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Pronounced Seasonal Diet Diversity Expansion of Golden Eagles (*Aquila chrysaetos*) in Northern Greece during the Non-Breeding Season: The Role of Tortoises

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Abstract: Golden Eagles are resident in Greece and known to feed mainly on tortoises when breeding. However, information on alternative prey is scarce, especially during the tortoise brumation, that roughly coincides with the eagles' non-breeding season. We analyzed 827 prey items collected from 12 territories over five territory years and 84 records of eagles hunting or feeding behavior. Tortoises dominated the breeding season diet (71% of prey categories on average) and over half of all hunting/feeding observations. While no spatial structure was evident, habitat variables such as forest canopy cover were important associates in golden eagle diet seasonally. A significant seasonal pattern emerged in diet diversity, using a subset of six territories with at least 10 samples per season. Eagles shifted from a narrow, reptile- based breeding season diet dominated by tortoises to a broader non-breeding season diet, that included more carrion, mammals and birds. Breeding season specialization on ectothermic prey is a trait usually associated with migratory raptors in the Western Palearctic. The observed dietary diversity expansion accompanied by residency in the absence of ectothermic prey, highlights the adaptability of the golden eagle, a generalist predator. Tortoise populations in Greece are of conservation concern and land use changes as well as climate change, such as development and land abandonment may increase the prevalence of catastrophic megafires, exacerbating the threats to the golden eagle's main prey when breeding. We discuss this and other diet related conservation implications for the species in northern Greece.

Keywords: *Aquila chrysaetos*; golden eagle; diet diversity; foraging; alternative prey; *Testudo* spp.; Greece; raptors; tortoise predation

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1. Introduction

Food is one of the major limiting factors for raptor populations [1], affecting several population parameters. Food availability and diet metrics have been thus documented to affect densities [2], breeding performance [3,4], convergence of individuals during dispersal in food rich areas [5], nestling condition metrics [6] and long-term population persistence [7]. It is therefore important to have a basic understanding of raptors' diets to inform conservation and further research efforts, such as assessing possible influences of dietary habits and availability of prey species on breeding and occupancy/survival.

Several raptor species tend to consume a few, readily available and profitable taxa given the opportunity, as demonstrated by population level scale studies. However, generalist species can shift their diets towards a broader range during main prey decline periods, according to the Alternative Prey Hypothesis [8].

Golden eagles *Aquila chrysaetos* in general, tend to consume medium sized prey that is abundant and accessible (0.5–4 kg, mainly gamebirds and leporids in Eurasia, and leporids and ground squirrels in N America [9–11]. However, the golden eagle is the most widespread Holarctic eagle, is highly adaptable in its diet as a generalist predator, despite often displaying specialism at low spatial and temporal scales. In northwest Scotland no evidence was found supporting higher productivity in relation to lower diet breadths in some areas; rather, a high diet breadth was attributed to a tendency of utilizing any profitable prey available [12]. In Japan, golden eagles showed considerable temporal plasticity as the breeding season progressed [13]. In Sweden, golden eagles displayed a plasticity on main prey depending on the habitat affecting its availability across its national distribution, and even high specialization locally [14,15]. I In Utah, USA, habitat variables explained best the occurrence of main prey types in golden Eagle diets [16].

In SE Europe, several breeding raptor species specialize on ectothermic prey or consume such prey at higher rates than elsewhere [17–20]. Golden eagles in Greece rely to a great extent on tortoises: Hermann's (*Eurotestudo hermanni*) and Spur-thighed (*Testudo graeca*) in the north, marginated (*T. marginata*) in Peloponnese to the south, especially during the chick rearing period. This raptor is considered the primary predator of adult tortoises in Greece [21]. However, there is scant evidence on alternative prey in periods when tortoises are scarce, as during the reptilian winter phase of brumation, when they should not be readily available to predators.

Our study had the following research objectives: to (a) investigate the diet of the species in northern Greece, (b) assess the variation of diet composition and breadth in the breeding/non-breeding season, (c) assess if the diet is related to spatial and habitat characteristics, (d) describe foraging techniques that may account for prey acquisition, and finally (e) interpret the results in the light of the adaptive significance of tortoise predation for golden eagles and relevant conservation pressures.

2. Materials and Methods

2.1. Study Population and Sampling Sites

The golden eagle is Endangered (EN) in Greece [22] and the national population has been estimated at 105–155 breeding pairs [23]. Productivity has been estimated at 0.5–0.55 fledglings per territorial pair per year, and mean nearest neighbor distance recorded between occupied nest sites in our study area was 8.47 km (±3.18 km) [24]. We sampled dietary material at 15 territories, across over 6600 km^2 in northern Greece (administrative regions of central and east Macedonia and Thrace) (Figure 1). The climate is Mediterranean/continental Mediterranean. The main vegetation types covering a buffer of 6 km around nests were broad leaved woodlands, conifers and sclerophyllous scrub, interspersed with openings and grasslands, and the mean altitude of territories was 440 ± 218 m (range 75–895 m). Main land uses were extensive grazing (goat, sheep, and cattle herds), forestry (usually selective logging) and crop-agriculture on lower altitudinal land.

2.2. Prey Item Sampling

Prey remains and pellets were collected mostly from autumn 2017 to summer 2021 from 15 occupied territories. We defined two sampling seasons: (a) the golden eagle breeding season (mid-March to late November) from egg laying to the late post-fledging dependence period for most pairs), coinciding with the high tortoise activity period; (b) the golden eagle non-breeding period (late November to mid-March) that largely coincides with the low activity period of tortoises that are either brumating or not yet very active [25]. We made 37 and 41 visits during the breeding and non-breeding season respectively (Table S1). We conducted active searching of prey remains and pellets in situ during visits to nests (11 visits to 9 territories), at the tops of nest cliffs, at the base of nest trees, diurnal perches and roosts on trees/cliffs within a buffer of 400 m around nest, where adult activity is more pronounced [26]. Searched areas at each visit were scoured for any signs of prey consumption.

