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Habitat Impacts on the Golden Eagle's Foraging Ecology and Nest Site Selection in Poland

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Abstract: The Golden Eagle *Aquila chrysaetos* (hereafter GE) is one of Europe's largest avian top predators. The present study recognizes the habitat characteristics and food composition of the GE in Poland. The research was carried out in the Polish part of the Carpathian Mountains. The GEs built nests mainly on old coniferous trees and strongly preferred the Silver Fir *Abies alba*. On average, within a 5 km buffer around the nest, forests covered about 2/3 of the area, while open land with villages was at 31% and water was about 1%. Birds preferred areas with less forest cover than in the random points, but the nests were significantly further from the countryside than the distance measured for the drawn points distributed in the GEs' range in Poland. Their diet during the breeding season was assessed by analyzing pellets and food remains. The proportion of birds was 55.7%, mammals was 43.4%, and reptiles was 0.9%. The ten most common prey species included the Domestic Pigeon *Columba livia*, the Ural Owl *Strix uralensis*, the Tawny Owl *Strix aluco*, the Buzzard *Buteo buteo*, the Roe Deer *Capreolus capreolus*, the Martens *Martes* sp., and the Red Fox *Vulpes vulpes*, which composed 70% of food items. Our results showed that the GE is a top predator, as evidenced by the high share of other predators—both mammal and bird species—in its diet, which constituted about 34% of identified preys. The diet of the studied GE population showed geographical variation, suggesting local adaptations to available prey species. The share of Roe Deer increased from west to east, indicating a higher availability in the less urbanized eastern part of the country. An analysis of general food categories showed that, as latitude increased, the share of captured birds among prey of the GEs declined, while the percentage of forest prey increased. Pigeons were prey of the GEs mainly in the western part of their range. The GEs often captured species with nocturnal activity—owls and martens, which were identified in most of the GEs' territories. The proportion of mammals in the diet of the GE increased with an increase in the proportion of open areas, while the abundance of birds of prey and owls in the diet correlated with a higher proportion of forests. The greatest threat to Poland's GE population is the reduction in semi-open areas with low human activity and low human population densities.

Keywords: *Aquila chrysaetos*; Carpathian Mountains; diet composition; habitat requirements; top predator

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1. Introduction

The study of the ecology of birds of prey provides a variety of information about ecosystems because of their critical role in the functioning of ecosystems [1]. Birds of prey may play different roles in ecosystems, such as flag-ships, surrogates, and umbrella species, as well as regulating prey populations and scavenging [2,3]. Due to their dependence on their prey, birds of prey may be considered as biodiversity indicators of their prey assemblage and overall biodiversity [4,5].

The large spatial requirements and specific environmental needs of birds of prey affect their low densities. Thus, the density of raptor populations depends mainly on the availability of good-quality habitats [6]. The identification of the habitat preferences of rare species of birds of prey is essential for their adequate protection, especially in changing climate and landscape conditions. Although many European raptors nest in forests, they obtain most of their food in open areas, so they belong to dual-habitat species [2]. Habitat protection should include breeding sites, as well as feeding areas, on the landscape scale. The relationship between habitat quality and diet composition is essential to understand the distribution and density of breeding pairs. To a great extent, nesting habitat parameters determine the diet composition of raptors during the breeding season [6]. Birds are sensitive to limited food availability; therefore, food resources are one of the most critical factors to address in conservation research [7].

The diet composition of birds of prey shows variability depending on specific habitat conditions and changes in primary prey availability. This variability is more pronounced in food generalists than in specialists. Food resources directly affect the fitness and survival of adults, breeding success, and the number of young raised, as well as their fitness [8]. The study of feeding ecology shows how habitat and foraging patterns affect food composition and how the choice of nesting site affects where to find food [9,10]. On the other hand, the study of the raptor diet can explain how a predator's exploitation of particular prey species affects their population dynamics. This is especially important for rare and endangered species of potential prey [11].

