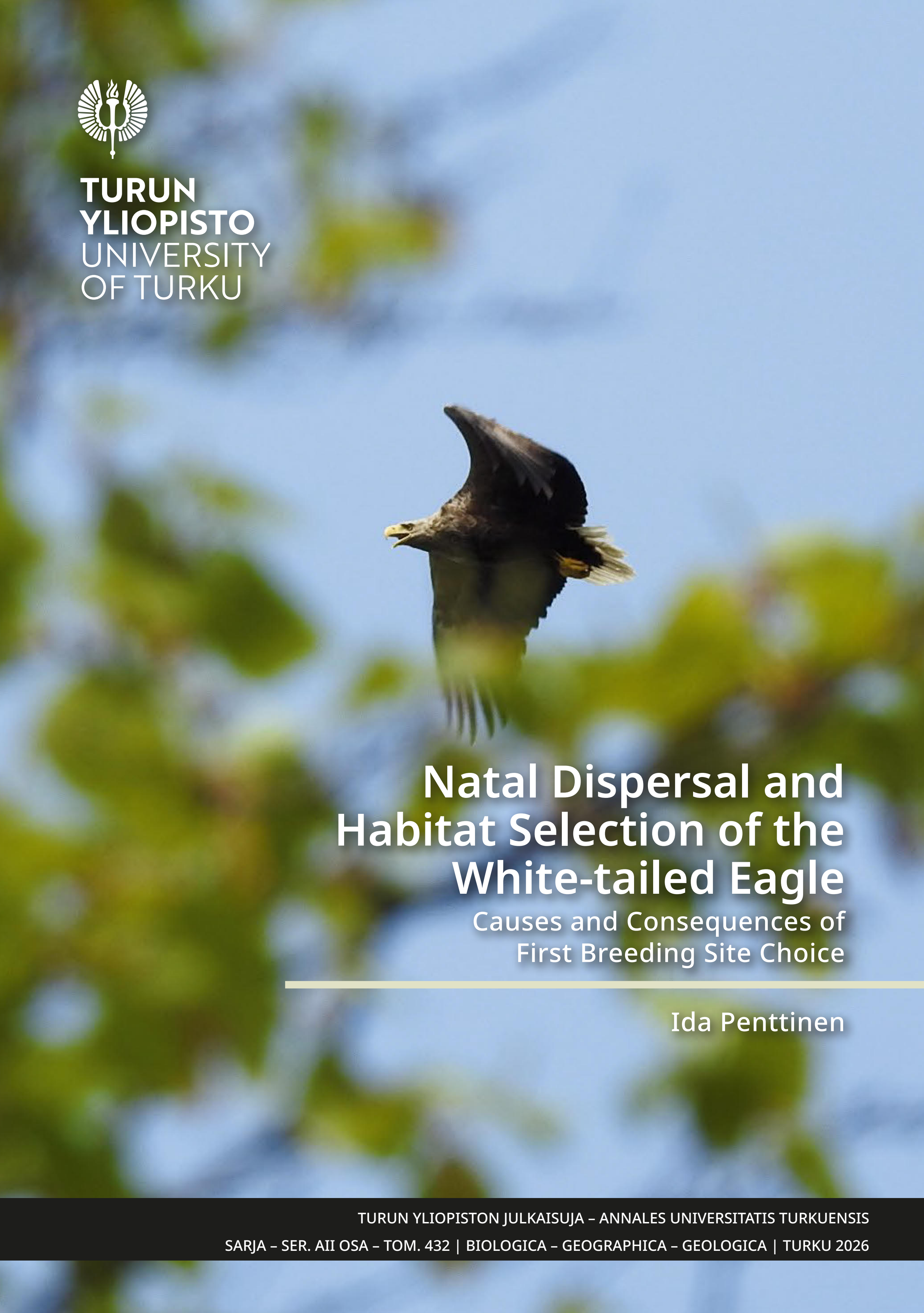

TURUN
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Natal Dispersal and Habitat Selection of the White-tailed Eagle

Causes and Consequences of First Breeding Site Choice

Ida Penttinen

TURUN YLIOPISTON JULKAISUJA – ANNALES UNIVERSITATIS TURKUENSIS
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From the expanse of the sky, the world looks completely different from what creatures crawling on the ground think. Seen from the stars, our Earth is just one star among others. To an eagle, space is like a shoreless sea where one can sail freely, and water and land together are like a large island below, from one side of which clouds rise and disappear behind the other shore, driven by the wind.

Translated from
Viimeiset Kotkat (The Last Eagles) by Bengt Berg

UNIVERSITY OF TURKU
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ABSTRACT

Natal dispersal refers to the movement of an individual from its birth site to its first breeding site. The choice of a breeding habitat is critical for fitness, and the consequences can be lifelong if the species exhibits high fidelity to breeding sites. However, individuals selecting their first breeding site have no experience with the fitness prospects of different habitats and must, therefore, base their decision on other cues. Whether these cues are reliably linked to reproductive success in those habitats remains unclear.

In this thesis, I investigated natal dispersal and habitat selection of the white-tailed eagle (*Haliaeetus albicilla*), a long-lived raptor with high breeding-site fidelity. Using a dataset of genetically and visually identified breeding individuals with known natal sites, I studied whether population density and habitat imprinting affect the settlement of white-tailed eagles, and whether these factors are associated with subsequent breeding success. I show that white-tailed eagles use conspecific density and natal habitat similarity as cues when choosing their breeding site. Eagles born in high-density areas tend to settle in lower-density areas in comparison, but dispersed over shorter distances. Breeding success was higher when the local breeder density was lower. White-tailed eagles also prefer their natal habitat type when choosing a breeding habitat, but this is not associated with improved breeding success. Since there were no effects of settling in natal-like habitats, this is likely a neutral behavioural pattern, or the benefits are gained in other ways. The habitat type seems to play a greater direct role in reproductive performance, since breeding success was higher in territories with a smaller proportion of water. I also found that older individuals seem to be more successful breeders than young ones.

The results shed light on the relationships between habitat selection mechanisms and the fitness prospects of chosen breeding habitats. Understanding these relationships is particularly important for long-lived species with high breeding site fidelity, such as large raptors. Many raptor populations are still recovering from past population declines or being reintroduced to their former range. Knowledge of the factors influencing movement and settlement can improve the success of reintroduction programmes and aid in predicting population growth and range expansion.

KEYWORDS: Natal dispersal, Habitat selection, Habitat imprinting, population density, reproductive success, microsatellites, ecological genetics

TURUN YLIOPISTO
Matemaattis-Luonnontieteellinen Tiedekunta
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TIIVISTELMÄ

Synnyindispersaali tarkoittaa yksilön siirtymistä syntymäpaikaltaan ensimmäiselle lisääntymispaikalle. Kelpoisuuden kannalta on olennaista, millaisen elinympäristön yksilö valitsee lisääntymiseen. Jos laji on lisääntymispaikkauskollinen, ensimmäisen paikan valinnalla voivat olla elinikäiset seuraukset. Ensimmäistä lisääntymispaikkaa valitessa yksilöillä ei vielä ole kokemusta eri elinympäristöjen kelpoisuusnäkymistä, vaan valinnan on perustuttava vihjeisiin, kuten samanlaisuuteen synnyinympäristön kanssa tai lajitovereiden läsnäoloon. On kuitenkin epäselvää, ennustavatko vihjeet lisääntymismenestystä valituissa ympäristöissä.

Tutkin väitöskirjassani, miten pesimäpopulaation tiheys ja habitaattileimautuminen vaikuttavat merikotkan (*Haliaeetus albicilla*) lisääntymispaikan valintaan ja ovatko ne yhteydessä myöhempään lisääntymismenestykseen. Tutkimus perustui aineistoon geneettisin ja visuaalisin menetelmin tunnistetuista yksilöistä, joiden synnyinpaikka tunnetaan. Pesimäpopulaation tiheys ja synnyin- ja pesimäympäristön samankaltaisuus ovat yhteydessä merikotkien lisääntymispaikan valintaan. Kun synnyinalueen tiheys on korkea, kotkat asettuvat suhteessa harvemman tiheyden alueille, mutta dispersoivat lyhyempiä matkoja. Lisääntymismenestys oli parempi alueilla, joilla pesimäpopulaation tiheys oli alhaisempi. Merikotkat näyttäisivät suosivan synnyinympäristöään muistuttavia pesimäympäristöjä. Tämä ei kuitenkaan johda parempaan lisääntymismenestykseen. Kyseessä on siis todennäköisesti neutraali käyttäytymismalli tai hyödyt ilmenevät muilla tavoin. Elinympäristöllä näyttää olevan suurempi vaikutus lisääntymismenestykseen, joka oli parempi reviireillä, joilla vesialueen osuus oli pienempi. Lisäksi havaitsin, että vanhemmat yksilöt vaikuttavat olevan menestyksekkäämpiä lisääntyjiä kuin nuoret yksilöt.