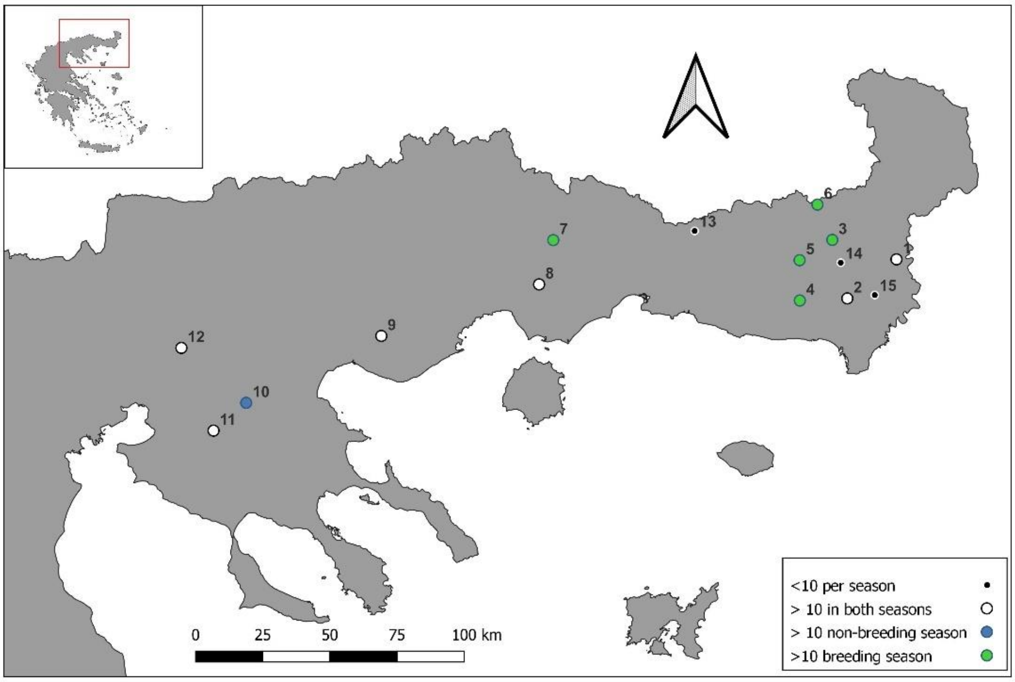

Figure 1. Sampled golden eagle territories in northern Greece. Only data from 11 and 7 territories with ≥10 prey items collected during the breeding and non-breeding seasons respectively were used in the analysis.

Material from localities outside the buffer were included in the analysis (as pertaining to the closest territory), only when members of the pair were known to perch there, or when cast golden eagle feathers were found. Material was not considered when there was evidence (cast feathers, observations) of other predatory species regularly utilizing the localities. Besides direct observations, roost and perch site localization was aided by telemetry data from three territorial adult birds (Movebank study ID 601374863).

2.3. Prey Item Identification and Counting

Prey remains and pellets were collected and removed from the sampling area either for identification in situ (e.g., hedgehog skins, tortoise shells) or in the laboratory. Collected tortoise carapaces were usually identified through the supracaudal scute; the presence of tail nails in pellets was indicative for *T. hermanni*. Whole bird feathers were identified to species when possible, using an online database [27]; feather fragments, mammalian hair and non-testudine reptilian scales were identified microscopically [28–30].

To estimate the number of prey items we combined finds in pellets and prey remains under the following protocol. Each visit to a territory was identified as a single collection event. The minimum number of individuals (MNI) at the lowest possible taxonomic level for each collection was calculated from distinctive anatomical features that were present (e.g., tortoise carapaces, jaws or humeri, flight feathers of birds, skulls or mammal jaws), either by taking the maximum number derived by each source or by combining them [31]. Thus, if for example in a collection we found plucked Eurasian Jay (*Garrulus glandarius*) feathers and a pellet of bones and feather fragments collected contemporaneously identified as belonging to the same species, it would be counted as one item. If on the other hand, we found plucked feathers and an entire head as prey remains and the pellet contained parts of a skull it was counted as two jays since the findings clearly belonged to two individuals. Similarly, one tortoise carapace in remains and two sets of jaws in a pellet were counted as two tortoises, one carapace and no distinct anatomical features in the pellet as one tortoise, one carapace with the head attached and two sets of jaws in a pellet as three tortoises, and so on.

The sum of all items from each collection per territory, comprised the final territory sample. The above approach is deemed conservative in estimating numbers of prey items per territory.

2.4. Spatial Structure and Environmental Parameters

We applied a Spearman correlation relating the inter-territory distance across all territory pairs and Renkonen's index, which measures dietary overlap [32], as a non sensitive index on the classification of findings to resource categories [33].

We utilised five habitat variables, in terms of percentage cover of four Corine Land Cover Classes: artificial land (codes 100), agricultural land (codes 200 apart from 231), open areas (codes 231, 321, 322, 324, 332 and 333), scrub (code 323) and forests (codes 311–313) [34]. We also calculated the average forest canopy cover using the 25 m resolution Pan–European forest cover dataset [35]. Given that golden eagles are known to range mainly in a radius of up to 6 km from their nests where they utilize mostly ridges [36], habitat variables were calculated in the following steps: we first ran a ridge selection algorithm [37], on a 50×50 m Digital Elevation Model, itself resampled from a global elevation dataset [38]. We subsequently converted the selected ridge pixels to polygons and applied a further 50 m buffer to include more area which eagles may have used, and to take account of possible edge habitats.

2.5. Field Observations

We analyzed a qualitative dataset of 198 observations of golden eagles feeding, hunting or otherwise interacting with prey, including the inspection of a few kill sites derived by telemetry data, collected during fieldwork and supplemented by 11 personal communications (2004–2021). Of these, 96 consisted of observations of golden eagles feeding on carcasses or offal deliberately left in specially designated areas (vulture feeding stations/trapping sites for telemetry purposes) and are just reported indicatively. Each individual recorded attempting to capture, carrying prey, or feeding at prey carcass was counted as one instance. The data were divided in the same categories as with other prey/food items and were examined as percentages. Field observations were not used in the main prey item analysis, but served as a secondary dataset cross-validating the results of prey analysis.

