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RESEARCH ARTICLE

Habitat imprinting in breeding territory selection of a long-lived bird of prey

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Abstract

1. Habitat imprinting is the phenomenon where exposure to cues in the natal habitat increases the probability of choosing a habitat with similar cues later in life. It is considered a key behavioural mechanism that decreases the costs associated with habitat selection. The similarity of breeding to natal habitats can be especially beneficial when choosing the first breeding site and when the choice has long-term consequences due to high site fidelity. Habitat imprinting in breeding habitat selection has rarely been documented in wild animals living in unmanipulated environments and is challenging to study in long-lived species with delayed maturity.
2. We used a combination of genetic and visual identification to identify 354 white-tailed eagles *Haliaeetus albicilla* hatched between 1991 and 2015 that were subsequently documented breeding between 2001 and 2023 along the Baltic Sea coast or in the inland environments.
3. We examined (a) the similarity of natal and breeding habitats and (b) the effects of natal dispersal distance on this similarity. Furthermore, (c) we were interested in breeding habitat selection and tested whether eagles showed a preference for natal-like habitats among suitable territories that were at the time still unoccupied.
4. We found that breeding habitats were similar to natal habitats, independent of natal dispersal distance. Eagles were also more likely to choose a natal-like breeding site among available alternative sites. These results indicate that habitat imprinting is a possible driving mechanism in the habitat selection of long-lived animals with delayed maturity and has important implications for conservation actions such as eagle reintroduction programmes.

KEYWORDS
ecological genetics, individual specialisation, microsatellites, Natal dispersal, Natal habitat preference induction, raptor

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Carina Nebel and Toni Laaksonen contributed equally to this work (shared senior authorship).

1 | INTRODUCTION

Mechanisms through which animals choose their breeding habitat are important for understanding population-level processes such as population structure, range dynamics and local adaptations (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 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, for example, result in individuals settling in natal-like habitats for reproduction (Davis, 2008; Piper, 2011) and has important implications for species conservation (Stamps & Swaisgood, 2007).

Breeding-site choice can have profound fitness consequences, especially for species with high breeding-site fidelity, since the consequences of the choice are potentially lifelong (Davis, 2004). When selecting a breeding habitat, animals typically lack complete information about the quality of available sites and not all habitats are equally suited for all individuals (Piper, 2011). Detecting and evaluating potential habitats can be both time- and energy-consuming (Clobert et al., 2009; Davis, 2004). Habitat imprinting may reduce search and evaluation costs by guiding individuals towards familiar conditions, a mechanism known as 'habitat cueing' (Davis, 2004). The similarity to the natal habitat might also provide information about habitat quality since the individual itself has survived to breeding age originating from the same kind of habitat (Stamps & Davis, 2006). In addition, the 'habitat training hypothesis' suggests that natal-like habitats may enhance survival and reproductive success through necessary foraging skills, physiological adaptations or immunological benefits acquired in their early life (Davis, 2004; Sol et al., 2003; Stamps, 2001; Stamps & Davis, 2006).

Preference for natal-like habitats has been documented in many animal groups, including birds (Camacho et al., 2016; Hildén, 1965; Sargent, 1965), insects (Ray, 1999; Rietdorf & Steidle, 2002) and fishes (Arvedlund & Nielsen, 1996). Most studies have been experimental studies conducted with insects in the laboratory or with passerine birds in aviaries or nest box systems (e.g. Grünberger & Leisler, 1990; Lewis & Tumlinson, 1988; Raach & Leisler, 1989). Many studies of passerines have found proof of NHPI or habitat imprinting as a mechanism of habitat choice and preference for natal-like habitat as behaviour learned in the rearing habitat (Camacho et al., 2016; Grünberger & Leisler, 1990; Klopfer, 1963; Sargent, 1965). A well-studied bird species is the common cuckoo *Cuculus canorus*, which has been shown to increase its probability of parasitising nests of its foster species by choosing a breeding habitat resembling their natal habitat. (e.g. Kolecek et al., 2020; Vogl et al., 2002; Yang et al., 2018). Studies in unmanipulated wild populations are still rare, and little is known about the effects of natal habitat in large-sized, long-lived species with delayed maturation. A likely reason is that studying this requires that both the natal and breeding sites of the individual are known, which can be challenging. Large-sized birds of prey are especially challenging to study due to their high mobility and often elusive behaviour.

