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Changes in Avian Top-Predator Diet in the 21st Century in Northeast (NE) Poland

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Abstract: The White-Tailed Eagle (WTE) *Haliaeetus albicilla* is a top avian predator that has rapidly increased in numbers and range in large parts of Europe in recent decades. In Poland, over the past 30 years, it has recolonized previously abandoned areas. In 1991, the first breeding pair in a large forest complex, the Augustów Forest (Northeast (NE) Poland), was recorded. In 2022, there were 13 breeding pairs. We analyzed changes in the diet composition of WTE in 2000–2023, divided into three periods: 2000–2005, 2009–2017, and 2018–2023. Throughout the 24 years of study, birds were the most frequently recorded food item, accounting for an average of 58% of food items, followed by fish (34%) and mammals (7%). During the study period, the most numerous food items were the Northern Pike *Esox lucius*, Coot *Fulica atra*, Common Bream *Abramis brama*, Mallard *Anas platyrhynchos*, and storks *Ciconia* sp. These species together accounted for 52% of food items. We recorded a long-term increasing share of Northern Pike, storks, and Great Crested Grebe *Podiceps cristatus*. Opposite changes, with declining frequency, were found for Coots and ducks. The share of the Coot, ducks, and Great Crested Grebe, as well as the total share of food connected with lakes in the WTE's diet, increased along the growing area of lakes in the territory of the WTE. The proportion of fish in the food did not show a relationship with the increase in the area of lakes, while the most frequently eaten fish species changed. Observed changes in food composition appear related to the settlement of the habitat-diverse areas by individual breeding pairs and changes the availability of main food categories.

Keywords: coot; diet composition; foraging pattern; Northern Pike; White Storks; White-Tailed Eagle

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1. Introduction

Birds of prey play extensive ecological functions, from top predators and scavengers to indicators of habitat changes. They require special attention from researchers due to their relatively low numbers and densities associated with large spatial requirements and potential conflict with human interest [1]. As top predators, large raptors strongly affect the trophic structure of the ecosystem. They regulate the number and distribution of prey by killing directly and having a negative impact on potential prey. Studies of food composition and feeding ecology make it possible to assess the impact of raptors on their prey populations. This includes the effects of predation on rare and endangered species, but also numerous species that can affect the functioning of ecosystems [2–4]. Food availability is a limiting factor for bird of prey populations, affecting reproductive parameters and population dynamics [5].

Intense human persecution led to a decline in raptor populations of most European species during the 20th century. However, in recent decades, comprehensive conservation efforts have brought population recovery [1]. The increase in numbers and range expansion in Europe over the last half-century has involved numerous species of birds of prey, but most spectacularly, the White-Tailed Eagle, hereafter WTE. Its population in Europe has rapidly decreased due to human persecution in the 20th century [6,7], but during the last decades, WTE's recovery and expansion have been observed [8].

The above-mentioned broader trends are exemplified by Poland. In 1994, the population of WTE was estimated at 223 breeding pairs, while in 2017—at 1400 pairs [9,10]. The development of the WTE population entailed the colonization of new areas and increased numbers within the former range [10]. The WTE is now a breeding species throughout the country except in the high mountains [11]. The recovery and growth of the WTE population affected the food webs, had consequences for prey species, and caused conservation and management conflicts [4,12,13]. The expansion of this raptor species was associated with the colonization of previously unused habitats, like fish ponds, and the exploitation of new food sources, like the White Storks *Ciconia ciconia* and Cranes *Grus grus* [14,15] or the Great Cormorant *Phalacrocorax carbo* [16].

As a dominant top predator, the WTE can impact, directly and indirectly, other co-occurring bird species, including other predators, by persecution, predation, kleptoparasitism, and competition [4,16,17]. A growing number of WTEs in central Europe may cause those raptors locally to lower the population of other protected bird species [17,18]. The WTE is listed in Annex I to the Directive 2009/147/EC of the European Parliament and the Council of 30 November 2009 on the conservation of wild birds and is strictly protected under Polish law.

Active conservation of breeding habitats and reduced chemical contamination of the environment influence the rapid increase in WTE numbers. Among others, food availability is one of the critical determinants of the development of the population. The composition of the diet is influenced by the diversity of the environment structure, mainly the share of the water area and its abundance of potential prey [13]. The WTE is associated with open water habitats: lakes, rivers, lagoons, and the sea coast [6,7]. Its food composition is dominated by fishes and water birds, in different proportions in particular studies. Mammals complete the list of prey. However, the diet composition of WTE shows a solid regional, environmental, and seasonal variation, reflecting primary prey species availability [13,14,18–21]. In central and eastern Europe, the most often consumed species include the Northern Pike *Esox lucius*, Common Bream *Abramis brama*, Carp *Cypinus carpio* and other *Cyprinidae*, Pikeperch *Sander lucioperca*, Coot *Fulica atra*, Mallard *Anas platyrhynchos*, the Great Crested Grebe *Podiceps cristatus*, as well as White Stork and Black Stork *Ciconia nigra* [3,6,15,18]. Wildfowl and large cyprinids contribute most to the diet, while corvids and mammals are locally important in Romania [22]. In northern Europe, WTEs consume mainly Northen Pike, waterfowl, predominantly Anatidae, and grouse [13,21].