2.6. Data Analysis

Diet diversity: We processed 711 prey remains and 182 pellets. We classified prey items in 13 prey categories: birds, mammals and reptiles comprised five, six and two categories respectively (Table 1). The database used in the analysis comprised 797 items (12 territories) out of 827 items (15 territories) collected overall: we included in the analysis only data from 11 territories (breeding season: 621 items) and from seven territories (non-breeding season: 176 items), where samples included at least 10 items [12]. Data from six territories were used for the seasonal comparison, satisfying the above criterion for both seasons. For each territory we calculated the frequency (%) of the prey category occurrence, as well as the Levin's Diet Breadth index (B) [33] that reflects the diversity of prey in terms of diet breadth, according to the equation $B = 1/\Sigma(p_i^2)$, where p_i is the proportion of each prey category in the territory sample. We also calculated for each prey category its prevalence (P), as the ratio of the number of territories where any item of the prey category was recorded vs. the number of all territories. We ran the same analysis for all territories taken together (population level).

Table 1. Seasonal and annual diet of the golden eagle in northern Greece in terms of number of prey items per category (N), average seasonal (AFs) and average annual (AF) frequency of prey category across territories, as well as prey category prevalence (P) across territories.

Prey Categories	Code	Breeding (n = 11)			Non-Breeding (n = 7)			Annual		
		N	AFs	P	N	AFs	P	N	AF	P
Birds		53	8.9	0.91	54	31.2	1	107	13.4	0.92
Birds all other	B_o	18	2.2	0.64	16	9.1	0.86	34	3.4	0.67
Corvids	B_c	11	3.1	0.73	7	3.7	0.71	18	3.7	0.75
Raptors and Owls	B_ro	2	0.1	0.18	2	0.8	0.29	4	0.3	0.25
Thrushes and Pigeons	B_tp	13	2.1	0.45	19	9.3	0.86	32	3.7	0.58
Waterbirds	B_w	9	1.3	0.36	10	8.2	0.86	19	2.4	0.5
Mammals		89	16.3	1	63	36.1	1	152	19.97	1
Carnivores	M_c	25	4.8	0.73	20	11.1	0.86	45	6.1	0.83
Glirids and Sciurids	M_gs	14	2.4	0.36	6	2.4	0.43	20	2.7	0.5
Hares	M_ha	8	2.7	0.73	6	3.7	0.71	14	2.9	0.83
Hedgehogs	M_he	20	2.6	0.55	13	7.2	0.57	33	3.4	0.58
Mammals all other	M_o	11	2.6	0.64	9	6.4	0.86	20	3.4	0.75
Ungulates	M_u	11	1.2	0.36	9	5.3	0.57	20	1.5	0.42
Reptiles		479	7.8	1	59	32.8	1	538	65.6	1
Snakes and Lizards	R_sl	30	4.6	0.73	12	8.5	0.57	42	6.0	0.75
Tortoises	R_t	449	70.3	1	47	24.2	1	496	60.7	1
Total		**621**			**176**			**797**	**100**	

Spatial and habitat analysis: We performed a Principal Component Analysis (PCA) to visualize in two-dimensional triplots the ecological distance of the territories sampled in terms of their diet composition, in relation to the five environmental variables considered. Due to the small sample size no constrained analysis was possible. Analysis was performed using CANOCO 5.12 [39]. Relationships detected were also checked with univariate Spearman correlations.

Seasonal variation: We ran a binomial chi-square test of proportions [40] for each category at the population level, i.e., prey items pooled per season from all territories of at least 10 items. To pinpoint any significant differences in diet categories between seasons, we first employed an analysis of similarity (ANOSIM) (n = 6 territories). We then ran both a paired Wilcoxon signed ranks test and a Simper test (restricting the permutations within territory blocks to retain the territory as the main sampling unit). For this analysis, since our expectations were for all non-reptilian categories to increase and for reptilian to decrease, we set a one tailed α level of $p \leq 0.1$ and accepted results as important when this was satisfied at both tests. To compare the seasonal diet breadth variation (six territories), we compared the Levin's diet breadth index in the two seasons (Wilcoxon signed rank test), after testing the assumption of symmetry with a Miao, Gel and Gastwirth [41] bootstrap test (Test statistic = 0.77, p= 0.41). We ran the above tests also at the taxonomic class level (birds, mammals, reptiles). Statistical analyses were conducted using vegan package [42] in R 1.12 [43], data were managed with Microsoft Excel^{TM}, and all habitat and spatial data were derived in QGis [44].

3. Results

3.1. Golden Eagle Diet

The overall golden eagle diet database included 827 items from 53 different taxa collected from 15 territories. We identified 21 mammal, 23 bird, and nine reptile species, of which 16 and 10 were unique for breeding and non-breeding seasons respectively (Appendix A). Bird taxa included corvids (mostly *Garrulus glandarius*), pigeons and thrushes (*Columba livia domestica*, *Columba palumbus* and *Turdus* spp.), raptors and owls, waterbirds (mostly *Larus michahellis* and Anatidae) and all other birds (Phasianidae, smaller passerines, and unidentified). Mammal taxa included carnivores (*Vulpes vulpes*, *Martes foina* and other mustelids, domestic dogs and cats), hares (*Lepus capensis*), hedgehogs (*Erinaceus* *roumanicus*), larger rodents (*Sciurus vulgaris*, *Glis glis*), domestic and wild ungulates (usually taken as carrion although roe deer (*Capreolus capreolus*) might be actively hunted), and others (smaller rodents and unidentified). Reptile taxa included tortoises, snakes and lizards. Reptiles and in particular tortoises comprised the mainstay of the eagle diet in northern Greece during the breeding period, followed by mammals (predominantly carnivores), and birds (Table 1).

3.2. Seasonal Variation of Golden Eagle Diet

During the breeding season golden eagles consumed more reptiles, and particularly tortoises. Birds and mammal prey item categories were not prevalent across all territories and their average frequencies did not exceed 5%. (Table 1, Table S2) In the non-breeding season, the importance of reptiles decreased, as expected, with a consequent increase in birds and mammals. Of all categories, only tortoises were again prevalent across all territories, but most other categories were more prevalent and exceeded 5 % of the total items per territory on average (Table 1, Table S2).

