments in the inner archipelago. However, the very rapid decrease of eiders calls for close monitoring and conservation efforts of the species. As top predators, the white-tailed eagles are prone to accumulation of pollutants and are as such excellent sentinel species for environmental pollution. However, consequently they are also vulnerable and thus, even though the population today is viable, a continuum of the thorough monitoring of the white-tailed eagles is important.

The ecosystem resilience is today severely challenged by anthropogenic impacts. Returning apex predators can improve the states of the ecosystems by e.g. preventing over-grazing, controlling the growth of prey populations and restricting invasive mesopredators. Successful co-existence with humans requires a general acceptance of the predators which only can be gained through cooperation and involvement of stakeholders and inhabitants that are affected by the matter.

KEYWORDS: Apex predator, Arctic, Baltic, Bird of prey, Breeding habitat, Conservation conflict, Mercury, Population dynamics, Prey use, Returning predator

TURUN YLIOPISTO
Matemaattis-luonnontieteellinen tiedekunta
Biologian laitos
Ekologia
CAMILLA EKBLAD: Merikotkan paluu: Peto-saalissuhteen ekologiaa Itämerellä ja Lapissa
Väitöskirja, 120 s
Biologian, maantieteen ja geologian tohtoriohjelma
marraskuu 2022

## TIIVISTELMÄ

Huippupedot säätelevät ekosysteemejä ylemmiltä trofiatasoilta alaspäin suuntautuvilla prosesseilla. Monien huippupetojen kannat romahtivat viime vuosisadalla ihmistoiminnan takia, mutta hiljattain joidenkin petojen kannat ovat elpyneet. Uudet yksilöt asettuvat usein samoille alueille, joilla laji alun perin esiintyi, mutta laajentavat myös asuinaluetta uusiin sopiviin elinympäristöihin. Huippupetojen äkillinen häviäminen tai paluu voi horjuttaa ekosysteemejä ja muutokset voivat aiheuttaa seurauksia sekä luontaisille saalislajeille että tuotantoeläimille. Merikotka (*Haliaeetus albicilla*) hävisi vainon ja ympäristömyrkkyjen takia lähes kokonaan Itämereltä 1900-luvun puoliväliin mennessä. Laajan suojelutyön tuloksena merikotkakanta elpyi ja kanta lähti nopeaan kasvuun 1980-luvulla, aiheuttaen samalla kasvavaa saalistuspainetta saalislajeille ja erityisesti haahkalle (*Somateria mollissima*), joka on merikotkan tärkein saalislaji Ahvenanmaalla, varsinkin ulkosaaristossa. Lapissa, jossa poronhoito on perinteinen elinkeino, merikotkakannan runsas kasvu on aiheuttanut huolta siitä, että merikotkat uhkaavat poronvasoja. Huippupetoina merikotkat itse ovat herkkiä elimistöön kertyville haitallisille aineille. Vaikka Itämeren myrkkypitoisuudet ovat laskeneet, Itämeri on edelleen maailman saastunein meri. Lapissa puolestaan elohopeatasot alueen suurimmissa vesistöissä, Porttipahdan ja Lokan tekoaltaissa, ovat korkeammat kuin Itämerellä.

Sekä merikotkan että sen saalislajien suojelun turvaamiseksi tarvitaan tutkimustietoa merikotkan ravinnosta ja sitä säätelevistä mekanismeista. Merikotkan paluu tarjoaa samalla ainutlaatuisen mahdollisuuden tutkia pedon ja saaliin välistä dynamiikkaa järjestelmässä, jossa peto palaa alueelle, josta se on käytännössä puuttunut usean vuosikymmenen ajan. Väitöskirjassani käsittelen (i) pesivien merikotkien saaliinkäyttöä ja pesimäympäristön maisemarakennetta Suomen rannikolla ja Lapissa, (ii) pesimäympäristön maisemarakenteen vaikutusta saalislajien esiintyvyyteen, (iii) poronvasojen esiintyvyyttä saaliissa, (iv) pesivien merikotkien yhteyttä haahkakannan paikallisiin ja ajallisiin muutoksiin, sekä (v) ravintolajien ja pesimäympäristön vaikutusta Lapin merikotkanpoikasten elohopeakuormitukseen.

Havaitsin, että merikotkien käyttämissä saalislajeissa oli ajallista vaihtelua Ahvenanmaalla, ja että eri saalislajien osuudet sekä saaristossa että sisämaassa olivat kytköksissä pesimäreviirien elinympäristöihin. Sisämaassa merikotkat suosivat reviirejä, joissa suurempi osuus kuin maisemassa keskimäärin koostui järvistä, kosteikoista ja avosoista. Merikotkat valitsivat näin ollen elinympäristöjä, joissa niiden ensisijaisen saaliin, kalan, saatavuus on paras. Saaristossa merikotkien tärkein

saalislaji oli haahka, jonka Itämeren kanta on laskenut voimakkaasti vuoden 1997 huippulukemista. Pesivien merikotkien läheisyydellä oli vaikutusta haahkakannan painopisteen ajalliseen ja paikalliseen muutokseen. Haahkamäärät vähenivät eniten ulkosaaristossa ja puuttomilla saarilla merikotkanpesien läheisyydessä. Sisäsaaristossa haahkakanta sen sijaan vahvistui alueilla, joilla pesi merikotkia. Saalislajeilla ja pesimäympäristön valinnalla oli vaikutusta myös itse merikotkiin. Saalislajien koostumus vaikutti Lapissa kuoriutuneiden merikotkanpoikasten kohonneisiin elohopeapitoisuuksiin. Korkeimmat pitoisuudet havaittiin poikasilla, joiden ravinto koostui korkean trofiatason saalislajeista, erityisesti alueen tärkeimmästä saalislajista hauesta. Toinen elohopeatasoja korottava tekijä oli pesän läheisyys paikalliseen kuormituslähteeseen, Porttipahdan tekoaltaaseen.

Joustavina opportunisteina merikotkat eivät kärsine ravinnonpuutteesta, vaikka joidenkin saalislajien populaatiot vähenisivätkin. Vastaavasti yksittäisiin saalislajeihin kohdistuva saalistuspaine ei kasvane ylisuureksi, koska merikotkat siirtyvät vaihtoehtoisiin saalislajeihin, jos jonkin lajin saatavuus vähenee. Haahkakannan painopiste on merikotkien vaikutuksesta siirtynyt sisäsaaristoon päin, eli pesimäympäristöihin, joissa saalistuspaine on matalampi. Haahkakannan nopea romahdus edellyttää kuitenkin kannan tarkkaa seurantaa ja suojelutoimenpiteitä. Huippupetoina merikotkat kerryttävät herkästi ympäristömyrkkyjä, ja soveltuvat täten erinomaisesti indikaattorilajeiksi ympäristömyrkkyjen seurantaan mutta ovat siksi myös haavoittuvia. Vaikka merikotkapopulaatio tällä hetkellä on elinkelpoinen, kannan huolellisen seurannan jatkaminen on tärkeää.

Elinympäristöjen sietokyky on nykyään vakavasti heikentynyt ihmistoiminnan takia. Huippupedot voivat palatessaan parantaa ekosysteemien tilaa mm. estämällä ylilaidunnusta, säätelemällä saaliskantojen kasvua ja rajoittamalla haitallisia vieraslajeja, varsinkin pienpetoja. Onnistunut rinnakkaiselo ihmisten kanssa edellyttää petoeläinten yleistä hyväksyntää, mikä on saavutettavissa vain yhteistyöllä ja osallistamalla petojen vaikutuspiirissä olevat sidosryhmät ja asukkaat.

# 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 **Ekblad, C.**, Sulkava, S., Stjernberg, T. & Laaksonen, T. 2016. Landscape-scale gradients and temporal changes in the prey species of the white-tailed eagle (*Haliaeetus albicilla*). *Annales Zoologici Fennici,* 53: 228–240.

II **Ekblad, C.**, Tikkanen, H., Sulkava, S. & Laaksonen, T. 2020. Diet and breeding habitat preferences of white-tailed eagles in a northern inland environment. *Polar Biology*, 43: 2071–2084.

III **Ekblad, C.**, Below, A., Lindén, A., Jaatinen, K., Lokki, H., Öst, M., Seimola, T., Tikkanen, H. & Laaksonen, T. Avoid your enemy: The return of an apex predator is associated with habitat shifts in a common but rapidly declining prey population. *Manuscript*.

IV **Ekblad, C.**, Eulaers, I., Schulz, R., Stjernberg, T., Søndergaard, J., Zubrod, J. & Laaksonen, T. 2021. Spatial and dietary sources of elevated mercury exposure in white-tailed eagle nestlings in an Arctic freshwater environment. *Environmental Pollution*, 290:117952.

# 1 Introduction

## 1.1 Recovery and expansion of apex predators

Apex predators are important regulators of ecosystems through top-down processes, where the predator regulates the population size of its prey species. During the last two centuries, populations of many large carnivores and raptors crashed because of human-induced persecution and habitat loss. Considered both competitors, a threat and 'cruel beings', they were widely and even legally persecuted (Pohja-Mykrä et al. 2012; Chapron et al. 2014). Moreover, large apex predators require large hunting areas and suffer from habitat loss and fragmentation caused by the spatial needs of the rapidly increasing human population (Chapron et al. 2014; Ripple et al. 2014). However, extensive conservation efforts and reintroduction projects have resulted in a recent recovery of some apex predator populations, including wolves in northern Europe and the US, and alligators and sea otters in the US, while the ban of problematic pesticides has contributed to the recovery of some birds of prey, such as ospreys (*Pandion haliaeetus*) and peregrine falcons (*Falco peregrinus*) (Ratcliffe 2003; Poole 2019). These apex predators are spreading back to areas where they once occurred, as well as into novel environments (Chapron et al. 2014; Ripple et al. 2014; Silliman et al. 2018). While beneficial for the biodiversity and functionality of the ecosystems, the return of apex predators might cause conflicts with humans because they are seen as competitors for resources, or as a threat to livestock (Nyhus 2016; Cammen et al. 2019; Salvatori et al. 2020). Furthermore, their return affects their prey species, which ultimately can cause conservation conflicts between the predator and the prey (Hipfner et al. 2012; Marshall et al. 2016).

### 1.1.1 Apex predators influence ecosystem dynamics

The sudden loss or arrival of a predator can have consequences for their prey species, destabilize the ecosystem and even cause a trophic cascade with effects through the entire food web (Terborgh and Estes 2010; Estes et al. 2011). The loss of an apex predator can lead to mesopredator release, which means that populations of smaller predators are able to increase, thus negatively affecting the number of smaller prey, such as rodents or passerines (Brashares et al. 2010). The removal of a carnivore might also release the predation pressure on its herbivore prey, which in turn causes increasing grazing pressure on the food plants of the herbivore. An extreme example of this comes from the eastern North Pacific Ocean coast, where former kelp forests transferred to barren grounds due to the removal of sea otters that had been regulating the sea urchins, which then were able to multiply and consume all the kelp (Estes et al. 2010). Moreover, trophic cascades seldom affect only a few species but have effects on multiple trophic levels and on many associated species through the ecosystem. Kelp forests form an important ecosystem providing living environment, food, and shelter for a variety of species ranging from algae to multiple invertebrate phyla as well as fish and even large mammals (Reed et al. 2016), and cascading effects on the next level were caused by the habitat loss of all these species using or inhabiting the kelp forests (Ripple et al. 2014).

Following the disappearance of apex predators, ecosystems can re-shape into alternative, predator-free states where a returning predator might encounter naïve prey individuals that have altered their behavior to match the predator-free environment (Berger et al. 2001; Bonnot et al. 2016). Appropriate antipredator responses can be lost in a prey population in just one generation (Blumstein et al. 2004; Kauffman et al. 2007), but can also rapidly be re-gained, provided that some individuals survive the encounter with the predator (Berger et al. 2001).

## 1.2 Feeding ecology in the context of territory characteristics

Foraging decisions are essential for the fitness, survival, and reproductive success of an animal. Classical optimal foraging theory predicts that an organism should prefer the most profitable prey when it is abundant, and switch to alternative prey when the availability of the preferred prey declines under a threshold (Stephens and Krebs 1986). Factors affecting the profitability of the prey include energy gain, availability and required searching effort, capture success and handling time but also toxicity avoidance and a varied and balanced intake of nutrients (Stephens and Krebs 1986; Sih 1993; Kohl et al. 2015). Concurrently, the organism is limited by its current condition and health as well as potential competitors or predators. The availability and profitability of a given prey can vary on a temporal scale ranging from the time of the day or different seasons to long-term temporal changes in the abundance of the prey (Sih 2011).

Predator avoidance is a crucial factor to consider while foraging, but for apex predators this is of lesser concern. Instead, the competition with conspecifics calls for individual territories. Defending a territory ensures access to suitable feeding grounds (Newton 1998). Subsequently, the choice of territory affects which prey is the most profitable, as the abundance and availability of prey differs in different habitats and areas (Sih 2011). Territories vary in quality, and especially for long-lived species with high site-fidelity, the territory choice can affect the life-long reproductive success of an individual. In addition to suitable feeding grounds, a good territory includes at least sufficient availability of food and a safe space for reproduction, in the case of raptors a convenient nesting place (Tapia and Zuberogoitia 2018). In dense or growing populations individuals may be forced to settle in suboptimal habitats.