Tulokseni selventävät elinympäristön valinnan mekanismien ja ympäristön kelpoisuusnäkymien välisiä yhteyksiä. Näiden tunteminen on tärkeää pitkäikäisten ja lisääntymispaikkauskollisten lajien, kuten suurten petolintujen, kohdalla. Monet petolintupopulaatiot toipuvat yhä menneistä populaatioromahduksista tai niitä ollaan palauttamassa alueille, joilta ne ovat hävinneet. Tieto liikkumiseen ja asettumiseen vaikuttavista tekijöistä auttaa parantamaan palautusistutusten onnistumista sekä ennustamaan populaatioiden ja levinneisyysalueiden laajenemista.

AVAINSANAT: Synnyindispersaali, habitaattileimautuminen, populaatiotiheys, elinympäristön valinta, lisääntymismenestys, mikrosatelliitit, ekologinen genetiikka

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 Penttinen, I., Nebel, C., Stjernberg, T., Kvist, L., Ponnikas, S., & Laaksonen, T. (2024). Large-scale genotypic identification reveals density-dependent natal dispersal patterns in an elusive bird of prey. *Movement Ecology*, *12*(1), 16. https://doi.org/10.1186/s40462-023-00447-5

II Penttinen, I., Nebel, C., & Laaksonen, T. (2025). Habitat imprinting in breeding territory selection of a long-lived bird of prey. *Journal of Animal Ecology*. https://doi.org/10.1111/1365-2656.70202

III Penttinen, I., Nebel, C., & Laaksonen, T. Habitat imprinting is not associated with reproductive benefits while habitat, density and parental age determine breeding success in a long-lived bird of prey. *Manuscript.*

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Author contributions to the original publications:

	Chapter I	Chapter II	Chapter III
Conceptualisation & methodology	IP, CN, TL	IP, CN, TL	IP, CN, TL
Funding acquisition	IP, CN, TL	IP, CN, TL	IP, CN, TL
Data collection & curation	IP, SP, LK, TS	IP	IP
Statistical analysis	IP, CN	IP, CN	IP, CN
Visualisation	IP	IP	IP
Supervision	TL, CN	TL, CN	TL, CN
Writing the original draft of the manuscript	IP	IP	IP
Reading and editing the manuscript	IP, CN, TL, SP, LK, TS	IP, CN, TL	IP, CN, TL

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1 Introduction

1.1 Natal dispersal

The movement of individual organisms is a fundamental factor in ecology and evolution that can occur at a variety of spatial and temporal scales for a range of underlying reasons throughout an individual's lifetime (Nathan et al., 2008; Swingland et al., 1983). The causes and consequences of movement have central roles as selective forces shaping communities, populations and individual fitness (Bowler & Benton, 2005; Clobert et al., 2001; Nathan et al., 2008). These are further affected by several ecological and behavioural factors, such as life-history stage, personality, seasonality and habitat (Clobert et al., 2001). Understanding animal movement is essential for effective conservation and management actions (Allen & Singh, 2016), since human activities limit animal movement, while movement is often the only way for animals to respond to rapid changes (Allen & Singh, 2016; Tucker et al., 2018).

A common form of movement in nature is dispersal (Baguette et al., 2012). Dispersal encompasses movements of individuals with potential consequences for gene flow across space (Ronce, 2007). There are two forms of dispersal: natal and breeding dispersal (Baguette et al., 2012; Bowler & Benton, 2005; Greenwood & Harvey, 1982; Matthysen, 2012). Natal dispersal refers to the movement of an individual from the site of birth to the site of first breeding, and breeding dispersal means the movement between subsequent breeding attempts (Matthysen, 2012). Natal dispersal is more common of the two and therefore has a larger impact on individual fitness and population structure (Matthysen, 2012), as it is largely responsible for gene flow and the colonisation of new areas (Bowler & Benton, 2005; Matthysen, 2012; Ronce, 2007). Natal dispersal is usually viewed as a three-stage process consisting of departure from the natal site, a transient phase and settlement to the new site (Matthysen, 2012).

The mechanisms driving natal dispersal are diverse and can differ across the three stages (Matthysen, 2012). Variation in dispersal can be explained by the interplay of internal conditions of the individual, such as body size, competitive ability and personality, and characteristics of the external environment, such as habitat quality, population density and local demographic structure (Bowler &

Benton, 2005; Matthysen, 2012). Dispersal reduces kin competition and risk of inbreeding, increases variance in expected fitness, and allows escape from unfavourable conditions (Bowler & Benton, 2005; Matthysen, 2012). However, it also involves costs in the form of time and energy needed for the movement itself and the search and evaluation of the settlement site, risks of moving through unfamiliar and unsuitable landscapes and the loss of advantage of local adaptation (Bonte et al., 2012; Bowler & Benton, 2005; Matthysen, 2012). Since costs and benefits differ among individuals, their responses to cues about their environment and internal state will vary, making dispersal phenotype- and condition-dependent (Ims & Hjermann, 2001; Matthysen, 2012).

1.2 Habitat selection

The last phase of the natal dispersal process, settlement at the first breeding site, involves habitat selection (Matthysen, 2012). The mechanisms involved in habitat selection have evolved to ensure that individuals recognise and utilise suitable habitats and hence maximise their fitness (Piper, 2011; Stamps & Davis, 2006). Habitat selection can be viewed as a three-stage process including search, settlement and residency phases (Stamps, 2001). The first two can be seen as being part of natal dispersal, but residency, living in the chosen habitat, is what determines the success of the choice (Stamps, 2001). This is what makes habitat selection a tricky endeavour: the costs of the process are paid during the search and settlement phases, but the benefits are reaped only during residency (Stamps, 2001).

Choice of a breeding habitat is an especially crucial decision, since it influences the fitness of not just the choosing individual but also its offspring, which can reflect on the entire population (Lack, 1954). Habitats differ in their potential to promote fitness, and each habitat has an innate quality (e.g. availability of food or shelter), which affects the breeding success of the individuals inhabiting them (Fuller, 2012; Hildén, 1965). The evaluation of the habitat's fitness prospects requires information on its quality. Many species evaluate breeding habitats based on personal experience, such as their own performance in those habitats. If breeding success is low, it is better to switch to another place, which might be better suited for breeding (Switzer, 1993). However, this information is not available when individuals are choosing their very first breeding habitat (Hildén, 1965; Piper, 2011), and if a species exhibits very high breeding site fidelity (Newton, 1979; Tapia & Zuberogoitia, 2018), the consequences of the first breeding habitat choice are potentially life-long. Without actual breeding experience, choices must be made based on other cues, such as resemblance to the natal habitat, the presence of conspecifics (Stamps, 2001), and social information about the breeding success of others (Seppänen et al., 2007).

1.3 Density-dependence in natal dispersal and habitat selection

Conspecific density is one of the key factors affecting dispersal patterns and habitat selection (Matthysen, 2005). The relationship between natal dispersal and population density can be positive or negative, and both mechanisms are supported by theory and empirical data (Lambin et al., 2001; Matthysen, 2005). Positive density-dependence means that dispersal distances or rates increase with increasing population density and is commonly observed in birds and mammals (Matthysen, 2005). It is likely a response to increased intraspecific competition, which forces maturing individuals to move farther to less-dense areas to find vacant settlement sites (Bowler & Benton, 2005; Lambin et al., 2001; Matthysen, 2005). Negative density-dependence means that dispersal distances or rates decrease with increasing population density. It can arise, for example, if the presence of conspecifics is used as a cue for high-quality breeding sites (Bowler & Benton, 2005; Lambin et al., 2001; Matthysen, 2005, 2012).