Our study aimed to examine whether the composition of the food of WTE in the extensive forest complex located on Lithuanian Lakeland in northeast Poland changes over a long time. Based on the observed increase in White-Tailed Eagle abundance in the study area [4,23], we expected to find changes in food composition related first to the occupation of more strongly environmentally diverse territories and noted changes in the availability of prey populations over a long time. We hypothesized that (i) the proportion of the main prey groups in the WTE's food is, over the long term, stable, but the frequency of the most frequently consumed species within a main group changes, and that (ii) an increase in the area of lakes within the territory influences an increase in the proportion of fish in the WTE's diet, while its smaller share results in greater consumption of birds or mammals.

2. Study Area

The Polish part of the Augustów Forest (after that AF) is in the country's northeast (at 23°15′ E, 53°54′ N). It extends over some 1400 km^2. The area is relatively flat, with elevations between 135 and 190 m a.s.l. The forest cover is around 90%, while lakes account for 6% of the area. Tree stands are dominated by the Scots Pine *Pinus sylvestris* (78%). The average age of trees here is 65 years, but stands older than 100 years account for about 15% of the forest area. Among the forest site types, mesic pine forest accounts for almost 40% of the area, while a further 27% comes from mesic mixed/coniferous forest. There are more than 100 post-glacial lakes in the AF, including 13 with an area of more than 1 km^2. The largest lake has an area of almost 22 km^2. The AF is included within Europe's Natura 2000 network—as the Special Protection Area for Birds PLB200002 "Puszcza Augustowska." Nevertheless, most of the area comprises commercial stands managed by six Forest Districts of Poland's State Forests National Forest Holding. The Lake Wigry National Park, covering some 150 km^2, is located in the northwestern part of the AF [24]. The studied WTE population was developed from the first breeding pair in 1999 to 13–15 in 2017 and a later period [4,23].

3. Methods

3.1. Food Data Collection and Identification

The current study was conducted in AF from 2009 to 2023. Additionally, data from earlier studies on the same area [14] were used to analyze and compare long-term WTE diet changes. During fieldwork, we searched for pellets and prey remains under the occupied WTE nests on the ground and under roosting trees in the vicinity of nests [14,24]. In total, food composition data were obtained from 13 different breeding territories. Nests were visited at least twice every breeding season from March to July. Methods for determining prey species were adopted from Zawadzka [19]. For the identification of food groups, we used all collected material. The skulls, bones, and hair of mammals, the feathers, bills, humeri, and tarsometatarsi of birds, and the scales and bones of fish were used for species-level identification. Bird feathers were identified to species when possible using author's feather collection. The guides for feathers [25,26] were used to identify bird species, and fish were identified after [27]. Feather fragments, mammalian hair, and jaws were identified microscopically; see procedure after [22,28].

In the case of remains found in both pellets and food remains, double counting of food items was avoided by assuming the lowest probable number of individuals eaten [19]. The minimum number of individuals (MNI) at each collection's lowest possible taxonomic level was calculated from distinctive anatomical features present by taking the minimum number derived from each source or by combining them. If we found, e.g., the bill and feathers of a White Stork, we counted them as only one prey. In the case of fish, scales of one species at a similar diameter collected during single control were treated as belonging to one individual [28].

For the identified prey species, the environment in which WTE hunted them was assigned. Distinctions were made between aquatic (W), forest (F), open area (O), and domestic species (D). The biomass of prey was not estimated; only its frequency was analyzed. The food niche breadth was calculated after Levins [29], $B = 1/\sum p_i^2$, where p_i is a fraction of each prey group distinguished as follows: mammals (divided for ungulate and other mammal species), birds (divided for *Anatidae*, Great Crested Grebe *Podiceps cristatus*, Coot *Fulica atra*, Storks *Ciconia* sp., Great Cormorant *Phalacrocorax carbo*, *Laridae* and others birds), fish (divided for the Northern Pike and Common Bream and other fish species), and all others species consumed. Index B varies from 1 (the narrowest niche) to 12 (the broadest niche possible).

We collected 660 pellets and 873 food remains from 2000 to 2023. In total, data from 77 nests/year were used for analysis. The collected data about WTE's diet were divided for analysis into three periods: 2000–2005 (partly published by [14]), 2009–2017, and 2018–2023. In 2018, we found the last two of the analyzed WTE nests, and their distribution in the study area finally settled and was sustainable until 2023. Therefore, having a different pool of nests with potential data collection per year, we divided the study time into three separate periods. In the first period, we collected 619 preys from 14 nests, from one to four nests per year. In the second period, we obtained 351 preys from 23 nests, from one to seven nests per year. In the third period, we collected 717 preys from 40 nests, from four to eight nests per year. The average value was 80 items for one year/season, the minimum value was 20, and the maximum was 212. The different number of nests in consecutive years is due to the variability in the effects of breeding. After early brood loss, no food remains were found under the nest.

3.2. Structure and Size of Territory

To assess the potential territory's environmental structure, we evaluated the surface proportion of different habitats. The percentage of lakes, forests, and open areas was measured in a buffer of 4,1 km around the WTE nests. The exact size and shape of the foraging area used by the eagles are not known in the study area, and the space used by WTE during breeding season shows a substantial variation depending on the habitat structure and food abundance as well as assessment methods [13]. For analysis, we assumed after [30] that the size of the territory is determined by half of the nearest neighbor distance (NND) between occupied nests, which in Augustów Forest amounts to 8.1 km [4]. Environmental data were taken from Poland's Forest Data Bank, run by the State Forest [31]. The share of water area was compared with the proportion of food categories associated with lakes and rivers.