The Golden Eagle *Aquila chrysaetos* is one of the biggest European bird of prey species. It is a widely distributed raptor whose range covers the southern and northern parts of Europe and northern Africa, as well as a large part of Asia and North America. The European population has been strongly reduced during the last two centuries due to human persecution [12,13]. The GE is regarded as a habitat generalist inhabiting mountainous and lowland areas with a low stand density [14]. It uses diverse environments: mountainous and upland areas, lowland forests, wetlands, and marginally even steppe and desert. It prefers inaccessible, low-density human population areas. This species nests on cliffs and trees [12,13]. In Poland, the GE inhabits only a limited area of the mountains. It selects vast forest areas, the highlands, and mountains with enormous meadows and river valleys. It establishes nests on rock shelves in high mountains and feeds above the upper forest border. In the lowlands, it lives in swamps and wetlands. Essential elements of the environment are dead-standing trees used for resting and perching [15].

The GE is considered to be a top predator, mainly preying on medium-sized vertebrates and also feeding on carrion [14]. The basis of its food is birds and mammals, and seldom reptilians, consumed in varying proportions. Numerous studies of food composition have documented the GE's strong ecological plasticity and ability to successfully prey on a variety of species, usually at a biomass from 0.5 to 3 kg, e.g., [16–21]. Diet composition shows a high variability depending on the availability of suitable prey in local conditions. Usually, this raptor opportunistically preys on the most available game of the proper size in its feeding area [12,22].

The European population of the GE is estimated at 19,200–25,600 adult individuals with a status of Least Concern and increasing population trend [23]. The largest populations of the GE inhabit Scandinavia, Russia, Spain, Italy, France, and Great Britain. Populations in central Europe are small, usually a few dozen pairs. The GE 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. In Poland, the GE is a red-listed species with category EN [24,25], and is strictly protected. Its nests are protected by creation zones where entry and habitat alteration are prohibited. Almost the entire GE population occurs in the Polish part of the Carpathians, as a part of the cross-border population [26]. Since 1993, the occupied nests or breeding territories of the GE have been monitored by members of the Eagle Conservation Committee [27]. During the last 30 years, the Polish population

was estimated at 30 breeding pairs, with some fluctuations. The previous two decades have seen a slight increase in numbers and expansion of range toward the west [28–30].

Our work aimed to examine the relationship between the habitat preference and diet composition of the GE in the Polish Carpathians over 24 years. We hypothesized that the GE's food composition would vary over its geographic range of occurrence. We assumed that the share of the main food groups, i.e., birds and mammals, would show no geographic variation. We expected that the proportion of raptors in the GE's diet, whose higher densities are outside the mountains, would increase as latitude and altitude increased. The second hypothesis relates to habitat requirements and assumes that the GE, as a secretive and persecuted species in the past, chooses nesting sites tucked away deep in the forest, away from human settlements. We expected the results to allow us to formulate recommendations for protecting the GE in Poland.

2. Study Area

The study covered selected areas of the Polish Carpathians, with a total area of about 8860 km^2 lying in the following subprovinces: (i) Outer Western Carpathians (Beskid Niski, Beskid Sądecki, Gorce, Beskid Wyspowy, and Beskid Żywiecki), (ii) Central Carpathians Western Carpathians (Tatra Mountains, Pieniny, Spisko-Gubałówka Foothills, and Orava-Novotarska Basin), and (iii) Eastern Carpathians (Western Bieszczady and Sanocko-Turczańskie Mountains). The Carpathian Mountains are characterized by high forest cover (33–80%). This is dominated by the Norway Spruce *Picea abies*, Beech *Fagus sylvaticus*, and Silver Fir *Abies alba*, which, together, form nearly 90% of forest stands. The Outer Western Carpathians are not very high mountains, with a few peaks exceeding 1000 m, while the central Western Carpathians have peaks reaching almost 2500 m above sea level [31]. The Eastern Carpathians within the Polish borders are characterized by extensive complexes of forests, meadows, and pastures of former state farms, and at 1200 m above sea level, there is a floor of mountain meadows. Human density here is low—4–5 people/km^2. In the Polish Carpathians, only the Tatra Mts have a storied vegetation system [29].