The few existing studies on raptors have primarily focused on medium-sized species. Some studies have found indications of early-life habitat preferences (Faccio et al., 2013; Fletcher et al., 2015; Orgeret et al., 2024) while others have not (Delgado et al., 2010; Mannan et al., 2007). Spatial scales of these studies range from nest-site features (Faccio et al., 2013; Mannan et al., 2007) to broader habitat characteristics at the territory level (Orgeret et al., 2024) to the entire settlement area (Delgado et al., 2010). Studies also vary in whether habitats are divided into distinct types (Faccio et al., 2013; Fletcher et al., 2015; Mannan et al., 2007; Orgeret et al., 2024) or whether continuous habitat variables are used. Only one study examined the difference between sexes in the context of habitat imprinting (Mannan et al., 2007), even though dispersal behaviour (Greenwood & Harvey, 1982) as well as habitat selection and use (Parrish & Sherry, 1994; Sunde & Redpath, 2006) can vary between sexes. Most of these studies report natal dispersal distances (Delgado et al., 2010; Faccio et al., 2013; Fletcher et al., 2015; Mannan et al., 2007; Orgeret et al., 2024), but only a few report the effects of distance to habitat similarity (Fletcher et al., 2015; Orgeret et al., 2024). Two studies compared the similarity of chosen habitats to available alternative habitats suitable for the study species (Fletcher et al., 2015; Mannan et al., 2007).

In habitat selection studies, selected habitats are often compared to random sites to find biases towards certain habitat characteristics. Randomly sampled points inevitably include habitats that are unsuitable for breeding, making it difficult to assess whether imprinting genuinely influences settlement decisions, or whether the observed pattern just reflects the selection bias. We suggest that a more realistic and accurate approach is to compare the selected site to ones that have been available and vacant, but will later be occupied by other individuals, verifying the suitability of the site for the species. This can be done, for example, in a recovering population where suitable territories are first vacant but filled over time.

In this study, we investigate whether there is an indication of habitat imprinting in the initial breeding site choice of a large, long-lived bird of prey, the white-tailed eagle *Haliaeetus albicilla*. This species is a top predator of a wide range of coastal and lakeside environments (BirdLife International, 2023), preying on fish, birds and mammals (Dementavičius et al., 2020; Ekblad et al., 2016). White-tailed eagles exhibit relatively strong natal area fidelity despite their ability to move long distances during their pre-breeding years, with most individuals settling for breeding within 65 km from their birthplace (Penttinen et al., 2024). Males show stronger area fidelity than females (Penttinen et al., 2024), and parental care is asymmetrical between sexes, which is typical for most raptors (Sonerud et al., 2014).

The Finnish population has grown from only a few pairs to over 700 known pairs, and is estimated to be ca. 1000 pairs (Lehikoinen et al., 2025), in recent decades and has been carefully monitored since the population low in the 1970s (Lokki et al., 2024). A long-term monitoring programme, including genetic sampling of nestlings and adults since 2003, allows us to identify breeding individuals and match them with their natal territories. Given the known ecologically important variation in breeding territories in a highly variable archipelago, these data provide a rare opportunity to study habitat imprinting in a wild bird population.

Specifically, we ask (a) whether the first breeding sites of white-tailed eagles are similar to their natal habitats, (b) whether the similarity between the natal and breeding sites is influenced by the distance between them or is there a difference between sexes and (c) whether the chosen breeding sites are more similar to natal habitats than other suitable habitats available and later occupied by the species, and thus known with certainty to be suitable for breeding. As far as we know, this approach has previously not been used for any species, while we expect it to provide a stronger test of habitat imprinting than the examination of habitat choice from random points in the landscape.

2 | MATERIALS AND METHODS

2.1 | Study area and field data collection

The Finnish Baltic Sea white-tailed eagle population (Figure 1) has been monitored since the 1970s by the volunteers of the white-tailed eagle working group (operating under WWF Finland 1973–2019 and under the Osprey Foundation since 2020). All known nest sites are checked annually, and new nest sites are actively searched for. The exact coordinates of newly found nests are taken using GPS devices. Nestlings are ringed with two rings (Helander, 2000) and photos of parent birds are taken to facilitate ring-reading. To supplement information about recruitment, feather samples for genetic identification have been collected since 2003. Two to three feathers are plucked from the back of each nestling, and shed adult feathers are collected from the nest site (typically from the ground under the nest).

The collection of adult feather samples was licensed by the Centre of Economic Development, Transport and the Environment (VARELY/985/2016, VARELY/971/2018). Nestling feathers for DNA extractions were collected under licences from the Finnish Animal Experiment Board (ESAVI-201-05480/Ym 23, ESAVI/3221/04.10.07/2013, ESAI/3021/04.10.07/2017).

2.2 | Laboratory protocol and genotype matching

DNA was extracted from 1519 nestling feathers (one per nestling) collected between 2008 and 2015 and 2564 adult feathers (one per nest per year) collected between 2012 and 2023. Different year ranges were chosen for nestlings and adults to allow individuals time to recruit to the breeding population. Additionally, 784 existing nestling genotypes from the years 2003 to 2007 (Ponnikas et al., 2013) were used.