At the population level, the consumption of tortoises decreased by 46 % from the breeding to non-breeding season and inversely the consumption of birds and mammals increased by 20% and 23% respectively (Table 1). Golden eagles took significantly more tortoises in the breeding season than in the non-breeding season, and significantly more thrushes and pigeons, waterbirds, other birds, carnivores, hedgehogs, ungulates, other mammals in the non-breeding season (Table 2).

Table 2. Seasonal variation of golden eagle diet in terms of Wilcoxon matched pairs test and Simper Analysis (n territories = 6, where the number of prey items was $\geq$10). Means and Binomial test of proportions considered 11 breeding territories and 7 non-breeding territories. Mean values refer to item proportions pooled across territories. p values: * $\leq$ 0.1, ** < 0.5, *** < 0.01, **** < 0.001.

Prey Category	Means ± SD (%)		Binomial Test of Proportions		Medians	Wilcoxon Matched Pairs Test		Simper Analysis	
	Breeding	Non-Breeding	x^2	p	Breeding/Non-Breeding	V	p	Contribution	p
Birds all other	2.2 ± 2.36	9.1 ± 6.16	11.4	****	0.04/0.09	1	*	0.06	*
Corvids	3.1 ± 3.35	3.7 ± 3.24	2.11	n/s	0.01/0.03	0	n/s	0.02	n/s
Raptors and Owls	0.1 ± 0.35	0.8 ± 1.37	0.55	n/s	0/0	1	n/s	0.01	n/s
Thrushes and Pigeons	2.1 ± 3.65	9.3 ± 9.56	24.7	****	0.027/0.07	3	n/s	0.07	n/s
Waterbirds	1.3 ± 2.77	8.2 ± 10.42	8.82	***	0.01/0.03	0	*	0.07	n/s
BIRDS	8.9 ± 6.61	31.1 ± 13.27	55.98	****	0.08/0.5	0	**	0.31	**
Carnivores	4.8 ± 5.60	11.1 ± 7.55	12.6	****	0.03/0.11	1	*	0.08	**
Glirids and Sciurids	2.4 ± 4.33	2.4 ± 3.29	0.35	n/s	0/0	1	n/s	0.02	n/s
Hares	2.7 ± 3.00	3.7 ± 3.22	2.45	n/s	0.01/0.04	2	*	0.03	*
Hedgehogs	2.6 ± 2.73	7.2 ± 9.78	4.99	**	0.04/0.01	5	n/s	0.07	n/s
Mammals all other	2.6 ± 3.04	6.4 ± 5.57	4.97	**	0.01/0.04	0	*	0.05	n/s
Ungulates	1.2 ± 1.85	5.28 ± 5.01	4.97	**	0.01/0.08	0	*	0.05	*
MAMMALS	16.3 ± 10.16	36.0 ± 13.34	39.55	****	0.14/0.52	0	**	0.38	***
Snakes and Lizards	4.6 ± 4.85	8.51 ± 13.21	0.72	n/s	0.04/0.01	14	n/s	0.07	n/s
Tortoises	70.2 ± 11.05	24.25 ± 11.18	119.4	****	0.72/0.25	21	**	0.4	***
REPTILES	74.8 ± 11.57	32.9 ± 15.11	116.92	****	0.91/0.49	21	**	0.31	***

The territory level analysis (n = 6) also showed significant difference in diet composition between the two seasons (ANOSIM: R = 0.79, p= 0.03 on 63 permutations, p< 0.01 on unrestricted 999 permutations). The prey categories of 'other birds', carnivores, hares were significantly higher in the non-breeding season than in the breeding season, and tortoises significantly lower, across both Wilcoxon and Simper tests. Differences were also significant across all tests at the class level (Table 2).

Diet diversity as expressed by the Levin's diet breadth was higher during the non-breeding season when considering both the 13 prey categories and the three classes (birds, mammals, reptiles) (V = 0, p= 0.03) (Figure 2).

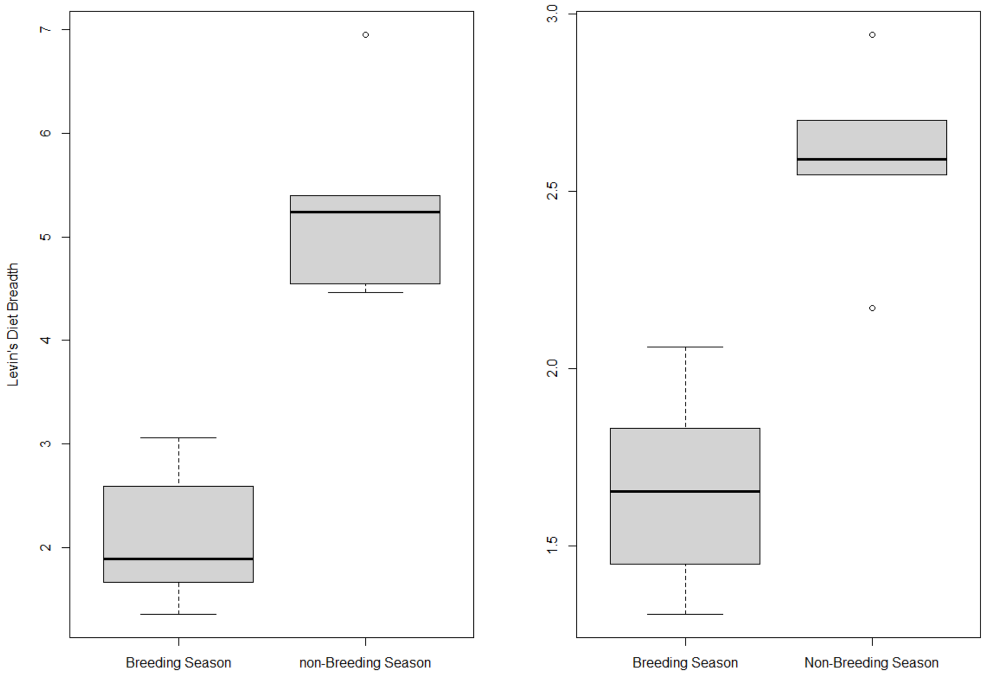

Figure 2. Seasonal Levin's diet breadth indices on the basis of 13 prey categories (see Table 1) (**left**), and the three broad taxonomic classes (birds, mammals, reptiles) (**right**).