3. Methods

3.1. The Distribution of Nesting Territories and Nesting Trees

From 2000 to 2023, the field study was based on long-term monitoring of the GE's breeding sites. During inspections in early spring (from 15.02 to 30.04), the occupation of known nests or territories was assessed. In addition, during peak mating activity, observations of the GE's mating behavior from viewpoints were made. Field works were conducted on sunny days between 9 a.m. and 1 p.m. from points 3–4 km apart for 2 h. Then, on this basis, new nests were searched for. Inspections were conducted throughout the entire known range of the GE in Poland, considering places where only single individuals were encountered and at the area's periphery, considering the potential for range expansion [30]. The species of the nest tree was identified and its age was determined from Poland's Forest Data Bank [32].

3.2. The Structure and Size of Territory

The exact size and shape of the foraging area used by the eagles are not known in the study area, and the area used by the GE during breeding season shows substantial variation depending on the habitat structure and food abundance, as well as the assessment methods. For analysis, we assumed [10] that the size of the territory was determined by 1/2 of the nearest neighbor distance (NND) between occupied nests, which, in our study, was 10.4 km. In order to assess the environmental structure of the potential territory, we evaluated the surface proportion of distinguished habitats in a 5 km buffer. We also measured the distance from the nest to the nearest forest edge, village, and river. Lastly, the length of rivers and hardened roads inside a 5 km buffer and the number of settlements were measured. Environmental data were taken from Poland's Forest Data Bank, run by the State Forests [32]. We used the Random point function in ArcMap to create 40 random

points in the study area. We measured all habitat characteristics described above for the random points to compare the GEs' habitat requirements with mean values in this part of Poland.

3.3. Dietary Data Collection and Prey Identification

Food remains and pellets were collected from the nests and the ground under the nests during inspections, combined with the ringing of chicks carried out in June or July. In total, food data came from 28 different GE territories. The guides [33–36] were used to identify some of the prey species remains. The number of prey was determined based on skeletal elements or feathers by identifying the individual prey. If the bones, feathers, or hair found belonged to one species and did not differ in size or degree of decomposition, it was assumed that they belonged to only one individual [20]. About 80% of the identified prey were collected as remains from the nests (bones, beaks, furs, and feathers). The analysis of pellets provided information on small- and medium-sized birds, mainly pigeons based on rings and Passerifomes based on feathers. The hair and furs contained in the spits were not determined and were not included in the analyses. In the case of remains found in both pellets and food remains, the double counting of food items was avoided by assuming the lowest probable number of the eaten individuals. The minimum number of individuals (MNI) at each collection's lowest possible taxonomic level was calculated from distinctive anatomical features by taking the minimum number derived from each source and combining them. If we found, e.g., the bill and feathers of the Ural Owl *Strix uralensis*, we counted them as only one prey [21]. For the identified prey species, the habitat in which the GE hunted them was assigned. Distinctions were made between forest species (F), open-area species (O), and anthropogenic species (A). Species were assigned to specific habitats based on characteristics in Polish regional monographs [27,33,37]. The biomass of prey was not estimated; only its frequency was analyzed.

3.4. Statistical Analysis

To check how the GE diet changed across the area of this species range in Poland, we used a generalized linear model (GLM), using data for each nest, for which sufficient numbers of food items were collected. In the GLM models, we used latitude or longitude as the dependent variable and data about the share of most frequent prey in single nests in seasons as independent variables. The shares of the six most frequent bird food categories and five most frequent mammal categories of the GEs' diet, each with a share above 2.5%, were used as independent variables. Only this threshold ensured the repeatability of food items across seasons in single nests. Nests with less than fifteen prey collected were deleted from detailed analyses (4 cases). After the preliminary data analysis, we decided to use as independent variables the proportions of Pigeons *Colubmbidae*, Corvids *Corvidae*, Buzzard *Buteo buteo*, Owls *Strigiformes*, Grouse *Galliformes*, Passerines, Roe Deer *Capreolus capreolus*, Hare *Lepus europaeus*, Red Fox *Canis vulpes*, and Martens *Martes* sp. Other predatory mammals were also used. The unit was a single nest from which at least 15 prey items were identified. The post hoc t-test was used to check the statistical significance of the analyzed parameters.