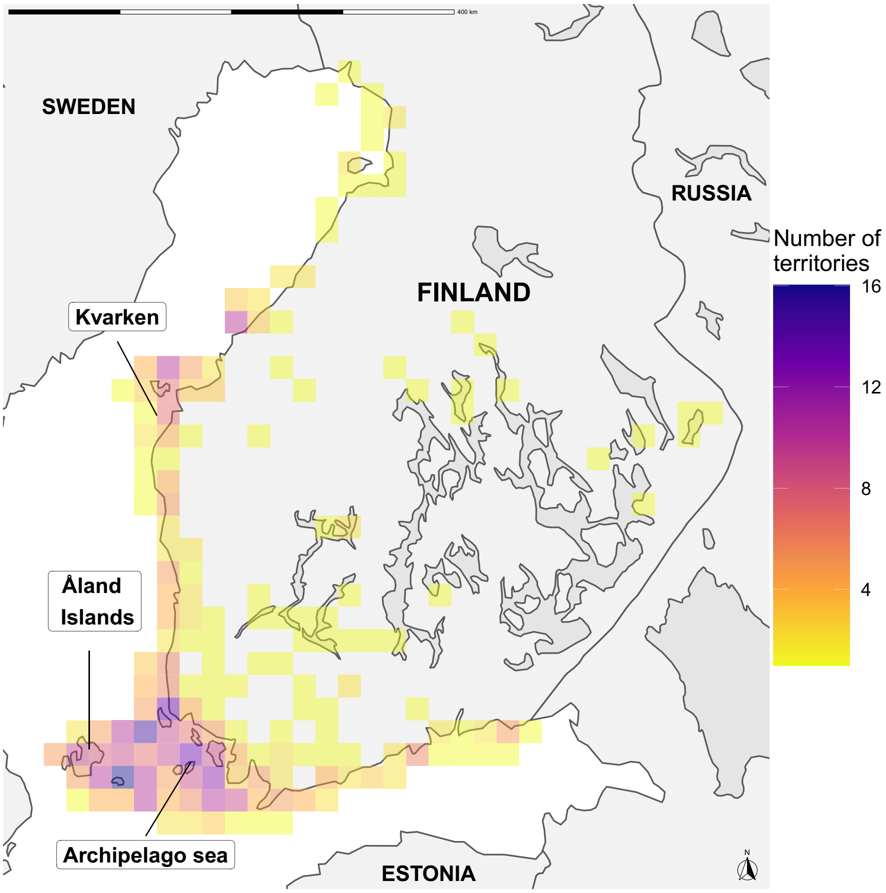

FIGURE 1 Map of the study area and the distribution of the white-tailed eagle population based on active territories in 2023. The core areas of the population are the Archipelago Sea, Åland Islands and the Kvarken area. Colours indicate the number of active territories within 20 × 20 km grid cells, with low densities in yellow and high densities in violet.

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 the adult feathers was extracted using a salt extraction method modified from Aljanabi and Martinez (1997). Samples were genotyped using 14 loci with 13 used for individual identification and one for sexing (Hailer et al., 2006; Ponnikas et al., 2013). Detailed laboratory protocols are described in the Supporting Information.

Genotype matching was used to identify nestlings that had recruited into the breeding population. Adult genotypes were screened against nestling genotypes using Cervus 3.0.7 software (Kalinowski et al., 2007), with a minimum of nine matching loci and allowing for one mismatch. The natal nest (where the nestling is ringed and sampled) and breeding nest (where the adult feather has been collected) were identified for each recruited individual. The suitability of the two sets of loci for individual identification was assessed by calculating the combined non-exclusion probability for identity and sibling identity in Cervus 3.0.7 (Kalinowski et al., 2007). Identification based on genotypes was supplemented with ring-readings from photographs of adults at nest sites during monitoring.

2.3 | Habitat characteristics

Here, territories were defined as circular areas with a 2 km radius around natal and breeding nests. This radius was selected to effectively characterise the landscape where the eagle is nesting, but it might not encompass the entire area that an eagle uses, for example, for hunting (Krone et al., 2009; Krone & Treu, 2018). A smaller radius would not describe the habitat as well, while a larger radius would give less difference and more overlap between habitats of different territories. Only one individual had a natal dispersal distance of <4 km, meaning that only a marginal proportion of the dataset had overlapping natal and settlement territory buffers. Habitat was characterised by the proportion of water (hereafter 'water area', which includes sea, lakes and rivers) within each territory. This variable was extracted from the CORINE land cover 2018 data (Härmä et al., 2019). 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 relies on (Fuller, 2012). It is also a key predictor of diet composition in this population. Eagles nesting in inner archipelago areas with less water cover rely more on fish, probably because these areas have more shallow waters with fish accessible for eagles. Eagles nesting in areas with more water cover consume more bird prey (Ekblad et al., 2016; Sulkava et al., 1997). The proportion of water in the territory also serves as a reliable indicator of the territory's position along the gradient from the outer archipelago (high water proportion) to the inner archipelago (medium water proportion) to inland environments (lowest water proportion). Because it remains stable over time, water proportion is well suited for use in long-term studies and analyses.

To quantify the level of similarity between natal and breeding sites, we calculated the absolute difference in water proportion between those territories (hereafter 'similarity' or 'habitat similarity'). Since the direction of the difference was not relevant to the study, all values were transformed into positive (absolute) differences. For the sake of clarity, the differences were subtracted from 1, so that higher values correspond to higher similarity.