3.3. Statistical Analysis

We used the chi-square test for multidimensional contingency tables to compare the generalized diet composition (fishes, birds, mammals, reptiles, and invertebrates in the three time periods (2000–2005, 2009–2017, 2018–2023)). The chi-square test (χ^2) was used to compare the proportion of food from different habitats and the value of food niche breadth among subsequent periods of our study. We used the Wilcoxon test to compare water share between older and newly located WTE territories.

To check how the WTE diet changed over time, we used a generalized linear mixed model (GLMM) using data for each territory for each year for which sufficient data about food have been collected. In the GLMM, we used the year as the dependent variable, while the shares of the eight most frequent food categories of WTEs, each with a share exceeding 3%, were independent variables. Only this threshold ensured the repeatability of food items across seasons in single nests. Nest/year with less than ten prey collected in a year were deleted from detailed analyses (8 cases); see [32]. The proportion of Northern Pike, Common Bream, storks, Great Crested Grebe, Coot, gulls, Great Cormorant, and ducks were used as independent variables. The unit was a single nest in a given year, from which at least ten preys were identified. We used a territory number as a random factor. An a priori Fisher's test and a post hoc t-test were used to check the statistical significance of analyzed parameters.

We used a generalized linear model (GLM) to check the dependence of the proportion of each of the most frequent food items according to the water surface area in the WTE's territory (in a 4.1 km buffer). The dependent variable was the water surface area expressed in km^2, and the independent variables were shares of the food items for each territory/year. A Gamma error distribution with a log link was used. An a priori Fisher's test and a post hoc t-test were conducted in this case. We used the simple GLM to check the size of the water area (in km^2) impact on the share of the non-water prey species.

The sjPlot package [33] was used to illustrate the results for individual species graphically. From the developed models, graphs of the model-predicted proportion of the studied species among WTE food during the study period were obtained. For the second model, the same procedure was used to obtain a graphical presentation of the share of individual species in the WTE food in the dependence on the water surface in a given territory. Statistical analyses were performed in the R (ver. 3. environment with the R-studio overlay).

4. Results

4.1. Diet Composition

We collected 1687 WTE food items during 24 years of the study (2000–2023), including 619 from 2000–2005 (Table 1). The WTE food consisted of fish, birds, mammals, and, exceptionally, reptiles and invertebrates. At least 68 species of animals were identified, including eight species of fish, 39 species of birds, and 18 species of mammals. Throughout the study period, the most numerous captured prey was the Northern Pike, followed by Coot, Common Bream, Mallard and Storks (mainly White Stork). These species together accounted for 52% of the frequency of food consumed (Table 1).

Table 1. Diet composition of White-Tailed Eagle in Augustów Forest in 2000–2023, abbreviations: W—water, O—open areas, F—forests, D—domestic.

Period		2000–2005		2011–2017		2018–2023		2000–2023	
Prey Species	**Habitat**	**N**	**%**	**N**	**%**	**N**	**%**	**N**	**%**
Esox lucius	W	29	5	77	22	115	16	221	13
Abramis brama	W	72	12	51	15	48	7	171	10
Tinca tinca	W	0	0	4	1	1	0	5	0
Perca fluviatilis	W	3	0	11	3	22	3	36	2
Rutilus rutilus	W	0	0	3	1	7	1	10	1
Carassius carassius	W	1	0	0	0	0	0	1	0
Coregonus lavaretus	W	1	0	0	0	0	0	1	0
Barbus barbus	W	1	0	0	0	0	0	1	0
Undetermined fish	W	84	14	23	7	22	3	129	7
Total Fish		187	31	169	48	215	30	571	34
Cygnus olor	W	7	1	1	0	5	1	13	1
Bucephala clangula	W	1	0	0	0	2	0	3	0
Spatula querquedula	W	0	0	0	0	1	0	1	0
Spatula clypeata	W	0	0	0	0	1	0	1	0
Mareca strepera	W	0	0	0	0	1	0	1	0
Anas platyrynchos	W	79	13	19	5	42	6	140	9
Anas crecca	W	0	0	1	0	0	0	1	0
Anas sp.	W	54	9	0	0	26	4	80	4
Domestic duck	D	0	0	0	0	1	0	1	0
Tetrastes bonasia	F	0	0	0	0	3	0	3	0
Gallus domesticus	D	2	0	2	1	20	3	24	1
Podiceps cristatus	W	9	1	11	3	37	5	57	3
Columba livia	D	0	0	0	0	3	0	3	0
Columba oenas	F	1	0	0	0	13	2	16	1
Columba palumbus	O	4	1	0	0	6	1	10	1
Gallinula chloropus	W	0	0	0	0	1	0	1	0
Fulica atra	W	93	15	31	9	62	9	186	11
Vanellus vanellus	O	1	0	0	0	4	1	5	0
Scolopax rusticola	F	0	0	0	0	1	0	1	0
Chroicocephalus ridibundus	W	8	1	13	4	11	2	32	2
Larus argentatus	W	1	0	0	0	3	0	4	0
Larus canus	W	1	0	0	0	1	0	2	0
Larus sp.	W	11	2	2	1	2	0	15	1
Sterna hirundo	W	0	0	0	0	2	0	2	0
Ciconia ciconia	O	26	4	35	10	79	11	140	8
Ciconia nigra	F	4	1	1	0	0	0	5	0
Ciconia sp.	O	13	2	0	0	0	0	13	1
Botaurus stellaris	W	1	0	1	0	1	0	3	0
Ardea cinerea	W	4	1	0	0	1	0	5	0
Ardea alba	W	0	0	0	0	1	0	1	0
Phalocrocorax carbo	W	7	1	14	4	48	7	69	4
Buteo buteo	F	0	0	2	1	3	0	5	0
Circus aeruginosus	W	0	0	1	0	0	0	1	0
Picus canus	F	0	0	0	0	1	0	1	0
Dryocopus martius	F	1	0	0	0	2	0	3	0
Dendrocopos major	F	0	0	2	1	0	0	2	0
Garrulus glandarius	F	7	1	1	0	5	1	13	1
Coloeus monedula	O	0	0	0	0	7	1	7	0
Corvus frugilegus	O	2	0	0	0	1	0	3	0