1.4 Natal habitat imprinting

Since individuals differ from each other by their genotypes, phenotypes and experiences, the quality of the same habitat can be different for different individuals (Piper, 2011). In addition to the innate value mentioned earlier, habitats can have private value based on an individual's experience and familiarity with them (Fuller, 2012; Piper, 2011). It is well documented across different taxa that animals tend to choose habitats resembling their natal habitat (Dixson et al., 2014; Kolecek et al., 2020; Merrick & Koprowski, 2016; Penttinen et al., 2025; Piper, 2011). Depending on the driving mechanism, this is known as habitat imprinting or natal habitat preference induction (NHPI) (Davis, 2004).

According to the concept of natal habitat preference induction (NHPI), early-life experiences from natal habitat can shape future habitat preferences (Davis, 2004; Stamps, 2001). NHPI most commonly increases preference for natal-like habitats, but in rare cases can also decrease it (Stamps & Davis, 2006). A specific case of NHPI is habitat imprinting, where the exposure to cues in the natal environment during a sensitive period increases preference for habitats with similar cues later in life (Stamps & Davis, 2006). This can result in individuals settling in natal-like habitats for reproduction (Davis, 2008; Piper, 2011). The only breeding habitat-related experience the recruiting individuals have is of their own natal habitat, which was good enough to enable their own survival to breeding age (Fuller, 2012; Stamps & Davis, 2006).

1.5 Reproductive consequences

Multiple mechanisms and cues through which animals choose their first, and sometimes only, breeding habitat have been proposed. However, their nature is determined by the fitness consequences in the chosen habitat. This determines whether following the cues is an adaptive behaviour, a merely behavioural pattern, or even maladaptive. Habitat imprinting may reduce search and evaluation costs because using the natal habitat type as a search image helps to spot and identify suitable habitats. This mechanism is known as 'habitat cueing' (Davis, 2004). The 'habitat training hypothesis' suggests that natal-like habitats may enhance survival and reproductive success by providing the necessary foraging skills, physiological adaptations, or immunological benefits acquired in early life (Davis, 2004; Sol et al., 2003; Stamps, 2001; Stamps & Davis, 2006).

When identifying a high-quality habitat, the presence of conspecifics or local population density can be a reliable source of information (Clobert et al., 2009; Fuller, 2012; Stamps, 2001). Conspecific attraction can lead, as mentioned earlier, to shorter natal dispersal distances. However, the innate quality of the habitat is inevitably affected by the presence of conspecifics (Fretwell & Lucas, 1969). A higher density of conspecifics can directly reduce breeding success by increasing interference competition (Lack, 1954), thereby lowering the population's reproductive success across all habitats. High density can also have indirect effects on individuals by forcing recruits to settle in lower-quality habitats, where their breeding success may be lower (the habitat heterogeneity hypothesis). These mechanisms are not mutually exclusive. After a certain density threshold, determined by the habitat's carrying capacity, it may be better for an individual to settle in a less optimal, but less crowded, habitat (Stamps, 1991) or delay recruitment to a later point in life (Stearns, 1998).

In a long-lived species, it must be considered that the potential effects of habitat imprinting or conspecific density on fitness may change with the individual's age. It is a common pattern that breeding success of individuals increases with age, reaches a plateau, and sometimes decreases again due to senescence (Forslund & Pärt, 1995). Older individuals are usually more successful and productive breeders (Forslund & Pärt, 1995; Sæther, 1990) which in a population could be due to better survival or delayed breeding of high-quality individuals or an individual gaining experience or improving in skills and abilities with age (Daunt et al., 1999; Fowler, 1995; Forslund & Pärt 1995; Laaksonen et al. 2002). There can also be an increase in reproductive effort with age, as life history theory predicts that older individuals should invest more than younger ones because of lower residual reproductive value (Williams, 1966).

1.6 Aims of the thesis

In this thesis, I investigated natal dispersal and habitat selection patterns of a long-lived raptor, the white-tailed eagle (*Haliaeetus albicilla*), using both genetic and visual identification of breeding individuals. The objective was to examine which factors affect the choice and settlement of the first breeding site for a species that rarely switches breeding sites thereafter. I also wanted to investigate the association between these factors and the subsequent breeding success. Due to challenges in tracking long-lived species with delayed maturity, neither natal dispersal nor the habitat imprinting behaviour of large raptors is well known.

In **Chapter I**, I use a dataset of identified individuals with known natal and breeding sites to calculate natal dispersal distances and utilise long-term monitoring data to determine whether the number of active territories (local breeder density) in individuals' natal areas is associated with natal dispersal distance.

In **Chapter II**, I compare the natal and breeding habitats of the identified white-tailed eagle individuals. I define habitat composition as the proportion of water area and calculate it for both the natal and breeding sites of individuals to determine whether eagles imprint on their natal habitat and show a preference for a similar habitat type when choosing their breeding habitat.

In **Chapter III**, I combine the individual identification and long-term monitoring datasets to compile nesting histories for the identified individuals and investigate whether local breeder density and the similarity between breeding and natal habitats affect breeding success and productivity. In addition, I investigate the association between breeding success and habitat type, the age of breeding individuals, and the timing of breeding.

2 Materials and Methods

2.1 Study species

The white-tailed eagle is a large bird of prey which is widespread in the northern Palearctic (Christie & Ferguson-Lees, 2010). It is a generalist top predator inhabiting a wide range of coastal and lakeside environments (Ekblad et al., 2020; Ekblad et al., 2016; Radović & Mikuska, 2009; Sulkava et al., 1997; Treinys et al., 2016). White-tailed eagles defend a small nesting territory within a larger home range, which can overlap with other pairs (Krone et al., 2009, 2013). A breeding pair can have one or more alternative nests within a territory, and territories are also defended outside the breeding season (Krone et al., 2013). They exhibit high breeding site fidelity (Nebel et al., 2024; Whitfield, Douse, et al., 2009). They have a long sub-adult phase and reach sexual maturity at 4–6 years of age (Struwe-Juhl & Grünkorn, 2007). The actual start of breeding can take even longer. Broods usually have one or two nestlings, sometimes even three.

White-tailed eagle was almost driven to extinction in Europe by heavy persecution in the 1800s and early 1900s (Hailer et al., 2006; Högmander et al., 2020; Saurola et al., 2013). The species was later protected by legislation but began suffering from environmental pollution, especially Dichlorodiphenyltrichloroethane (DDT), which impaired breeding ability in the 1950s - 1970s (Helander et al., 2008). At its lowest point, the population in Finland consisted of only few nesting pairs with poor breeding success (Högmander et al., 2020; Saurola et al., 2013). Extensive conservation efforts and the ban on DDT facilitated the recovery of the white-tailed eagle. In 2025, the Finnish population exceeds 700 known active territories (Osprey Foundation, unpublished data).

2.2 Study area and field procedures

In Finland, the majority of the breeding population is situated in the archipelago and along the coastal areas, but also in Lapland and near large inland water bodies (Fig. 1). The core population areas are the Åland Islands, the Archipelago Sea in Southwest Finland, and the Kvarken area. I studied the entire Finnish population in chapter I. In chapters II and III, I included only coastal and non-arctic inland areas (Fig. 1).