## 1.3 Predator and prey population fluctuations in the Baltic Sea and Arctic inland

### 1.3.1 The return of the white-tailed eagle

Due to persecution and pollutants, the white-tailed eagle (*Haliaeetus albicilla*) was virtually absent from the Baltic Sea for decades during the 20th century. Extensive conservation efforts initiated by the new-formed white-tailed eagle working group of WWF Finland in the early 1970s led to an accelerating recovery of the eagle population, considered one of the greatest success stories in conservation history (Hildén and Hario 1993; Högmander et al. 2020). In 2019, the Finnish population exceeded 500 breeding pairs and its' status was set to least concern (LC) in the red list of Finland (Lehikoinen et al. 2019). The rapid growth of the eagle population from the 1980s onward however caused increasing predation pressure on its prey species, in particular the common eider (*Somateria mollissima*, hereafter eider) (Ekroos et al. 2012a; Öst et al. 2022), an abundant but rapidly decreasing waterfowl species. Recovering sea eagle (*Haliaeetus* sp.) populations have been shown to contribute to both local and wider scale declines in seabirds in both the US and Europe (Hipfner et al. 2012; Henson et al. 2019; Bregnballe et al. 2022).

In Lapland in northern inland Finland, the construction of two large artificial water reservoirs in the late 1960s created a novel suitable breeding habitat for white-tailed eagles. Historically, only a few nests were known in the area, but the reservoirs initiated a rapid colonization by white-tailed eagles. The population around the reservoirs is now, half a century later, quite dense and new recruits are settling also further away from the reservoirs. In Lapland, husbandry of semi-domestic reindeer is a traditional livelihood. The diet of the white-tailed eagles includes mammals and also reindeer calves (Sulkava et al. 1997), and concerns are rising that the growing white-tailed eagle population poses a threat to the reindeer calves.

### 1.3.2 Waterfowl in the Baltic Sea

Populations of seabirds and waders nesting in the Baltic have undergone substantial changes in the last century. The causes are multifaceted and, in many cases, unclear. Early information is scarce, but the waterbird populations in the early 20th century were considerably smaller than today due to hunting pressure and serious over-exploitation caused by the development of more efficient weapons by humans. The establishment of sanctuaries in the 1920s along with released hunting pressure resulted in increasing waterbird populations (Hildén and Hario 1993). The first population-wide peaks with subsequent declines thereafter were observed in the 1970s in e.g. the tufted duck (*Aythya fuligula*) and turnstone (*Arenaria interpres*), followed by peaks and decreases of several species in the 1990s (Pöysä et al. 2013; Below et al. 2019). Concurrently, many species have increased significantly and even recolonizing species such as the cormorant (*Phalacrocorax carbo*) have established viable breeding populations (Lehikoinen 2006). In general, large herbivorous species such as swans (*Cygnus* sp.) and geese (*Anser/Branta* sp.) are increasing, while smaller duck species feeding on e.g. invertebrates are decreasing (Elmberg et al. 2020; Holopainen et al. 2022). Declines have been attributed to e.g. eutrophication (Pöysä et al. 2013; Lehikoinen et al. 2016), climate change (Pavón-Jordán et al. 2019), environmental pollutants in the overwintering areas, reduced availability of landfills (Below et al. 2019) as well as increasing predation pressure by invasive mammalian and native avian predators (Brzeziński et al. 2020; Dahl and Åhlén 2019; Bregnballe et al. 2022; Jaatinen et al. 2022).

The eider is one of the most numerous waterfowl in the Baltic. The Finnish breeding population grew rapidly from the 1970s in a landscape that was almost free from predators. The population peaked in the mid-1990s, after which it experienced a rapid decline (Ekroos et al. 2012b). The decline started already a decade earlier in the eastern Gulf of Finland, while the population in the SW archipelago still was increasing (Desholm et al. 2002). The initial decline in the 1980s was attributed to pathogens in chicks and females (Hollmén et al. 2002) while the large-scale population crash has been addressed to thiamine deficiency (Balk et al. 2009; Mörner et al. 2017), reduced mussel stocks due to low nutrient levels in the wintering areas (Laursen and Møller 2014) and predation by the invasive mammalian predators mink and raccoon dog as well as the rapidly increasing white-tailed eagles (Jaatinen et al. 2022; Öst et al. 2022).

## 1.4 Herding of semi-domesticated reindeer

Reindeer herding is a traditional livelihood with important cultural and financial value for many people in Lapland, including the indigenous Sámi people (Jernsletten and Klokov 2002). The reindeer herding area comprise the northernmost third of Finland, where semi-domesticated reindeer (*Rangifer tarandus*) are allowed to graze freely. The area is divided into 54 reindeer-herding cooperatives and the maximum numbers of reindeer in each cooperative is regulated by the Ministry of Agriculture and Forestry of Finland (Reindeer Husbandry Act 848/1990). The cooperatives are separated by fences but within them the reindeer are migratory and utilize large areas that vary between seasons, depending on snow conditions, food availability and avoidance of disturbing insects (Kumpula et al. 2011). The total number of live reindeer in the entire area after the autumn roundups, where part of the animals are separated for slaughter, is about 200 000, with higher numbers in higher latitudes (Reindeer herder's association 2020).

## 1.5 Pollutants in the Baltic and Arctic

The Baltic Sea is a shallow brackish water basin with limited water exchange with the ocean, and as such prone to accumulate substances received from the catchment area. In the mid-20th century, it was found to be widely polluted by organochlorines, e.g. PCB and DDT, as well as heavy metals such as lead (Pb) and mercury (Hg)(Vallius 2014; Nyberg et al. 2015). These contaminants are bio-accumulating and magnifying through the food-web, hence having the potential to lead to high burdens in apex predators. The organochlorines cause eggshell thinning, which was the main reason for the poor reproductive success and population crash of the white-tailed eagles in the Baltic (Helander et al. 2002; Helander et al. 2008). DDT was banned and the use of PCB was restricted in the countries surrounding the Baltic Sea during the 1970s and since then, the levels of most of these pollutants have decreased considerably in the area. However, the levels of other persistent organic pollutants (POPs) such as per- and polyfluoroalkyl substances (PFAS) have increased, and even legacy pollutants can still cause problems (Sonne et al. 2020). In the Swedish coast of the Bothnian Sea, the levels of PCB and DDT along with other POPs in white-tailed eagle eggs are elevated compared to the rest of the Baltic Sea. This coincides with decreased productivity of the eagles nesting in this area (Bignert and Helander 2015; Hellström 2015).

Heavy metals can cause organ damage (Tchounwou et al. 2012) and lead poisoning due to ingestion of ammunition in carcasses or waterfowl is indeed the main and second most common cause of death in sub-adult and adult white-tailed eagles, respectively (Bignert and Helander 2015; Isomursu et al. 2018). Even non-lethal levels can be of concern. Accumulation of sublethal levels of Hg can lead to problems with reproduction, neurology, and immune responses (Dietz et al. 2019). Mercury is emitted to the atmosphere via both anthropogenic activities and natural processes, where it can be transported anywhere, also reaching pristine ecosystems in the Arctic (AMAP 2019). In aquatic environments, microbes methylate Hg to methyl mercury (MeHg), a toxic organic form that bioaccumulates in food webs (Jernelöv and Martin 1975; Lavoie et al. 2013; Paranjape and Hall 2017). Artificially flooded reservoirs provide excellent conditions for the process, causing high levels of MeHg especially in newly flooded reservoirs (Friedl and Wüest 2002; Hsu-Kim et al. 2018). Dietary factors associated with increased MeHg accumulation in animals involve high trophic position or aquatic origin of the prey (Lavoie et al. 2013; Ackerman et al. 2016). Mercury levels in white-tailed eagles in the Baltic are today at background levels (5 µg $g^{-1}$ in feathers) in Poland and at the Finnish coast, but still slightly elevated at the central Swedish Baltic Sea coast (Kalisinska 2014; Sun et al. 2019). Elevated levels have been measured also in nestlings in Lapland in northern inland Finland (Johansson 2019).

## 1.6 Aims of the thesis

Even though human-induced ecosystem changes tend to be negative, and we only are beginning to see the consequences of climate change and biodiversity loss, there are also encouraging cases of successful conservation actions. One of these is the recovery of some apex predator populations formerly on the brink of extinction. However, the rapid return of apex predators has consequences on their prey species. The aim of this thesis was to gain an in-depth understanding of factors affecting the prey use and predator-prey interactions of the rapidly increasing population of the white-tailed eagles in the Baltic and in the Arctic inland. This is crucial for successful conservation and management of both the predator and prey populations. In the first chapters (I, II), I examined the prey use of white-tailed eagles in the Finnish archipelago and northern inland as well as connections between the prey use and the nesting habitat of these birds. In the latter chapters (III, IV), I explored impacts of the predation on the main prey in the archipelago and consequences of the diet and habitat choice on the white-tailed eagles themselves.

To begin with, I performed a thorough examination of the prey use in the Åland Islands (I), a large archipelago in the middle of the Baltic Sea. Using an extensive dataset of identified prey remains collected at the nests during 25 years, I explored spatial differences and temporal changes in the prey use of eagle pairs nesting in different archipelago zones. In the following chapter (II), I focused on the diet of the white-tailed eagles nesting in a very different inland environment in northern Finland. In addition to the diet, I studied their territory habitat choice and explored how the habitat of the breeding territory affected the diet composition and occurrence of reindeer calves. In chapter III, I performed a large-scale assessment of the impact on the growing white-tailed eagle population on the distribution of its rapidly decreasing main prey along the Finnish coast, the eider. Here, I used extensive long-term monitoring data for both species. This system provides a unique opportunity to study the effect of a returning predator on its prey. In the last chapter (IV), I examined consequences of the prey use and nesting habitats of the white-tailed eagles by linking elevated mercury concentrations in nestlings in Lapland with the diet and territory characteristics.

# 2 Material and methods

## 2.1 Study species

The main study species of this thesis is the white-tailed eagle (I – IV), a large apex raptor closely associated with water (Ferguson-Lees and Christie 2001). It feeds solely on meat but is a generalist with a large spectrum of prey species, including both fish, birds and mammals (Sulkava et al. 1997). Sub-adult white-tailed eagles are highly mobile and fly widely around on areas covering thousands of square kilometres before they settle on a territory (Balotari-Chiebao et al. 2018). The white-tailed eagle matures at an age of about five years but does not necessarily settle until some years later. After settling, it however has high site-fidelity and defends a nesting territory, on which it has one or several nests (Cramp 1980). The one to two, seldom three, chicks hatch in mid to late April in southern Finland and in late May to early June in northern Finland. The core nesting areas in Finland are in the Åland islands, the

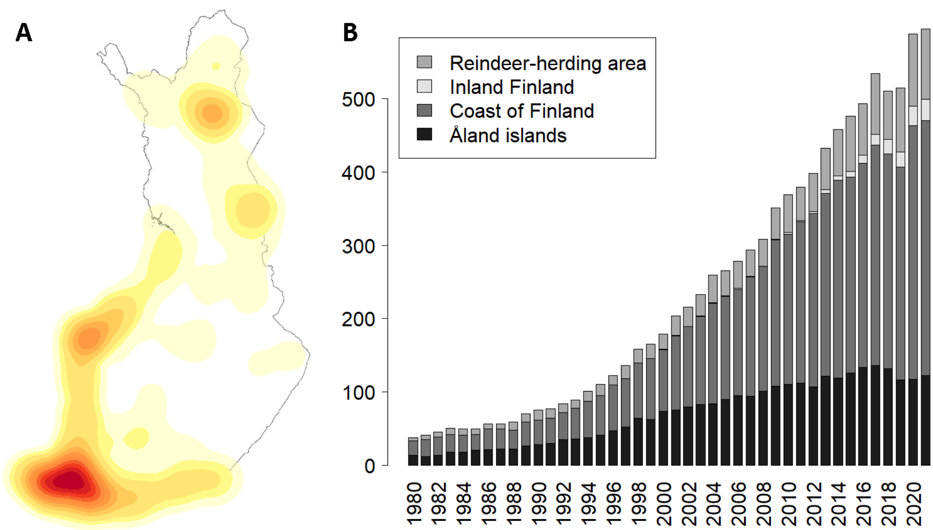


**Fig. 1**. A) The distribution of nesting white-tailed eagles in Finland. The heatmap shows territories that have been active at least once in the past five years (2017 – 2021). B) Number of occupied white-tailed eagle territories in Finland 1980 – 2021.

SW-archipelago and the Kvarken area, but the distribution covers the entire coast as well as Lapland and Kuusamo in the northern inland (Fig. 1). Recently, pairs have settled also in the southern inland.

The reindeer (II) is a medium-sized ungulate. The Semi-domesticated reindeer in Scandinavia originate from the subspecies mountain reindeer (*R. t. tarandus*) (Rankama and Ukkonen 2001; Røed et al. 2008). In most cooperatives, calving takes place on the spring pastures in the wild, but in some areas the reindeer are gathered into calving enclosures (Kumpula et al. 2011). The calves, one or occasionally two per female, are born in May-June and has a birthweight of 4-6 kg.

The eider (III) is a large diving duck and one of the main preys of white-tailed eagles in the archipelago. It winters in the Danish waters and nests on islands in the Finnish archipelago, mainly in areas where the salinity is at least 4.5 ‰, determining the boundaries for its main prey blue mussels (*Mytilus edulis*) (Westerbom et al. 2002). It nests on the ground, preferably behind vegetation that offers protection, or exposed in a crevice, where it relies on its protective color (Öst and Steele 2010). The eagle predation targets mainly incubating females (Lehikoinen et al. 2008; Ramula et al. 2018) and, after hatching, the chicks when the eider families gather on the water (Öst et al. 2003). The males gather offshore and leave to moulting areas when the ducklings hatch.