We used a logistic regression model (GLM) to compare nesting habitats and drew random points in the surrounding habitat. A layer including forests and mountains was created to draw potential nest points. We rejected water areas, villages, towns, and agricultural areas as habitats impossible for GE nesting. Nest or random points were used as a dependent variable. The data on non-forest area, distance to open area, distance to villages, distance to river, the length of rivers, the length of roads, and the number of villages were used as independent variables. The post hoc z-test was conducted in this model. Statistical analyses were performed in the R environment (ver. 4.1.3 with the R-studio overlay).

4. Results

4.1. Habitat Requirements

We found from 27 to 30 breeding pairs of the GE in the Polish part of the Carpathians Mountains in successive years. The GEs' nests were distributed over 265 km between the most distant east–west and 65 km between the most distant north–south nests (Figure 1). The area inhabited by the Polish GE population covered about 6500 km^2. The average NND between the GEs' nests in Poland was 10.4 km, and the nearest occupied nests were 5 km apart.

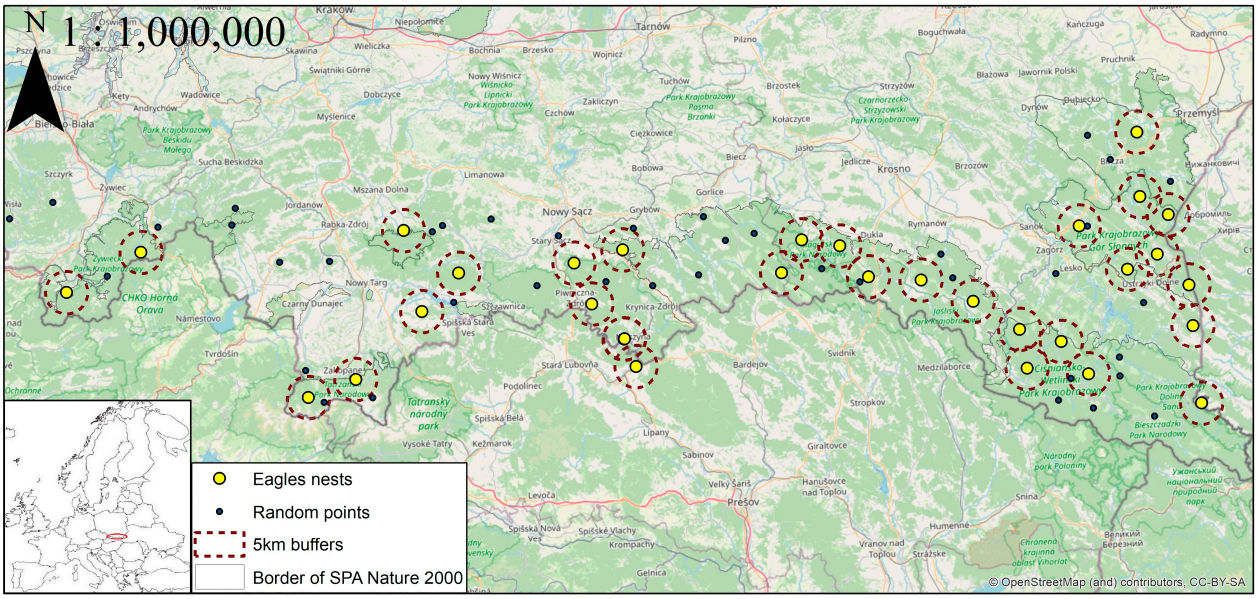

Figure 1. Distribution of GE nests in the Polish part of the Carpathians Mountains.

GEs built nests in Poland mainly on old coniferous trees and strongly preferred the Silver Fir. Among 100 known nests, 95 were placed on the Fir, 2 each on Larch *Larix decidua* and Beech, and only 1 on Scots Pine *Pinus sylvestris*. Nesting trees were aged from 100 to 160 years; on average, they were 126 years old. Three nests on rocks shelves were located only in the Tatra Mountains. The GEs' nests were from 390 to 1450 m above sea level. The nests were located 28 m from the base of the rock and 250 m from the valley bottom. Nests were usually located behind the mountain peak on the northern side of the ridge. On average, the GEs' nests were located in the middle of the forest—i.e., about 600 m from the forest edge and open area—about 1500 m from the village, and about 2000 m from the nearest river (Table 1). In the average territory, forest covered 67% of the area, while about 31% was open land and villages, and about 1% was water cover (Table 1).