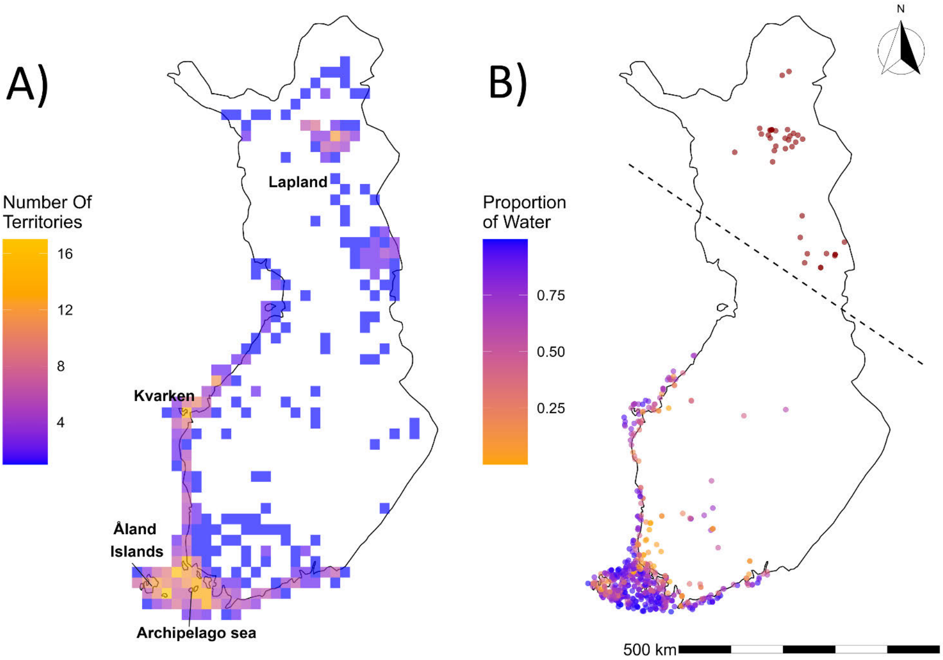

Figure 1. A) Distribution of the white-tailed eagle territories in Finland. Colours indicate the number of active territories within 20 x 20 km grid cells, with low densities in violet and high densities in orange. All territories that were active at least once between 2020 and 2024 are included. The core areas of the population are the Archipelago Sea, Åland Islands, and the Kvarken area. B) All the white-tailed eagle territories studied in this thesis, including natal territories, observed breeding territories and assumed breeding territories of the identified individuals. Territories across Finland were considered in chapter I, and territories below the dashed line were considered in chapters II and III. The colour of these territories indicates the proportion of water area within each territory, with high proportions shown in violet and low proportions in yellow.

Systematic Finnish white-tailed eagle population monitoring was initiated in the 1970s, when the population was near extinction (Lokki et al., 2024; Stjernberg & Koivusaari, 1995). Since then, all known nest sites have been checked annually by the volunteers of the white-tailed eagle working group (operating under WWF Finland 1973 – 2019 and under the Osprey Foundation since 2020) every spring. New nests are also actively searched for, and their exact coordinates are recorded with GPS devices. The volunteers report the status and breeding outcome of the nests: unoccupied (no signs of eagle presence), unsuccessful (clear signs of nesting initiated but no nestlings), or successful (produced nestlings). Brood size is recorded, and, when possible, nestlings are ringed with two metal rings. One has an engraved 5-digit individual ID code, and the second has a larger, shorter unique alphanumeric code allowing adult identification from a distance. Photos of parent birds are taken during monitoring visits to facilitate ring reading. Since 2003, feather samples have been collected for DNA identification. Two to three feathers are plucked from the back of each ringed nestling, and the nests and their surroundings are searched for shed adult feathers.

2.3 DNA extraction and genotyping

Laboratory procedures were carried out by the Centre of Evolutionary Applications (CEA) at the University of Turku. DNA was extracted from 1,764 nestling feathers (one per nestling) collected between 2008 and 2016 and 2,896 adult feathers (one per nest per year) collected between 2012 and 2024. Different year ranges were chosen for nestlings and adults to allow individuals time to recruit to the breeding population.

Nestling and adult feathers were prepared for DNA extraction by cutting a small piece (approx. 0.5 cm) from the basal tip of the calamus. DNA extraction from the nestling feathers was done with a silica fine and filter-based method modified from Elphinstone et al. (2003). DNA from adult feathers was extracted using a salt-extraction method modified from Aljanabi & Martinez (1997). Samples were genotyped using 14 loci. The following 13 were used for individual identification: Hal-01, Hal-07, Hal-09, Hal-03, Hal-13, Aa-27, IE-12, Hal-04, Hal-05, IE-04, Hal-06, Aa-11, IE-11 and Hal-14. One locus was used for sexing (Hailer et al., 2006; Ponnikas et al., 2013; Dawson et al., 2015). 784 existing nestling genotypes from the years 2003 – 2007 (Ponnikas et al., 2013) were used. This dataset included allele sizes for 9 loci: Hal-01, Hal-03, Hal-04, Hal-05, Hal-06, Hal-07, Hal-09, Hal-13, and Hal-14. Details of the DNA extraction success rate are presented in Table 1.

Table 1. The success rate of DNA extraction from the feathers of adult and nestling white-tailed eagles. Samples were genotyped with 14 microsatellite markers: 13 for individual identification and 1 for sexing. Successful extraction means that any number of markers were obtained, and failed extraction means that no markers were obtained. Full genotype refers to samples from which all 13 markers used for identification were obtained. Samples that provided at least 9 markers were used in the analysis.

Sample type	Adult		Nestling	
	n	%	n	%
Total	2896	100	1764	100
Extraction successful	2765	95,5	1725	97,8
Extraction failed	133	4,6	40	2,3
Min. 9 markers	2643	91,3	1705	96,7
Full genotype	2268	78,3	1576	89,3

2.4 Individual identification by genotype matching

I used genotype matching to identify nestlings that had recruited into the breeding population (Fig. 2). Adult genotypes were screened against nestling genotypes using Cervus 3.0.7 software (Kalinowski et al., 2007), with a minimum of 9 matching loci and allowing for one mismatch. Matching adult and nestling genotypes reveals the natal nest (where the nestling is ringed and sampled) and breeding nests (where the adult feathers have been collected) of the individual. Identification based on genotypes was supplemented with ring-readings from photographs of adults at nest sites during monitoring. These were obtained from the ringing office operating under the Finnish Natural History Museum (LUOMUS).

The nesting history of individuals for chapter III was compiled from identification and long-term monitoring data. The gaps between confirmed identifications were filled using the monitoring data. For example, if an individual was identified in a territory in 2010 and 2015, the status and breeding outcomes from that territory in 2011 – 2014 were assumed to be of this individual and included in the data. Since white-tailed eagles are territorial and exhibit very high breeding-site fidelity (Nebel et al., 2024; Whitfield et al., 2009), I consider it reasonable to assume that the same individual occupied that territory between the two confirmed identifications.

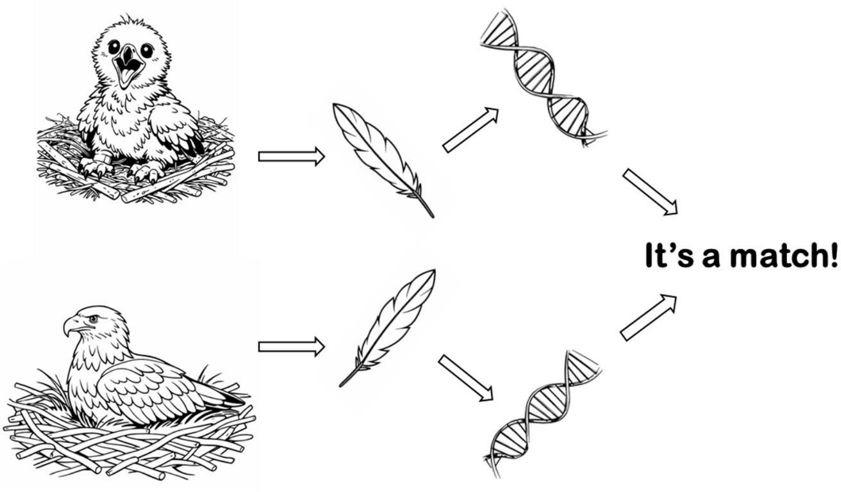

Figure 2. Illustration of the process of identifying breeding individuals and their natal nest by genotype matching

Each confirmed (individual identified) or assumed (supplemented from monitoring data) breeding attempt was scored as successful ('1') if it had produced ringing-aged nestlings and otherwise failed ('0'). The number of nestlings (1–3;

hereafter, productivity) was reported for each successful breeding. Since the proportion of breeding events that produced three nestlings was very small (4% of successful breeding attempts), broods with two or three nestlings were pooled and coded as '1', whereas one-nestling broods were coded as '0'. The ages of nestlings were estimated based on the wing length at the time of ringing from a wing growth curve (Helander, 1981), and hatching date (Julian day, 1 = 1st of March) calculated based on this. Hatching date was used to describe the timing of breeding.