## 2.2 Study areas

The study area of this thesis covers the distribution of most of the breeding area of white-tailed eagles in Finland, except for the coast of the Bothnian bay north of the city of Kokkola and the southern inland. Chapters I and III consider the coastal population while chapters II and IV consider the population in northern inland Finland (Fig. 2).

The study in chapter I is conducted in the Åland islands, a large archipelago in the middle of the Bothnian bay spanning 13 300 km², of which 1550 km² is land. Of the land area, 70 % is situated on the main island. The remaining land consists of more than 27 000 smaller and larger islands (Lindqvist 2021). Approximately 25 % of the Finnish white-tailed eagle population nests in this area. The study area in chapter III includes the archipelago of the Finnish coast from the city of Virolahti at the eastern border to the city of Kokkola at latitude 63° 57' in the Bothnian bay, excluding the Åland islands. The distance between the cities along the waterway is approximately 800 km. The width of the archipelago varies. In the Gulf of Finland (S) and along the western coast (W) the distance from the outermost islands to the mainland is less than 20 km, while the width of the Kvarken archipelago (NW) is 47 km and the southwestern archipelago (SW) more than 80 km. There are approximately 55 000 islands with a size between 0.01 and 20 ha.


**Fig. 2**. Map of the study area. Names of waters are indicated with italics. The circle shows the Åland islands (I) and the archipelago at the Finnish coast considered in chapter III is situated in the square. The reindeer herding area in northern Finland (II, IV) is shown in a darker color.

In Chapters II and IV, the study area is situated in Lapland in inland Northern Finland. Chapter II considers the entire reindeer herding area of 123 000 km$^2$ where reindeer are allowed to graze freely, which in addition to Lapland includes an extension to the south covering the northern parts of North Ostrobothnia and Kainuu. Lakes and rivers constitute 6.7 % of the area. Other habitat types include low forests, peat bogs, and fells. In chapter IV only the part north of the Arctic circle is considered. The human settlement in the area is sparce. The largest water bodies are the two artificial reservoirs, Lokka and Porttipahta, flooded in 1967 and 1971, respectively (Hellsten et al. 1993).

## 2.3 Monitoring of white-tailed eagles

Since 1973, almost all known white-tailed eagle nests in Finland are surveyed yearly by volunteers from the Finnish white-tailed eagle working group, that until 2019 was affiliated with WWF Finland and thereafter with the Osprey Foundation.

The nation-wide survey is extensive and most of the territories at the coast and in Åland are known. The coverage in the inland and especially the northern part is not as comprehensive, due to the vast and mostly roadless areas. If the known nests are unoccupied, an effort is made to locate alternative nests, if possible. New nests are often found with public help. In Lapland, the surveys are first conducted by helicopter, after which successful nests are visited from the ground. In the last years helicopter surveys have been conducted also in Kainuu and in Åland. The nests are visited in May-June, when the breeding status is monitored, and nestlings are measured and ringed when possible. A breeding attempt is considered, if at least one of the nests has been decorated (Balotari-Chiebao et al. 2016; Högmander et al. 2020). Since 2003, three to five body feathers of each nestling have been plucked from the back to be used for DNA-analyses. In Lapland, the monitoring is coordinated by the governmental organization Metsähallitus since 1994. The data about the location of the white-tailed eagle nests and breeding status on a yearly basis in Finland is administered by the white-tailed eagle working group.

## 2.4 Collection and identification of prey remains

The diet of the white-tailed eagles (I, II, IV) was determined by prey remains collected at the nests. In Åland, prey remains from under almost all nests have been systematically collected from 1980 to 2015 during the nest visits. In Lapland, prey remains were systematically collected in 2017–2018 from a number of nests. Supplementary information in the form of thorough field notes about prey found in nests was available for 1993–2013 from Lapland. Identified prey remains of 7734 specimens collected from nests with successful breeding in Åland during 1985–2010 were used for spatial and temporal analyses (I), and 720 identified prey remains from 1993–2013 and 2017–2018 were used for spatial analyses (II) and as mercury sources (IV) in Lapland.

The prey remains were identified mainly by the late prof. emeritus Seppo Sulkava to the highest possible level; species, genus, or bird/fish/mammal sp. The identifications were supported by reference collections (osteological, feathers) as well as guide books (e.g. (März 1987) The number of individuals was determined by the 'minimum method' (Oehme 1975). In this method every remain of one species is considered to originate from one individual, unless there are multiple remains that cannot originate from the same individual, e.g. beaks, feathers with distinct sex colors or different sized jaws. The total number of individuals is considered to be the maximum number of remains that inevitably originates from different individuals. The Åland dataset was large enough to be analyzed on a yearly base in chapter I. The Lapland prey material was pooled on territory level in articles II and IV.

Prey data originating from remains does not allow for determining the absolute amount of different prey species in the diet of the white-tailed eagles. Diet studies based on prey remains tend to be biased towards species with large, hard bones while small species with soft bones might not be found (Sulkava et al. 1997). Fish, except for pike (*Esox Lucius*), might hence be underestimated. Furthermore, I used the number of prey items as units which gives somewhat different results than the mass of the prey species. However, the same method was used for all territories and areas, thus the biases are constant in space and time. Therefore, it is possible to make conclusions about differences in the diet in regards of areas, time, and territory characteristics.

## 2.5 Stable isotopes as proxies for diet

In chapter IV, stable isotopes were used in parallel with prey remains to assess the diet of the white-tailed eagles. Stable isotope ratios of carbon ($\delta^{13}$C) and nitrogen ($\delta^{15}$N) can be used to trace the diet of an animal, if measured from a body part or e.g. a feather. $\delta^{13}$C is used to evaluate whether the origin of the prey is marine, freshwater or terrestrial, while $\delta^{15}$N is an indicator for the trophic position of the prey (Peterson and Fry 1987; Boecklen et al. 2011). $^{15}$N accumulates in the food-web and higher ratios of the heavier isotope indicates a higher trophic position. $^{13}$C is quite straightforwardly depleted in the terrestrial food web and enriched in the marine. However, with lake ecosystems, $\delta^{13}$C ratios are often even more depleted than in terrestrial systems.

## 2.6 Spatial data

Spatial analyses were used as a part of the study in all four chapters, and I used several open spatial datasets available from different sources. I determined the center of a white-tailed eagle territory by the nest if the pair only had one nest, and by the mean coordinates of the nests, if the pair had multiple nests. In chapter I, I used the program MapInfo to calculate proportions of land and water from maps obtained from the National Land survey of Finland. Here, I used a radius of two km from the territory center. This does not include the entire hunting range of the eagles, but instead serves as a measure of the archipelago type where the eagles nest in the Åland islands. In chapters II and IV, I used the open-source CORINE 2012 landcover data with a resolution of 20 m x 20 m obtained from the Finnish Environment Institute (Härmä et al. 2013). I used R version 3.5.0 and Qgis version 3.2.2 to calculate the distance to the reservoirs of Porttipahta and Lokka and the proportions of six major landscape types (forest, sparse forest, open areas, peatbogs, marshlands and lakes), within a 10 km radius of the territory center of the eagles, which more or less covers the actual hunting grounds of the eagles (Krone and Treu 2018).

In chapter III, I used Qgis ver 3.12 to calculate a variety of geographical constrains for islands in the Finnish archipelago, on which eiders have been counted. I used a map obtained from the National land survey of Finland to calculate the island's area, longitude, latitude, yearly distance to the closest occupied white-tailed eagle nest and proportion land within a radius of 5 km for the islands (hereafter land ratio, not to be confused with the land proportion in white-tailed eagle territories). The dataset used to calculate forest cover data was obtained from the Natural Resources Institute Finland. I created a three-level variable for the proximity of an occupied white-tailed eagle nest in the previous year with the levels 'nests within a radius of 2 km from the island', 'nests within 2–10 km from the island' or 'no nests within 10 km'.

## 2.7 Eider surveillance data

Eider occurrence in the Finnish archipelago is monitored through the archipelago bird censuses in Finland, initiated in 1984. The number of breeding eider pairs is estimated at counts following published guidelines (Koskimies and Väisänen 1991), coordinated by the governmental organization Metsähallitus and the Finnish Environment institute, from where I obtained the eider count data used in chapter III. The monitoring frequency varies in different areas, islands and years due to the large area and resource-intensive work required. This monitoring data was extended with data series obtained from municipalities, associations, and private persons. The final dataset on surveyed islands consisted of 18191 island-counts from 3648 islands during the time-period 1997–2020.

## 2.8 Laboratory work: Feather preparation and analyses of stable isotopes and mercury

Of the feathers sampled for DNA-analyses from nestlings in Lapland, I received permission to use one of each nestling for Hg- and stable isotope analysis (chapter IV). Feathers were available from 85 nestlings spanning the years 2007–2018. The collected feathers had been transported from the nests and stored in paper envelopes in -24°C. I performed the Hg analyses at the accredited trace element laboratory of the Department of Bioscience at Aarhus University in Denmark. The feathers were washed with distilled water, covered with analytical-grade laboratory paper and left to dry overnight in a controlled laboratory environment. The dry feathers were cut in 1 mm pieces with scissors, and the calamus was removed.

A subsample of the homogenized feather (1.5–10.9 mg) was used to analyse the total Hg content (μg $g^{-1}$, dw) with a Milestone DMA-80 Direct Hg Analyzer (Sorisole, Italy) following the U. S. EPA Method 7473 (EPA 1998). To verify the analytical quality, blanks, duplicates (1:10), aqueous standards and the Certified Reference Material (CRM) DORM-4 were analyzed concurrently. All samples as well as CRMs were corrected in accordance with these.

The stable isotope analyses for carbon ($\delta^{13}C$) and nitrogen ($\delta^{15}N$) were performed at the Stable Isotope Lab of the University of Koblenz-Landau in Germany. A subsample of each homogenized feather (mean, sd 1.48 ± 0.06) was used to determine ratios of carbon ($^{13}C$:$^{12}C$) and nitrogen ($^{15}N$:$^{14}N$) in the feather with a Flash 2000 HT elemental analyser coupled via a ConFlo IV interface to a Delta V Advantage isotope ratio mass spectrometer (Thermo Fisher Scientific, Bremen, Germany).

## 2.9. Statistical methods

I used general linear (GLM) and generalized linear mixed models (GLMM) to investigate spatial and temporal trends in the proportions of different prey types in the diet of the white-tailed eagles (I), nesting habitat choice of white-tailed eagles and the connection between the nesting habitat and prey use (II), the effect of white-tailed eagles on population-scale distribution shifts in breeding eiders (III), and dietary factors and territory characteristics affecting elevated Hg levels in white-tailed eagle nestlings (IV).

In chapter I, I used a binomial GLMM to investigate whether the proportion of different target prey species in the diet of a white-tailed eagle pair was affected by the land proportion in the nesting territory, if there were any temporal trends among the prey use, and using an interaction term, if the possible trends were consistent or differed in different parts of the archipelago. Territory ID and year as a categorical variable were included as random effects to control for repeated sampling from the same territories and possible correlations within years.

To determine if the white-tailed eagles nesting in the northern inland in the reindeer herding area showed a preference for some habitat types (II), I assigned random points (n= territories x 2) in the area. I used a binomial GLM to test whether the proportion of six major habitat types differed between real and random territories. Thereafter, I used a binomial GLM to test if the proportion of some target prey groups and species were affected by the territory habitats. Latitude was included in the models to test for possible geographical gradients.

In chapter III, I used a GLMM with Poisson distribution to explore spatiotemporal factors affecting the number of eiders breeding on islands at the Finnish coast, and whether the numbers were affected by the proximity of breeding white-tailed eagles. The general model included the island's size, an interaction between latitude, longitude and year, land ratio within 5 km radius as a proxy of archipelago type, and forest cover. I then formulated 12 hypotheses testing different variations of the model, i) without additional spatiotemporal interactions, ii) with temporal effects on archipelago type, iii) with temporal effects on land cover and iv) with temporal effects of both, a) without eagle effect, b) with eagle effect and c) with a temporal eagle effect. To control for the differing monitoring frequencies of the islands and to avoid pseudo-replication, island ID and year as a categorical variable were included as random effects in all models along with a parameter accounting for the spatial autocorrelation of the observations. The best model was selected by AIC (Burnham and Anderson 2002).

The connections between Hg concentrations in white-tailed eagle nestlings in Lapland and dietary sources, nesting habitat and geographical constraints (IV) was explored by a set of GLMMs, where i) dietary variables, ii) long-range transport, iii) territory habitat, iv) point sources and v) a combination of all non-correlated factors were considered. The model(s) best explaining the differences was selected by AIC (Burnham and Anderson 2002). To control for repeated sampling from some territories and possible differences between years, territory ID and year as categorical variable were added as random factors in the models.

All statistical analyses were performed by program R (R core Team 2020).

# 3 Results and Discussion

## 3.1 Spatial and temporal trends in the diet of white-tailed eagles in Finland (I, II)

In the archipelago of Åland, remains of 99 different prey species were identified. The main prey was common eiders (21,4 %) and pike (11,9 %). An additional 17 species could be considered common as they constituted more than 1 % of the prey. In Lapland in northern inland Finland, the number of prey species was 47 and the main prey was pike (49,8 %). Of all prey species, 34 species (27 birds, 4 fish) were eaten in both areas, while 65 species (39 birds, 14 fish) were found only in the Åland material and 13 (11 birds, 2 fish) only in Lapland. The diet in Åland consisted of 69,6 % birds, 27,3 % fish and 3,1 % mammals. In Lapland, fish was the main prey group constituting 64,3 % of the diet, while the proportion of birds was 28,5 % and of mammals 7,2 %. The proportion of reindeer calves was 3.1 %.

