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ORIGINAL PAPER

Diet and breeding habitat preferences of White-tailed Eagles in a northern inland environment

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Abstract

Many apex predator populations are recolonizing old areas and dispersing to new ones, with potential consequences for their prey species and for livestock. An increasing population of the White-tailed Eagle (*Haliaeetus albicilla*) has settled north of the Arctic Circle in northern Finland, mainly at two big water reservoirs but also in areas with mainly terrestrial habitat. We examined nesting habitat preferences and prey use of White-tailed Eagles in this environment, where reindeer husbandry is a traditional livelihood and concerns are rising that the growing White-tailed Eagle population poses a threat to reindeer calves. Lakes, peat bogs, and marshlands were preferred habitats in the nesting territories. Fish constituted 64.3% of the identified prey items, with birds accounting for 28.5% and mammals 7.2%. The nesting territory habitat within a 10 km radius and the latitude influenced the prey composition at both the group and species level. The occurrence of reindeer calves as prey increased with latitude but was not associated with any habitat. Knowledge of the diet and territory preferences can be used to predict future dispersal and local prey use of this species. Nesting White-tailed Eagles do not seem to pose a threat to traditional reindeer herding, but further research is needed regarding non-breeding sub-adults and whether the White-tailed Eagles actually kill reindeer calves or simply exploit their carcasses.

Keywords Bird of prey · Breeding territory · Human-wildlife conflict · Lapland · Raptor

Introduction

Apex predators play a key role in top-down regulation of ecosystems, often with cascading effects when an apex predator leaves or enters a system (Estes et al. 2011). In the past century, many apex predator populations crashed (Prugh et al. 2009; Estes et al. 2011), but some populations have recovered recently; for example large carnivores in Europe and wolves (*Canis lupus*), sea otters (*Enhydra lutris),* and alligators (*Alligator mississippiensis*) in different parts of the USA (Chapron et al. 2014; Ripple et al. 2014; Silliman et al. 2018). Following the ban of organochloride pesticides and reduced persecution, the populations of apex raptors, such as Peregrine Falcons (*Falco peregrinus*) and Ospreys (*Pandion Haliaeetus*), have also recovered (Ratcliffe 2003; Poole 2019). The growing populations are spreading into new areas, often re-colonizing areas they once inhabited (Silliman et al. 2018). This return of apex predators is a complex issue. Even though their importance as regulators of food webs is commonly acknowledged, they cause conflicts with humans because they are considered competitors for prey resources or a threat to humans and/or livestock (Valkama et al. 2005; Prugh et al. 2009; Ripple et al. 2014; Nyhus 2016). The return of the predators may also conflict with the conservation of the prey species (Hipfner et al. 2012).

According to classical foraging theory, apex predators, as well as other foragers, should prefer the most profitable prey when it is abundant, and switch to less preferred prey when the abundance of the preferred prey declines below a certain threshold (Stephens and Krebs 1986). More recently,

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it has been noticed that predators also seek variation in their diets (Kohl et al. 2015). However, different predator individuals do not necessarily have equal opportunities for choosing prey. The abundance and availability of different prey species varies between habitats, thereby altering which prey is the most profitable (Ontiveros et al. 2005; Sih 2011) or available (Amar et al. 2004; Newsome et al. 2015). Territorial species therefore have to pay attention to prey availability when choosing a breeding territory. Species that select nesting site annually can choose different places in subsequent years if the environmental conditions or prey availability change (Arroyo et al. 2009; Vasko et al. 2011; Navarro-López et al. 2015). For species that generally choose a territory for life, the consequences of the selection are often lifelong and the associations between habitat and diet need further investigation.

Many raptor species are prime examples of territorial species that remain faithful to their breeding territory. They typically have relatively large territories that cover various types of habitats (Tapia and Zuberogoitia 2018). Some evidence supports habitat-driven intraspecific differences in the diet of raptors, as landscape characteristics can impact the diet of individual raptor pairs (Amar et al. 2004; Frey et al. 2011; Shin et al. 2013; Terraube et al. 2014; Bildstein 2017). Nevertheless, research has focused on species that specialize in a few prey species and habitats, whereas almost nothing is known about the connections between the use of multiple prey species and territory habitat characteristics.

The White-tailed Eagle (*Haliaeetus albicilla*) is a large raptor that typically lives and nests close to water. It was driven to the brink of extinction in the twentieth century in the area around the Baltic Sea due to persecution and to pollution by organochlorine pesticides, but after extensive conservation efforts the population started to grow in the 1980s (Stjernberg et al. 2005, 2016). In Finland, the core nesting areas are along the Baltic coast. As the population has grown, the White-tailed Eagles have expanded to new areas, as well as to areas where they historically have occurred but were missing for several decades (Högmander et al. 2020).

The reappearance of White-tailed Eagles in food webs from which they have been virtually absent in the recent past can have consequences for the prey species and cause management and conservation conflicts (Hipfner et al. 2012). In parts of the Baltic Sea, the Common Eider (*Somateria mollissima*) population has crashed in the outer archipelago since its peak in the 1990s (Below et al. 2019), probably in part due to growing White-tailed Eagle populations (Ekroos et al. 2012; Öst et al. 2018). This has created a conflict with eider hunting, as well as a concern for the survival of this prey species, which is classified as endangered in the Finnish red list (Hyvärinen et al. 2019). However, where the White-tailed Eagle has been re-introduced in Scotland and Ireland, financially more important conflicts with livestock herding have arisen with sheep herders (Simms et al. 2010; O'Rourke 2014). The original dissensus about the level of threat posed by the White-tailed Eagles to the lambs, and the viability of the lambs eaten, has been met by the development of an action plan in Scotland (Scottish Natural Heritage 2017).

In the late 1960s, two big water reservoirs, Lokka (417 km^2) and Porttipahta (214 km^2), were constructed inland in northern Finland (Lapland). Historically, occasional White-tailed Eagle nestings were known in the area (Ollila et al. 2007), but the reservoirs provided novel breeding habitats that launched the expansion of the White-tailed Eagle population to the area. The first nesting event at Lokka was observed in 1977 (Sulkava et al. 1997), and by 2019, 86 nesting pairs were recorded in the reindeer herding area (WWF Finland, unpublished) (Fig. 1). The majority of the current territories in Lapland are located around these two water reservoirs, but today nests are present in other areas as well, with the second largest aggregation in the Kuusamo region in the southeastern part of the area (Fig. 2).

Molecular genetics has shown that the Lapland White-tailed Eagle population has a northeastern origin and thus does not originate from the Baltic population (Ponnikas et al. 2013). The diet of the White-tailed Eagles nesting in Lapland was studied in the 1980s, when it consisted mostly of fish (69.2%), followed by birds (29.2%) and mammals (3.6%). Reindeer calves (*Rangifer tarandus tarandus*) constituted 0.5% of the diet (by number of prey items; Sulkava et al. 1997). An update of the diet of White-tailed Eagles in the area is important, as the former study did not discriminate between habitats and the population has grown tenfold since, thereby enhancing the competition for territories and possibly inducing dispersal to sub-optimal habitats.