We also considered other habitat variables for which white-tailed eagles show a preference (Ekblad et al., 2020; Evans et al., 2010; Radović & Mikuska, 2009; Treinys et al., 2016). However, the water area explained most of the habitat variability (Table S1), and was highly correlated with forest area (correlation coefficient = −0.94, Figure S1); thus other habitat variables were omitted from further analyses and only water area was considered. Further details on habitat description and variable correlations are available in the Supporting Information.

2.4 | Accounting for spatial proximity in habitat similarity

To account for the possibility that natal and breeding territories in closer proximity might be more similar, we examined the effect of natal dispersal distance on habitat similarity. Natal dispersal distance was calculated as the geodesic distance (km) between the coordinates of the natal nest and the first breeding nest where the individual was detected.

2.5 | Identification of available territories

To test whether eagles select natal-like habitats over other available options, we compared chosen breeding territories with alternative available territories within 65 km of the natal site – the average natal dispersal distance (65.2 km, SD = 64.3, Penttinen et al., 2024). 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. Therefore, these are sites that we know to be suitable for white-tailed eagles and have been available for the given individual with high probability. Using real eagle territories gives a more accurate picture since they differ from randomly sampled points in the landscape (Figure S1). The proportion of water in the available territories was calculated the same way as for natal and breeding territories, and the similarity between natal and available territories was computed for comparison. We used the fixed year of expected settlement (year of birth +5), since at this time, the white-tailed eagles have reached sexual maturity, and can be assumed to have started looking for a mate and territory. While it would be ideal to use the actual year of settlement, it is difficult to estimate, as the year of first detection may not coincide with the first breeding attempt, despite the high monitoring efforts of our population.

2.6 | Data and Statistical Analysis

The combination of genotype matching and ring-reading from photographs resulted in a dataset of 354 individuals with known natal and breeding locations. The dataset included 174 females, 144 males and 36 individuals of unknown sex. After excluding individuals of unknown sex and those younger than 5 calendar years ($n = 13$, before breeding age), the final dataset used in the analyses comprised 305 individuals (167 females and 138 males). The combined non-exclusion probability values confirmed the reliability of the loci set for individual identification (identity <0.0001, sib identity = 0.0003). The proportion of water in the territories ranged from 0 to 0.99 (mean = 0.65, SD = 0.30). The habitat similarity ranged from 0.03 (not similar) to 1 (identical), with a mean of 0.74 (SD = 0.23; note that the absolute value of the difference is always positive).

We used three models corresponding to our research questions. In the first model (a), we used a generalised linear mixed model (GLMM, beta family) to test whether the proportion of water (continuous) around the natal nest predicted the proportion of water around the first breeding nest. In a second GLMM (beta family) (b), we assessed whether the similarity of natal and breeding habitats (continuous) was influenced by natal dispersal distance (continuous, 3–352 km) and sex (factor, male or female). Beta family was used in the models because it met the model assumptions, while a normal distribution was not suitable for the proportional data that was skewed towards maximum values and bounded between zero and one. Since beta models cannot handle boundary values (exact zero or one), a correction advised by Cribari-Neto and Zeileis (2010) was made for the response variables. The expected settlement year was included as a covariate in both models (a and b) to account for potential temporal trends caused by the growing population. The third model (c) was a generalised linear mixed model (GLMM, binomial family) to test whether chosen breeding territories (1) were more natal-like than available territories (0). The explanatory variable was habitat similarity. The number of available territories per individual was added as a covariate, as it varied between individuals (1–29, mean = 11.5, SD = 5.8) and affects the probability of a territory being chosen. In all models, natal territory ID and expected settlement year were included as random effects on the intercept to account for potential non-independence of the observations from the same territory or same year. In the binomial model, individual ID was also added as a random effect on the intercept. All models were tested for multicollinearity (VIFs = 1–1.04). The binomial GLMM model was tested for overdispersion (dispersion = 0.997, $p = 0.92$) and zero-inflation (ratio of observed to simulated zeros = 0.999, $p = 1$).

Analyses were performed in R v.4.1.3 (R Core Team, 2019). Data wrangling and visualisation were done using the 'tidyverse' package (Wickham et al., 2019), with spatial calculations via 'geosphere' (Hijmans, 2021) and habitat variable extraction using 'sp' (Pebesma & Bivand, 2005), 'rgeos' (Bivand & Rundel, 2023) and 'raster' (Hijmans, 2023). Available alternative territories were identified with 'sf' (Pebesma, 2018). Maps were obtained from 'naturalearth' (South, 2017a) and 'naturalearthdata' (South, 2017b). Correlations of habitat variables were calculated with 'psych' (Revelle, 2007). GLMMs were fitted with 'lme4' and effect sizes were obtained with 'ggeffects' (Lüdecke, 2018). Dispersion and zero-inflation were tested with 'DHARMa' (Hartig et al., 2024).