Table 1. *Cont.*

Period		2000–2005		2011–2017		2018–2023		2000–2023	
Prey Species	**Habitat**	**N**	**%**	**N**	**%**	**N**	**%**	**N**	**%**
Corvus corax	F	1	0	1	0	1	0	3	0
Corvus cornix	O	0	0	0	0	0	0	0	0
Turdus merula	F	0	0	0	0	1	0	1	0
Turdus sp.	F	0	0	0	0	6	1	6	0
Undetermined birds		27	4	24	7	41	5	92	6
Eggs of Heron	W	2	0	0	0	0	0	2	0
Total birds		375	61	162	46	446	62	983	58
Talpa europaea	O	2	0	0	0	2	0	4	0
Ondatra zibethica	W	0	0	1	0	0	0	1	0
Arvicola terrestris	W	1	0	1	0	0	0	2	0
Myodes glareolus	F	0	0	1	0	0	0	1	0
Microtus arvalis	O	0	0	3	1	0	0	3	0
Microtus oeconomus	O	1	0	0	0	0	0	1	0
Microtus sp.	O	2	0	0	0	0	0	2	0
Undetermined *Rodentia*	O	1	0	0	0	1	0	2	0
Lepus europaeus	F	1	0	2	1	11	2	14	1
Lepus timidus	F	1	0	1	0	0	0	2	0
Lepus sp.	F	0	0	0	0	1	0	1	0
Canis familiaris	D	1	0	1	0	9	1	11	1
Nyctereutes procyonoides	F	1	0	0	0	0	0	1	0
Martes martes	F	0	0	2	1	1	0	3	0
Mustela putorius	F	1	0	0	0	1	0	2	0
Neogale vison	W	0	0	0	0	2	0	2	0
Felis catus	D	0	0	0	0	3	0	3	0
Sus scrofa	F	2	0	5	1	12	2	19	1
Capreolus capreolus	F	9	2	1	0	6	1	16	1
Cervus elaphus	F	5	1	0	0	1	0	6	0
Refuse from slaughter-house	D	0	0	0	0	4	1	4	0
Undetermined mammals		8	1	0	0	2	0	10	1
Total Mammals		37	6	19	5	55	8	111	7
Natrix natrix	W	3	0	1	0	1	0	5	0
Total Reptiles		3	0	1	0	1	0	5	0
Lumnea stagnalis	W	3	0	0	0	0	0	3	0
Coleoptera	F	6	1	0	0	0	0	6	0
Total Invertebrates		12	1	1	0	1	0	14	1
TOTAL		619	100	351	100	717	100	1687	100

In the first period, birds were almost twice as numerous as fish and accounted for 61%; in the second period, they were almost as numerous—46%; and in the last period, they were significantly more numerous—62%. WTEs captured almost twice as many birds as fish for the entire study period. The proportion of eaten fish fluctuated from 29 to 48% in the study period, with an average of 34% (Figure 1). Changes in the share of fishes and birds were significant among the study periods (χ^2 = 13.98, df = 6, p = 0.03). The percentage of mammals in the diet was small and showed no evident change over time. A long-term proportion of food items from a predominated water habitat was 65 to 75% of animals consumed. The share of food categories obtained from open areas changed to a greater extent (Figure 2). The difference in categories of food percentage from each habitat was statistically insignificant (χ^2 = 7.29, df = 6, p = 0.29). The breadth of food niche B for the subsequent periods amounted to 7,80, 8,26, 9,15, but differences were insignificant (χ^2 = 2.51, df = 2, p = 0.28).

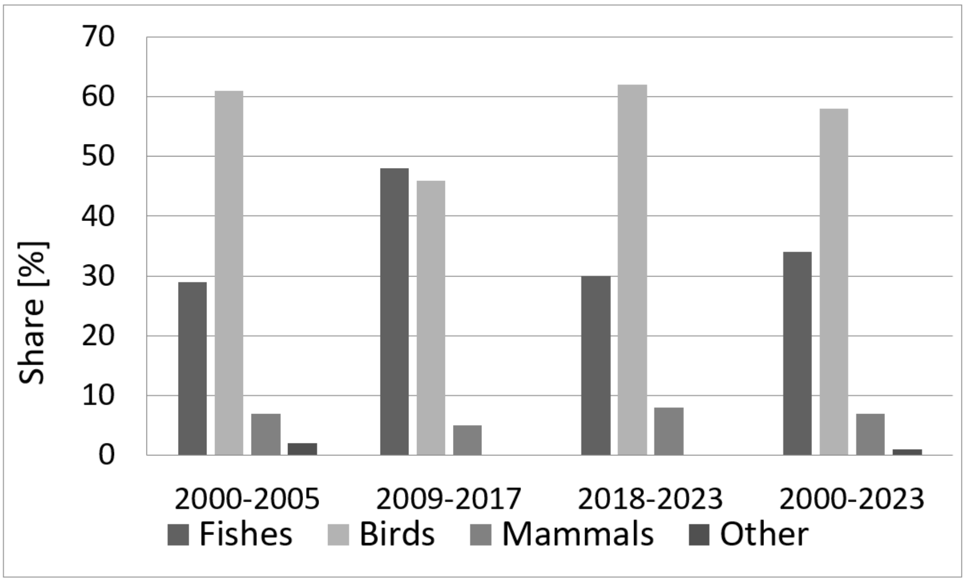

Figure 1. The share of general WTE food categories in three distinguished periods and the whole study period.