### 3.1.1 The connection between breeding territory habitat and prey use

In the archipelago (I), the location of the territory affected the prey use of the white-tailed eagle pairs. The archipelago type was proxied by the proportion land within 2 km from the nest (or the center of multiple nests), where higher land cover indicates inner archipelago and lower land cover outer archipelago. The proportion of fish increased with the increasing proportion of land cover, being close to zero in the outermost archipelago but constituting almost half of the diet in the inner archipelago. Consequently, the proportion of birds was highest in the outer archipelago and decreased towards the inner archipelago (Fig. 3a). Of 11 bird prey groups, 10 increased in the outer archipelago (including eider, velvet scooter (*Melanitta fusca*), cormorants, mergansers (*Mergus* sp.), and gulls and terns (*Larus* sp., *Sterna* sp.)) while only one, coot (*Fulica atra*), increased towards the inner archipelago. No fish species increased towards the outer archipelago.

In the northern inland environment in Lapland (II), the prey use of the white-tailed eagles was affected by the habitat types in the hunting territory, which was determined by the proportions of six major habitat types within 10 km radius from the nest (or the center of multiple nests). As could be expected, the proportion of fish increased when there was more lake area in the territory (Fig 3b), but an increasing proportion of marshland actually had an even stronger positive effect on the proportion fish, especially pike, in the diet. The marshlands are suitable spawning places for pike and make eligible hunting grounds for white-tailed eagles. The proportion of birds in the diet, in particular grouse (Tetraonidae spp.), in the diet increased when the proportion of sparse forest in the territory increased. In a single bird species, cranes (*Grus grus*), the proportion in the white-tailed eagle diet increased with increasing proportions of peatbog. Furthermore, the proportion of birds increased, and the proportion of fish decreased towards north. The proportion of reindeer calves in the diet was not associated with any habitat type but increased towards north.

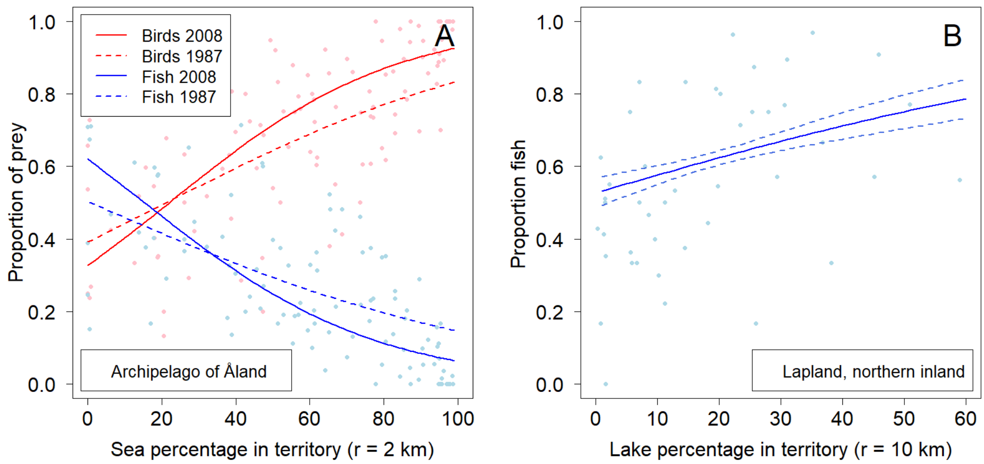


**Fig. 3**. Connections between the territory habitat and diet of white-tailed eagles (I, II). In both graphs, the x-axis shows the proportion of water (sea or lake) in the territory. The land proportion is highest to the left (0) and decreases to the right. A) In the archipelago, the proportion of birds (red) increased and fish (blue) decreased towards the outer archipelago (proxied by proportion of land within a radius of 2 km from the nest, here shown as the reverse sea proportion for comparability reasons). Furthermore, during the time period 1985–2010, the proportion of birds increased overall and especially in the outer archipelago, while the proportion of fish decreased except for in the inner archipelago. The dotted lines show the estimates in the beginning of the time period, and the solid lines the estimates in the end of the time period. B) In the northern inland, the proportion of fish in the diet increased with increasing proportions of lakes in the territory (within a radius of 10 km). The solid line shows the estimated proportion of fish in a territory, along with standard errors (dotted lines).

### 3.1.2 Temporal trends in Åland (I)

During the time period 1985–2010, the overall proportion of birds in the diet increased and the proportion fish decreased (Fig. 3a). On a spatiotemporal scale, the proportion of birds increased in time in the outer and middle archipelago but decreased in the innermost archipelago, while the situation for the fish was reverse, with a decrease in time in the outer and middle archipelago but an increase in the inner archipelago. On species level, the proportion of cormorants, swans, goldeneyes (*Bucephala clangula*) and gulls increased temporally while velvet scooters and mergansers decreased. Regarding fish, pike and perch (*Perca fluviatilis*) decreased but bream (*Abramis brama*) increased.

### 3.1.3 Dietary conclusions

The detailed examination of the diet of white-tailed eagles strengthens the picture of the white-tailed eagle as an opportunistic hunter, foraging on the prey that is available in the surroundings of the nest. The energetically most efficient hunting method for the eagles is perching (Nadjafzadeh et al. 2016), which is a suitable method for catching fish in shallow waters. White-tailed eagles do not catch fish deeper than 50 cm under the surface (Helander 1983) and as shallow waters are scarce in the outer archipelago, the eagles nesting there have to rely on a waterfowl-based diet. On the other hand, fish is the most profitable prey for white-tailed eagles in inland Germany (Nadjafzadeh et al. 2013) which is consistent with our findings that the white-tailed eagles in the inland environment of Lapland as well as the innermost archipelago of Åland, with highest land cover, have a fish-dominated diet. The same gradient from inner to outer archipelago was also observed by Helander (1983), while the fish-dominated diet in inland areas with more lakes is consistent with later findings from Lithuania (Dementavičius et al. 2020). Hence, in inlands, white-tailed eagles eat more fish in areas where lakes are abundant, but in the archipelago environment the pattern is different, as fish availability is better in the inner archipelago containing suitable shallow fishing waters (Fig. 3).

Furthermore, I showed that in areas with other terrestrial habitat types the white-tailed eagles used prey species associated explicitly with the particular habitats. White-tailed eagles do not hunt in closed forests but can hunt in forests with low canopy cover, where grouse is abundant. Open peat bogs are very abundant in Lapland and suitable hunting grounds for eagles, where they utilize cranes, that breed on peat bogs. To my knowledge, this is the first time prey utilization in different terrestrial habitats have been assessed for white-tailed eagles.

Waterfowl time-series from Åland are scarce, but the temporal trends detected in the eagle prey material in Åland corresponds with the waterfowl time-trends at the Finnish coast. The two bird species with the highest proportional temporal increase in the prey was swans, which population is increasing, and the recolonizing cormorants. The effect of eutrophication can also be seen in the prey use, as eagles nesting namely in the inner archipelago are including increasing amounts of cyprinid fishes in their diet. Cyprinid biomass grows in eutrophicated waters and cyprinid fish has increased with time in the Baltic, especially in Åland (Ådjers et al. 2006; Bergström et al. 2016). The most significant decline in the diet occurred in the important prey species pike, which is declining in the Baltic (Lehtonen et al. 2009).

Hence, white-tailed eagles should not be food deprived even if the populations of some prey species decline, as they are flexible and use the prey that is available in space and time, as later concluded also by (Dementavičius et al. 2020). Correspondingly, if the number of any prey species falls so low that they are not profitable prey for the white-tailed eagles, they should switch to more abundant prey. The results also indicate, that breeding white-tailed eagles do not seek reindeer calves in any particular habitat, but rather exploit them if they are available and encountered.

A majority of all raptor species are generalists, utilizing tens to hundreds of prey species (Bildstein 2017). Habitat-dependent differences in the diet of individuals of generalist raptors have been found also for e.g. harriers (*Circus* sp.) (Amar et al. 2004; Terraube et al. 2014) and owls (*Bubo bubo, Tyto alba*) (Frey et al. 2011; Shin et al. 2013). Large-scale spatial and temporal changes in prey use of eagle owls were demonstrated in Slovakia, where human-induced habitat changes resulted in both a turnover in the available prey species as well as dispersal to less suitable habitats by the owls (Obuch 2021). The white-tailed eagles are restricted to vertebrate prey, but use a very broad spectrum of prey species of fish, birds and mammals. Their ability to exploit a wide range of habitats and prey species makes them resilient to annual fluctuations in prey populations unlike e.g. the sympatric golden eagle (*Aquila chrysaetos*), which diet mainly consists of grouse (Tetraonidae sp.) and mountain hare (*Lepus timidus*) (Sulkava et al. 1998; Johnsen et al. 2007), thus possibly suffering from food shortage in years with low prey numbers. This could explain why the white-tailed eagle population in Finland is growing, but the golden eagle population, that here lives at the northern edge of its distribution and hence has lower breeding success (Schweiger et al. 2015), is not.

## 3.2 Territory habitat choice (II)

The white-tailed eagles in the Lapland inland preferred to breed in territories containing larger proportions of lakes, peat bogs and marshlands than the proportional availability in the area. The preference for aquatic habitats in the territory was expected and has earlier been documented in Croatia (Radović and Mikuska 2009) and Lithuania, where also a preference for wetlands was detected (Treinys et al. 2016). In Finland, peat bogs are a preferred habitat also for subadult white-tailed eagles (Tikkanen et al. 2018). As the territory habitat for birds with high site-fidelity defines which prey will be available, the territory choice has consequences for the whole productional lifespan of the individual. The habitat preferences of the eagles coincide with the habitat types associated with higher proportions of fish, indicating that the eagles seek nesting places with good availability of fishing grounds. Peat bogs provide suitable open and prey-rich hunting habitats for the eagles. The population in the surroundings of the largest water bodies is dense and quite saturated, which may be why territories are emerging also in other areas with alternative habitats, potentially forcing the eagles to prey on less preferred prey.

## 3.3 Relationships between eagle occupancy and prey population development (III)

The eider is the main prey of the white-tailed eagles in the Åland islands (I) and the southwestern archipelago of Finland (unpublished own data). In chapter III, I explored the effects of the returning white-tailed eagle on the eider population since its peak in 1997. Of the 12 hypotheses, the most complex one was the best according to AIC: number of eiders breeding on an island ~ time*latitude*longitude + land ratio within 5 km* time*white-tailed eagle occurrence + forest cover*time* white-tailed eagle occurrence.

The results showed that the temporal change in eider numbers was different depending on the archipelago type and the proximity to white-tailed eagle nests (Fig. 4). In the beginning of the period the highest eider numbers were found in the outer archipelago, within 2 km from eagle nests. During the time period 1997–2020 the eiders declined in the outer archipelago, most on islands close to eagle nests. In the end of the period, the highest eider numbers in the outer archipelago were found on islands > 10 km from eagles. In the inner archipelago, contrary, the eider numbers increased in time on islands in the vicinity of eagle nests. On islands with no or little forest cover, the eiders declined more in the vicinity of white-tailed eagles (< 2 km) than further from the white-tailed eagle nest, while on islands with high forest cover there was less decline in general and no apparent association with white-tailed eagle nest proximity. General spatiotemporal trends showed that the temporal decrease in eider numbers was most severe in the core areas in the southwestern archipelago. In the Gulf of Bothnia in northwest the eider numbers are generally low, and there the decrease was more modest. The eider numbers in the eastern part of the Gulf of Finland on the other hand showed a small temporal increase. This might be because the area is densely populated, and humans are shown to have frightening effect on white-tailed eagles (Tikkanen et al. 2018; Balotari-Chiebao et al. 2021), while the eiders have learned to use humans as protective umbrella species (Fox et al. 2015). Furthermore, the number of white-tailed eagle territories is lower in the eastern Gulf of Finland.