The growth of the White-tailed Eagle population in Lapland may awaken conflicts if the birds prey upon popular game species. So far, the main concern has been that they may kill reindeer calves, causing financial losses for reindeer herders. Herding of semi-domesticated reindeer is a traditional livelihood practiced in Lapland and plays important cultural and financial roles for the indigenous Sámi people in the northernmost municipalities (Kumpula et al. 2011), as well as for other inhabitants in the rest of the reindeer herding area (Jernsletten and Klokov 2002). The semi-domesticated reindeer graze freely in the spring- and summer pastures, also calving there. This makes them vulnerable to predators that are large enough to capture calves. In some parts of this area, around 10% of the Golden Eagle (*Aquila chrysaetos*) diet, as measured by prey items, consists of reindeer calves (Sulkava et al. 1998; Johnsen et al. 2007). Concern has been raised that the growing population of White-tailed Eagles could also contribute to calf losses, as

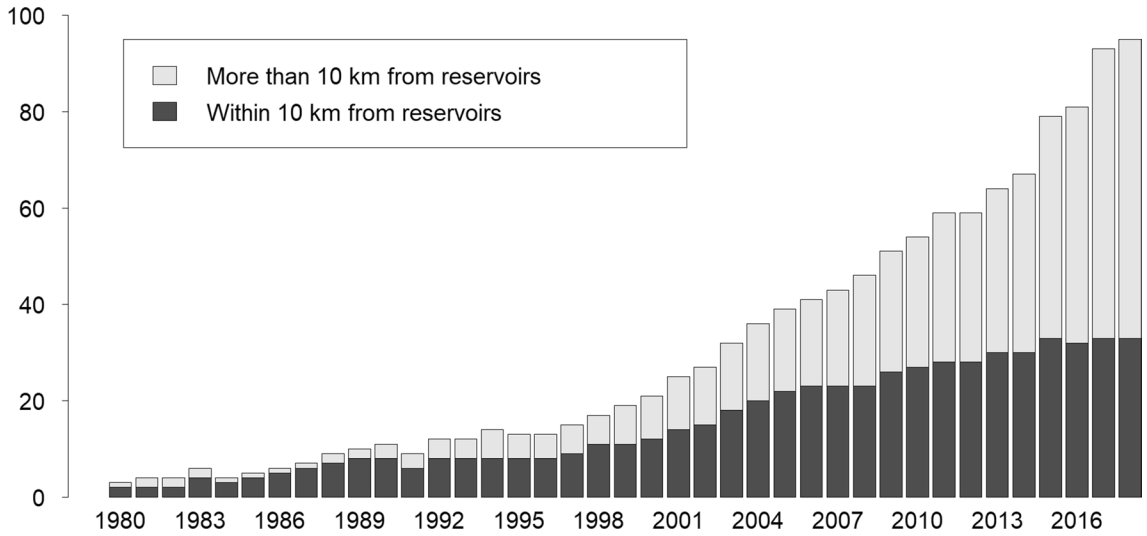

Fig. 1 The number of occupied White-tailed Eagle territories in the reindeer herding area each year since 1980. Territories within 10 km from the Lokka and Porttipahta reservoirs (dark bars) and farther than 10 km from them (light bars) are shown

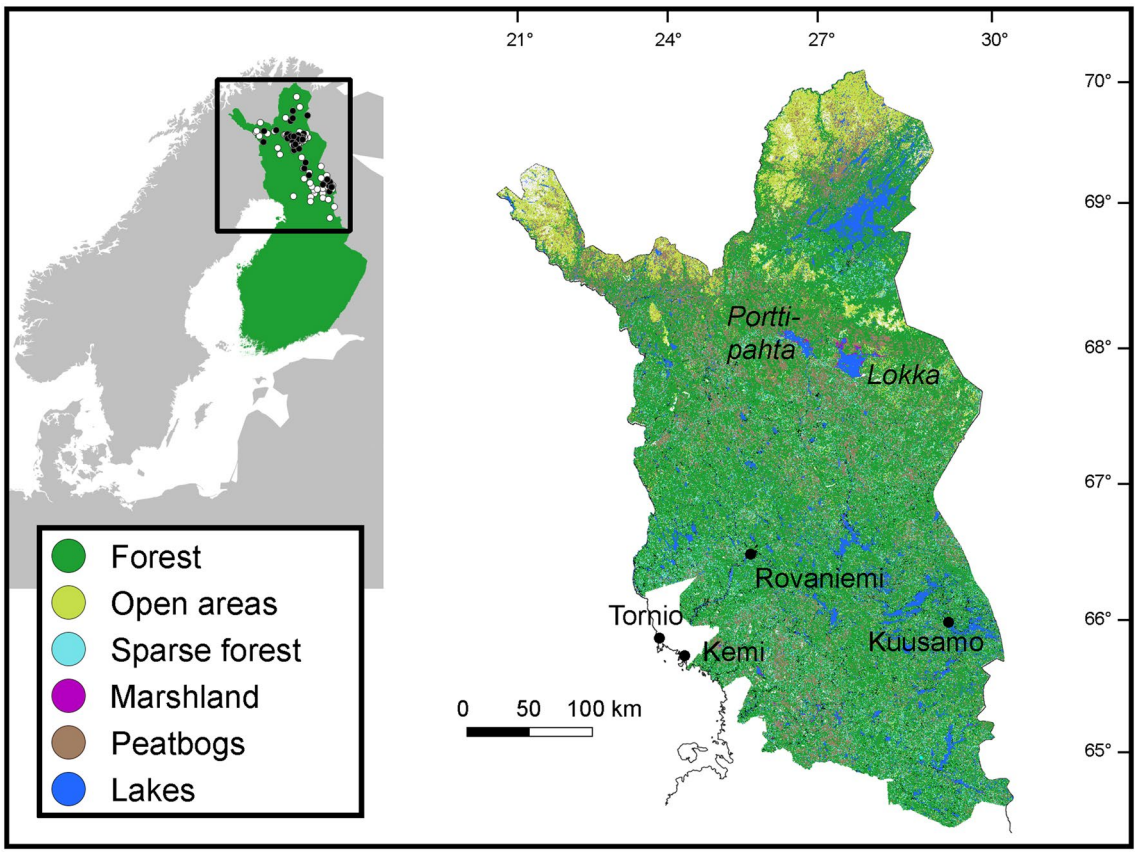

Fig. 2 The map shows the location of the reindeer herding area in Lapland in northern Finland. The habitat types in the area are shown in different colors. All known current and historical White-tailed Eagle territories in the area, as of 2018, are plotted on the location map. Black dots indicate territories from which prey data are available, while white dots are territories with no available prey data. The densest aggregation is around the water reservoirs of Porttipahta and Lokka

the White-tailed Eagle is about the same size as the Golden Eagle and has a partially overlapping diet.