Table 1. Values of analyzed environmental parameters in 5 km buffers around the Golden Eagle's nests.

	Min	Max	Median	Mean	SE. Mean	Std. Dev	Coef. Var
Non-forest area [%]	0.10	0.69	0.32	0.31	0.02	0.114	0.37
Distance to open area [m]	50	2000	500	614	74.5	429	0.69
Distance to villages [m]	550	4600	1300	1581	147	842	0.53
Distance to the river [m]	300	4000	1900	1925	193	111	0.58
Length of rivers [km]	5.0	42.0	13.5	15.6	1.33	7.7	0.49
Length of roads [km]	4.3	71.0	42.0	39.7	3.07	17.7	0.44
Number of villages	2.0	23.0	7.0	7.24	0.69	3.9	0.54

The results of the GLM comparing the surroundings of nests and random points indicated significant environmental requirements of the GE. The birds preferred areas with

less forest cover than in the random points, but the nests were significantly further from the countryside than the distance measured for the drawn points distributed in the GEs' range in Poland. Another significantly differentiating environmental element in the surrounding buffer was the length of roads. More roads were around nests than around random points (Table 2).

Table 2. Logistic model results comparing differences between environmental parameters around GE's nests and random points.

	Estimate	Std. Error	z Value	Pr (>|z|)
(Intercept)	−2.87	1.47	−1.96	0.05
Non-forestarea [%]	−5.93	2.80	−2.12	0.03
Distance to open area [km]	0.0004	0.0009	0.50	0.62
Distance to villages [km]	0.001	0.0004	2.83	0.005
Distance to the river [km]	−0.0001	0.0003	−0.46	0.64
Length of rivers [km]	−0.02	0.04	−0.36	0.72
Length of roads [km]	0.10	0.03	2.99	0.003
Number of villages	0.02	0.06	0.40	0.69

4.2. Diet Composition

An analysis of remains and pellets from the nests of 28 pairs made it possible to determine 821 GE prey belonging to three clusters and 50 species. The proportion of birds was 55.7%, mammals was 43.4%, and reptiles was 0.9%. Prey classified as being associated with forest accounted for 32.4%, prey from open areas accounted for 47.8%, and anthropogenic prey composed 19.8% of the identified prey. The most common prey included the Domestic Pigeon *Columba livia*, the Ural Owl, the Tawny Owl *Strix aluco*, the Buzzard, the Roe Deer, the Martens, and the Red Fox (Table 3).

Table 3. The diet composition of the Golden Eagle in the Polish part of the Carpathians Mountains from the period of 2000–2023, abbreviations: O—open areas, F—forests, and A—anthropogenic habitat.

Prey Species	Habitat	N	[%]
Phasianus colchicus	O	15	1.83
Tetrao urogallus	F	1	0.12
Tetrastes bonasia	F	3	0.37
Domestic hen	A	21	2.56
Numida meleagris	A	1	0.12
Platalea leucorodia	O	1	0.12
Accipiter gentilis	F	7	0.85
Buteo buteo	F	52	6.33
Pernis apivorus	F	1	0.12
Dendrocopos major	F	1	0.12
Picus viridis	O	1	0.12
Scolopax rusticola	F	1	0.12
Strix aluco	F	37	4.51
Strix uralensis	F	42	5.12
Asio otus	O	3	0.37
Columba livia	A	121	14.74
Columba palumbus	O	24	2.92
Columba oenas	F	3	0.37
Apus apus	O	1	0.12
Corvus frugilegus	O	2	0.24
Corvus corax	F	24	2.92
Garrulus glandarius	F	10	1.22
Pica pica	O	3	0.37
Corvidae	F	4	0.49
Sturnus vulgaris	O	2	0.24