3.3. Relationships of Golden Eagle Diet to Spatial and Habitat Characteristics

No spatial structure was evident in the data, as the distance between nests was not significantly correlated with the Renkonen Index of similarity (Spearman rho =0.06, p = 0.55) and this was reflected in the spacing of the territories across the PCA axes. The two first PCA axes explained 92.5% and 67.9% of the diet variability of the breeding and non-breeding datasets respectively (Figure 3). Tortoises (R_t) were more prominent as prey in territories with high canopy cover during the breeding season and in territories with low canopy cover in the non-breeding season (Figure 3, Table S3), the latter also pinpointed by Spearman correlation (rho= −0.86, p = 0.02). Inversely, golden eagles preyed on hares in lower canopy cover habitats during the breeding season (rho = −0.63, p < 0.04) and in more closed habitats during the non-breeding season. Carnivores (M_ca), hedgehogs (M_he) and other birds (B_o) were prominent prey in territories with significant agricultural land cover during the non-breeding season.

3.4. Field Observations

Tortoises comprised 55.1% of the 102 observations of golden eagle hunting/feeding behavior as apparent targets and, combined with snakes and lizards, reached 65.3% (Appendix B). Of the actual instances where the eagles were successful (86), the same percentages reached 67.4 and 76.6% respectively. Only 10% of the reptilian observations happened during the non-breeding season (Appendix B).

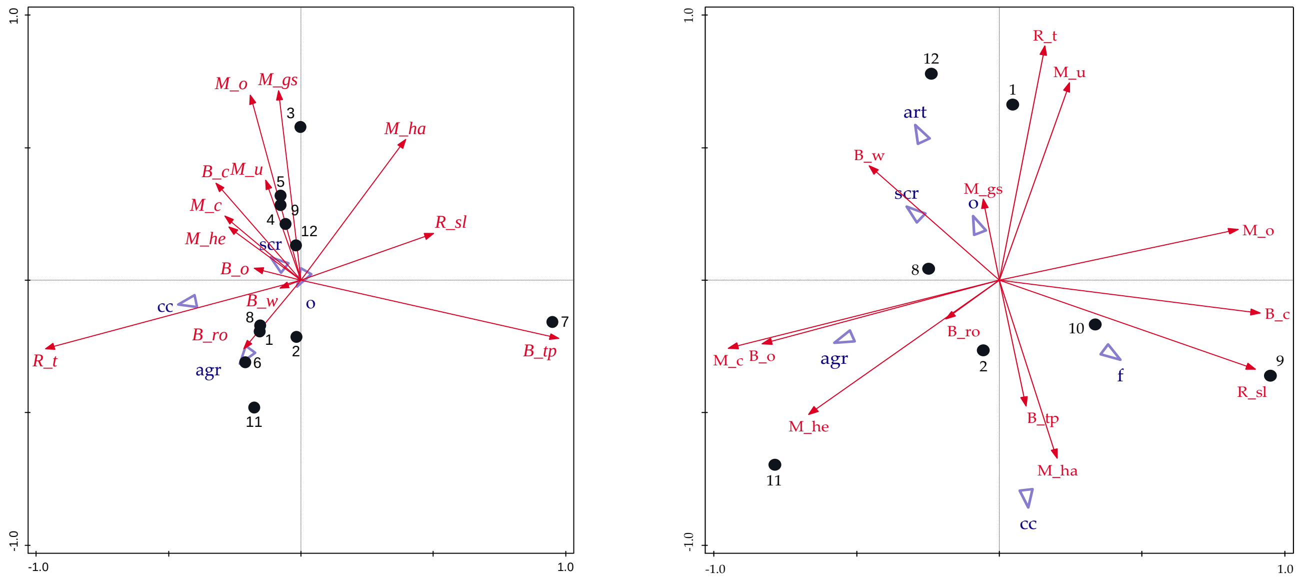

Figure 3. PCA triplot for breeding (**left**) and non-breeding (**right**) seasons, showing the position of territories (dots), environmental parameters (triangles) on ridges at 6.5 km around nests and prey categories (red arrows). agr: agricultural land, cc: canopy cover, scr: scrub and o: open land. Prey categories codified as in Table 1.

The typical reptile hunting method which was observed involved slow descent from a moderate height gained through circling and low gliding flight, prospecting the ground. Eagles were capturing reptilian prey descending slowly, sometimes in seemingly dense canopy, even landing and walking to the base of scrub. Carnivores comprised 6.9% of the 102 records and at least five of the seven instances related to already dead animals visited by pairs. Ungulates comprised also 6.9% and involved mostly carrion and offal but include unsuccessful attempts by a pair on roe deer and attempt at attacking young chamois (*Rupicapra r. balcanica*). All other mammalian categories comprised a further 4.9% of instances. One particular behavior, potentially explaining the presence of glirids in eagle diet was a capture of a small mammal (could not be identified) after an individual perched on a tree canopy, plunged suddenly into the tree. Birds comprised 12.7% of observations with a small percentage of success (3 out of 13 instances). Birds were hunted with aerial maneuvers, including tandem hunting of smaller raptors by pairs (3 instances), corralling of flocking birds by a pair (1), nest raiding (2), aerial chases (3) and near vertical stoops (2) at very high speeds. 10 instances regarded scavenging divided equally between ungulates and carnivores (including a roadkill). An additional 96 observations of eagles feeding on carrion and offal deliberately left for avian scavengers were also registered, 75 of which in the non-breeding season, when the majority of such disposals were made.