Evaluation of the possible impacts of the growing White-tailed Eagle population on their prey species requires an understanding of how the selection of territorial habitat by nesting eagles will affect the availability of prey species in each territory and, thereby, the eagle's diet. Only a few studies have addressed nesting habitat preferences for White-tailed Eagles. In Lithuania, a preference for various water bodies, as well as semi-open areas, was found within a calculated territory with a radius of 6 km (Treinys et al. 2016), whereas all White-tailed Eagle nests in Croatia are found within 1 km of some kind of water body (Radović and Mikuska 2009). Associations between the diet and the habitat in the nesting territory have, to our knowledge, been made only regarding the share of water and land (Helander 1983; Ekblad et al. 2016). A very recent paper from Lithuania examined the diet in different aquatic environments, but the terrestrial habitats were not further discriminated (Dementavičius et al. 2020). Nothing is known about these connections at high latitudes, such as in Lapland.

In the present study, we examined the diet and nesting habitat preferences of the recently expanded population of White-tailed Eagle in Finnish Lapland in an effort to understand the drivers behind the prey choice. A second goal was to evaluate to what extent the occurrence of reindeer calves in the diet of White-tailed Eagles is driven by these factors. Our aim is for this to be a first step toward understanding the possible impacts of this predator on its prey and the potential for conflicts in prey use between White-tailed Eagle and humans. Specifically, the aims of this study were (1) to investigate whether the White-tailed Eagles prefer certain habitats over others when choosing nesting territory; (2) to examine the diet of the nesting White-tailed Eagles and the connections between habitats in the territory and prey species in the diet; and (3) to identify possible factors that predict the occurrence of reindeer calves in the White-tailed Eagle diet.

Material and methods

Study area

Our study area is located mostly in Lapland, the northernmost region of Finland. The reindeer herding area, where reindeer are allowed to graze freely within the borders of 54 reindeer herding cooperatives, covers almost the same area. Exceptions are an area around the city of Kemi, which is excluded, and an extension in the south that belongs to the regions of North Ostrobothnia and Kainuu. Because we consider the reindeer aspect, our study takes place in the entire reindeer herding area, which, for simplicity, we refer to hereafter as Lapland. The study area is located north of latitude 64° 28′ N and has a size of 122 936 km^2, covering a third of Finland (Anon. 2015) (Fig. 2). The landscape is a mosaic of lakes, low forests, and peat bogs, with a growing proportion of tree-covered and open fells towards north. Human settlements are very scarce (mean 1.4 people km^{-2}, Statistics Finland 2019). Fresh water covers 6.7% of the area (National Land Survey of Finland 2019). Conditions are harsh, with mean temperatures in April, when the White-tailed Eagles start nesting, of −1.5° C at the reservoirs and −0.1 °C in the Kuusamo region (2009 – 2018). At the reservoirs, the ground loses its snow cover, on average, on the 13th of May and in Kuusamo on the 9th of May (Official Statistics of Finland 2019).

Study species and nest surveillance

The White-tailed Eagle (*H. albicilla*) is a large bird of prey, with a wingspan of 195–245 cm and a weight of 4–7 kg. It lives and nests close to water (Ferguson-Lees and Christie 2001). Annually, almost all known nests are surveyed in Finland (Högmander et al. 2020). In Lapland, the monitoring has been coordinated and supported by Metsähallitus, a governmental organization. The nests are visited in May–June, when the breeding status of the pair is monitored. The number of nestlings is recorded, and if possible, the nestlings are measured and ringed by volunteers. In 2019, 86 occupied territories of White-tailed Eagles were detected in the reindeer herding area (WWF Finland, unpublished).

The reindeer (*R. tarandus tarandus*) is a medium-sized ungulate. The calves, usually one per female, are born between May and June in the study area. They have a birthweight of 4–6 kg and their weight doubles in the first month (Anon. 2015). The maximum number of reindeer that can be left alive in the autumn, in total and in each cooperative, is set by the Ministry of Agriculture and Forestry of Finland (Reindeer Husbandry Act 848/1990). In 2017, the actual number of reindeer was 193 140. The number and density of reindeer increases with latitude. Data about the number of reindeers in different reindeer herding areas was obtained from the LIITERI database (Finnish Environment Institute 2019).

Territorial size and habitat

Breeding White-tailed Eagles show site fidelity; they have one or several nests in their territory and use them year after year (Cramp 1980). No unambiguous size for White-tailed Eagle territories has been determined; therefore, we investigated the habitat around each known nest using three territory sizes based on information from other studies. In Germany, home ranges varied from 6–392 km^2 (Krone and Treu 2018). This translates to a radius between 1.38 and

11.17 km, if the territories were perfect circles. At the Baltic Sea coast, a radius of 2 km around the nests was used to describe habitat characteristics of the nesting landscape (Ekblad et al. 2016). In a study from Lithuania a radius of 6 km around the nests was used (Treinys et al. 2016). Unpublished data from two nesting White-tailed Eagles equipped with GPS-transmitters in Finland also reveal that 95% of all positions were within 11.8 and 13.2 km of their respective nests. The positionings were mainly from the coast or the vicinity of water bodies, while a large proportion of large water-free areas were not used. Thus, the territory sizes of White-tailed Eagles can vary widely depending on the environment.

The centers of the White-tailed Eagle territories were defined as their nests or, in cases with several nests, as the geometric average coordinates. We calculated the proportions of different landscape types (habitats) within buffers around the nests with 2 km, 5 km, and 10 km radiuses. The landscape types were obtained from the open source CORINE 2012 Landcover data, with a resolution of 20 m × 20 m, produced by the Finnish Environment Institute (Härmä et al. 2013). The types considered were forests, open areas, forests with a canopy cover of 10–30% (hereafter sparse forest), marshlands (including overgrown lakes, reeds, flooded lands, and small water surfaces > 25 ha), peat bogs, and lakes. Additional information about the Corine landscape data is given in Online Resource 1. The calculations were performed with R version 3.5.0, and QGIS version 3.2.2. The calculations were made for every known White-tailed Eagle territory in the reindeer herding area ($n = 113$).

Diet data

For this study, we have used all available data about White-tailed Eagle diet in Lapland that can be assigned to a territory level. We identified prey remains from 763 different individuals; the remains were collected from nests at 83 different visits at 45 territories. The methods of data collection varied somewhat between years due to personnel turnover. The majority of the data was collected in 2017 and 2018 and was supplemented with information from 1993–2013. Additional data about sampled territories per year is provided in Online Resource 2.

In 2017, prey remains were collected from 15 active nests in July–August, both during the nest visits and after the breeding season. All prey remains found under the nests and, in some cases, in the nests were collected. In 2018, prey remains were collected from 14 nests, but only during the nest visits, in June–July. In total, we collected and identified prey items from 258 prey individuals in 2017 and 161 in 2018. In addition, the prey remains in four nests in 2017 and two in 2018 were photographed, which added a total of 10 items. In 2017, additional notes were made about 9 nests, stating the occurrence or non-occurrence and number of reindeer calves in each nest along with 17 other identified prey items, and documentation of the evidence for whether there was no, few, or many fish, birds and mammals. This was interpreted so, that 'few' was two and 'many' was five prey items, adding 46 items. After these additions, the total number of identified prey items from 2017–2018 was 463.