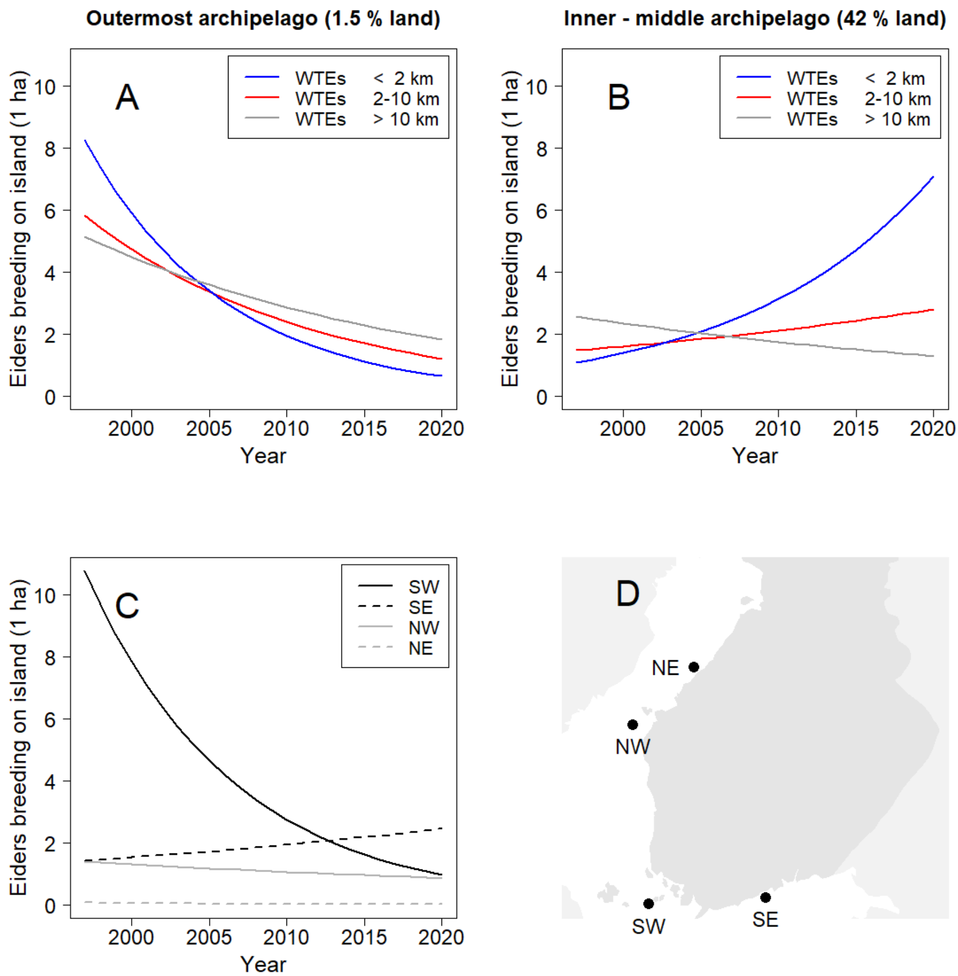


**Fig. 4**. Modelled spatiotemporal changes in numbers of eiders breeding on islands of 1 ha along the Finnish coast. Panels A and B show temporal changes of estimated eider numbers in different archipelago zones (proxied by the land ratio in a 5 km buffer around each island) and with regards to the proximity to white-tailed eagle (WTE) nests. A) estimates for the outermost archipelago (1.5 % land; 10 % percentile) and B) for the inner-middle archipelago (42 % land; 90 % percentile). C) General spatiotemporal trends modelled for four regions at the Finnish coast, shown on the map in panel D. Here, land ratio and forest cover were set to their medians and eagle occurrence to 2–10 km.

During the time period 1997–2020, the core of the eider population has shifted from the breeding grounds in the outer archipelago towards the inner archipelago, and our results indicate that the presence of territorial white-tailed eagles contributed to this shift. In the absence of eagles, the eiders could exploit the barren, distant islands that were safest in regards of mammalian predators, but where they were exposed to the eagles when they returned. The eider is a long-lived species with high site-fidelity, that seldom changes nesting island (Öst et al. 2011), while new recruits are less site-faithful to their natal islands (Öst et al. 2005; Kurvinen et al. 2016). Hence, the eiders likely disappeared from the outer archipelago because they were depredated or stopped to breed, while the shift of the core of the population towards the inner archipelago probably was induced by new recruits successfully settling in less exposed islands. Besides the protective attributes of the more sheltered inner archipelago, it provides more profitable prey for the white-tailed eagles, that feeds predominantly on fish in the inner archipelago (I). However, mammalian predators pose a threat in this environment and the removal of invasive alien predators is crucial for eider conservation (Jaatinen et al. 2022).

Nest-site selection is influenced by predation risk (Lima 1998) and avoidance of nesting close to raptor nests has been documented for several land bird species (Lima 2009; Møller et al. 2017) but rarely for waterbirds. Displacement of nesting sites following the re-colonisation of an apex avian predator, the eagle owl, has in Germany been found also for the northern goshawk (*Accipiter gentilis*), an intraguild mesopredator (Chakarov and Krüger 2010; Mueller et al. 2016). The predator presence can furthermore, even years after it has disappeared, influence the distribution of both its prey, that avoids nesting close to the predator nest, and the distribution of smaller species, that seek the proximity of large raptor nests because their frightening effect on the subordinate predators (Burgas et al. 2021).

## 3.4 Consequences of the nesting environment and diet on white-tailed eagle nestlings (IV)

In chapters I-II, I showed that the choice of nesting territory affects the prey use of the white-tailed eagles. Hence, possible anthropogenic effects on some prey types or in certain areas could affect the nesting and foraging eagles. I examined mercury levels in feathers of white-tailed eagle nestlings hatched in Lapland and found them to be elevated, with a geometric mean of 11.48 $\mu g\ g^{-1}$ (4.97 $\mu g\ g^{-1}$–31.02 $\mu g\ g^{-1}$ dw). This exceeds the considered background level of 5 $\mu g\ g^{-1}$ (Scheuhammer 1991), but is below the proposed threshold for adverse health effects, 40 $\mu g\ g^{-1}$ (Sun et al. 2019). The main drivers for the elevated levels were the trophic position of the prey as proxied by $\delta^{15}N$, the proportion of pike in the diet, and the proximity to the Porttipahta reservoir (Fig. 5).

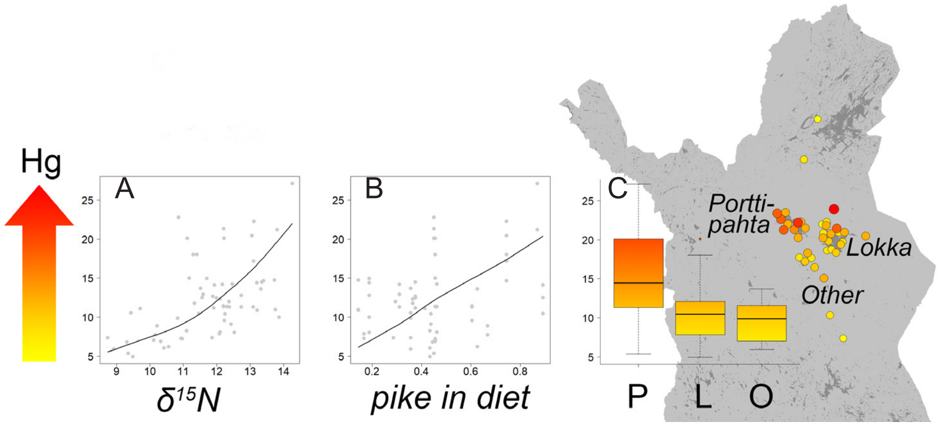


**Fig. 5**. Factors affecting the Hg burden of white-tailed eagle nestlings in Lapland. Elevated Hg levels are linked with A) a diet on high trophic level species (as proxied by $\delta^{15}N$), B) a pike-rich diet and C) the proximity to the Porttipahta reservoir. Figure from Ekblad et al. 2021, Environmental Pollution.

As expected, because of the bioaccumulating attribute of Hg, a diet consisting of higher trophic level species was the major contributor to elevated Hg burdens in the nestlings. This is consistent with a study of Bonelli's eagles in Spain, where multiple contamination pathways were compared (Badry et al. 2019). Pike is a long-lived, predatory fish with the potential to accumulate high amounts of Hg (Pierce 2012). The Porttipahta reservoir has historically had higher Hg burdens than Lokka. As the reservoirs were flooded already 50 years ago, the levels have decreased and are officially not considered elevated anymore. My results however show that the levels in Porttipahta still are elevated, especially in long-lived high-trophic-level predatory fish, affecting the fish-eating apex predators such as the white-tailed eagles in the terrestrial food web. I showed that elevated Hg levels in biota can depend on multiple factors, and that it is important to consider several simultaneous aspects when assessing Hg exposure to wildlife. Furthermore, I identified a potential evolutionary trap, as white-tailed eagles that consume large amounts of their preferred prey, pike, accumulate the highest Hg burdens.

# 4 Conclusions

The return of apex predators affects the densities of their prey, which can create conflicts and challenges for the conservation of both the predator and prey populations, as well as for livestock. In this thesis, I examined different aspects of the prey use of a rapidly returning population of an apex predator, the white-tailed eagle, that was practically missing from the Baltic Sea for several decades. Although in Finland traditionally an inhabitant of the seacoast, an expanding population of the eagles has settled also in northern inland Finland, where herding of semi-domesticated reindeer is a traditional livelihood. This thesis covers the landscape-scale prey use of nesting white-tailed eagles in the Åland islands archipelago and its temporal changes during 25 years (I), the prey use and territory habitat choice of the Lapland population as well as the connection between the diet and nesting habitats (II), consequences of the expanding population on the population-level distribution of the main prey in the Baltic, the common eider (III) and consequences of the diet and hatching location on the mercury burden on the eaglets (IV). The research builds on material collected over a time span of up to four decades by countless volunteers.

The thorough diet studies (I, II) showed that the white-tailed eagle is an opportunistic forager capable of utilizing a variety of prey species including birds, fish and mammals. The diet varies with the nesting environment and the eagles make use of prey species that occur in the territory, and switch to other prey when the availability changes. An example of this was the shift of main prey in the Åland Islands (I) from pike to eider in the late 1980s, probably due to decreasing pike stocks, growing abundance of eiders and a shift of the expanding white-tailed eagle population towards the outer archipelago, where fishing grounds are scarce. The opportunistic and flexible prey use of the white-tailed eagle indicate that the species will not become food deprived, even though the number of certain prey species would decline.

In the arctic inland environment, the white-tailed eagles preferred to nest in territories with large proportions of lakes, peat bogs and marshlands (II). The prey use in the territories reflected the species occurring in the habitat, and the habitats preferred by the eagles were mainly the ones where their preferred prey occurred. The habitat preference information can be used to predict to which areas the eagle population is expanding, and what kind of prey composition pairs in different habitats are expected to use. The results indicated that the nesting white-tailed eagles did not explicitly seek for reindeer calves in any habitat, but rather exploited these if encountered. Further, the proportion of reindeer calves in the diet was small. Nesting white-tailed eagles should hence not pose a threat to the traditional reindeer herding. However, the role of sub-adult and adult non-breeders would require additional research.

In the Baltic Sea, the populations of some waterfowl, especially the common eider, have declined drastically during the past decades. The eider is the main prey of the white-tailed eagles in the Åland Islands (I), and the growing white-tailed eagle population is proposed to be one of the reasons for the decline. I demonstrated that population-wide breeding distribution shifts of the highly philopatric eiders at the Finnish coast were associated with the proximity of nesting white-tailed eagles (III). The number of eiders decreased steepest in the outer archipelago in the vicinity of eagle nests, probably due to excess-mortality on exposed islands, while eider numbers in the inner archipelago were positively correlated with the presence of eagle nests. In the inner archipelago the predation pressure by white-tailed eagles is lower, but instead the predation risk by invasive alien mammalian predators is higher. I showed that a returning predator can affect the distribution of its prey in different ways in different habitats, and the potentially different outcomes and needs are important to consider when planning large-scale conservation measures for prey species.

The diet and feeding grounds can affect the pollutant burden of predators, and white-tailed eagles are excellent sentinel species for bioaccumulating hazardous substances in ecosystems (Helander et al. 2008). I showed that elevated mercury levels in white-tailed eagle nestlings in Lapland were associated with a diet on high trophic level prey, especially pike, and the proximity of a point source, the artificial reservoir of Porttipahta (IV). The study highlights the importance of considering multiple potential pathways when examining mercury exposure as well as the importance of thorough long-term monitoring of Hg in artificial reservoirs with an emphasis to include also larger and older fish specimens. Hg levels can still be elevated decades after the flooding and even low levels can accumulate to considerable burdens in long food webs involving long-lived species. No eaglets in this study had Hg burdens exceeding the proposed health effect levels and no fitness effects were measured, but elevated levels in the biota are however important to be aware of and follow up if needed. Also, the study concerned eaglets, and as Hg is bioaccumulating the levels in these birds might be even higher when they reach adulthood. Furthermore, it is of some concern that the elevated Hg burdens were tied to increased consumption of the preferred prey, pike, which could be an evolutionary trap.

In the past half century, the white-tailed eagle population has gone from critically endangered and almost extinct in Finland to viable and finally labelled least concern (LC) in the red list of 2019 (Lehikoinen et al. 2019). In 2021, its population in Finland had reached almost 600 breeding pairs. This thesis covers only the effects of nesting white-tailed eagles, but in addition to them the sub-adult floaters are affecting the prey populations, in many cases probably in an even higher degree than the adults, and their role should be targeted in subsequent research. The exact number of floaters is impossible to estimate, but calculated based on vital population parameters (breeding pairs, mean offspring production, survival, and population growth rate), it could be of the order of 2000-3000. With the current status and growth rate of the population it would be important to limit any artificially boosted over-survival of subadult WTEs by minimising subsidies in the winter, such as discarded hunting remains. However, continued thorough monitoring of this indicator species of the state of the Baltic (HELCOM) is needed. Although the eagle population now exceeds the threshold population size for LC, 500 pairs, even small fluctuations might reverse the development of the population.

The resilience of today's ecosystems is severely challenged by anthropogenic impacts in the form of habitat loss, climate change, pollutants, and invasive alien species. Apex predators are important regulators of ecosystems, but in the unstable ecosystems their return or loss might lead to unexpected fluctuating outcomes and trophic cascades. At the same time, they can act as sentinel species, alerting for rising pollutant levels or other disturbances in the ecosystems (Helander et al. 2008; Hazen et al. 2019), prevent over-grazing (Ripple et al. 2001; Estes et al. 2011) and suppress the distribution of invasive mesopredators (Cunningham et al. 2020; Selonen et al. 2022). Involvement of the local human stakeholders and inhabitants is essential for the successful co-existence between humans and apex predators (O'Rourke 2014). Thorough monitoring of species and ecosystems at all trophic levels is crucial to ensure the conservation of both the predator and prey populations, as well as to enable a proper response to both familiar and possible new and unexpected challenges in the environment in the future.