2.5 Natal dispersal distance and local breeder density

I measured natal dispersal distances as the geodesic distance (km) between the coordinates of the natal nest and the nest where the same individual was first detected as a breeding adult. Breeding dispersal is rare in the white-tailed eagle (Nebel et al. 2024), and thus it is safe to assume that the site of first detection is also the site of the first breeding attempt.

The local breeder density was measured as the number of active territories. The territory was defined as active if any of the nests within that territory had any signs of eagle presence (at least some new nest material brought in). I calculated the breeder density within a 30 km radius of the natal nest in the expected recruitment year (birth year + 5, chapter I), within a 10 km radius around the natal site and the first breeding site in the expected recruitment year, as well as the absolute difference between these density values (I), and within a 10 km radius from the breeding nest for each breeding attempt (III). I also calculated the expected density difference (I) for each individual by extracting the active territories within the actual observed natal dispersal distance from their natal nest, calculating the density within a 10 km radius for each of these and subtracting the natal site density from the average of these densities.

The 30 km radius was chosen based on the median natal dispersal distances found in this study (I). The 10 km buffer corresponds to the maximum mean home range for territorial adults (Krone & Treu, 2018). Even though the actual areas defended by the eagles are much smaller than a 10 km radius, they can still utilise areas this large when, for example, foraging, and are, therefore, likely to interact with other eagles residing within this distance. I used a fixed year of expected recruitment, since at this time, the white-tailed eagles can be assumed to have reached sexual maturity and started looking for a mate and territory (Struwe-Juhl & Grünkorn, 2007)and the year of first detection may not coincide with the first breeding attempt, despite the high monitoring efforts in our population.

2.6 Habitat characteristics & similarity

Habitat composition in the territories was characterised by the proportion of water area (including sea, lakes, and rivers) within each territory. Water area is a coarse landscape-scale characteristic that can be assessed in flight, the type of which the choice of the very first breeding territory and the initial identification of potential habitats most likely rely on (Fuller, 2012). It describes well the location of the nest on the gradient from inland territories (0% water) to territories in the outermost archipelago (99% water). It also has ecological significance as a predictor of diet composition (Ekblad et al., 2016) and remains stable over time, which is fitting for a long-term study. A territory was defined as a circular area around the nest with a radius of 2 km, which was selected to effectively characterise the landscape where the eagle is nesting (Krone et al., 2009; Krone & Treu, 2018). The water area variable was extracted from the CORINE land cover 2018 data (Härmä et al., 2019).

To quantify the level of similarity between natal and breeding sites, I calculated the absolute difference in water proportion between those territories. I transformed the resulting values into positive (absolute) differences. Finally, I subtracted the differences from 1, so that higher values correspond to higher similarity. The habitat similarity was calculated between natal territory and the first breeding territory (I), between natal territory and alternative available territories within 65 km of the natal nest (II), and between natal nest and each nest an individual had been identified or assumed to be nesting in (III). Available territories considered were existing white-tailed eagle territories that were established at the individual's expected settlement year (birth year + 5) or the subsequent year.

2.7 Statistical analysis

All analyses were performed in R v.4.1.3 (R Core Team, 2019). I used linear mixed models (LMM) and generalised linear mixed models (GLMM) to investigate the effects of local breeder density (I) and habitat similarity (II) on the settlement and habitat selection behaviour, and how these factors, as well as habitat composition and age of the breeder, might reflect on the reproductive performance (III) of the white-tailed eagles.

In chapter I, I used an LMM to explore how natal dispersal distance was affected by natal area breeder density, sex and the year of expected recruitment. In a second LMM, the difference between breeding and natal area density was the response variable, and natal area breeder density and expected recruitment year were the explanatory variables. The expected density difference was included as a control variable. Natal territory ID and expected recruitment year were included as random effects in both models to account for potential non-independence of observations from the same year and same territory.

In chapter II, I used a GLMM of the beta family to test whether the proportion of water area around the natal nest predicted the proportion of water around the first breeding nest. In a second GLMM (beta family), I assessed whether the similarity of natal and breeding habitats was influenced by natal dispersal distance and sex. The beta family was used in these models because it is suitable for data that is skewed towards maximum values and bounded between zero and one. However, since beta models cannot handle boundary values (exact zero or one), a correction proposed by Cribari-Neto and Zeileis (2010) was applied to the response variables. The expected settlement year was included as a covariate in both models to account for potential temporal trends driven by population growth. The third model was a binomial GLMM to test whether chosen first breeding territories (1) were more natal-like than other available territories in the same general area (0). The explanatory variable was habitat similarity. The number of available territories per individual was added as a covariate because it varied among individuals and affects the probability of a territory being chosen. In all models, natal territory ID and expected settlement year were included as random effects. In the binomial model, individual ID was also added as a random effect.

In chapter III, I used two binomial GLMMs to explore how habitat similarity, habitat composition, local breeder density, and individual age affect breeding success and productivity. The first model had breeding success (0 = fail, 1 = successful) as the response variable, and the second model had productivity (number of nestlings; 0 = 1 nestling, 1 = 2 or 3 nestlings) as the response variable. The explanatory variables for both models were habitat similarity, local breeder density, individual age, and water area in the breeding territory. Breeding year and latitude were included as covariates to account for potential temporal and spatial trends. Hatching date (scaled separately for each year) was included as a covariate in the productivity model. It was not possible to include it in the breeding success model, as this is available only for successful breeding events in which nestlings are ringed and measured. Individual ID was included as a random effect in both models to account for pseudoreplication and potential between-individual differences in breeding success.

3 Results & Discussion

3.1 Natal dispersal distance (I)

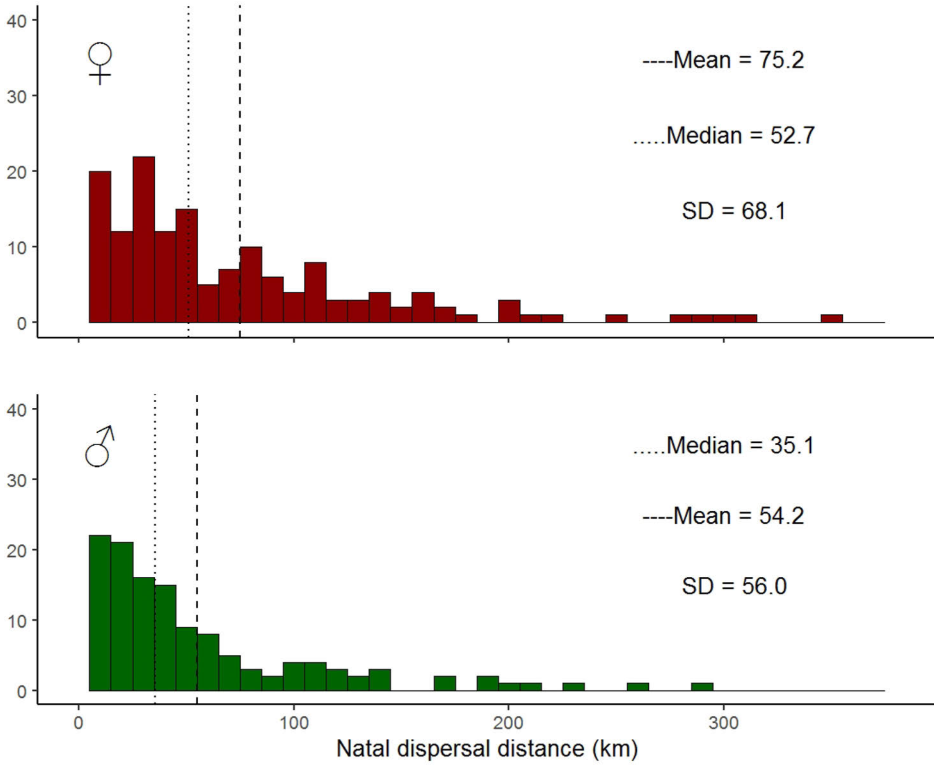

Figure 3. Distributions of natal dispersal distances of white-tailed eagle females (top) and males (bottom).