3 | RESULTS

There was a significant positive relationship between the proportion of water in natal and breeding territories: individuals born in territories with a high proportion of water were more likely to breed in territories with a high proportion of water. The slope translates into a 2.5% increase in breeding site water proportion per 10% increase in natal habitat water proportion. (Table 1; Figure 2a). Visual examination of the raw data scatterplot (Figure 2a) suggests that the relationship between water area in the natal and breeding territories could be mainly driven by territories with a high proportion of water.

There was no obvious association between natal dispersal distance and habitat similarity (Table 1; Figure 2b). There was also no difference between sexes and no change in habitat similarity over time (effect of expected settlement year) (Table 1). The probability of a territory being chosen increased with increasing habitat similarity (Table 1; Figure 3), indicating that white-tailed eagles are more likely to settle in territories resembling their natal territory than in other available territories within the area.

4 | DISCUSSION

Our study provides an indication of habitat imprinting in white-tailed eagles. Using genotype matching and individual marking for identifying individuals in their natal and breeding sites, we found that breeding white-tailed eagles were more likely to settle in habitats resembling their natal environment. Specifically, 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. This pattern persisted regardless of natal dispersal distance, suggesting that habitat selection was not merely a by-product of spatial proximity. We could further show, using comprehensive large-scale monitoring data, that individuals showed a preference for territories that resembled their natal sites among available territories within the same general area, supporting the role of habitat imprinting in breeding habitat selection.

TABLE 1 Parameter estimates of the models examining the habitat imprinting in white-tailed eagles.

Response variables	Explanatory variables	Estimate	SE	χ^2	Ndf	*p*
(a)						
Water area (breeding site)	**Water area (natal site)**	**1.040**	**0.231**	**20.35**	**1**	**<0.001**
	Intercept	−0.249	0.162	2.37	1	0.124
(b)						
Habitat similarity	Natal dispersal distance (scaled)	−0.096	0.061	2.47	1	0.116
	Sex (male)	−0.066	0.119	0.31	1	0.578
	Expected settlement year	−0.047	0.066	0.52	1	0.473
	Intercept	**1.021**	**0.092**	123.39	**1**	**<0.001**
(c)						
Chosen/Available	**Habitat similarity**	**0.769**	**0.271**	**8.05**	**1**	**0.005**
	No. territories available	**−0.097**	**0.011**	**71.90**	**1**	**<0.001**
	Intercept	**−1.741**	**0.240**	**52.75**	**1**	**<0.001**

Note: Model (a) describes the relationship between the proportion of water in natal and breeding sites. The response variable is the proportion of water (continuous) in the breeding territory, and the explanatory variable is the proportion of water (continuous) in the natal territory (both within a 2 km radius of the nest). Model (b) describes the effect of natal dispersal distance on similarity of the natal and breeding territories. The response variable is habitat similarity (continuous, proportion of water in the breeding territory subtracted from the proportion of water in the natal territories). The explanatory variables are natal dispersal distance (km, continuous, scaled), sex (factor, male or female; here reference category is male) and expected settlement year (continuous, scaled). Model (c) examines the effect of habitat similarity on the probability of a territory being chosen. The response variable is chosen or available territory (binomial, real territory chosen by the individual [1] or territory available for the individual but not chosen [0]), and the explanatory variable is the habitat similarity (continuous). Availability (number of available territories per individual, numeric, range 1–29) was included as a covariate. Estimates, SE, χ^2, numerator degrees of freedom (ndf) and *p*-values are shown. The R^2-values (marginal/conditional) of the models are (a) 0.291/0.291, (b) 0.066/0.557 and (c) 0.092/0.092. Natal territory ID and expected settlement year were set as random effects on the intercept in all three models, and individual identifier (ID) in model c. Natal territory ID variance contributions were 0.000, 0.055 and 0.000 in models a, b and c, respectively. Expected settlement year variance contributions were 0.000, 0.018 and 0.005 in models a, b and c, respectively. Individual ID contributed to 0.000 variance. Significant variables are highlighted in bold.

4.1 | Mechanisms of habitat imprinting

Habitat imprinting likely functions as an adaptive strategy to optimise habitat selection. According to the 'habitat cueing hypothesis', individuals rely on environmental cues experienced during early life to identify suitable breeding habitats, reducing the costs of searching for and evaluating new sites (Davis, 2004). This may be particularly important for long-lived species with strong breeding site fidelity, such as white-tailed eagles, which appear to start breeding at a median age of 9 calendar years (in Finland, unpublished data), can live over 30 years and show very low rates of breeding dispersal (Nebel et al., 2024; Whitfield et al., 2009). For such species, the initial choice of a breeding site may have long-lasting consequences, making natal habitat imprinting a potentially valuable mechanism for evaluating habitat quality.

While many species can use their breeding success as a direct cue for habitat quality and switch accordingly (Schmidt, 2001; Switzer, 1993), this is not applicable during the initial settlement phase or in species with strong breeding site fidelity. In these cases, individuals cannot use prior breeding success as a cue, and the only habitat they have direct experience of is their natal site (Davis, 2004). Therefore, imprinting on the natal habitat may serve as a crucial mechanism guiding first-time breeders in their settlement decisions.