4. Discussion

4.1. Golden Eagle Diet

To our knowledge, our analysis has been the first to incorporate findings from the non-breeding season across the Mediterranean. We found 53 taxa in the entire dataset, among which unusual items e.g., a European free-tailed bat (*Tandarida teniotis*) and birds as small as blue tits (*Cyanistes caeruleus*). The number of taxa recorded was unusually large for Balkan golden eagle prey composition [45–47] but higher numbers have been reported, e.g., in Scotland and Bavaria [12,48]. Our findings stressed the importance of tortoises in the golden eagle diet in Greece. Unlike most other studies, we also included data for the non-breeding season and found a shift towards a wider variety of prey categories during that period.

Our tortoise estimate of 62.2% across the entire dataset is within the range of the reported values for the Balkan populations [45–47], with the overall importance of tortoises not diminishing, despite the inclusion of non-breeding season data (28.3% of the entire dataset). The rest of the prey categories, apart from the hares, are within the limits of published values for the Palearctic [9] and the Balkans [45–47]

Hares accounted for 1.8% in our dataset. This is a relatively low percentage, as is the 3.7 % in the non-breeding season, although during that period consumption increased. Leporids in general and hares where rabbits are absent, will usually form an important part of the eagle's diet, exceeding 10% in several Palearctic populations [9]. Low percentages however for the Mediterranean are not uncommon (e.g., [4] as is the case for the Balkans [45–47]. Hares were generally considered important for golden eagles in Greece [49] and this is even reflected in several common names and traditions in the country [50]. A similar result was recorded with partridges, another species that was considered important [49].

Carrion consumption was relatively low compared to many other populations where it might exceed 10% [9]. However, the consistent response of golden eagles to carrion and offal, supplied or naturally occurring in our behavioral dataset, indicates that especially in winter, carrion would be utilized when encountered, as is the normal for golden eagle populations [2] and carrion did increase substantially during the non-breeding season.

Regarding the role of the golden eagle as a super predator, raptors and owls had a limited incidence, but carnivores were the most important non-reptilian category, especially in the non-breeding season. Carnivores are important at similar magnitudes of 5–20% in several palearctic populations [4,9]. It has been suggested that the presence of golden eagles might alter carnivore and raptor incidence and behavior, thus incurring benefits to small game populations [51,52].

4.2. Seasonal Variation of Eagle Diet

We found a considerable shift from a reptile based diet to a more inclusive of other classes in winter, despite the incidence of tortoises that did not disappear altogether. The only raptor with higher dependence on ectothermic and hibernating prey (reptiles only in this case) in SE Europe, the short–toed eagle (*Circaetus gallicus*), is a Palearctic-Paleotropic migrant [17]. Adult golden eagles in similar latitudes stay year-round in their territories [9] and in our population, they can compensate for the temporary low availability of their main prey by expanding their diet breadth through a shift on other taxa and carrion.

Eagles switch part of their diet on whatever is available during the non-breeding season. At the population level, almost all the non-reptilian prey categories showed considerable increases in the non-breeding season diet. Of avian taxa, increased frequencies of waterbirds and thrushes and pigeons, have been found also in other eagle diet studies during winter, possibly as these taxa more abundant and flocking at this period [53,54]. A tendency to exploit a locally abundant food source was apparent in territory 12 where waterbirds (gulls) were taken at relatively high frequencies as the site is situated close to a large refuse dump (category artificial land). Besides, the fact that some categories were significant at the population level only, indicates that they are highly consumed only in certain territories, instead of uniformly across the population. Across the population, only carnivores, a variety of smaller birds, carrion and hares were retained in both our territory analyses. We believe all the above to indicate that golden eagles respond as generalists in the absence or lower incidence of their main prey, expanding their diet to several taxa and could be thus classified as facultative specialists [55].

4.3. Habitat Variables and Diet

We found that golden eagle hunted tortoises in closed habitats during the breeding season and in more open habitats in the non-breeding season. The higher tortoise abundance in the breeding season, combined with limited escape capabilities, could allow hunting in the more forested areas, whilst in the non-breeding season, any active tortoises during mild, sunny days might be more prevalent in open areas. The inverse pattern was found for hares. Hares might be more abundant in openings [56], and their higher sensory ability and agility facilitates capture in larger openings. In the non-breeding season, the absence of leaf cover might facilitate detection, allowing hare hunting in more dense areas [13]. Agriculture (in the ridges of our territories mostly low input such as cereal and alfalfa crops) was associated with more carnivores, hedgehogs and other birds. Small scale, low input agriculture increases habitat mosaics and edges and can plausibly attract several taxa on which Mediterranean raptors might feed [57].

4.4. Tortoise Dependence

Golden eagles in the Balkans, including our population, display an unusual diet and to our knowledge, are the highest recorded adult tortoise predators both between conspecific populations and other avian taxa [9,10,17–19,45–47,58–64]. Only [62] noted a 31.9 % of tortoise incidence in golden eagle diet outside the region. From other species in the Balkans, similar magnitude (31.5% albeit on mostly young tortoises) was reported for the Egyptian vulture (*Neophron percnopterus*) [19,64] and for some pairs (up to 30%) of the now locally extinct bearded vulture (*Gypaetus barbatus*) [65].

Eagles capture tortoises in even small openings and to break the carapace open, drop them in a near suitable rocky surface, in a manner similar to the bone dropping behavior of the bearded vulture [66]. Prey and nut dropping to access the interior of hard shells is widely recorded and studied among several bird taxa from different orders, where it has arisen independently and is considered a borderline tool-using behavior, directly linked to foraging innovation rate [67] and such innovations are generally associated with diet-generalist species with larger relative brain metrics [68,69]. This learned behavior might be acquired culturally through vertical transmission. Raptors are known to train through play during the post fledging dependence period, benefitting by adult experience [70,71]. We did observe juveniles following adults with tortoises during this period and even dropping items (pieces of carrion) for which this behavior is unnecessary. Additionally, observations of immature eagles failing to break carapaces in unsuitable substrate (ploughed field), suggest that experience might also be involved.