In chapter I, I show that white-tailed eagles return to breed close to their natal area, even though the range of natal dispersal distances is large. Natal dispersal distances ranged from 2.4 to 352.3 km, with females dispersing farther than males (fig. 3). The median distance was 51.5 km for females, 35.5 km for males (Fig. 3) and 43.2 km for all individuals. The distribution of natal dispersal distances is strongly skewed towards shorter distances, and the occurrence of long-distance dispersal is relatively rare. Similar patterns have been found in numerous natal dispersal studies in raptors (e.g. Limiñana et al., 2012; Morton et al., 2018; Passarotto et al., 2022; Steenhof & Heath, 2013) and other species (Carle-Pruneau et al., 2022; Martin et al., 2008; Morton, 1992; Wheelwright & Mauck, 1998). Natal dispersal distances did not change during the study period.

Individuals are inevitably lost when the study area is limited. However, eagles born on the coast of Finland, especially on the Åland Islands, can find suitable breeding territories on the Swedish side of the Baltic Sea without moving longer than average distances. Therefore, dispersers are lost across all distances, and the dispersal distance distribution presented here likely gives a fairly accurate reflection of dispersal behaviour and distances of the white-tailed eagle.

3.2 Local breeder density affects settlement (I)

Local breeder density in the natal area in the year of expected recruitment significantly affected the settlement behaviour of the white-tailed eagle. White-tailed eagles settle in higher-density areas in comparison to their natal area when they originate from relatively low-density areas, as opposed to the highest-density areas, from where the eagles will settle in a lower-density area (Fig. 4B). Individuals born in high-density areas, however, dispersed over shorter distances than those originating from a low-density natal site (Fig. 4A).

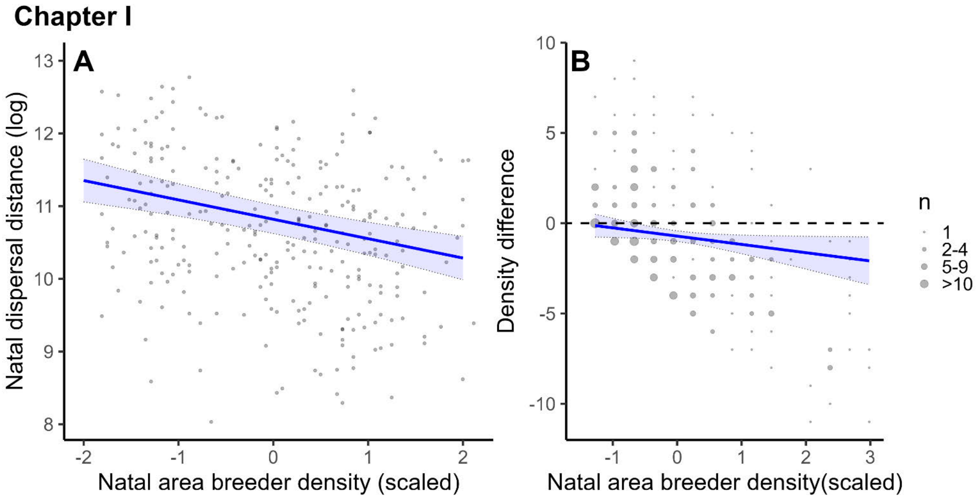

Figure 4. Main results of chapter I. The association between natal area breeder density and natal dispersal distance (A) and between natal area breeder density and the density difference between natal and breeding site (B). Regression lines depict model predictions and shaded areas the 95% confidence intervals.

The results indicate both negative and positive density dependency. Settlement in higher-density areas when the natal site density is low could be in line with the conspecific attraction hypothesis, meaning that eagles can use social information to identify high-quality breeding sites (Clobert et al., 2009). The presence of conspecifics can reduce the costs of detecting and evaluating suitable breeding sites. The attraction towards higher densities can also be due to the prospecting of mates. Natal dispersal distances were longer when the natal site density was low, which could mean that longer travels are needed from low-density areas to find a mate. This has been shown in translocated sub-adult Spanish imperial eagles (*Aquila adalberti*), which despite an advantageous competitive environment, left the translocation area to explore breeding populations over 100 km away (Muriel et al., 2016).

In line with negative density-dependency, I found an indication that areas of the highest density of conspecifics are keeping new white-tailed eagles from settling there, causing them to settle in lower-density areas instead. However, the rather short dispersal distances from high-density natal territories indicate that those individuals move short distances, for example, to the edge of high-density areas or into pockets of lower breeder density in between high-density areas rather than disperse over large distances. Negative density-dependence can be caused by intraspecific competition. White-tailed eagles are territorial and regularly engage in territorial fights (Isomursu et al., 2018; Saurola et al., 2003; Stjernberg et al., 2003). At low densities, this intraspecific competition might occur less frequently than at higher densities. The lack of temporal trend in dispersal distances despite the population growth also tells us that white-tailed eagles might have occurred in high densities at specific hotspots and expanded their ranges continuously from there, leading to an increased variation in local breeder densities and an overall consistent natal dispersal behaviour in relation to local breeder densities over time. This could also indicate that population saturation is occurring locally.

Shorter natal dispersal distances from higher-density areas may be associated with habitat quality (Briggs et al., 2012; Swift et al., 2021). It has previously been observed that the home ranges of white-tailed eagles are smaller in optimal habitats (Krone et al., 2013). Thus, high-quality habitats can support higher densities. In such habitats, finding a good territory with less competition may not require moving as far as in lower-quality habitats. In my dataset, the median age of individuals at the first observation as breeders was 10 calendar years, which is relatively high given a maturation age of 4–6 cy. This could indicate that many individuals adopt a floater strategy, in which they postpone breeding to wait for good territories to become vacant (Cooper et al., 2009; Ferrer et al., 2004; Katzenberger et al., 2021). This has been speculated to be one of the reasons for negative density-dependence in raptor dispersal: individuals choose to remain as floaters rather than dispersing over long distances in search of a good territory or settling for a worse one (Penteriani et al., 2011; Penteriani & Delgado, 2009). It is important to note, however, that age at first breeding in our data is, to an unknown extent, an overestimate because it is not always clear when exactly a nest was built, or the breeding career started.

3.3 Local breeder density affects breeding success (III)

In addition to being associated with the natal dispersal distances and settlement behaviour, I found in chapter III that local breeder density is associated with the breeding success of the white-tailed eagles, but not with productivity. Breeding success decreased with increasing local breeder density (Fig. 6A). Other studies of density-dependent reproductive success of the white-tailed eagle have reported larger (Krüger et al., 2012) or smaller brood sizes associated with higher density (Heuck et al., 2017) or no effect of density (Dementavičius et al., 2022). The differences could be due to different stages of population recovery and the population's saturation level, which are affected by the overall carrying capacity. As for productivity, growing density could increase the proportion of failed breeding attempts, but not affect the average productivity of successful ones (Fasce et al., 2011; Sternalski et al., 2013), or affect the physical condition of the nestlings (Byholm et al., 2007; Dementavičius et al., 2022; Nebel et al., 2023).

Based on these results, it is difficult to confirm the mechanism behind density-dependent reproductive success. However, it seems that it is beneficial for white-tailed eagles to select nesting sites from lower-density areas. The benefits do not seem to be habitat-dependent, since there was no interactive effect of water area and density. The tendency to engage in territorial fights, which take time and energy, forces parents away from their nests and reduces survival (Isomursu et al., 2018; Krone et al., 2013; Saurola et al., 2003; Stjernberg et al., 2003). This points towards the interference hypothesis, according to which increasing interference competition directly reduces breeding success. However, it is difficult to say whether the movement towards lower-density areas to breed is due to active avoidance of competition, local saturation forcing individuals elsewhere (the habitat heterogeneity hypothesis), or both. A population-level examination of the association between population density and the mean and variance of breeding success in Spanish imperial eagles provides support for the habitat heterogeneity hypothesis (Ferrer & Donazar, 1996).

3.4 Habitat imprinting affects settlement, not breeding success (II, III)

The results in chapter II show that the proportion of water in the natal territory is positively associated with the proportion of water in the breeding territory.

Individuals born in territories with a large proportion of water were more likely to breed in territories with a large proportion of water, while those from territories with a lower proportion of water tended to settle in areas with lower water coverage (Fig. 5A) The level of similarity was not associated with natal dispersal distance (Fig. 5B), suggesting that habitat similarity is not merely a by-product of spatial proximity. Individuals showed a preference for territories that resembled their natal sites among available suitable territories within the same general area (Fig. 5C), supporting the role of habitat imprinting in breeding habitat selection.