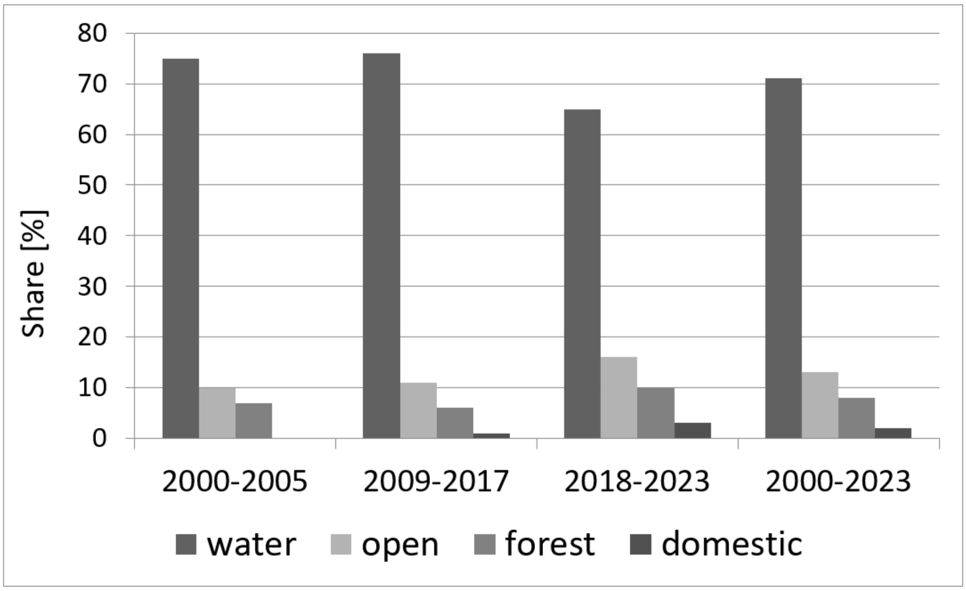

Figure 2. The share of WTE food categories belonging to the various habitats.

4.2. Changes in the Abundance of Primary Prey Species in the WTE Diet

The GLMM model calculated for eight groups of WTE food items showed that during the whole study period, the share of some of them changed significantly (Tables 2 and 3, Figure 3). The substantial changes during a long time were noticed for Great Crested Grebe (DF = 60, F = 17.78, $p < 0.001$), storks (DF = 58, F = 4.97, $p = 0.04$), Northern Pike (DF = 57, F = 11.95, $p = 0.001$), ducks (DF = 53, F= 7.05, $p = 0.01$) and Great Cormorant (DF = 55, F = 5.97, $p = 0.02$). Other food-type changes were not crucial in the a priori test. In post hoc analyses, the share of Great Crested Grebe increased significantly, while the share of Northern Pike also increased, but only near a significant level, and the proportion of ducks declined significantly (Table 3, Figure 3).

Table 2. The percentage of main categories of WTE food in analyzed study periods, bold type for the nine most common prey species, taken into account in GLM and GLMM.

Period / Food Category	2000–2005	2009–2017	2018–2023	2000–2023
	%	%	%	%
Northern Pike	5	22	16	**13.2**
Common Bream	12	15	7	**10.1**
Eurasian Perch	1	3	3	2.2
Other fishes	13	9	4	8.2
Storks	8	10	11	**9.9**
Coot	13	9	9	**10.1**
Mallard	14	5	6	**8.6**
Other ducks	8	0	4	**4.7**
Great Cormorant	1	4	7	**4.2**
Corvids	2	1	2	1.7
Great Crested Grebe	1	3	5	**3.5**
Gulls	4	4	2	**3.2**
Domestic hen	0	1	3	1.7
Woodpeckers	0	1	0	0.4
Birds of prey	0	1	0	0.4
Mute Swan	1	0	1	0.8
Pigeons	1	0	3	1.7
Herons	1	0	0	0.7
Other birds	6	7	8	6.9
Predatory mammals	1	1	2	1.4
Ungulate	3	2	3	2.8
Hares	0	1	2	1.1
Rodents	1	2	0	1.1
Reptiles	1	0	0	0.3
Invertebrates	2	0	0	0.6

Table 3. GLMM results for relationships between the year of study and the share of most frequent groups of WTE food (Intercept = study year).