An alternative mechanism to habitat cueing is provided by the 'habitat training hypothesis', which suggests that individuals develop habitat-specific skills or characteristics in their natal environment and these enhance survival and reproductive success in similar environments (Davis, 2004; Provenza & Balph, 1987; Stamps, 2001). For white-tailed eagles, diet composition varies with habitat type (Dementavičius et al., 2020; Ekblad et al., 2016), and expertise in handling specific prey types may provide a selective advantage (Nebel et al., 2023). In the geomorphologically highly variable northern Baltic Sea archipelago, the proportion of water area in the territories affects the proportions of fish, birds and mammals in the diet composition (Ekblad et al., 2016). After fledging, young white-tailed eagles remain in their natal territory for up to 3 months (Balotari-Chiebao et al., 2016; Engler & Krone, 2022; Eskildsen et al., 2024), during which they learn foraging techniques adapted to local prey availability. There is also indication from several animal species that early experience of a certain diet type simply induces a preference for this kind of diet (Immelmann, 1975). This could also explain why individuals favour natal-like habitats when establishing breeding territories (Nebel et al., 2023).

There might also be physiological and immunological benefits of choosing a natal-like habitat, in particular, associated with polymorphisms of MHC class II genes. A study from Poland found that MHC class II polymorphisms varied between white-tailed eagle nestlings raised in different habitats (Minias et al., 2021). MHC genes are associated with receptors identifying extracellular pathogens and therefore variation in polymorphisms reflects differing parasite fauna between habitats (Minias et al., 2021). By choosing a breeding site

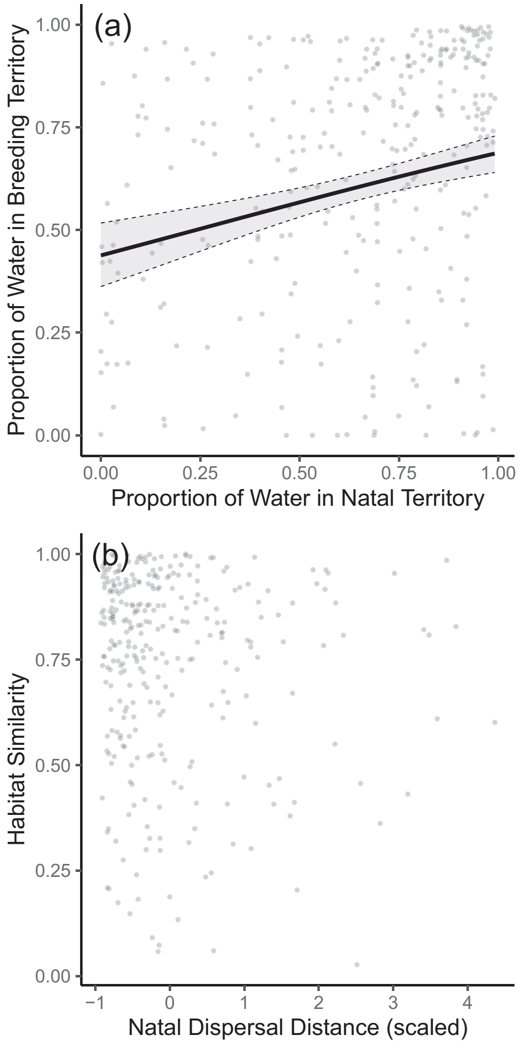

FIGURE 2 Relationship between (a) the proportion of water in natal and breeding territories (2 km radius from the nest) and (b) natal dispersal distance and the habitat similarity (difference of water area between natal and breeding sites). The regression line represents model predictions, with shaded areas indicating the 95% confidence interval.

with habitat characteristics resembling the natal site, eagle individuals could improve their own as well as their offspring's resilience to local pathogens.

The concept of habitat imprinting includes the idea that exposure to certain habitat cues during a certain time period (sensitive period) induces preference for those cues later in life (Davis, 2004; Immelmann, 1975; Stamps, 2001). The duration of the sensitive periods can range from hours to several months (Immelmann, 1975). Therefore, it is possible that the entire post-fledging pre-dispersal period can affect the later habitat preferences of white-tailed eagles. The imprinting effect is expected to persist even after exposure to other cues (Immelmann, 1975). Before breeding, white-tailed eagles spend years roaming over vast distances, and occasionally return to their natal area (Mee, 2016; Nygård et al., 2000; Whitfield et al., 2009). Experiences during these sub-adult years might shape the habitat preferences, as has been shown, for example, in eagle owls *Bubo bubo* (Delgado et al., 2010), and the lack of data from those years is inevitably a shortcoming for the present study. However, our results suggest that the preference for natal-like habitats persists through those vagrant years.