Table 3. *Cont.*

Prey Species	Habitat	N	[%]
Turdus philomelos	F	4	0.49
Turdus merula	F	2	0.24
Turdus pilaris	O	1	0.12
Turdus viscivorus	F	3	0.37
Turdus sp.	F	1	0.12
Passeriformes undetermined		14	1.71
Birds undetermined		51	6.2
Total Birds		457	55.7
Erinaceus concolor	F	4	0.49
Glis glis	F	6	0.73
Arvicola terrestris	O	3	0.37
Sciurus vulgaris	F	11	1.34
Marmota marmota	O	1	0.12
Rodentia undetermined	O	5	0.61
Lepus europaeus	O	23	2.80
Felis domesticus	O	14	1.71
Felis sylvestris	F	3	0.37
Nyctereutes procyonoides	F	2	0.24
Mustela erminea	O	4	0.49
Meles meles	F	3	0.37
Martes sp.	F	84	10.23
Vulpes vulpes	O	29	3.53
Mustela nivalis	O	1	0.12
Mustela putorius	O	2	0.24
Sus scrofa	F	2	0.24
Cervus elaphus	F	4	0.49
Capreolus capreolus	O	131	15.96
Sus domestica	A	1	0.12
Ovis aries	A	1	0.12
Bison bonasus	F	1	0.12
Mammals undetermined		21	2.56
Total Mammals		356	43.4
Anquis fragilis	O	1	0.12
Natix natrix	O	4	0.49
Vipera berus	F	3	037
Total Reptilians		8	0.9
Total		821	100.0

4.3. Geographical Variations in Food Composition

It was shown that there was a relationship between latitude and food composition, and a much weaker association with this longitude parameter (Tables 4–7). As latitude increased, the proportion of Corvidae (mainly the Raven) increased, while the share of pigeons sharply decreased (Table 4). Changes in other categories of consumed birds were insignificant (Table 4).

Table 4. GLM results for relationships between latitude and the share of most frequent birds group in the GEs' diet (Intercept = latitude).

Estimate	Std. Error	t	Value	Pr (>|t|)
(Intercept)	22.51	0.35	63.72	<0.001
Pigeons	−6.51	1.44	−4.51	<0.001
Corvids	10.42	4.19	2.48	0.025
Raptors	0.76	2.20	0.35	0.73
Owls	−3.37	1.92	−1.8	0.10
Galliformes	4.64	3.10	1.50	0.16
Passerines	−4.89	2.81	−1.74	0.10

Table 5. GLM results for relationships between latitude and the share of the most frequent group of mammals in the GEs' diet (Intercept = latitude).

	Estimate	Std. Error	t Value	Pr (>|t|)
(Intercept)	20.78	0.48	42.86	<0.001
Roe Deer	4.14	1.66	2.50	0.024
Hare	2.52	5.91	0.43	0.68
Red Fox	−3.45	8.03	−0.43	0.67
Predatory mammals	1.08	5.34	0.20	0.84
Martens	0.87	6.76	0.13	0.90

Table 6. GLM results for relationships between longitude and the proportion of the most frequent group of birds in the GEs' diet (Intercept = longitude).

	Estimate	Std. Error	t Value	Pr (>|t|)
(Intercept)	49.44	0.05	951.6	<0.001
Pigeons	−0.19	0.22	−0.87	0.40
Corvids	0.60	0.62	0.96	0.35
Raptors	0.61	0.32	2.04	0.038
Owls	−0.86	0.28	−3.07	0.007
Galliformes	0.57	0.47	1.20	0.24
Passerines	0.53	0.42	1.27	0.22

Table 7. GLM results for relationships between longitude and the proportion of the most frequent group of mammals in the GEs' diet (Intercept = longitude).

	Estimate	Std. Error	t Value	Pr (>|t|)
(Intercept)	49.48	0.06	809.0	<0.001
Roe deer	−0.09	0.20	−0.47	0.64
Hare	−0.28	0.73	−0.39	0.70
Red Fox	0.20	0.99	0.20	0.84
Predatory mammals	−0.07	0.66	−0.10	0.92
Martens	0.15	0.84	0.18	0.86

Fewer dependencies could be indicated for the analyzed groups of eaten mammals, where only the proportion of Roe Deer changed significantly. The share of Roe Deer increased from west to east, indicating a higher availability of this prey in the less urbanized eastern part of the country (Table 5).

The variation in food composition related to longitude was less pronounced. With a change in longitude, the share of raptors and owl food of the GE changed significantly (Table 6). In the gradient from south to north, the percentage of owls decreased (the Tawny owl and the Ural owl), while the share of raptors (mainly the Buzzard) increased. The other categories of bird prey did not change considerably (Table 6). Interestingly, we did not discover significant correlations between longitude and the share of mammals or general prey categories in the GEs' diet (Table 7).