	Estimate	Std. Error	t	Value Pr (>|t|)
(Intercept)	2013.12	2.886	697.51	<0.001
Great Crested Grebe	54.42	14.56	3.78	<0.001
Storks	8.24	5.20	1.66	0.11
Northern Pike	9.24	5.59	1.82	0.07
Common Bream	−15.60	27.24	−0.57	0.57
Coot	−2.80	7.13	−0.39	0.70
Ducks	−14.63	8.61	−2.05	0.05
Great Cormorant	14.77	6.16	2.40	0.02
Gulls	−11.82	6.15	−0.76	0.46
Random effect	Std. dev.			
Territory	2.59			
Residuals				
ε_{ij}	4.95			

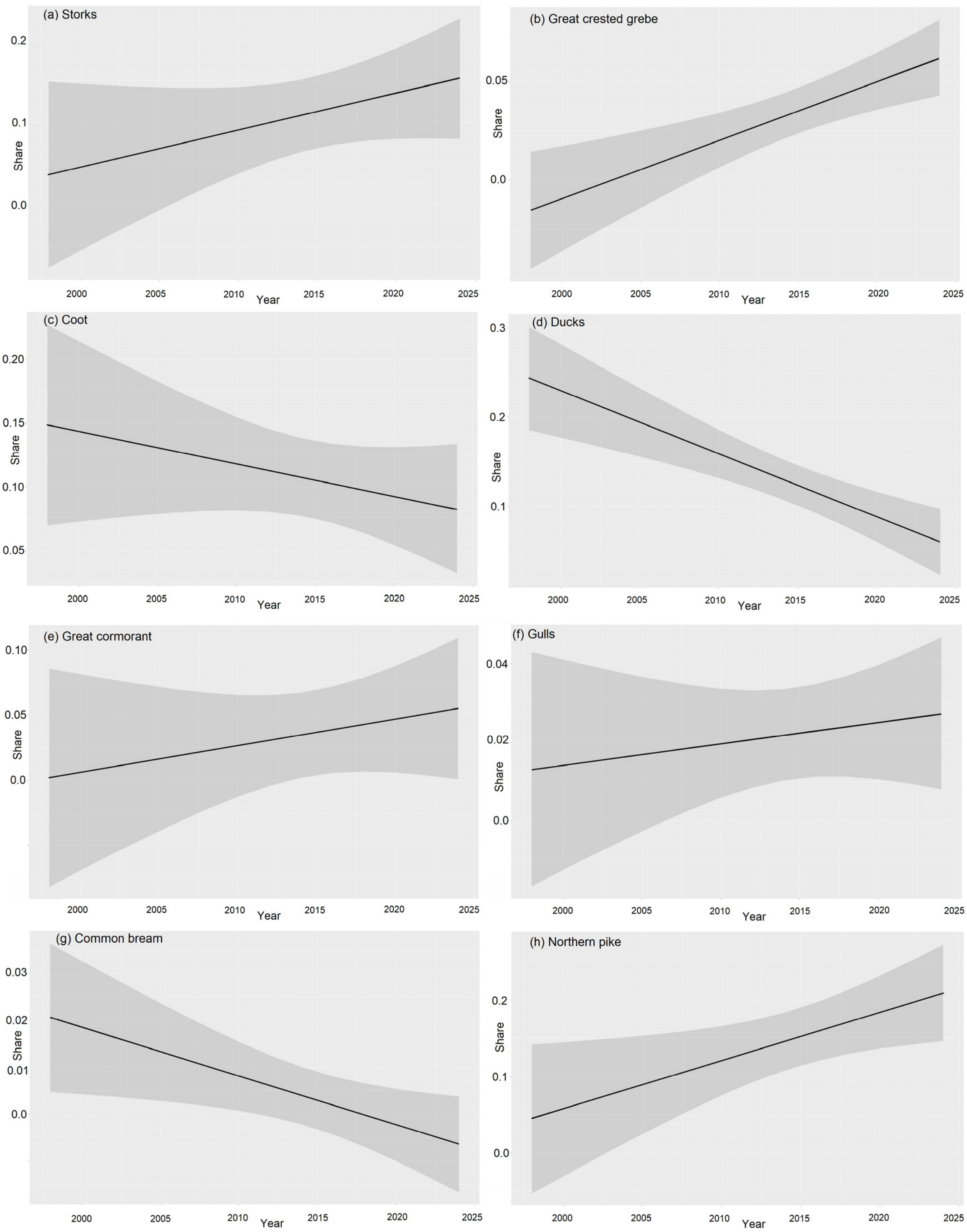

Figure 3. Results of GLMM model of time changes impact on the share of most frequent WTE food categories. The grey shading represents the 95% confidence interval.

4.3. Water Area Impact

The shares of the water area in a 4.1 km buffer around the WTE nests differed among individual territories. The smallest percentage of water area was 0% (0 ha), while the most significant share of the water surface was about 40% (2150 ha). The mean value of the water surface in a 4.1 km buffer around the WTE nest in the study area was about 15% (14.56%, 771 ha). Nests in the Lake Wigry National Park were encircled by about 40% of an open water area (37–41%), while the surrounding buffer of the rest of the WTE nests contained less than 10% of the water area. Territories established after 2005 did not differ from those previously occupied by raptors in the water area size (W = 37.5, $p = 0.28$).

The territory's water area share impacts WTE diet composition (Table 4, Figure 4). A priori test in GLM results indicated that the shares of the Coot (F = 14.08, DF = 56, $p < 0.001$), Storks (F = 8.09, DF = 59, $p = 0.006$), Great Crested Grebe (F = 7.59, DF = 60, $p = 0.008$) and ducks (F = 4.09, DF = 53, $p = 0.05$) were significantly correlated with the proportion of water surface in WTE territories. With post hoc test results, we found that bigger areas of open water in WTE territories impact a higher share of the Coot, Great Crested Grebe, and ducks in the raptor's diet (Table 4, Figure 4). Other food category shares showed no dependence on the percentage of water area.