4.2 | Natal area Fidelity and habitat imprinting

White-tailed eagles have been shown to exhibit natal area fidelity, which means that eagles return to breed fairly close to their natal areas (Penttinen et al., 2024). This is typical for most raptors and many bird species (Greenwood, 1980; Greenwood & Harvey, 1982). The strong site fidelity also produces a conceptual issue: habitat imprinting can be challenging to distinguish from site fidelity (Fuller, 2012), as both can result in settlement in natal-like habitats. In cases of site fidelity, this is due to spatial proximity, whereas habitat imprinting indicates active preference despite distance (Stamps & Swaisgood, 2007). Snail kites *Rostrhamus sociabilis* have been shown to prefer their natal-like wetland types independent of the natal dispersal distance (Fletcher et al., 2015). A study of Scandinavian wolves *Canis lupus*, in contrast, has shown that settlement in natal-like habitats mostly occurred by individuals with the shortest natal dispersal distances (Sanz-Pérez et al., 2018). Since for white-tailed eagles, there is no obvious connection between habitat similarity and natal dispersal distance, and individuals preferred natal-like habitats among alternatives within the same general area, our results indicate that habitat imprinting of white-tailed eagles is not merely a by-product of proximity but rather an active preference. However, natal area fidelity might be a simple and effective strategy for individuals to maximise their chances of encountering natal-like habitats.

4.3 | Asymmetric parental care and sex-specific habitat choice

In raptors, including the white-tailed eagle, males are primarily responsible for foraging during incubation and nestling periods (Sonerud et al., 2014). Therefore, it could be that males would benefit more from settling in a natal-like habitat than females if there are advantages for individuals to nest in natal-like habitats (Trochet et al., 2016). However, we found no difference in habitat similarity between sexes. A possible explanation is that white-tailed eagle pairs stay in their territories year-round (Dementavičius & Treinys, 2009; Krone et al., 2013), meaning that, in terms of foraging, both sexes might benefit similarly from settling in a natal-like habitat.

4.4 | Variability and constraints in habitat selection

Experience in the natal habitat can increase the preference for similar habitats in later life stages, but it does not mean that

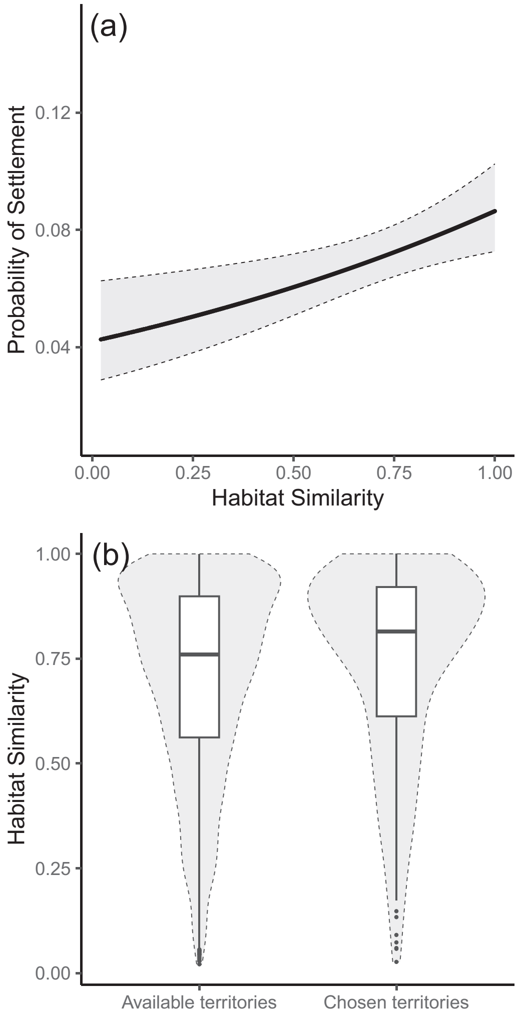

FIGURE 3 (a) Probability of a territory being settled in relation to habitat similarity (water area difference between natal and available (chosen or not-chosen) territories). The regression line depicts model predictions, and the shaded area is the 95% confidence interval. (b) The distribution of habitat similarity in chosen breeding territories and available alternative territories. The proportion of water is measured within a 2 km radius of the nest sites.

individuals would always choose similar habitats (Stamps, 2001). While our results indicate an imprinting effect, there was substantial individual variation in the degree of natal habitat similarity. This was particularly seen in habitat similarity being stronger in individuals whose natal territories had a large proportion of water than in those with a smaller proportion of water. 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). Density of the breeding population can also affect the settlement of the white-tailed eagles (Penttinen et al., 2024).

Territory sizes can differ in different habitats, contributing to the number of eagles certain habitats can support (Krone et al., 2013). Eagles from habitats with more water are known to have narrower diets (Ekblad et al., 2016). These individuals could benefit more from settling in similar habitats, whereas individuals with wider diets can be more flexible (Nebel et al., 2023). A similar pattern of preference for natal-like habitats depending on the natal habitat type has been detected in red kites *Milvus milvus* (Orgeret et al., 2024). This was attributed to additional resources and habitat features needed for reproduction, that is, variation of breeding potential among different habitats.