5. Discussion

5.1. Habitat Requirements

Despite its low numbers, the Polish population of the Golden Eagle occupies a vast area, within which active territories are distributed unevenly; more numerous are those in the eastern part of the area. In the Polish Carpathians, this raptor species occurs abundantly in sparsely human-populated areas with low anthropopression. Due to high spatial requirements, the GE has a low breeding density. Its breeding territories are dispersed. This finding is in line with the general pattern. Environmental conditions strongly influence local density, and home range size shows significant variation [12,14]. A Finnish study with

GPS transmitters documented the GE using vast areas up to 300 km^2 and a range of 14 km, although the raptor did not use their home range evenly [38]. In turn, the home ranges of the GE in Sweden range from 60 to 605 km^2. The size of this home range has declined along with the increase in the proportion of open areas within the territory [39].

In Polish mountainous conditions, the GE built nests mainly on the Silver Fir. These tree species allow for stable placement and good concealment of the GEs' nests. The selectivity of nest trees is completely opposite to that of other large arboreal nest-building birds in Poland—namely the White-tailed Eagle *Haliaeetus albicilla* and the Black Stork *Ciconia nigra*, which prefer Pines and Oaks *Quercus* sp. [40]. In turn, in Belarussian Polessya, Scots Pines dominated among nesting trees of the GE [41]. The small percentage of nests located on rocks in Poland indicates the great importance of appropriately sized and aged nest trees, as well as the protection of patches of old forests to preserve the GEs' nesting habitats in upland and lower mountain conditions.

The studied GEs in Poland showed a great extent of avoidance of anthropogenic areas close to the nests. This pattern of nest distribution confirms the hypothesized need for tranquility and isolation of this species from human settlements, and the reasonableness of protecting nesting sites. Eagles usually avoid areas intensively penetrated by humans [12,41,42]. At the same time, the birds chose areas with surroundings characterized by lower-than-average forest cover for nesting sites. This is due to the use of open areas as the main feeding ground for the GE. Open areas are essential, despite the human settlements there; however, they are under low human population density. Non-forest spaces contain a few human settlements, where livestock is used as a source of the GEs' food. The greater length of roads in the 5 km buffers is challenging to explain. It could potentially indicate a more willing use of the carrion of larger prey fallen on these roads. Still, the verification of this assumption would require a thorough survey of eagle hunting methods in the study area. Our food data came from the breeding season, and the road and carrion component may be important in the fall and winter seasons with less available prey [20].

5.2. Difference in Diet Composition

The eagle is described as an environmentally plastic food opportunist [12]. The spectrum of prey species consumed by the GE in the Carpathians Mts. was broad, although birds were caught more often than mammals. The studied raptor preyed in forest and open areas. Essential prey of the GE were medium-sized birds and mammals: the Roe Deer, the Domestic Pigeon, the Martens, the Buzzard, the Tawny Owl, the Ural Owl, the Red Fox, the Wood Pigeon *Columba palumbus*, the Raven, and the Hare. These 10 prey species (in order from most to least frequent) constituted almost 70% of the GE's diet. Among the Roe Deer and Hares brought to nests, juveniles predominated, while the eaten birds were dominated by adults [20]. By comparison, only five prey species comprised 80% of frequency in Finland [16]. Despite the distinctiveness of the food composition of the Carpathian GE population related to local conditions, some categories of prey are also often used in other parts of the wide range of these raptors. Ungulate calves have been important prey in the Italian Alps [43] and the tundra region [16,17]. Hares and other *Leporidae* were the vital prey of the GE in Finland [16], Belarussian Polessya [41], the Pyrenees [19], Great Britain [12,18], the mountain tundra [17], as well as in the western United States [21]. Almost throughout its range, the GE often captured larger rodents [12,16,17,19].