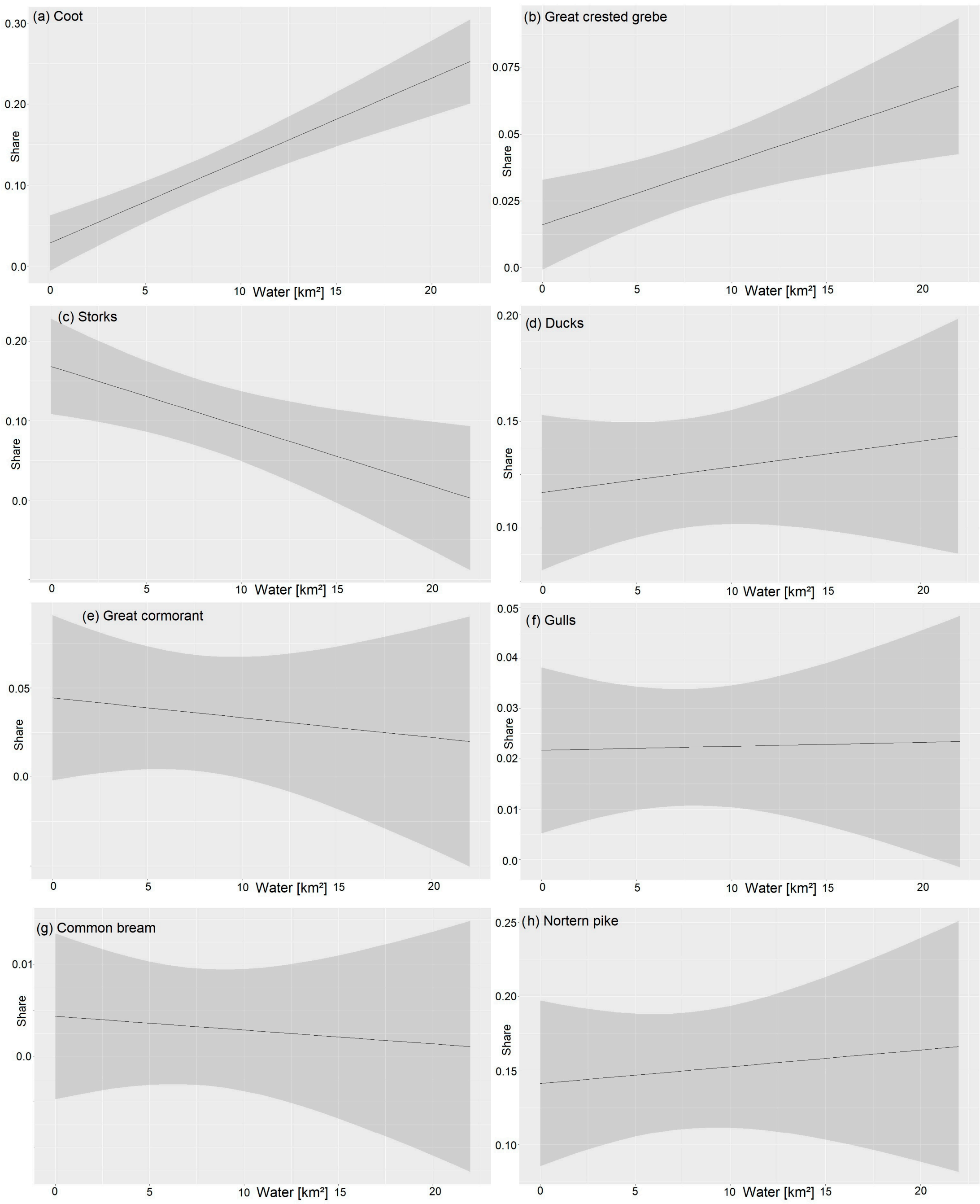

Figure 4. Results of correlation test between main groups of WTE food and proportion of water area in 4.1 km buffer around WTE nest in Augustów Forest. The grey shading represents the 95% confidence interval.

Table 4. GLM results for relationships between the water area in the 4.1 km buffer around the WTE nest and the share of most common groups of WTE food (Intercept = water area, Gaussian error distributed with inverse link).

	Estimate	Std. Error	z Value	Pr (>∣z∣)
(Intercept)	5.14	0.43	11.89	<0.001
Great Crested Grebe	5.48	2.43	2.26	0.028
Storks	0.09	0.82	0.11	0.910
Northern Pike	1.44	0.89	1.619	0.111
Common Bream	−5.16	4.86	−1.062	0.293
Coot	4.33	1.08	4.026	<0.001
Ducks	3.10	1.46	2.119	0.039
Great Cormorant	1.11	0.97	1.146	0.257
Gulls	−0.57	2.58	−0.22	0.827
AIC: 939.8				

Attempts to find valuable GLM of individual prey categories with other parameters (the share of forest; the percentage of open areas; or the number of villages) did not show significant dependencies; nor were results obtained for general groups of food (fishes; birds; mammals).

The share of terrestrial WTE food categories was significantly tied with water surface (F = 11.58, DF = 2, $p = 0.001$). The share of terrestrial WTE prey was estimated at 0.43 (SE = 0.04, t = 14.02, $p < 0.001$) and decreased by about 1.2% with each water area square km (SE = 0.001, t = −3.40, $p = 0.001$).