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. The Finnish white-tailed eagle population has gone through a bottleneck, and at the lowest point of the population, the eagles were breeding mostly in three regions on the coastal areas: the Åland islands, the Archipelago Sea close to mainland Finland, and the Kvarken region close to the Bothnian Bay. 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). However, this has not led to a temporal trend in habitat similarity, which could be explained by the archipelago environment not becoming saturated yet (Penttinen et al., 2024) and individuals born there still being able to acquire natal-like habitats. 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 contributed to sustaining and increasing the inland population.

While habitat imprinting induces preference for natal-like habitats, the wider concept of NHPI states that experience in the natal habitat can also cause 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, for example, weather conditions during the time spent in the natal habitat (Fletcher et al., 2015). Unpredictable perturbations in the environment can also cause the individual to move away from the given habitat as a response (emergency life-history tactics, Wingfield, 2003).

Resemblance to natal habitat is just one possible source of information about the quality of the potential breeding habitat. The choice of habitat can also be affected by the presence (social information) and breeding success of conspecifics (public information) (Danchin et al., 2001).

4.5 | Implications for conservation

Understanding habitat imprinting has important conservation implications, particularly for reintroduction programmes of raptors, which are among the most threatened animal taxa in the world (McClure et al., 2018). In Finland, the white-tailed eagle population is thriving (Lokki et al., 2024), but this is not the case everywhere in Europe, where several active reintroduction programmes are attempting to establish a breeding population of white-tailed eagles (Carver et al., 2022; Juste et al., 2023; Meyrier et al., 2025). Other raptors, such as the bearded vulture *Gypaetus barbatus* (Schaub et al., 2009) and Spanish imperial eagle *Aquila adalberti* (Ferrer et al., 2013), have also been assisted in their recovery by reintroduction programmes. Unfortunately, reintroduction programmes often face problems, a major one being that released individuals not accepting the new habitat and dispersing away from the intended settlement sites (Berger-Tal et al., 2020). Habitat imprinting may contribute to these challenges if individuals fail to recognise unfamiliar environments as suitable. Incorporating knowledge of early life exposure to natal habitat preferences into release strategies—such as exposing the individuals to characteristics of desired settlement habitat prior to release—could improve retention and breeding success in reintroduced populations (Stamps & Swaisgood, 2007).

4.6 | Limitations and future directions

Further studies would be needed to understand in more detail how habitat imprinting is developed in white-tailed eagles. Based on current results, it is not clear if the habitat imprinting behaviour of white-tailed eagles is due to 'habitat cueing' or 'habitat training'. Furthermore, it would be interesting to understand whether habitat imprinting results in fitness benefits for individuals, which would require, for example, investigating the effects of habitat similarity on breeding success. Clarifying the association between natal habitat type and habitat imprinting would also need further examination. The effects of population density should also be studied since it affects the availability of habitats and the intensity of competition. Habitat preferences during the prospecting phase should also be studied because imprinted habitat selection can vary between different phases of dispersal (Orgeret et al., 2024).

5 | CONCLUSION

Our study shows that white-tailed eagles exhibit natal habitat imprinting when selecting breeding territories. This preference persists regardless of dispersal distance and is evident even when alternative suitable habitats are available. These findings add to the understanding of the role of early-life experience in habitat selection, with implications for conservation, population ecology and evolutionary processes. Recognising the influence of habitat imprinting is important for effective species management, particularly in reintroduction efforts where habitat suitability assessments should consider the natal habitat preferences of translocated individuals. Future research should focus on identifying the mechanisms driving habitat imprinting and assessing its long-term ecological and evolutionary consequences.

AUTHOR CONTRIBUTIONS

Ida Penttinen (Conceptualisation, data curation, formal analysis, funding acquisition, investigation, methodology, visualisation and writing—original draft). Carina Nebel (Conceptualisation, formal analysis, funding acquisition, methodology, supervision and writing—review and editing). Toni Laaksonen (Conceptualisation, funding acquisition, methodology, project administration, supervision and writing—review and editing).

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CONFLICT OF INTEREST STATEMENT

The authors declare no conflict of interest.

DATA AVAILABILITY STATEMENT

Data are available from Figshare repository https://doi.org/10.6084/m9.figshare.28920065 (Penttinen et al., 2025).

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SUPPORTING INFORMATION

Additional supporting information can be found online in the Supporting Information section at the end of this article.

Table S1. The results of the principal component analysis (PCA) of the habitat variables in white-tailed eagle territories. Habitat variables were extracted from Corine land cover data and calculated as proportions within a 2 km radius of nests.

Figure S1. Correlations of habitat variables in white-tailed eagle territories. Variables used were the proportion of water area (sea, lakes, rivers, clc-classes 47–49), marshes (clc-classes 41–42 and 45–46), sparse forests (canopy cover < 30%, clc-classes 33–36) and forests (canopy cover > 30%, clc-classes 23–30). Variables were extracted from the Corine land cover 2018 data and measured as proportions within a 2 km radius from the nest.

Figure S2. Density plot visualising the proportion of water area in white-tailed eagle territories (blue, *n* = 449) and randomly generated sites in the same landscape (green, *n* = 1100).

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