Golden eagles are reported in N.E. Greece (Dadia National Park) to prefer male individuals over females, *E. hermanni* over *T. graeca* and show a tendency to catch medium sized individuals of both species (1–1.5 kg) [72]. Tortoise predation is costly in terms of prey handling, as golden eagles might need to drop them repeatedly sometimes to break the carapace sufficiently open for consumption. During handling, tortoises might be lost if they roll into very dense vegetation or otherwise inaccessible spots after the drop. However, golden eagles show a clear preference to tortoises for several reasons. First, tortoises are in general easy to capture, and according to our results, they can be captured in fairly dense vegetation where the high speed and maneuverability required to capture other typical eagle prey taxa (e.g., Leporids and birds) is not possible. Indeed, our observed tortoise capture behaviors correspond to the "Low flight and slow descent attack" and "walk and grab attack" described by Watson [9]. Second, tortoises can reach high densities especially during the breeding season, reaching up to 20 tortoises/ha [73], compared to e.g., a reported 0.036 hares/ha [74] reported from Greece. Third, they have a nigh nutritional value, despite the carapace entailing a 31% wastage component [75], further enhanced by scales and bones. Anything apart from the carapace and intestines may be consumed by the eagles although limbs and heads are found nearly intact in pellets and they are not always taken as sometimes they are found attached in carapaces. Data on nutritional value show tortoises to be comparable if not higher to e.g., Leporids (134 Kcal/100 g vs. 112 Kcal/100 g [75,76]. An adult Hermann's tortoise in the preferred size of 1.5 kg, would therefore provide ~950 g of edible mass to a growing chick (7% and 17% dry weight of fat and protein). Finally, specific tortoise behaviors, e.g., sunning in early morning in openings may further augment encounter rates [72]. It is possible therefore, that all the above factors, have contributed to this facultative prey specialization, consistent with the Prey Availability Hypothesis of [12].

We found an unexpectedly high incidence of tortoises in the non-breeding season, in some territories exceeding 25%. Tortoises may become active in mild winter days [25], and during our sampling winters they could be active during prolonged spells of mild weather. The earliest we have observed eagles with tortoises was the 8th of February, again more than a month before our latest non-breeding period collection. It is possible that only repeated, very intensive sampling before and after very cold spells would provide an accurate picture of the eagle's responses to a complete absence of tortoises.

Our results concerned low to mid-attitude golden eagles' territories. Pairs in the Balkans nesting at higher altitudes may not have access to tortoises, whose distribution is limited at 1500 m asl [46,77] where hares and partridges might be more important as prey. Comparisons of the productivity of pairs with and without access to tortoises (i.e., nesting in the high altitude mt ranges of the Balkans) would provide further answers about the adaptive significance of tortoise hunting.

4.5. Methodological Insights

Non-breeding season samples were smaller than the breeding season in relation to the effort invested (Table S1). Collecting non-breeding season data might yield smaller samples as eagles do not have to feed growing chicks and spread their time in wider areas than the immediate perimeter of the nest [78,79]. Despite the differences in sample sizes, we believe the differences we detected to be genuine due to our minimum requirement for sample inclusion (10 items) and the fact that reptiles would be in any case less abundant.

All raptor diet assessment methods have to some degree inherent biases and different methods might yield different results [31]. In our case, there is the possibility that tortoise carapaces are more prone to detection during prey item collections as they are relatively larger and more persistent in time compared to e.g., fur or feather pellets [19]. However, we believe that the high tortoise predation is not overestimated. Adult golden eagles are known to discard persistent prey remains away from nests, including tortoise carapaces, and even consume pellets [26]. Tortoises also comprised majority of prey remains in nests where the search area is very small and standardized. Furthermore, the overall frequency of tortoises observed as prey during field observations was very high, confirming the dietary dataset. Additionally, our prey item analysis, the MNI method combining pellets and prey remains that has been suggested as the less biased for golden eagles elsewhere, tends to underestimate the most common prey [80]. Ungulates on the other hand might be underrepresented in pellets, especially if the eagles feed on soft parts of a carcass and this might explain a relatively low incidence in diet samples.

Finally, a larger dataset of territories sampled would allow a more robust analysis of the impact of environmental variables on diet selection. However, our results have plausible explanations, and can be considered as a basis for further research in this direction.

4.6. Conservation Implications

Our findings have potentially serious conservation implications for our study population. Golden eagle breeding metrics can be negatively affected where main prey availability (tortoises in our case) declines or altogether collapses [3,81,82]. Both tortoise species have an unfavourable conservation status and a declining population trend, the Hermann's tortoise populations are considered Vulnerable (VU) [77,83], threatened by excess mortality and habitat loss through agricultural intensification, land abandonment, development and wildfires [84]. Such pressures are widespread in Mediterranean woodlands and garrigue [85] that dominate much of our population's distribution range.

Wildfires, endemic in our study area (Table S4), can have abrupt, catastrophic mortality effects on tortoise populations, particularly in the widespread among our territories scrub cover [73]. Especially megafires, are expected to increase in incidence concurrently with extreme heat events [86]. While e.g., hares might recover quickly [74], tortoise population recovery after fires is slow [87], hindered by limited recolonization due to low mobility [88] and the slow growth rates of any new hatchlings that can reach 500 g under optimal conditions only after four years [89]. Wildfire likelihood is enhanced also by the land abandonment that incurs increased fuel loads through the expansion of woody vegetation where grazing and small-scale farming declines [90]. The land abandonment-induced expansion of canopy cover is documented in parts of our study area [91,92] in the Rhodope mts and Dadia forest. This trend, apart from other negative biodiversity impacts [93,94] reduces the open areas raptors such as the golden eagle rely for hunting [95–97], like the small openings where reptile capture is possible [13] and the open ridges that we found to favor hare predation in the breeding season. Both tortoises and hare abundance has been found to be greater in open habitats such as pasture and scrubland mosaics [56,87,98]. Habitat loss through wildfires and increased canopy cover has been found to affect golden eagle populations and particularly pairs in areas of high density that cannot compensate for this loss through range expansion [99,100]. Habitat management such as grazing and prescribed burning [101,102] promoting habitat mosaics will thus reduce megafire incidence [103], and the associated biodiversity benefits will promote both the main and alternative prey availability [104–106].