# Acknowledgements

This journey started at the 40th anniversary of the WWF White-tailed Eagle working group, where I got invited to speak because I had written my master's thesis about the diet of white-tailed eagles back in the days. There I met my supervisor-to-be Toni, who asked if I wanted to do a PhD about white-tailed eagles. Toni, I want to thank you with all my heart for providing me this opportunity and getting me through with it. Even though the path has been far from straight, you did not lose faith in me. Thank you for all the help along every step of the way.

This thesis builds on the workload of countless volunteers and members of the white-tailed eagle working group, originally affiliated by WWF Finland and since 2019 with the Osprey Foundation. Without you, we would not have the thorough monitoring data, prey remains or feathers that are used in these studies. I want to thank each and every one of you, for collecting the data, letting me use it, and for saving the species. I have also greatly enjoyed all the shared eagle experiences and seminars. Thank you for so kindly welcoming me in your association (it was about time to get female representation!). I am forever grateful to Totti, who first introduced me to the world of sea eagles. You have been most encouraging and have shared of your life-long experience with these birds, not to mention your amazing work with the monitoring and prey remain collection in Åland. Olli-Pekka, you have been of invaluable help in Lapland, both in the field and as a source of local knowledge. Heikki, thanks for maintaining the Finnish white-tailed eagle database and providing me with any information whenever I needed it (which was often and a lot). Olli, thank you for the fantastic cover photo of the fishing eagle. Most of the prey remains were identified by the incredible professor emeritus Seppo, who sadly passed away in 2019 at an age of 87 years and worked with the identifications to the very end.

Igor, thank you for providing ecologist-me the opportunity to do some actual lab work abroad, it was both valuable and fun. I also want to thank you for your big help with both the hands-on work, the analyses and the fourth manuscript. Eiderguys, thank you for collaborating with me on the paper about eagles and eiders. Special thanks to Andy for the help with the insane statistics in that work. Hannu, I can't thank you enough for all your help, your friendship and for believing in me even when I did not do it myself. Rimgaudas and Johan, my sincere thanks for your time and effort in pre-evaluating this thesis as well as your valuable improvement suggestions. Oliver, thank you for agreeing on being my opponent.

This PhD project spanned quite many years during which there has been turnovers in both fellow doctoral students and the state of the world. The BGG environment has been a great place throughout and I have met so many interesting and wonderful people during this journey. Jon, thanks for organizing PhD-seminars, teaching R and all the help with various matters. Sari, thanks for the always fast replies regarding practical issues. Mari, you helped with all my confused questions in the very beginning when I had no idea of how anything worked and what I was doing. Maria, Pirjo, Pauliina, Tytti, Tuuli and the girls, thank you for the interesting discussions, the company, the fish poetry and for always making me feel welcome even though I was an overaged satellite member of the community. Fabio, you were my "PhD-brother" and it was a pleasure to share the experience with you. Thank you for all the support, eagle talk, and friendship. Animal Ecology Lab fellows, you are the perfect mix of relaxed, smart, fun, outdoorsy, nerdy and slightly insane people I enjoy surrounding me with. Tiia, special thanks for all the help in the final steps and for being such a good friend, and Carina and Ida for the joy of finally having peer sea eagle girls.

To my dear friends Mella and Titti, thank you for making me think and talk about anything and everything else than work, for all the late, wet and weird evenings and for walking and kayaking company. Heidi and Helena, thanks for the open-hearted discussions about life, the universe and everything, the karaoke-nights and for keeping the bridge to the world of insects open.

Mum, dad, Hannele. Thank you for encouraging me and always believing in me. Mum, thank you for the food-supply, and dad, thank you for all the help with the kid logistics during these years. Kim, thank you for sharing my ups, my downs and my life, and for so patiently listening to my endless talk about eagles (with a genuine interest!) as well as for the help with unexpected technical problems like how to build a nest-camera. Lea, Tor, Else and Alvin, thank you for pulling up with all the eagle talk and the spontaneous songs about cat food, for your support, and for filling my life with joy.

This PhD-project and spin-offs of it has brought me on adventures from Romania to our beautiful archipelago to the high fells of Lapland. I have also had the privilege to see the entire archipelago of Åland from an eagle-view, when participating in the helicopter monitoring. Countless hours have been spent at the computer. ERA, Mika and Jon Henrik Fjällgren – thank you for being the soundtrack of my thesis. Funding for this thesis, for which I am truly grateful, was obtained from a variety of sources: The Swedish Cultural Foundation in Finland, The Finnish Foundation for Nature Conservation, Victoriastiftelsen, Waldemar von Frenckells stiftelse, Nordenskiöld-samfundet, Otto A. Malm foundation, BGG doctoral programme, Societas pro Fauna et Flora Fennica and Oskar Öflunds stiftelse.

# References


Ackerman JT, Eagles-Smith CA, Herzog MP, Hartman CA, Peterson SH, Evers DC, Jackson AK, Elliott JE, vander Pol SS, Bryan CE 2016. Avian mercury exposure and toxicological risk across western North America: A synthesis. Sci Total Environ 568:749–769. https://doi.org/10.1016/j.scitotenv.2016.03.071

Ådjers K, Appelberg M, Eschbaum R, Lappalainen A, Minde A, Repečka R, Thoresson G 2006. Trends in coastal fish stocks of the Baltic Sea. Boreal Environ Res 11:13–25.

AMAP/UN Environment 2019. Technical Background Report for the Global Mercury Assessment 2018:viii + 426 pp Including E-Annexes.

Amar A, Arroyo B, Redpath S, Thirgood S 2004. Habitat predicts losses of red grouse to individual hen harriers. J Appl Ecol 41:305–314. https://doi.org/10.1111/j.0021-8901.2004.00890.x

Badry A, Palma L, Beja P, Ciesielski TM, Dias A, Lierhagen S, Jenssen BM, Sturaro N, Eulaers I, Jaspers VLB 2019. Using an apex predator for large-scale monitoring of trace element contamination: Associations with environmental, anthropogenic and dietary proxies. Sci Total Environ 676:746–755. https://doi.org/10.1016/j.scitotenv.2019.04.217

Balk L, Hägerroth P-A, Akerman G, Hanson M, Tjärnlund U, Hansson T, Hallgrimsson GT, Zebühr Y, Broman D, Mörner T, Sundberg H 2009. Wild Birds of Declining European Species Are Dying from a Thiamine Deficiency Syndrome. Proceedings of the National Academy of Sciences - PNAS 106:12001–12006. https://doi.org/10.1073/pnas.0902903106

Balotari-Chiebao F, Brommer JE, Niinimäki T, Laaksonen T 2016. Proximity to wind-power plants reduces the breeding success of the white-tailed eagle. Anim Conserv 19:265–272. https://doi.org/10.1111/acv.12238

Balotari-Chiebao F, Brommer JE, Saurola P, Ijäs A, Laaksonen T 2018. Assessing space use by pre-breeding white-tailed eagles in the context of wind-energy development in Finland. Landsc Urban Plan 177:251–258. https://doi.org/10.1016/j.landurbplan.2018.05.012

Balotari-Chiebao F, Brommer JE, Tikkanen H, Laaksonen T 2021. Habitat use by post-fledging white-tailed eagles shows avoidance of human infrastructure and agricultural areas. Eur J Wildl Res 67. https://doi.org/10.1007/s10344-021-01482-6

Below A, Lehikoinen A, Mikkola-Roos M, Kurvinen L, Laaksonen T 2019. Saaristolintukantojen kehitys vuosina 1980–2018. Linnut-vuosikirja 56-57 [in Finnish with English summary]

Berger J, Swenson JE, Persson I-L 2001. Recolonizing Carnivores and Naïve Prey: Conservation Lessons from Pleistocene Extinctions. Science (1979) 291:1036–1039. https://doi.org/10.1126/SCIENCE.1056466

Bergström L, Heikinheimo O, Svirgsden R, Kruze E, Ložys L, Lappalainen A, Saks L, Minde A, Dainys J, Jakubavičiūtė E, Ådjers K, Olsson J 2016. Long term changes in the status of coastal fish in the Baltic Sea. Estuar Coast Shelf Sci 169:74–84. https://doi.org/10.1016/j.ecss.2015.12.013

Bignert A, Helander B 2015. Monitoring of contaminants and their effects on the common Guillemot and the White-tailed sea eagle. J Ornithol 156:173–185. https://doi.org/10.1007/s10336-015-1240-3

Bildstein KL 2017. Raptors: The Curious Nature of Diurnal Birds of Prey. Cornell University Press, Ithaca, NY.

Blumstein DT, Daniel JC, Springett BP 2004. A Test of the Multi-Predator Hypothesis: Rapid Loss of Antipredator Behavior after 130 years of Isolation. Ethology 110:919–934. https://doi.org/10.1111/j.1439-0310.2004.01033.x

Boecklen WJ, Yarnes CT, Cook BA, James AC 2011. On the Use of Stable Isotopes in Trophic Ecology. Annu Rev Ecol Evol Syst 42:411–440. https://doi.org/10.1146/annurev-ecolsys-102209-144726

Bonnot NC, Morellet N, Hewison AJM, Martin JL, Benhamou S, Chamaillé-Jammes S 2016. Sitka black-tailed deer (*Odocoileus hemionus sitkensis*) adjust habitat selection and activity rhythm to the absence of predators. Can J Zool 94:385–394. https://doi.org/10.1139/CJZ-2015-0227

Brashares J, Prugh L, Stoner C, Epps C 2010. Ecological and Conservation Implications of Mesopredator Release. In: Terborgh J and Estes J (eds) Trophic cascades: predators, prey, and the changing dynamics of nature. Island Press, Washington, pp 221–240.

Bregnballe T, Tofft J, Kotzerka J, Lehikoinen A, Rusanen P, Herrmann C, Krone O, Engström H, Rattiste K, Reich J and Kouzov SA 2022. Occurrence and Behaviour of White-Tailed Eagles *Haliaeetus albicilla* in Great Cormorant *Phalacrocorax Carbo Sinensis* Colonies in Countries around the Baltic Sea. Ardea 109:565–582. https://doi.org/10.5253/arde.v109i2.a24

Brzeziński M, Żmihorski M, Nieoczym M, Wilniewczyc P, Zalewski A 2020. The expansion wave of an invasive predator leaves declining waterbird populations behind. Divers distrib 26: 138-150. https://doi.org/10.1111/ddi.13003

Burgas D, Ovaskainen O, Blanchet FG, Byholm P 2021. The Ghost of the Hawk: Top Predator Shaping Bird Communities in Space and Time. Front Ecol Evol 9. https://doi.org/10.3389/fevo.2021.638039

Burnham KP, Anderson DR 2002. Model Selection and Multimodel Inference: A Practical Information-Theoretic Approach, 2nd edn. Springer-Verlag, New York.

Cammen KM, Rasher DB, Steneck RS 2019. Predator recovery, shifting baselines, and the adaptive management challenges they create. Ecosphere 10(2):e02579 https://doi.org/10.1002/ecs2.2579

Chakarov N, Krüger O 2010. Mesopredator release by an emergent superpredator: A natural experiment of predation in a three level guild. PLoS One 5:e15229–e15229. https://doi.org/10.1371/journal.pone.0015229

Chapron G, Kaczensky P, Linnell JDC, von Arx M, Huber D, Andrén H, López-Bao JV, Adamec M, Álvares F, Anders O, Balčiauskas L, Balys V, Bedő P, Bego F, Blanco JC, Breitenmoser U, Brøseth H, Bufka L, Bunikyte R, Ciucci P, Dutsov A, Engleder T, Fuxjäger C, Groff C, Holmala K, Hoxha B, Iliopoulos Y, Ionescu O, Jeremić J, Jerina K, Kluth G, Knauer F, Kojola I, Kos I, Krofel M, Kubala J, Kunovac S, Kusak J, Kutal M, Liberg O, Majić A, Männil P, Manz R, Marboutin E, Marucco F, Melovski D, Mersini K, Mertzanis Y, Mysłajek W. R, Nowak S, Odden J, Ozolins J, Palomero G, Paunović M, Persson J, Potočnik H, Quenette P-Y, Rauer G, Reinhardt I, Rigg R, Ryser A, Salvatori V, Skrbinšek T, Stojanov A, Swenson JE, Szemethy L, Trajçe A, Tsingarska-Sedefcheva E, Váňa M, Veeroja R, Wabakken P, Wölfl M, Wölfl S, Zimmermann F, Zlatanova D, Boitani L 2014. Recovery of large carnivores in Europe's modern human-dominated landscapes. Science 346:1517–1519. https://doi.org/10.1126/science.1257553

Cramp S 1980. Handbook of the birds of Europe, the Middle East and North Africa: the birds of the Western Palearctic. Vol. 2, Hawks to bustards. Oxford University Press, Oxford.

Cunningham CX, Johnson CN, Jones ME, Ostfeld R 2020. A native apex predator limits an invasive mesopredator and protects native prey: Tasmanian devils protecting bandicoots from cats. Ecol Lett 23:711–721. https://doi.org/10.1111/ele.13473

Dahl F, Åhlén PA 2019. Nest predation by raccoon dog *Nyctereutes procyonoides* in the archipelago of northern Sweden. Biol Invasions 21:743–755. https://doi.org/10.1007/s10530-018-1855-4

Dementavičius D, Rumbutis S, Virbickas T, Vaitkuvienė D, Dagys M, Treinys R 2020. Spatial and temporal variations in the White-tailed Eagle *Haliaeetus albicilla* breeding diet revealed by prey remains. Bird Study 67:206–216. https://doi.org/10.1080/00063657.2020.1808591

Desholm M, Christensen T, Scheiffarth G, Hario M, Andersson Å, Ens B, Camphuysen C, Nilsson L, Waltho C, Lorentsen S-H, Kuresoo A, Kats R, Fleet D, Fox A 2002. Status of the Baltic/Wadden Sea population of the Common Eider *Somateria m. mollissima*. Wildfowl 53:167–203.