In our study, somewhat surprising is the high frequency of Domestic Pigeons in the diet of the GE, which could be precisely identified by the found rings. Pigeons were the prey of the GE mainly in the western part of its range. The GE often captured species with nocturnal activity, namely owls and martens, identified in most of the GEs' territories. It is probable that GEs effectively search for them while resting during the day or moving between hiding places. Our results showed that the GE is a top predator, which is in line with what other researchers of the feeding ecology of the GE have pointed out [12]. This is evidenced by the high share of other predators, mammal and bird species, in its diet—about

34% of the identified prey. Almost 10% of the food items were owls, and 6% were Buzzards. The most often caught predatory mammals were Martens, followed by Red Foxes. The GE was also an effective predator of another large avian food generalist—the Raven. This indicates its top role in the food pyramid of the mountain ecosystems in the Polish part of the Carpathians. Predation on subordinate predator species (mammals and birds), on the one hand, reduces food competition and, on the other, eliminates the possibility of smaller predators destroying GE broods [44]. According to a British study of another apex predator—the Goshawk *Accipiter gentilis*—the proportion of mesopredators in its diet increased in parallel with the recovery of the Goshawk population. This increase in the consumption of predators is explained by a decline in the availability of alternative prey. The authors concluded that predation has different effects on the populations of particular mesopredators, affecting or not a decrease in their numbers [45]. In our long-term study, the population size of the GE was almost unchanged, and the exploited population of the Ural Owl showed no decline in numbers [46].

Contrary to our expectations, the diet of the studied GE population showed geographical variation, indicating local adaptations to available prey species. The differences were mainly in the frequency of pigeons and Corvids. A high share of pigeons in the diet was recorded in densely populated Silesia in the western part of the GEs' range in Poland. Pigeon breeding is very popular in Silesia, unlike in the sparsely populated eastern Carpathians. In turn, the higher share of Corvids in the diet of the GE, mainly associated with forest Ravens and Jays *Garrulus glandarius*, were found in territories in the east of the Polish range of the GE, in the region with a small number of domestic pigeons kept. Most captured Corvids were forest species, more numerous in the east than in the west of the GEs' area [46]. The higher share of the Roe Deer in the eastern part of the GEs' range in Poland indicates the greater importance of this prey in high forested areas.

Surprising varieties in the diet composition of the GE were found—not east–west over a distance of 250 km, but only 60–70 km north–south. These were differences in the eagle's diet shares of owls and birds of prey. The percentage of owls decreased northwards, while the share of birds of prey increased. In local conditions, an increase in latitude also means a decrease in height above sea level. These changes may be related to the lower forest cover in the north of the GEs' range, which results in lower densities of the Ural Owl in the north of its range and higher densities of birds of prey, which reach lower densities in the mountains, as they do not hunt as effectively as owls in mountain forests [46]. The analysis of the food composition showed no apparent geographical differences in the proportion of the Red Fox, martens, and other mammalian predators, so those species could be considered as universal prey. The lack of a spatial pattern in diet also characterized the proportions of hares, grouses, and songbirds.

5.3. Conclusions and Protective Recommendations

Our research indicates that the GE population in Polish Carpathians nests is dispersed, with nests of neighboring pairs averaging 10 km apart. Their density is higher in the east of the region, a less populated part with higher forest cover. The eagles avoid nesting near human settlements, but choose areas with lower forest cover for nesting sites. Open areas are essential for foraging. The GE selects old coniferous forests near open spaces with a low human population density and activity for a breeding habitat. Preserving an extensive agricultural landscape, with grazing, is an important condition for the occurrence of this eagle. The emergence of new settlements and scattered developments is unfavorable.

The GE effectively uses a wide range of prey, with ten of the most often consumed prey species constituting almost 70% of its diet. The Red Deer, the Domestic Pigeon, owls, and predatory mammals are the most important prey. Predators account for 34% of the frequency of food items, indicating the crucial ecological role of the eagle as a top predator, castigating the trophic structure in the ecosystem. Within the Polish population, geographic variation in the proportions of several prey species was noted, related to their variable availability. In conclusion, conservation efforts should consistently include preserving old

stands as breeding sites, protecting the structure of the semi-open landscape of foraging grounds, and reducing anthropopressure. The GEs' feeding opportunism suggests that reducing the availability of specific prey species would not be a limiting factor. The greatest threat to Poland's GE population is the reduction in semi-open areas with low human activity and low human population densities.

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