The newly collected and the photographed prey items were identified to the highest possible level by SS with the help of reference material and guidebooks (März 1987). The number of items of each species was determined by the 'minimum method' (Oehme 1975). In this method, every prey remain from one species is considered to originate from the same individual, unless multiple remain parts are found that cannot originate from only one individual, such as beaks, lower jaws from one side (left or right), or feathers with differing distinct sex colors. The total number of individuals from a species is considered to be the number of the remains from maximum number of different individuals.

In 1993–2013, White-tailed Eagle ringer Seppo Ojala made notes about the prey in the nests during nests visits. Notes were made only for large and identifiable prey remains. Hence, notes are available only for some nests and from some years. The occurrence of reindeer calves, however, was always noted. In total, notes are available from 31 territories from 1993 to 2013, totaling 288 prey individuals.

The identified prey remains were pooled at the territory level for the analyses.

Biases of prey data

When collecting prey items, large and hard bones are better preserved than soft and small ones, which means that small fish and ducklings are underrepresented (Mersmann et al. 1992; Sulkava et al. 1997). The hard jaw bones of pike (*Esox lucius*) are found easily, so pike tend to be overrepresented (Sulkava et al. 1997). Bones of reindeer calves are also well preserved, and as all cases of reindeer calves were noted even if no other prey remains were collected, the proportion of reindeer calves is also overrepresented. Conversely, we use the number of prey items as units, which gives a somewhat different result than if biomass was used. We have no data regarding the density of the prey species in the territories; therefore, our data cannot be used to evaluate the choice of prey with regards to prey availability. No proportions based on weight estimates are given, as they are not essential for the analyses between diet and habitat.

These data consist both of systematically collected and identified prey items (2017–2018, 'new data', extended with some notes), as well as notes of easily identifiable remains (1993–2013, 'old data'). This means that the samples are not directly comparable in the two data sets. The old data set has a higher proportion of fish, whereas the new data contains

more birds. In particular, the proportion of waterfowl (new data 17.8%, old data 5.9%) and of cyprinid fishes (new 3.2%, old 15.3%) showed considerable variation. As a precaution, we verified the analyses with different subsets of the data. The results regarding the connections between habitats and diet were highly consistent in the different subsets. The only differences were associated with the marshlands, which did not show any trend with only the new data. Regarding the occurrence of reindeer calves, a large proportion originated from the notes and did not show any trends if the data originating from the notes was discarded. Hence, we used all the data in the final analyses, as the results were almost identical, but the larger dataset gave better weight to the analyses and also detected a trend for the reindeer calves. Importantly, the sampling effort was the same, regardless of the surrounding landscape; hence, the bias in prey remain collection and identification in both the old and new data is similar in all habitats. Therefore, the results of the subsequent analyses can be considered robust despite the biases in the data.

Statistical methods

All statistical tests were performed with R, version 3.5.0 (R Core Team 2020). Prior to the actual analyses, we determined the best suited territory size for analyzing the diet composition in relation to the habitats. We concluded that it was a 10 km radius, so this size was used in all subsequent analyses. The analyses and results regarding the territory size are presented in Online Resource 3.

Nesting habitat selection

We examined whether some habitats were preferred by the White-tailed Eagles when choosing nesting territory. In addition to feeding grounds, the choice of nesting territory depends on different characteristics, such as disturbance factors and the availability of nesting trees. In this paper, we address only the feeding ground aspect. We used the dataset with all known current and past territories of White-tailed Eagles in Lapland ($n = 113$). In QGIS, we assigned 226 random points (= territories × 2) with a minimum distance of 4 km from each other in the research area and calculated the habitat proportions for a radius of 10 km in R in the same way as for the actual territories. We removed five random territories, that had more than 50% of their areas located outside the boundaries of the research area, leaving 221 random territories. The proportion of forests was removed from the analysis due to the high collinearity with the proportion of lake area, as indicated by the variance inflation factor (*VIF*) with threshold 3 (Zuur et al. 2010). A binomial generalized linear model (*GLM)* was used to test for differences between real and random territories, with real and random (1/0) territories as response variables and the proportion of different habitats as explanatory variables. If the proportion of some habitat differed significantly between the real and random territories, the White-tailed Eagles would show a preference for that habitat. The goodness of the predictors was tested by k-fold cross-validation (Picard and Cook 1984; Kohavi 1995) with the "cvAUC" package in R (LeDell et al. 2014). The data were divided randomly into five same-sized groups. Four of the groups were used to predict the habitat use in the last group. The confidence limits for the AUC-values were calculated by repeating all the analyses 100 times.

Connections between diet and territory habitat

The diet analyses were made at the territory level; all identified remains collected over the years from the same territory were pooled together to form the total number of prey for the particular territory. We used a binomial *GLM* to analyze the general diet composition of the major prey groups (fish, birds, and mammals), in different habitats within a 10 km radius from each nest. The number of target prey groups from each territory was used as the response variable, with the number of all prey items as the denominator. As explanatory variables we used the proportions of the different habitats (a value between 0 and 1). With proportional data, such as the habitats here, the variables inevitably may correlate with each other as they sum up to 100%. We therefore used a *VIF* to test for correlation between the variables and a threshold of 3 for not including the variables in the same model (Zuur et al. 2010). The proportion of lakes and forest correlated and could not be used in the same model. As lakes are more suitable than forests as hunting grounds for White-tailed Eagles, the proportion of forest was excluded from the analyses to avoid the correlation issue. Latitude was included in all models to test for geographical gradients. Consistently, latitude was also scaled to a value between 0 and 1, as (latitude – min(latitude))/ δ(latitude), where min(latitude) is the southernmost latitude of the data and δ(latitude) is the range of latitudes in the data.

We also investigated the finer scale relationships between the occurrence of some species (or species groups) in the prey remains and nesting habitats. As with the major groups, we used a binomial *GLM* with the number of target species from each territory as the response variable, and the number of all prey items as the denominator. As explanatory variables, we used only the habitats considered relevant for the target prey, along with latitude. Hence, lake and marshland were used as a proxy for predicting the availability of fish species; lake, peat bog and marshland were used for waterfowl and gulls (*Larus* spp.); peat bog and marshland for Common Cranes (*Grus grus*) and forest, sparse forest, and open areas for grouse (Tetraonidae spp).

To investigate all possible relationships between habitats and reindeer calves in the diet we also included, in addition

to the habitats, the density of reindeer in each cooperative, calculated by the number of reindeer divided by the land area of the cooperative. Consistently, this value was scaled to a value between 0 and 1.