5. Discussion

Our study examined changes in the diet composition of a local population of WTE inhabiting a vast forest complex in NE Poland. The list of WTE food items in the breeding season from the Augustów Forest included at least 68 species identified in pellets and prey remains. In the long term, the number of prey species captured increased. During the 24 years of study, the share of the most numerous preys did not exceed 13%, although it reached a slightly higher value in a particular period. Among the most important preys of the WTE were the Northern Pike and Common Bream, followed by Coot, storks, and ducks. The feeding specialization of the studied WTE population was weak. WTE is a food opportunist, primarily preying on medium- and large-sized animals and the list of the most frequent species consumed and its proportions show regional and local variations [6]. The relatively high value of the food niche breadth and the low variability of this index among studied periods confirm such a foraging pattern in our study. The proportion of representatives of the various systematic clusters—fish, birds, and mammals—did not show evident variability over time. The most numerous group of the WTE food items was birds, although their proportion fluctuated. In the diet composition of the WTE from the AF, the share of fish was lower, and that of birds was higher than in most other study areas [2,3,6,13,15,18]. This may be due to the methodology adopted (collection of food remains only from the ground), as small remnants of fish may remain only in the nest. Birds prevailed in the diet of WTE only in a long-term study from Finland [21] and in the Danube Delta, Romania [22]. In our research, the share of mammals consumed was at a stable low level of 5–7%. This does not differ from the results reported by other researchers [2,3,6,13,18,22] and indicates that mammals only supplement the diet of the WTE.

As expected, in the long term, the observed changes in the WTE diet occurred among the most abundantly captured species within the main food groups. Evident changes over time involved more frequent capture of storks, Great Crested Grebes, and Northern Pike. A downward trend was documented in the consumption of the Coot, ducks, and Common Bream. Considering earlier data from the first breeding WTE pair in Augustów Forest, the percentage of the Coot preyed on declined from 40% in the diet in 1991–1998 [19] to only

9% in 2018–2023. The reason is a general decline in the number of this species in Poland. Still, it is also connected with smaller lake areas in later occupied territories, which affects the lower proportion of Coots in the WTE diet. It is probable that population decline is also the reason for the decrease in the number of captured ducks [10]. Explaining the change in consumed Common Bream and the Northern Pike is difficult and may result from the method used to collect food remains only on the ground. The hypothesis of an increase in the proportion of fish consumed as the area of lakes increases within the territory was not confirmed. The share of fish in the diet did not correlate with the water surface proportion, while the proportion among the most frequently captured fish species slightly changed. The proportion of gulls in the diet did not vary over time or by water surface area. The lack of the same dependence in the consumption of the Great Cormorant may be due to the low representativeness of the data, as this species of bird was eaten in great numbers by only one pair of the WTE nesting near the colony of the Cormorant. As reported in [16], the WTE exploits Great Cormorants locally, just by pairs of raptors nesting in their colonies. However, in AF, the number of all prey caught in the aquatic environment increased along the growing lake surface, confirming the opportunistic foraging pattern of the WTE. It is a flexible predator that successfully preys mainly on fish and water birds. In AF, the WTE population inhabits a typical, semi-natural habitat—lakes surrounded by vast forests, with a different proportion of open areas. Such environments offer the WTE a varied food supply. Our study suggests that lakes were these raptors' most important feeding habitat. The opportunistic foraging behavior of the WTE may indirectly document changes in the availability, and therefore abundance, of its most important prey. This is one of the ecological functions that apex predators can perform [34].

The increase in the number of storks eaten in the overall food composition may result from successive pairs of the studied WTE population settling in areas with a lower proportion of lakes and a higher proportion of open areas [14,19,24]. In such environments, which may be defined as suboptimal, an increase in the proportion of large prey not directly related to water in the diet is observed, as documented in a nearby area [15]. In addition, the WTE nesting in such areas also used other non-traditional prey, such as domestic poultry, leftover carcasses, and dogs and cats. However, their share in the overall diet composition was small.

The WTE as a top predator is often cited as impacting other predator species [4,35–37]. It is considered a regulator of the population of medium-sized mammals and birds of prey [14], but our study did not confirm this influence through direct predation. Birds of prey and predatory mammals combined accounted for only 0.5% of the frequency of food items consumed. The impact of the WTE is likely more important by indirect effects (facilitating nest predation with its presence around other predators as well as its nests), which affects the reduction in numbers and changes in distribution, as well as exerting of fear, as has been shown for the Black Stork in the AF [4], the Great Cormorant around the Baltic Sea [16] and was suggested in Lithuania in relationship to Black Stork and diurnal birds of prey [17,36]. The establishment of a WTE nest near the Great Cormorant colony caused some birds to move to a new colony in the middle of the village near the lake.

6. Conclusions

The White-Tailed Eagles in Augustów Forest consumed primarily birds and fish. During 24 years of study, the share of those two leading food groups fluctuated, but birds (mainly waterfowl) were captured more often than fish. The proportion of the main food categories did not change in time, but the proportions of each of the most frequently eaten species changed. Evident changes over time involved more frequent consumption by the WTE of storks, Great Crested Grebes, and Northern Pike. A declining trend was documented in the consumption of the Coot, ducks, and Common Bream. Over the long term, there was a sharp decline in Coot consumption. The proportion of fish in the food did not correlate with the change in the area of the lakes, while the most frequently captured fish species changed. Changes in diet composition might be due to both a decline in prey populations and the settlement of new pairs of the WTE in areas with a smaller share of lakes. Food composition analysis did not demonstrate an apparent effect on medium-sized predators by direct predation. The composition of the food and the observed changes indicate opportunism in the foraging of the WTE, so the availability of food is not a factor limiting the further development of the studied Augustów Forest population of this protected raptor species. The existing methods of protection are sufficient.

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