Dietz R, Letcher RJ, Desforges J-P, Eulaers I, Sonne C, Wilson S, Andersen-Ranberg E, Basu N, Barst BD, Bustnes JO, Bytingsvik J, Ciesielski TM, Drevnick PE, Gabrielsen GW, Haarr A, Hylland K, Jenssen BM, Levin M, McKinney MA, Nørregaard RD, Pedersen KE, Provencher J, Styrishave B, Tartu S, Aars J, Ackerman JT, Rosing-Asvid A, Barrett R, Bignert A, Born EW, Branigan M, Braune B, Bryan CE, Dam M, Eagles-Smith C, Evans M, Evans TJ, Fisk AT, Gamberg M, Gustavson K, Hartman CA, Helander B, Herzog MP, Hoekstra PF, Houde M, Hoydal K, Jackson AK, Kucklick J, Lie E, Loseto L, Mallory ML, Miljeteig C, Mosbech A, Muir DCG, Nielsen ST úni, Peacock E, Pedro S, Peterson SH, Polder A, Rigét FF, Roach P, Saunes H, Sinding M-HS, Skaare JU, Søndergaard J, Stenson G, Stern G, Treu G, Schuur SS, Víkingsson G 2019. Current state of knowledge on biological effects from contaminants on arctic wildlife and fish. Sci Total Environ 696:133792. https://doi.org/https://doi.org/10.1016/j.scitotenv.2019.133792

Ekroos J, Öst M, Karell P, Jaatinen K, Kilpi M 2012a. Philopatric predisposition to predation-induced ecological traps: habitat-dependent mortality of breeding eiders. Oecologia 170:979–986. https://doi.org/10.1007/s00442-012-2378-9

Ekroos J, Fox AD, Christensen TK, Cervencl A 2012b. Declines amongst breeding Eider *Somateria mollissima* numbers in the Baltic/Wadden Sea flyway. Ornis Fenn 89:81–90.

Elmberg J, Arzel C, Gunnarsson G, Holopainen S, Nummi P, Pöysä H, Sjöberg K 2020. Population change in breeding boreal waterbirds in a 25-year perspective: What characterises winners and losers? Freshw Biol 65:167–177. https://doi.org/10.1111/fwb.13411

EPA US 1998. Mercury in Solids and Solutions by Thermal Decomposition, Amalgamation, and Atomic Absorption Spectrophotometry.

Estes J, Peterson C, Steneck R 2010. Some effects of apex predators in higher-latitude coastal oceans. In: Terborgh J, Estes J (eds) Trophic Cascades: Predators, Prey, and the Changing Dynamics of Nature. Island Press, Washington, pp 37–54.

Estes JA, Terborgh J, Brashares JS, Power ME, Berger J, Bond WJ, Carpenter SR, Essington TE, Holt RD, Jackson JBC, Marquis RJ, Oksanen L, Oksanen T, Paine RT, Pikitch EK, Ripple WJ, Sandin SA, Scheffer M, Schoener TW, Shurin JB, Sinclair ARE, Soulé ME, Virtanen R, Wardle DA (2011) Trophic downgrading of planet Earth. Science 1979. 333:301–306. https://doi.org/10.1126/science.1205106

Ferguson-Lees J, Christie D 2001. Raptors of the world. Christopher Helm Publishers, London.

Fox AD, Jónsson JE, Aarvak T, Bregnballe T, Christensen TK, Clausen KK, Clausen P, Dalby L, Holm TE, Pavón-Jordan D, Laursen K, Lehikoinen A, Lorentsen S-H, Møller AP, Nordström M, Öst M, Söderquist P, Roland Therkildsen O 2015. Current and Potential Threats to Nordic Duck Populations – A Horizon Scanning Exercise. Ann Zool Fennici 52:193–220. https://doi.org/10.5735/086.052.0404

Frey C, Sonnay C, Dreiss A, Roulin A 2011. Habitat, breeding performance, diet and individual age in Swiss Barn Owls (*Tyto alba*). J Ornithol 152:279–290.

Friedl G, Wüest A 2002. Disrupting biogeochemical cycles – Consequences of damming. Aquat Sci 64:55–65. https://doi.org/10.1007/s00027-002-8054-0

Härmä P, Hatunen S, Törmä M, Järvenpää E, Kallio M, Teiniranta R, Kiiski T, Suikkanen J 2013. GIO Land Monitoring 2011 – 2013 in the framework of regulation (EU) No 911/2010. Final Report, Finland. 47 p.

Hazen EL, Abrahms B, Brodie S, Carroll G, Jacox MG, Savoca MS, Scales KL, Sydeman WJ, Bograd SJ 2019. Marine top predators as climate and ecosystem sentinels. Front Ecol Environ 17:565–574. https://doi.org/10.1002/fee.2125

Helander B 1983. Food ecology of the white-tailed sea eagle *Haliaeetus albicilla* in Sweden. In: Helander, B. Reproduction of the white-tailed sea eagle *Haliaeetus albicilla* (L.) in Sweden, in relation to food and residue levels of organochlorine and mercury compounds in the eggs. p 87-155. PhD-thesis, Department of Zoology, Stockholm.

Helander B, Bignert A, Asplund L 2008. Using Raptors as Environmental Sentinels: Monitoring the White-tailed Sea Eagle *Haliaeetus albicilla* in Sweden. Ambio 37:425–431. https://doi.org/10.1579/0044-7447(2008)37[425:URAESM]2.0.CO;2

Helander B, Olsson A, Bignert A, Asplund L, Litzén K 2002. The Role of DDE, PCB, Coplanar PCB and Eggshell Parameters for Reproduction in the White-tailed Sea Eagle (*Haliaeetus albicilla*) in Sweden. Ambio 31:386–403. https://doi.org/10.1579/0044-7447-31.5.386

Hellsten SK, Virtanen MO, Nenonen OS, Kinnunen KA, Riihimäki JM 1993. Relative Importance of Internal Sources of Phosphorus and Organic Matter in Northern Finnish Reservoirs. Water Sci Technol 28:85–94. https://doi.org/10.2166/wst.1993.0132

Hellström P 2015. Rapportering från undersökning av DDT-PCB-HCB-HCH, PBDE-HBCD, PFAS och stabila isotoper i ägg från havsörn 2015. Naturhistoriska riksmuseet, Stockholm. [In Swedish]

Henson SM, Desharnais RA, Funasaki ET, Galusha JG, James |, Watson W, Hayward JL 2019. Predator-prey dynamics of bald eagles and glaucous-winged gulls at Protection Island, Washington, USA. Ecol evol 9:3850–3867. https://doi.org/10.1002/ece3.5011

Hildén O, Hario M 1993. Muuttuva saaristolinnusto. Forssa. 317 p. [In Finnish]

Hipfner MJ, Blight LK, Lowe RW, Wilhelm SI, Robertson GJ, Barrett RT, Anker-Nilssen T, Good TP 2012. Unintended consequences: how the recovery of sea eagle *Haliaeetus* spp. populations in the northern hemisphere is affecting seabirds. Mar Ornithol 40:39–52.

Högmander J, Lokki H, Laaksonen T, Stjernberg T 2020. The Finnish White-tailed Eagle *Haliaeetus albicilla* population no longer endangered [in Finnish with English summary]. Linnut-vuosikirja 2019: 60–71

Hollmén T, Franson JC, Kilpi M, Docherty DE, Hansen WR, Hario M 2002. Isolation and Characterization of a Reovirus from Common Eiders (*Somateria mollissima*) from Finland. Avian Dis 46:478–484. https://doi.org/10.1637/0005-2086(2002)046[0478:IACOAR]2.0.CO;2

Holopainen S, Čehovská M, Jaatinen K, Laaksonen T, Lindén A, Nummi P, Piha M, Pöysä H, Toivanen T, Väänänen V-M, Lehikoinen A 2022. A rapid increase of large-sized waterfowl does not explain the population declines of small-sized waterbird at their breeding sites. Glob Ecol Conserv 36:e02144. https://doi.org/10.1016/j.gecco.2022.e02144

Hsu-Kim H, Eckley CS, Achá D, Feng X, Gilmour CC, Jonsson S, Mitchell CPJ 2018. Challenges and opportunities for managing aquatic mercury pollution in altered landscapes. Ambio 47:141–169. https://doi.org/10.1007/s13280-017-1006-7

Isomursu M, Koivusaari J, Stjernberg T, Hirvelä-Koski V, Venäläinen E-R 2018. Lead poisoning and other human-related factors cause significant mortality in white-tailed eagles. Ambio 47:858–868. https://doi.org/10.1007/s13280-018-1052-9

Jaatinen K, Hermansson I, Mohring B, Steele BB, Öst M 2022. Mitigating impacts of invasive alien predators on an endangered sea duck amidst high native predation pressure. Oecologia 198:543–552. https://doi.org/10.1007/s00442-021-05101-8

Jernelöv A, Martin AL 1975. Ecological implications of metal metabolism by microorganisms. Annu Rev Microbiol 29:61–77. https://doi.org/10.1146/annurev.mi.29.100175.000425

Jernsletten J-L, Klokov K 2002. Sustainable Reindeer Husbandry. Centre for Saami Studies, University of Tromsø, Tromsø.

Johansson V 2019. Spatial Trends in Mercury Exposure, its Dietary Sources and Clinical Health Effects in Finnish White-Tailed Eagle Nestlings. Dissertation, University of Helsinki, Faculty of Veterinary Medicine.

Johnsen T, Systad G, Jacobsen K, Nygård T, Bustnes J 2007. The occurrence of reindeer calves in the diet of nesting Golden Eagles in Finnmark, northern Norway. Ornis Fenn 84:112–118.

Kalisinska E 2014. Total and Methylmercury in Soft Tissues of White-Tailed Eagle (*Haliaeetus albicilla*) and Osprey (*Pandion haliaetus*) Collected in Poland. Ambio 43:858–870. https://doi.org/10.1007/s13280-014-0533-8

Kauffman MJ, Varley N, Smith DW, Stahler DR, MacNulty DR, Boyce MS 2007. Landscape heterogeneity shapes predation in a newly restored predator-prey system. Ecol Lett 10:690–700. https://doi.org/10.1111/j.1461-0248.2007.01059.x

Kohl KD, Coogan SCP, Raubenheimer D 2015. Do wild carnivores forage for prey or for nutrients? BioEssays 37:701–709. https://doi.org/10.1002/bies.201400171

Koskimies P, Väisänen R 1991. Monitoring Bird Populations - A Manual of Methods Applied in Finland. Zoological Museum, Finnish Museum of Natural History, University of Helsinki.

Krone O, Treu G 2018. Movement patterns of white-tailed sea eagles near wind turbines. J Wildl Manage 82:1367–1375. https://doi.org/10.1002/jwmg.21488

Kumpula J, Stark S, Holand Ø 2011. Seasonal grazing effects by semi-domesticated reindeer on subarctic mountain birch forests. Polar Biol 34:441–453. https://doi.org/10.1007/s00300-010-0899-4

Kurvinen L, Kilpi M, Nordström M, Öst M, Kilpi M, Öst M 2016. Drivers of decline and changed nest-site preference of the Baltic eider: an island-level analysis from south-western Finland. Ornis Fenn 93:55–66.

Laursen K, Møller AP 2014. Long-term changes in nutrients and mussel stocks are related to numbers of breeding eiders *Somateria mollissima* at a large Baltic colony. PLoS One 9:e95851–e95851. https://doi.org/10.1371/journal.pone.0095851

Lavoie RA, Jardine TD, Chumchal MM, Kidd KA, Campbell LM 2013. Biomagnification of Mercury in Aquatic Food Webs: A Worldwide Meta-Analysis. Environ Sci Technol 47:13385–13394. https://doi.org/10.1021/es403103t

Lehikoinen A 2006. Cormorants in the Finnish archipelago. Ornis Fenn 83:34–46.

Lehikoinen A, Christensen TK, Öst M, Kilpi M, Saurola P, Vattulainen A 2008. Large-scale change in the sex ratio of a declining eider *Somateria mollissima* population. Wildlife Biol 14:288–301. https://doi.org/10.2981/0909-6396(2008)14[288:LCITSR]2.0.CO;2

Lehikoinen A, Jukarainen A, Mikkola-Roos M, Below A, Lehtiniemi T, Pessa J, Rajasärkkä A, Rintala J, Rusanen P, Sirkiä P, Tiainen J, Valkama J 2019. Birds. In: Hyvärinen E, Juslén A, Kemppainen E, Uddström A, Liukko U-M (eds) The 2019 Red List of Finnish Species. Ministry of the Environment & Finnish Environment Institute, Helsinki, pp 560–570.

Lehikoinen A, Rintala J, Lammi E, Pöysä H (2016) Habitat-specific population trajectories in boreal waterbirds: alarming trends and bioindicators for wetlands. Anim Conserv 19:88–95. https://doi.org/10.1111/acv.12226

Lehtonen H, Leskinen E, Selén R, Reinikainen M (2009) Potential reasons for the changes in the abundance of pike, Esox lucius, in the western Gulf of Finland, 1939-2007. Fish Manag Ecol 16:484–491. https://doi.org/10.1111/j.1365-2400.2009.00701.x

Lima SL (1998) Nonlethal Effects in the Ecology of Predator-Prey Interactions: What are the ecological effects of anti-predator decision-making? Bioscience 48:25–34. https://doi.org/10.2307/1313225

Lima SL (2009) Predators and the breeding bird: behavioral and reproductive flexibility under the risk of predation. Biol Rev Camb Philos Soc 84:485–513. https://doi.org/10.1111/J.1469-185X.2009.00085.X

Lindqvist G (2021) Statistical Yearbook of Åland 2021. Mariehamn.