Chapter II

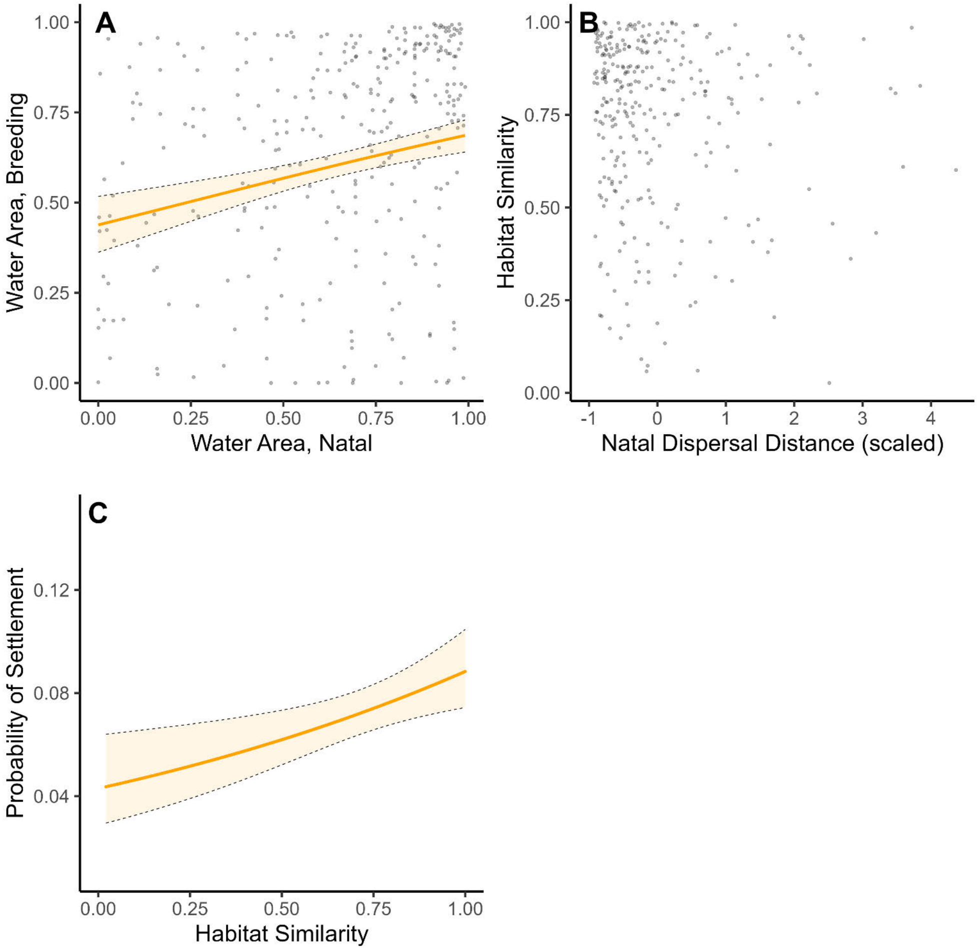

Figure 5. Main results of chapter II. The associations between water area in the natal and breeding sites (A), between natal dispersal distance and habitat similarity (B) and habitat similarity and the probability of a territory being settled in (C). Regression lines depict model predictions and shaded areas the 95% confidence intervals.

However, the results of chapter III reveal that habitat similarity is not associated with breeding success or productivity. This result indicates that white-tailed eagles do not gain reproductive benefits by settling in a natal-like habitat to breed (III). Habitat imprinting does not necessarily lead to the most fitness-maximising choice if other cues signalling high-quality habitats are ignored or unfamiliar (Piper et al., 2013; Tims et al., 2004). However, since there seems to be no negative association between natal habitat preference and breeding success either, it is possible that habitat imprinting is a neutral behavioural pattern, or that the benefits are gained in other ways, for example, through better lifetime reproductive success, increased survival or faster settlement (Brown et al., 2008). By choosing a breeding site with natal habitat characteristics, eagle individuals could improve their own as well as their offspring's resilience to local pathogens (Minias et al., 2021). Natal-habitat type could, in any case, serve as a search image for a suitable breeding habitat, and it could, at the very least, help to avoid completely unsuitable habitats (Chalfoun & Schmidt, 2012).

Familiarity with the habitat and its characteristics starts accumulating quickly (Piper, 2011). As mentioned earlier, the age at first breeding in our dataset appears relatively high. One advantage of the floater strategy could be gaining familiarity with some subset of habitats and a competitive foothold when those become vacant (Piper, 2011; Zack & Stutchbury, 1992). White-tailed eagles have a vagrancy period lasting several years before sexual maturation and the start of breeding (Whitfield, Duffy, et al., 2009). Subadult and non-breeding adult eagles roam over vast distances (Balotari-Chiebao et al., 2018; Eskildsen et al., 2024; Halgunset, 2024) and thus have plenty of time and opportunities to encounter different types of habitats.

Experience in the natal habitat can increase the preference for similar habitats in later life stages, but it does not mean that individuals would always choose similar habitats (Stamps, 2001). It could simply be that there are no natal-like habitats available for all individuals, or there is variation in individuals' ability to compete over such habitats (Fuller, 2012). Individuals may adapt to different environments due to necessity or opportunity. This behavioural flexibility is essential for range expansion, as it allows populations to colonise new areas and habitats. While habitat imprinting induces a preference for natal-like habitats, the broader concept of NHPI holds that experience in the natal habitat can also lead to avoidance of such habitats (Fletcher et al., 2015; Milleret et al., 2019). It can be caused by characteristics of the natal habitat (Milleret et al., 2019) or by negative early-life experiences, such as severe weather conditions during time spent in the natal habitat (Fletcher et al., 2015).

3.5 Habitat-dependent breeding success (III)

Habitat composition plays a greater role in the reproductive performance of white-tailed eagles than similarity to natal habitat. Eagles nesting in territories with a smaller proportion of water have a higher probability to breed successfully (Fig. 6B). The general landscape structure could contribute to this if the conditions in territories with a large proportion of water area are, all in all, harsher and nest sites less sheltered. Our results contradict the findings of Heuck et al. (2017) in Germany, where the breeding success of white-tailed eagles increased with increasing water surface area around the nest sites. This probably reflects general differences in the habitats of white-tailed eagles in Finland and Germany.

White-tailed eagles breed earlier in territories with a smaller proportion of water (Nebel et al. 2023), and earlier breeding is commonly associated with better breeding success (Klomp, 1970). The white-tailed eagle diet is habitat-dependent; in territories with a large proportion of water and a mostly bird-based diet (Ekblad et al. 2016), food availability is likely affected by the timing of waterfowl migration, potentially resulting in less stable food sources. More land-based territories might have a higher diversity of alternative prey options (Byholm et al., 2007; Kujala et al., 2024; Lõhmus & Väli, 2004; Sumasgutner et al., 2019), which could be utilised during a shortage of preferred prey, for example, early in the breeding season, when prey availability is not yet at its peak. These habitats also potentially provide additional anthropogenic food sources, such as feeders, hunting carcasses, or fish left by fishers, which are especially beneficial outside the breeding season. This could help eagle individuals stay in the vicinity of their territories year-round (Krone et al., 2013) and help females reach the body condition needed to start breeding earlier.

The proportion of water area was not associated with productivity. A Lithuanian study found that white-tailed eagle brood sizes did not differ across habitats, but nestling body condition was better in habitats with shallow, fish-rich waters (Dementavičius et al., 2022). Nebel et al. (2023) have also shown that early-life diet composition affects the physical condition of nestlings. Habitat composition has been shown to affect nestling condition also in northern goshawks (*Accipiter gentilis*) (Byholm et al., 2007).

When investigating habitat-dependent fitness, it is challenging to distinguish between the quality of the habitat and the quality of the individual inhabiting it. Individual ID as a random term explained a large portion of the variation in breeding success (III). In peregrine falcons (*Falco peregrinus*), individual quality has been shown to explain variation in breeding success better than territory quality (Zabala & Zuberogoitia, 2015). If the habitats with better breeding success, like habitats with more land cover, are assumed to be the most optimal for white-tailed eagles, the highest-quality individuals may be able to occupy and defend them.