Results

Nesting habitat

The main landscape types in the territories within a 10 km radius from the nest were forest, peat bogs, and lakes. Additionally, sparse forest, open areas, and marshes each constituted a mean percentage of 1.4–7.7 (Table 1). Other landscape types each constituted a mean of less than 0.6% and were excluded from the analyses.

The White-tailed Eagles clearly preferred some landscape types in the vicinity of their nests. The proportional area of lakes and peat bogs within a radius of 10 km (an area of 314 km^2) from their nests was significantly higher than expected by random choice of territories (Table 1). The proportional area of marshlands was also higher in the real territories (Table 1 and Fig. 3). The accuracy of the predictors was high, as the distribution of 1/0-points was determined to be correct in 81% of the occasions (AUC = 0.81, CI 0.76/0.86).

Diet in general

The prey brought to White-tailed Eagle nestlings in Lapland (identified as prey remains) consisted mostly of fish (64.3%), birds (28.5%), and, to a smaller extent, mammals (7.2%) (Table 2). By far, the most common prey species was the pike *E. lucius*, which constituted half of all the prey items. Other important prey species or groups were waterfowl, grouse, and ides *Leuciscus idus* (Table 2). Reindeer calves constituted 3.1% of the prey items in these data (Table 2); however, as noted before, this number is an overestimate because the data in 1993–2013 and the notes from recent years included recordings of reindeer calves on occasions when no other species were recorded. Hence, the total proportion of mammals is also a slight overestimate, while the proportion of fish other than pike is likely underestimated, as the data have not been corrected for biases regarding prey remains detection.

Diet in relation to habitat in the breeding territory

For all the major prey groups, diet was associated with habitat. The proportion of fish increased with the proportions of lakes, marshlands, and peat bogs (Fig. 4a), and decreased with increasing proportions of sparse forest and with latitude (Table 3).

As fish and birds were the major prey groups, their proportions in the diet correlate with each other. The proportion of birds increased with the proportion of sparse forest and latitude and decreased with the increasing proportion of marshland (Table 3). The proportion of mammals decreased with an increasing proportion of marshland (Table 3).

The proportion of the most common prey remains, namely pike, increased with the increasing proportion of marshland and decreased with increasing latitude, while cyprinid fish increased with the increasing proportion of lakes (Fig. 4b) and marshlands, and burbot increased with lakes (Table 4).

Bird species (or groups of species) in the diet also varied with habitats. The proportion of waterfowl increased with latitude and decreased with the increasing proportion of peat bogs and marshlands (Table 4). Grouse increased with the increasing proportion of sparse forest (Fig. 4c) and Common Cranes increased with the increasing proportion of peat bogs

Table 1 Proportion (%) of the major habitat types in the White-tailed Eagle territories with a radius of 10 km from the nest or the mean location of multiple nests and nesting territory habitat preferences of White-tailed Eagles obtained with a resource selection function (*RSF*, logistic regression) model comparing real territories with randomly assigned points

Landscape type	Proportion in territory			Territories with prey data ($n = 45$)	Tot. n territories = 334 n real = 113, n random points = 221		
	All territories ($n = 113$)						
	Mean	Min	Max	Mean	Estimate	Z	P
(Intercept)					−2.68 ± 0.67	-4.00	
Forest	50.05	4.38	77.61	44.69			
Lakes	14.95	0.32	59.00	19.78	**0.11 ± 0.02**	**5.13**	**< 0.0001*****
Peat bogs	19.55	2.75	44.29	19.63	**0.08 ± 0.02**	**4.51**	**< 0.0001*****
Marshlands	1.37	0.00	6.82	4.02	**0.32 ± 0.14**	**2.29**	**0.0222***
Open areas	4.03	0.15	46.41	3.16	−0.04 ± 0.02	−1.75	0.0795
Sparse forest	7.73	0.05	16.52	6.94	0.05 ± 0.04	−1.23	0.2196
Other	2.31	0.06	9.73	2.14	0.07 ± 0.07	1.03	0.3052

The estimate shows the coefficient for the changes in the probability of the presence of a nest (vs. a random spot) in the landscape in relation to the habitat variable. Significant ($p < 0.05$) results are shown in bold. The habitat proportions are shown separately for all territories ($n = 113$) and territories with prey data ($n = 45$). Sparse forest is forest with low (10–30%) canopy cover

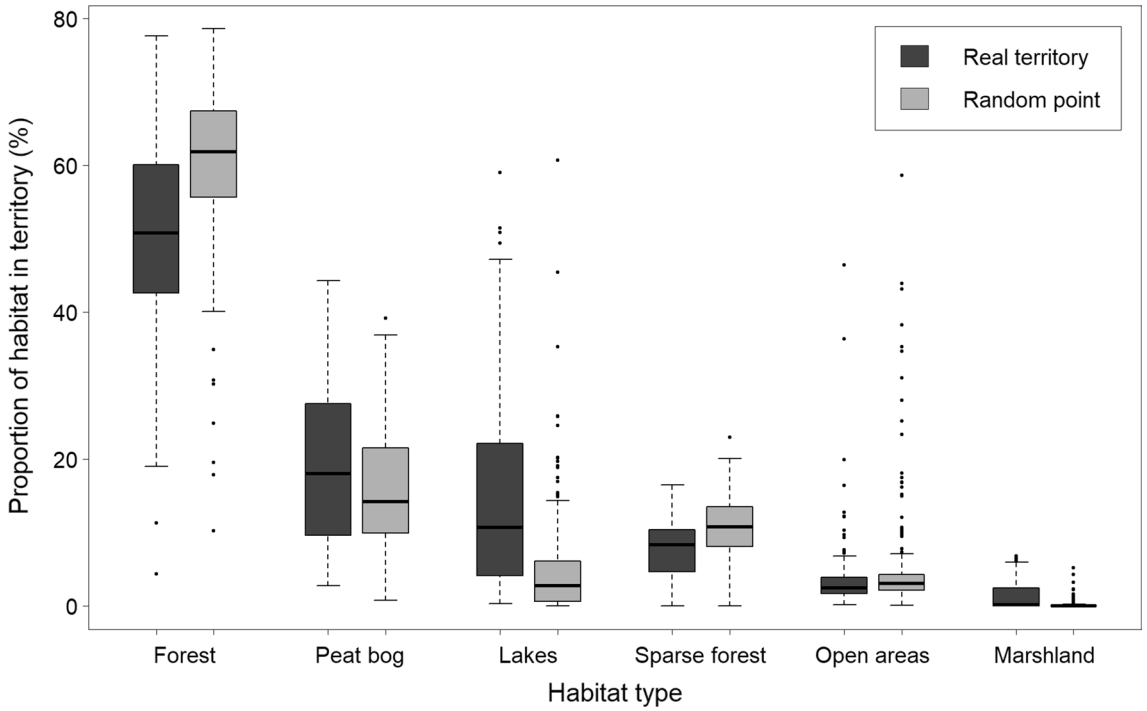

Fig. 3 Comparison between habitats in territories ($n=113$) of White-tailed Eagles (within 10 km radius from the nest) and random points ($n=221$) of same size in the same area. The White-tailed Eagles show a preference for lakes, peat bogs, and marshlands

(Fig. 4d, Table 4). The proportion of gulls in the diet was not associated with any habitat type (Table 4).