Marshall KN, Stier AC, Samhouri JF, Kelly RP, Ward EJ (2016) Conservation Challenges of Predator Recovery. Conserv Lett 9:70–78. https://doi.org/10.1111/conl.12186

März R (1987) Gewöll- und Rupfungskunde. Akademie-Verlag, Berlin.

Møller AP, Kwiecinski Z, Tryjanowski P 2017. Prey reduce risk-taking and abundance in the proximity of predators. Curr Zool 63:591–598. https://doi.org/10.1093/cz/zow114

Mörner T, Hansson T, Carlsson L, Berg A-L, Ruiz Muñoz Y, Gustavsson H, Mattsson R, Balk L 2017. Thiamine deficiency impairs common eider (*Somateria mollissima*) reproduction in the field. Sci Rep 7:14451–7. https://doi.org/10.1038/s41598-017-13884-1

Mueller A, Chakarov N, Heseker H, Krüger O, Quinn J 2016. Intraguild predation leads to cascading effects on habitat choice, behaviour and reproductive performance. J Anim Ecol 85:774–784. https://doi.org/10.1111/1365-2656.12493

Nadjafzadeh M, Hofer H, Krone O 2016. Sit-and-wait for large prey: foraging strategy and prey choice of White-tailed Eagles. J Ornithol 157:165–178. https://doi.org/10.1007/s10336-015-1264-8

Nadjafzadeh M, Hofer H, Krone O 2013. The link between feeding ecology and lead poisoning in white-tailed eagles. J Wild Manage 77:48–57. https://doi.org/10.1002/jwmg.440

Newton I 1998. Population Limitation in Birds. Elsevier Science. https://doi.org/10.1016/B978-0-12-517365-0.X5000-5

Nyberg E, Faxneld S, Danielsson S, Eriksson U, Miller A, Bignert A 2015. Temporal and spatial trends of PCBs, DDTs, HCHs, and HCB in Swedish marine biota 1969–2012. Ambio 44:S484–S497. https://doi.org/10.1007/s13280-015-0673-5

Nyhus PJ 2016. Human–Wildlife Conflict and Coexistence. Annu Rev Environ Resour 41:143–171. https://doi.org/10.1146/annurev-environ-110615-085634

Obuch J 2021. Spatial and temporal changes in the diet composition of the Eurasian eagle-owl (*Bubo bubo*) in Slovakia comparing three historical periods. Raptor Journal 15:17–55. https://doi.org/doi:10.2478/srj-2021-0002

Oehme G 1975. Zur Ernährung des Seeadlers, *Haliaeetus albicilla* (L.), unter besonderer Berücksichtigung der Population in den drei Nordbezirken der DDR. Inaugural-Dissertation, Ernst-Moritz-Arndt-Universität Greifswald.

O'Rourke E 2014. The reintroduction of the white-tailed sea eagle to Ireland: People and wildlife. Land use policy 38:129–137. https://doi.org/10.1016/j.landusepol.2013.10.020

Öst M, Lehikoinen A, Jaatinen K 2022. Top–down effects override climate forcing on reproductive success in a declining sea duck. Oikos 2022:e08762. https://doi.org/10.1111/OIK.08762

Öst M, Lehikoinen A, Jaatinen K, Kilpi M 2011. Causes and consequences of fine-scale breeding dispersal in a female-philopatric species. Oecologia 166:327–336. https://doi.org/10.1007/S00442-010-1855-2

Öst M, Steele BB 2010. Age-Specific Nest-Site Preference and Success in Eiders. Oecologia 162:59–69. https://doi.org/10.1007/s00442-009-1444-4

Öst M, Vitikainen E, Waldeck P, Sundström L, Lindström K, Hollmén T, Franson JC, Kilpi M 2005. Eider females form non-kin brood-rearing coalitions. Mol Ecol 14:3903–3908. https://doi.org/10.1111/j.1365-294X.2005.02694.x

Öst M, Ydenberg R, Kilpi M, Lindström K 2003. Condition and coalition formation by brood-rearing common eider females. Behavioral Ecology 14:311–317. https://doi.org/10.1093/beheco/14.3.311

Paranjape AR, Hall BD 2017. Recent advances in the study of mercury methylation in aquatic systems. FACETS 2. https://doi.org/10.1139/facets-2016-0027

Pavón-Jordán D, Clausen P, Dagys M, Devos K, Encarnaçao V, Fox AD, Frost T, Gaudard C, Hornman M, Keller V, Langendoen T, Ławicki Ł, Lewis LJ, Lorentsen S, Luigujoe L, Meissner W, Molina B, Musil P, Musilova Z, Nilsson L, Paquet J, Ridzon J, Stipniece A, Teufelbauer N, Wahl J, Zenatello M, Lehikoinen A, Zurell D 2019. Habitat- and species-mediated short- and long-term distributional changes in waterbird abundance linked to variation in European winter weather. Divers Distrib 25:225–239. https://doi.org/10.1111/ddi.12855

Peterson BJ, Fry B 1987. Stable Isotopes in Ecosystem Studies. Annu Rev Ecol Syst 18:293–320. https://doi.org/10.1146/annurev.es.18.110187.001453

Pierce R 2012. Northern Pike Ecology, Conservation, and Management History. University of Minnesota Press.

Pohja-Mykrä M, Vuorisalo T, Mykrä S 2012. Organized persecution of birds of prey in Finland: historical and population biological perspectives. Ornis Fenn 89:1–19

Poole A 2019. Ospreys: The Revival of a Global Raptor. Johns Hopkins University Press, Baltimore.

Pöysä H, Rintala J, Lehikoinen A, Väisänen RA 2013. The importance of hunting pressure, habitat preference and life history for population trends of breeding waterbirds in Finland. Eur J Wildl Res 59:245–256. https://doi.org/10.1007/s10344-012-0673-8

R Core Team 2020. R: A language and environment for statistical computing. R Foundation for Statistical Computing.

Radović A, Mikuska T 2009. Population size, distribution and habitat selection of the white-tailed eagle *Haliaeetus albicilla* in the alluvial wetlands of Croatia. Biologia 64:156–164. https://doi.org/10.2478/s11756-009-0011-0

Ramula S, Öst M, Lindén A, Karell P, Kilpi M 2018. Increased male bias in eider ducks can be explained by sex-specific survival of prime-age breeders. PLoS ONE 13(4):e0195415 https://doi.org/10.1371/journal.pone.0195415

Rankama T, Ukkonen P 2001. On the early history of the wild reindeer (*Rangifer tarandus* L.) in Finland. Boreas 30:131–147. https://doi.org/10.1080/03009480119600

Ratcliffe D 2003. The Peregrine saga. In: Thompson D (ed) Birds of prey in a changing environment. The Stationery Office, Edinburgh, pp 91–98.

Reed DC, Nelson JC, Harrer SL, Miller RJ 2016. Estimating biomass of benthic kelp forest invertebrates from body size and percent cover data. Mar Biol 163. https://doi.org/10.1007/s00227-016-2879-x

Ripple WJ, Estes JA, Beschta RL, Wilmers CC, Ritchie EG, Hebblewhite M, Berger J, Elmhagen B, Letnic M, Nelson MP, Schmitz OJ, Smith DW, Wallach AD, Wirsing AJ 2014. Status and ecological effects of the world's largest carnivores. Science (1979) 343:151–162. https://doi.org/10.1126/science.1241484

Ripple WJ, Larsen EJ, Renkin RA, Smith DW 2001. Trophic cascades among wolves, elk and aspen on Yellowstone National Park's northern range. Biol Conserv 102:227–234. https://doi.org/10.1016/S0006-3207(01)00107-0

Røed KH, Flagstad Ø, Nieminen M, Holand Ø, Dwyer MJ, Røv N, Vilà C 2008. Genetic analyses reveal independent domestication origins of Eurasian reindeer. Proc R Soc B 275:1849–1855. https://doi.org/10.1098/rspb.2008.0332

Salvatori V, Balian E, Blanco JC, Ciucci P, Demeter L, Hartel T, Marsden K, Redpath SM, von Korff Y, Young JC 2020. Applying Participatory Processes to Address Conflicts Over the Conservation of Large Carnivores: Understanding Conditions for Successful Management. Front Ecol Evol 8. https://doi.org/10.3389/fevo.2020.00182

Scheuhammer A 1991. Effects of acidification on the availability of toxic metals and calcium to wild birds and mammals. Env Pol 71:329–375. https://doi.org/https://doi.org/10.1016/0269-7491(91)90036-V

Schweiger A, Fünfstück H, Beierkuhnlein C 2015. Availability of optimal-sized prey affects global distribution patterns of the golden eagle *Aquila chrysaetos*. J Avian Biol 46:81–88. https://doi.org/10.1111/jav.00396

Selonen V, Brommer JE, Holopainen S, Kauhala K, Krüger H, Poutanen J, Väänänen V-M, Laaksonen T 2022. Invasive species control with apex predators: increasing presence of wolves is associated with reduced occurrence of the alien raccoon dog. Biol Invasions. https://doi.org/10.1007/s10530-022-02850-2

Shin D-M, Yoo J-C, Jeong D-M, Shin D-M 2013. Spatial variation of Eurasian eagle-owl diets in wetland and non-wetland habitats in west-central Korea. J Raptor Res 47:400–409. https://doi.org/10.3356/JRR-13-00006.1

Sih A 1993. Effects of ecological interactions on forager diets: competition, predation risk, parasitism and prey behaviour. In: Hughes RN (ed) Diet selection. Blackwell Scientific Publications, Cambridge, pp 182–211.

Sih A 2011. Foraging theory. In: Scheiner S, Willig M (eds) The Theory of Ecology. University of Chicago Press, Chicago, pp 65–90.

Silliman BR, Hughes BB, Gaskins LC, He Q, Tinker MT, Read A, Nifong J, Stepp R 2018. Are the ghosts of nature's past haunting ecology today? Current Biology 28:532–537. https://doi.org/10.1016/j.cub.2018.04.002

Sonne C, Lakemeyer J, Desforges J-P, Eulaers I, Persson S, Stokholm I, Galatius A, Gross S, Gonnsen K, Lehnert K, Andersen-Ranberg EU, Tange Olsen M, Dietz R, Siebert U 2020. A review of pathogens in selected Baltic Sea indicator species. Environ Int 137:105565. https://doi.org/10.1016/j.envint.2020.105565

Stephens DW, Krebs JR 1986. Foraging theory. Princeton U.P, Princeton, N.J

Sulkava S, Huhtala K, Rajala P, Tornberg R 1998. Changes in the diet of the Golden Eagle *Aquila chrysaetos* and small game populations in Finland in 1957-96. Ornis Fenn 76:1–16.

Sulkava S, Tornberg R, Koivusaari J 1997. Diet of the White-tailed Eagle *Haliaeetus albicilla* in Finland. Ornis Fenn 74:65–78.

Sun J, Bustnes JO, Helander B, Bårdsen B-J, Boertmann D, Dietz R, Jaspers VLB, Labansen AL, Lepoint G, Schulz R, Søndergaard J, Sonne C, Thorup K, Tøttrup AP, Zubrod JP, Eens M, Eulaers I 2019. Temporal trends of mercury differ across three northern white-tailed eagle (*Haliaeetus albicilla*) subpopulations. Sci Total Environ 687:77–86. https://doi.org/10.1016/j.scitotenv.2019.06.027

Tapia L, Zuberogoitia I 2018. Breeding and nesting biology in raptors. In: Sarasola JH, Grande JM, Negro JJ (eds) Birds of prey: biology and conservation in the XXI century. Springer International Publishing, pp 63–94.

Tchounwou PB, Yedjou CG, Patlolla AK, Sutton DJ 2012. Heavy Metal Toxicity and the Environment. EXS 101:133–164. https://doi.org/10.1007/978-3-7643-8340-4_6

Terborgh John, Estes JA 2010. Trophic cascades: predators, prey, and the changing dynamics of nature. Island Press, Washington DC.

Terraube J, Guixé D, Arroyo B 2014. Diet composition and foraging success in generalist predators: Are specialist individuals better foragers? Basic Appl Ecol 15:616–624. https://doi.org/10.1016/j.baae.2014.08.008

Tikkanen H, Balotari-Chiebao F, Laaksonen T, Pakanen V-M, Rytkönen S 2018. Habitat use of flying subadult White-tailed Eagles (*Haliaeetus albicilla*): implications for land use and wind power plant planning. Ornis Fenn 95:137.

Treinys R, Dementavičius D, Rumbutis S, Švažas S, Butkauskas D, Sruoga A, Dagys M 2016. Settlement, habitat preference, reproduction, and genetic diversity in recovering the white-tailed eagle *Haliaeetus albicilla* population. J Ornithol 157:311–323. https://doi.org/10.1007/s10336-015-1280-8

Vallius H 2014. Heavy metal concentrations in sediment cores from the northern Baltic Sea: Declines over the last two decades. Mar Pollut Bull 79:359–364. https://doi.org/10.1016/j.marpolbul.2013.11.017

Westerbom M, Kilpi M, Mustonen O 2002. Blue mussels, *Mytilus edulis* at the edge of the range: population structure, growth and biomass along a salinity gradient in the north-eastern Baltic Sea. Mar Biol 140:991–999. https://doi.org/10.1007/s00227-001-0765-6