3.6 Age-dependent breeding success (III)

A study in Scotland found that breeding success and productivity of white-tailed eagles improved with age, but also showed a decline starting already between ages of 14 – 20 years (Murgatroyd et al., 2018). I also found that breeding success of the white-tailed eagles improved with age (Fig. 6C) but did not show signs of later decline. This could be due to the small sample size of individuals older than 20 calendar years and the lack of very old individuals in my data.

Older birds of prey are more efficient at hunting and feeding nestlings, deliver a greater mass of prey and are better at utilising alternative prey than young individuals (Byholm et al., 2011; Rutz et al., 2006; Sasvári et al., 2000). I did not find any indication of the effect of age being sex-specific (Murgatroyd et al., 2018). Males and females have different roles in parental care (Møller & Nielsen, 2014; Sonerud et al., 2014), and increased experience in both may contribute to higher breeding success.

3.7 Timing of breeding & productivity (III)

Productivity was only affected by the timing of breeding, with the probability of producing more than one nestling being higher in earlier broods (Fig. 6C). This same pattern has been observed in white-tailed eagles by Nebel et al. (2023), and it is also well established across bird taxa (Klomp, 1970; Verhulst & Nilsson, 2007). This pattern is attributed to the overall breeding conditions deteriorating towards the end of the season, or better-quality individuals managing to breed earlier (Grüebler & Naef-Daenzer, 2010).

To keep the disturbance to nesting white-tailed eagles minimal, nest sites are usually visited only once when the nestlings are of ringing age. This means that the original clutch size or the number of fledglings is unknown. The incubation and early nestling periods have been identified as the time when breeding failure occurs most often (Newton, 1979). The time of the young becoming independent can also be a critical period (Newton, 1979). If the number of nestlings changes before or after the visit to the nest, it will not show up in our data. If the variables of interest have the greatest effect during incubation or the early nestling period, disturbances to nesting appear in our data as failed breeding attempts, not as smaller brood sizes.

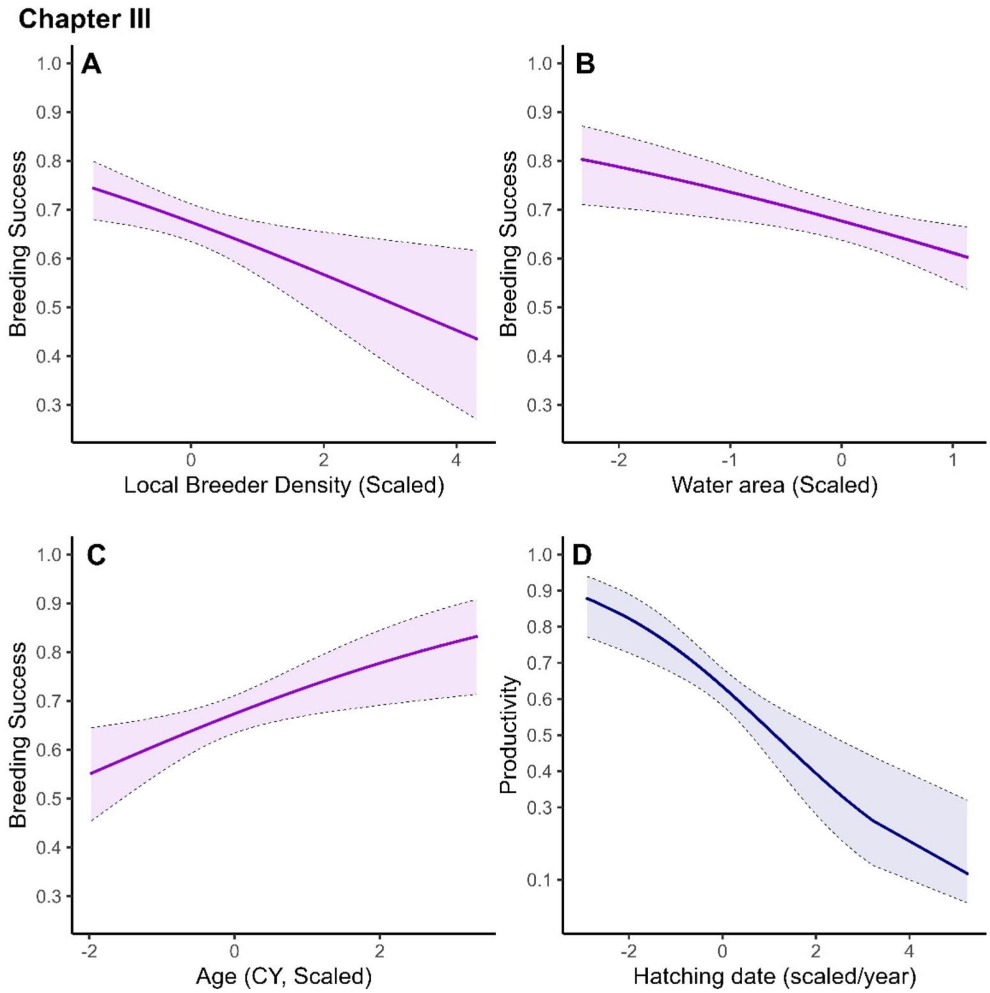

Figure 6. Main results of chapter III. The associations between local breeder density (A), water area in the territory (B), and age of the breeder (C) on breeding success. The association between hatching date and productivity (D). Regression lines depict model predictions, and the shaded areas the 95% confidence intervals.

3.8 Population patterns

Settlement patterns identified in this study are reflected in the population and range history of Finnish white-tailed eagles. Between 1989 and 2024, the number of known active territories in Finland increased from about 70 to over 700 (Osprey Foundation, unpublished data). The Finnish white-tailed eagle population has undergone a bottleneck. At its lowest point, the eagles were breeding mostly in three coastal regions: the Åland Islands, the Archipelago Sea near mainland Finland, and the Kvarken region near the Bothnian Bay. The range expansion began from these three points, which are still areas with the densest population. After the population started recovering, it took several decades for individuals to establish breeding territories further inland. In recent years, the proportion of the population breeding far away from the coastline has been increasing (Lokki et al., 2024). A combination of habitat imprinting and site fidelity may have initially hindered inland colonisation, but once pioneering individuals settled in these areas, habitat imprinting likely helped sustain and increase the inland population. The population of Finnish Lapland was included only in chapter I. This part of the data shows that there has so far been no dispersal between the Lapland population and the population in the rest of Finland (unpublished data).

4 Conclusions

In this thesis, I have studied factors affecting the settlement of white-tailed eagles on their first breeding site and the subsequent breeding success. Chapter I shows that settlement can be positively or negatively density dependent, depending on the natal area density. The inclusion of settlement site density reveals novel insights into the complexity of the process. Chapter II reveals the role of natal habitat imprinting as a driver of settlement behaviour, while also hinting at behavioural flexibility. In chapter III, I show that cues used during settlement at the first breeding site do not necessarily lead to better performance. The breeding success of individuals choosing natal-like breeding sites is similar to that of individuals choosing natal-unlike ones. Local breeder density and habitat type do affect the reproductive performance.

Based on my findings, it seems that white-tailed eagles can utilise several features of the environment as cues when choosing their first (and possibly only) breeding site. These features differ in how well they predict the fitness in the given habitat. While the density of breeding conspecifics in an area can pinpoint a site of high quality as well as high competition, similarity to natal habitat at best separates suitable habitats from unsuitable ones. Even if the choice of a natal-like breeding site does not maximise breeding success, there is no indication of negative effects on it. Habitat imprinting, therefore, is not maladaptive. Either it affects fitness in some way other than breeding, or it is a neutral behaviour. However, recognising the influence of habitat imprinting is important for reintroduction efforts where habitat suitability assessments should consider the natal habitat preferences of translocated individuals.

In the end, it comes down to the essentials: fitness potential offered by different habitats and the quality of individuals inhabiting them. In addition to clear patterns, I also found substantial variation in the data. Despite the patterns found, it is clear that the white-tailed eagle is behaviourally flexible and able to adapt to diverse habitats. Flexibility has ensured the growth and expansion of this once-almost-extinct population to the point where it is simply thriving

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