Reindeer calf remains solely increased with latitude. The habitat types in the territory and the density of reindeer in the cooperative did not correlate with reindeer calf remains. In 2017, remains of 9 reindeer calves were found at White-tailed Eagle nests. In 2018, the remains of only one calf were found. Whether the calves were taken alive or as carcasses could not be determined.

Discussion

We showed that the diet of White-tailed Eagles nesting in Lapland is associated with the habitat in their nesting territory, and that some habitats, namely lakes, peat bogs, and marshlands, are strongly preferred in the nesting habitat. According to our results, the White-tailed Eagles prefer to nest in the vicinity of good fishing grounds. However, they also appear to be opportunistic and exploit common birds in terrestrial habitats. The use of reindeer calves and other mammals seems to be mainly occasional.

Habitat preferences

As the White-tailed eagles traditionally nest along the coast and are strongly associated with water, their preference for higher proportions of lakes in their territories was highly expected, and was also found to be the case in Lithuania (Treinys et al. 2016) and Croatia (Radović and Mikuska 2009). Although the proportion of lakes was the most significant habitat variable for nesting territories of the White-tailed Eagles, they also showed a preference for peat bogs. Consistently, subadult White-tailed Eagles have been shown to prefer peat bogs as well at the Finnish coast (Tikkanen et al. 2018a). Peat bogs are probably good hunting grounds for White-tailed Eagles, as they fit their hunting techniques well. White-tailed Eagles are large raptors unable to hunt in closed forests. Their preferred hunting technique is to sit and perch over the landscape (Nadjafzadeh et al. 2016), making open peat bogs ideal. The proportion of marshland in Lapland is low compared to many other habitat types; nevertheless, the White-tailed Eagles showed a preference for them. In the area, marshlands often occur at shallow lake shores, which are good fishing grounds. The preference for marshlands might also be a proxy for shallow lake shores. In contrast to the birds in Lithuania (Treinys et al. 2016), the White-tailed Eagles in Lapland did not show a preference for open areas or sparse forests, even though those could also potentially fit their hunting techniques.

Estimating the available foraging habitat types within a certain radius of the nest is somewhat problematic as the White-tailed Eagles are known to use only some of the area for foraging, and they can exploit distant fishing grounds

Table 2 Main prey groups and species of white-tailed eagles nesting in Lapland, in terms of numbers of prey individuals and the percentage of all prey items identified (in groups containing > 1% of items)

	n	%
Fish	**490**	**64.2**
Pike (*Esox lucius)*	380	49.8
Ide *(Leuciscus idus)*	42	5.5
Other Cyprinid fish spp. (Cyprinidae)	9	1.2
Burbot *(Lota lota)*	21	2.8
Perch *(Perca fluviatilis)*	9	1.2
Other or undefined fish	29	3.8
Birds	**218**	**28.6**
Waterfowl	88	12.6
- Mallard *(Anas platyrhynchos)*	21	2.8
- Common Teal *(Anas crecca)*	12	1.6
- Goldeneye *(Bucephala clangula)*	12	1.6
- Mergansers *(Mergus & Mergellus spp.)*	21	2.8
Grouse	45	5.9
- Capercaillie *(Tetrao urogallus)*	19	2.5
- Willow Ptarmigan *(Lagopus lagopus)*	10	1.3
- Black Grouse *(Lyrurus tetrix)*	10	1.3
Common Crane *(Grus grus)*	18	2.4
Waders (Scolopacidae)	9	1.2
Gulls (*Larus spp.*)	16	2.1
Other or undefined birds	51	6.7
- Geese (*Anser / Branta* spp.)	8	1.1
- Corvids (Corvidae)	16	2.1
Mammals	**55**	**7.2**
Reindeer calves	24	3.1
Other mammals	31	4.1
- Hares *(Lepus sp.)*	14	1.8
- Adult reindeer *(Rangifer tarandus)*	8	1.1
Tot	**763**	**100**

located up to 12–14 km away from their nest. A perfect model would take into account only the areas actually used by the individual White-tailed Eagles, but determining these areas would require satellite transmitters or extensive fieldwork to follow each individual pair, which is not possible to execute on a large scale. Forest is the main landscape type in the area, and White-tailed Eagles require robust trees for their nests, but they did not explicitly select forest in their nesting territory as hunting ground. The unused areas consist mainly of forest; hence, the proportions of preferred hunting habitats should be a good proxy for the areas actually used by the White-tailed Eagles. We showed that the White-tailed Eagles prefer some habitats in their nesting territories associated with foraging, and we linked these habitats to different use of prey species. In addition, White-tailed Eagles nesting in territories with larger proportions of a non-preferred habitat were able to utilize it, as shown by the prey composition. The landscape composition of a theoretical circular territory with radius 10 km can therefore be used to predict the diet composition of White-tailed Eagle pairs in northern Finland.

Diet in general

Fish, especially pike, form the core of the diet of White-tailed Eagles nesting in Lapland. As expected, the proportion of fish increased with proportion of lake and marshland in the nesting habitat. For burbot (*Lota lota*), the increase was just associated with lakes, but for cyprinid fish and pike, marshland also caused an increase. For pike, the increase was larger for marshlands than for lakes. Pike spawn in the spring, just after the ice melting, in shallow waters such as flooded marshlands (Casselman and Lewis 1996), where they are easy prey for White-tailed Eagles. Outside the spawning season, mature pike also often occur in shallow, vegetation-rich areas (Casselman and Lewis 1996). The marshland habitat is mainly found at the shores of lakes, indicating shallow waters suitable for fishing. These factors could explain why the proportion of fish and pike in the diet of a pair is better explained by the proportion of marshland than by the lake area in the territory.

Bird species occur in much more diverse habitats (in the available GIS data) than fish do, which complicates the investigation of their occurrence as a group. The most significant association with habitat for birds as a group was that their occurrence in the diet increased with sparse forest. This relationship was clearly driven by grouse that inhabit this kind of forests and are the most available bird prey in the size-span suitable for White-tailed Eagles in the habitat (Väisänen et al. 2011).

Waterfowl and gulls are typically associated with marshlands and lakes, but their proportion as remains did not increase in territories with higher proportions of these habitats. Instead, their proportion decreased with marshland. The White-tailed Eagle pairs that ate waterfowl and gulls were often nesting close to lakes or rivers, but remains of these species were also completely missing from the nests of many pairs nesting close to water. This negative relationship may mirror the high occurrence of pike in this habitat. White-tailed Eagles nesting close to water may principally choose fish in these habitats and use waterfowl and gulls opportunistically when encountered. Fish are shown to be the preferred prey of White-tailed Eagles in inland landscapes of Germany (Nadjafzadeh et al. 2013), in agreement with the findings in the present study, and this seems to hold true as well in northern inland landscapes. The same study showed that mammals were the least preferred prey (Nadjafzadeh et al. 2013), which also seems to be the case in Lapland. First, their share of the total prey is small. Second, no habitats where mammals mainly occur were preferred by the White-tailed Eagles. Third, the only habitat types

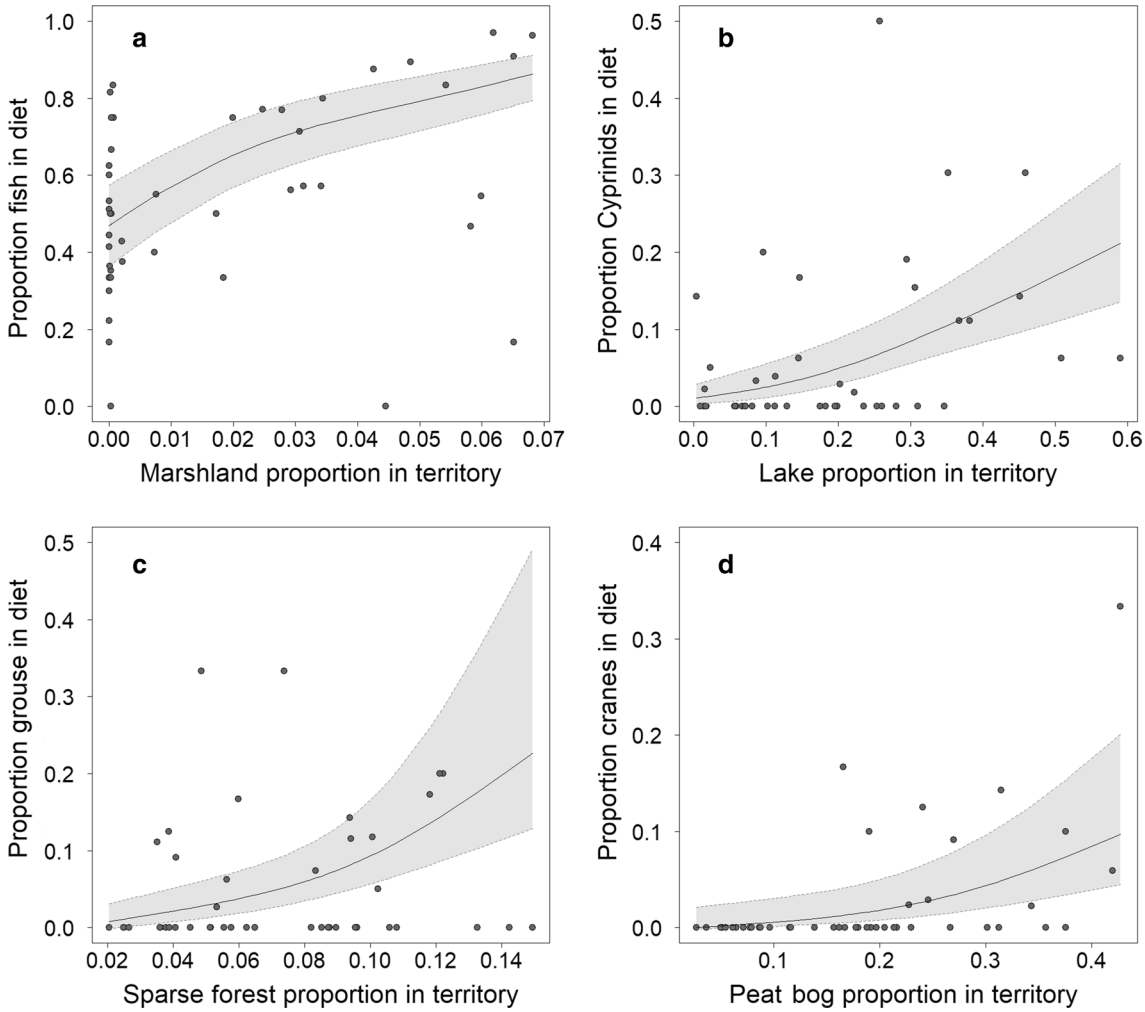

Fig. 4 Relationships between proportion of habitat around the nest at a 10 km radius and prey items in the diet of White-tailed Eagles in Lapland. The x-axis shows the proportion of the particular habitat type in the territory, and the y-axis shows the proportion of prey in the identified prey material. Only significant relationships are shown (see Table 4). The dots are actual means (over all the years, if many) for each territory, while the lines are model-based estimates with confidence intervals (grey shade)

Table 3 Estimates of the occurrence of major prey groups of White-tailed Eagles depending on proportions of different habitats around their nests within a radius of 10 km as obtained from a generalized linear model (*GLM)*

Habitat	Fish ($n=490$)			Birds ($n=218$)			Mammals ($n=55$)		
	Estimate	z	P	Estimate	z	p	Estimate	z	P
(Intercept)	1.01 ± 0.50	2.05	0.0406*	− 1.81 ± 0.53	− 3.43	0.0006***	− 1.63 ± 0.86	− 1.90	0.0581
Latitude	**− 2.12 ± 0.46**	**− 4.62**	**< 0.0001*****	**1.85 ± 0.46**	**4.00**	**< 0.0001*****	0.84 ± 0.70	1.21	0.2282
Marshland	**18.7 ± 4.97**	**3.77**	**0.0002*****	**− 12.3 ± 5.30**	**− 2.33**	**0.0199***	**− 22.6 ± 9.23**	**− 2.45**	**0.0143***
Sparse forest	**− 8.49 ± 3.83**	**− 2.21**	**0.0268***	**11.8 ± 4.02**	**2.93**	**0.0034****	− 4.85 ± 6.33	− 0.77	0.4442
Lake	**1.99 ± 0.75**	**2.65**	**0.0081****	− 1.15 ± 0.79	− 1.46	0.1455	**− 2.77 ± 1.55**	**− 1.79**	**0.0737**
Peat bog	**2.42 ± 1.13**	**2.14**	**0.0322***	**− 1.88 ± 1.11**	**− 1.69**	**0.0909**	− 1.31 ± 1.61	− 0.82	0.4151
Open areas	4.26 ± 4.79	0.89	0.3733	− 6.36 ± 5.21	− 1.22	0.2217	3.58 ± 6.43	0.56	0.5777

Significant ($p<0.05$) and indicative ($p<0.1$) results are shown in bold. Sparse forest stands for transitional forests with low canopy cover (10–30%)

Table 4 Occurrence of prey types in the prey of White-tailed Eagles in relation to their nesting territory habitats within a radius of 10 km from the nest

Proportion habitat in territory	Pike *Esox lucius* ($n=380$)			Cyprinid fish ($n=51$)			Burbot *Lota lota* ($n=21$)		
	Estimate	Z	p	Estimate	Z	P	Estimate	Z	P
(Intercept)	0.59 ± 0.21	2.77	0.0057**	−4.28 ± 0.62	−6.85	< 0.0001***	−7.31 ± 1.93	−3.79	0.0002***
Lake	0.14 ± 0.55	0.26	0.7990	**3.74 ± 0.99**	**3.77**	**0.0002*** **	**4.73 ± 1.52**	**3.11**	**0.0019** **
Marshland	**18.0 ± 3.73**	**4.82**	**< 0.0001*** **	**19.1 ± 7.23**	**2.64**	**0.0084** **	14.8 ± 10.5	1.41	0.1586
Latitude	**−1.87 ± 0.35**	**−5.38**	**< 0.0001*** **	0.03 ± 0.99	0.03	0.9751	2.93 ± 2.55	1.15	0.2504

Proportion habitat in territory	Waterfowl ($n=87$)			Gulls *Larus* sp. ($n=16$)			Common Crane *Grus grus* ($n=18$)		
	Estimate	Z	P	Estimate	Z	P	Estimate	Z	p
(Intercept)	−1.79 ± 0.39	−4.60	< 0.0001***	−4.27 ± 0.97	−4.39	< 0.0001***	−5.99 ± 1.31	−4.56	< 0.0001***
Lake	0.05 ± 1.01	0.05	0.9581	1.68 ± 2.01	0.84	0.404			
Peat bog	**−3.87 ± 1.27**	**−3.04**	**0.0024** **	−1.68 ± 3.73	−0.45	0.652	**9.93 ± 3.45**	**2.88**	**0.0040** **
Marshland	**−25.1 ± 7.19**	**−3.50**	**0.0005*** **	4.78 ± 12.6	0.38	0.703	7.71 ± 13.2	0.59	0.5585
Latitude	**1.60 ± 0.46**	**3.51**	**0.0005*** **	0.32 ± 1.31	0.25	0.806	−0.47 ± 2.25	−0.21	0.8330

Proportion habitat in territory	Grouse ($n=45$)			Reindeer calves ($n=24$)		
	Estimate	Z	p	Estimate	Z	p
(Intercept)	−4.92 ± 1.22	−4.03	< 0.0001***	−4.44 ± 1.81	−2.46	0.0139*
Forest	−0.46 ± 1.57	−0.29	0.771			
Sparse forest	**26.2 ± 6.15**	**4.25**	**< 0.0001*** **	−7.57 ± 10.9	−0.70	0.4854
Open areas	5.46 ± 9.73	0.56	0.575	5.39 ± 7.16	0.75	0.4519
Lake				−1.21 ± 2.25	−0.54	0.5896
Peat bog				1.21 ± 2.44	0.50	0.6191
Marshland				**−22.29 ± 13.1**	**−1.70**	**0.0890**
Latitude	0.14 ± 0.80	0.17	0.862	**3.80 ± 1.71**	**2.23**	**0.0260***
Reindeer density				−1.43 ± 1.48	−0.96	0.3361

All models are in the form [Proportion of target species] ~ intercept + habitat_x + habitat_y + … + habitat n + latitude. For the choice of potential explanatory habitat variables for each prey group, see methods

Significant ($p<0.05$) and indicative ($p<0.1$) results are shown in bold. *n* is the number of identified prey items of each species or group. *df* for all species = 44

that were associated with mammals, namely marshlands and lakes, showed negative correlations. The White-tailed Eagles did not choose mammals in any habitat and avoided them in environments where fish were abundant.

The general prey composition in this study was very similar to the previous one described in the 1980s (Sulkava et al. 1997), indicating that no major turnovers have happened regarding the prey availability. The Common Crane, however, occurred to a greater extent in this study (2.4% of the prey) than in the previous one (0.4%). Crane occurrence grew with peat bog, which also was a preferred habitat. It is possible that the population is about to be saturated around the reservoirs, and new pairs are now occupying alternative habitats with more peat bogs. Grouse were also slightly more abundant in this study (5.9% vs. 3.7%), which could indicate that more pairs inhabit areas with sparse forest. This habitat is suitable as a hunting ground for White-tailed Eagles, albeit not preferred in this area.

Reindeer calves in the diet

The reindeer calf remains were not associated with any habitat type, nor with reindeer density in a cooperative. However, their appearance in the diet increased with latitude. The number and density of free ranging reindeer also grows towards north (Finnish Environment Institute 2019), where the forests are sparser and the trees grow shorter. Reindeer calves should hence be easier to access in the north, both by availability and approachability.

In 2017, considerably more reindeer calf remains were found at the White-tailed Eagle nests than were found in 2018. The snow cover in the winter of 2017–2018 around the water reservoirs was thicker than in the winter 2016–2017, but spring and the snow melt were earlier in 2018 (Official Statistics of Finland 2019). In Norway, deep snow in the spring negatively affects the survival of reindeer calves (Tveraa et al. 2003) and the reproductive rates are lower for reindeer in springs when the snow melt is late (Helle and Kojola 2008). A majority of the calf mortality occurs at birth or within a week thereafter (Miller and Barry 2009). The higher occurrence of reindeer calves in nests in 2017 may be explained by a weaker condition and higher mortality of the calves due to the late spring snow melt. This research concerns only the connections between territory habitats and prey use by nesting White-tailed Eagles and does not allow for answering other important questions regarding the matter. Our findings, however, indicate that the nesting White-tailed Eagles do not seek out reindeer calves in any habitat; rather, the eagles exploit the calves when the calves are available. Scavenging birds are commonly mistakenly assumed by herders to have killed their prey (Duriez et al. 2019), even though they are just utilizing available resources. We currently do not know whether White-tailed Eagle have killed the reindeer calves or are scavenging them. However, successful co-existence between these predators and livestock herders crucially requires the involvement of the herders, along with conservation biologists, in the management, as well as consideration of the socio-economic aspects of that co-existence (Bennett 2016; O'Rourke 2014).

Conclusions and implications

To conclude, our research highlights preferences of nesting habitat of White-tailed Eagles in an inland environment and how these preferences are associated with the nestling diet. The remains of prey species mostly reflect the habitat preferences of the prey, while the preferred territory habitats in turn reflects the occurrence of the preferred prey.

Comprehensive monitoring of raptor populations, where the individuals use large areas in vast, inaccessible landscapes, is difficult, expensive, time-consuming, and often simply impossible. Our results can be used to predict the prey use of White-tailed Eagles at the landscape-level and potentially also the future dispersion of a growing population in Lapland. Additional research is needed to refine predictors beyond habitats and feeding grounds using models that take into account additional factors, such as the availability of nesting trees, the distance to other White-tailed Eagle nests, and human disturbance (Tikkanen et al. 2018b).

Reindeer calves are included in the diet of White-tailed Eagle nestlings in small proportions, with a slightly larger proportion in the northern areas. The numbers of reindeer calves eaten, but not necessary killed, by the nesting White-tailed Eagles are so small that at least the nesting white-tailed eagles do not appear to pose a threat to reindeer herding. More research is needed, however, to estimate the total loss of calves due to predation by White-tailed Eagles in the area, including the predation by sub-adult White-tailed Eagles and the viability of the calves that are eaten.

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