Game species encountered in the golden eagle diet collection and behavioral datasets include the wild boar (*Sus scrofa*, whose offal is usually discarded in situ), hares, *Turdus* thrushes, ducks and woodpigeons, that are legally hunted in Greece during the winter months. Especially in winter and by immature individuals, the consumption of such items might be a possible pathway of lead ingestion as has been found elsewhere for this and other eagle species [107–110]. Lead levels have only been investigated incidentally in Greek raptors [111] and relevant studies incorporating tissues of dead birds, feathers and whole blood of handled specimens are required (preliminary findings in four of our territorial eagles have found small but detectable levels, Azmanis and Sidiropoulos, unpublished data).

We found that carrion, although the most likely class taken as such (ungulates) is underrepresented in pellets, can be important for golden eagles. The main carrion source in our area are livestock herds, declining concurrently to extensive grazing with land abandonment [112,113]. It might be particularly important in winter and for inexperienced, dispersing birds [9,114] and can be utilized even during the summer months [115]. Declining carrion availabilities are also exacerbated by the EU legislation on carrion and offal management that forbids the in situ disposal especially as the article 14 of the EC1069/2009 that amends this situation in Special Protection Areas has not been embodied in Greek legislation. Carrion can also be a potential hazard. Wildlife poisoning using offal and carcasses as baits is widespread in the Greek countryside [116] and is the main mortality factor for carrion eating birds. It has devastated vulture populations in mainland Greece [117,118] and accounts for >60% of the recorded golden eagle mortality in our study area in the last 30 years.

5. Conclusions

In conclusion, golden eagles have shown a considerable seasonal dietary plasticity in our study area, shifting from a narrow, reptile based diet to a broader diet more inclusive of various mammalian and avian taxa in the non-breeding season. The declining tortoise populations should be monitored and protected across the golden eagle range in our study area, in terms of management implications, with habitat management promoting landscape heterogeneity. The latter, based on our results where some prey categories where only locally important, should be considered on a territory basis after consideration of local features such as habitat conditions and stocking densities [12].

Supplementary Materials: The following are available online at https://www.mdpi.com/article/10.3390/d14020135/s1, Table S1: Time schedule of the 37 and 41 visits conducted during the breeding (March-November) and non breeding (November-March) season for prey remain collection at the 15 territories. Table S2: Percentage of prey categories and classes, n of items and Levins diversity index per territory and season for sample sizes of at least 10 items. Table S3: Percentage cover of habitat types in the 12 territories and average canopy cover. Table S4: Incidence of wildfires in the regional units of our study territories in the period 1983–2008.

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Conflicts of Interest: The authors declare no conflict of interest.

Appendix A

Table A1. The 53 prey taxa of the golden eagle diet in northern Greece, with reference to the 13 class categories used in the analysis. N: the number of prey items, -: unidentified at this taxonomic level. Superscripts indicate prey item found only during the breeding season (^{b}) or only at the non-breeding season (^{nb}).

Class Category	Class	Order	Family	N	%	Lowest Taxonomic Level Identified
Mammals all other	Mammalia	-	-	4	0.5	
Mammals all other		Cheiroptera	Molossidae	1	0.1	*Tandarida teniotis* ^{b} (1)
Hedgehogs		Eulipotyphla	Erinaceidae	34	4.1	*Erinaceus concolor* (35)
Mammals all other		Eulipotyphla	Soricidae	3	0.4	-
Hares		Lagomorpha	Leporidae	15	1.8	*Lepus capensis* (15)
Mammals all other		Rodentia	Muridae	15	1.8	*Mus musculus* (1), *Apodemus sp* (3), *Rattus sp* (2), unidentified (9)
Glirids and Sciurids		Rodentia	Gliridae	13	1.6	*Glis glis*
Glirids and Sciurids		Rodentia	Sciuridae	10	1.2	*Sciurus vulgaris*
Carnivores		Carnivora	Canidae	16	1.9	*Canis sp* ^{nb} (2), *V vulpes* (14)
Carnivores		Carnivora	Mustelidae	29	3.5	*M Meles* ^{b} (2), *Martes foina* (19), *Martes sp* (5), *Mustela nivalis* ^{b} (2), *M putorius* ^{b} (1)
Carnivores		Carnivora	Felidae	2	0.2	*Felis catus* ^{nb}
Ungulates		Artiodactyla	Bovidae	15	1.8	*Caprini* (5), *Capra hircus* (7), *Ovis aries*^{nb} (2), *Bos taurus* ^{b} (1)
Ungulates		Artiodactyla	Cervidae	3	0.4	*Capreolus capreolus* ^{nb}
Ungulates		Artiodactyla	Suidae	2	0.2	*Sus domestica* ^{b}
Ungulates		Perissodactyla	Equidae	1	0.1	*Equus sp* ^{b}

Table A1. *Cont.*

Class Category	Class	Order	Family	N	%	Lowest Taxonomic Level Identified
Birds all other	*Aves*	-	-	11	1.3	
Warerbirds		Pelecaniformes	Phalacrocoracidae	1	0.1	*Phalacrocorax carbo* [b]
Waterbirds		Anseriformes	Anatidae	2	0.2	*Anas strepera* [b] (1)
Raptors and Owls		Accipitriformes	Accipitridae	2	0.2	*Buteo buteo* [b] (1)
Raptors and Owls		Falconiformes	Falconidae	1	0.1	
Birds all other		Galliformes	Phasianidae	3	0.4	*Alectoris graeca* [b] (2), *C coturnix* [b] (1)
Waterbirds		Charadriiformes	Laridae	16	1.9	*Larus michahellis* (14), *Larus sp* (2)
Thrushes and pigeons		Columbiformes	Columbidae	12	1.5	*Columba palumbus* (5), *C livia domestica* (5), *Streptopelia turtur* [b] (1), unidentified 1
Birds all other		Apodiformes	Apodidae	1	0.1	*Apus melba* [b]
Birds all other		Caprimulgiformes	Caprimulgidae	2	0.2	*Caprimulgus europaeus* [b]
Raptors and owls		Stringiformes	Stringidae	1	0.1	*Athene noctua* [nb]
Birds all other		Passeriformes	-	9	1.1	
Birds all other		Passeriformes	Alaudidae	1	0.1	*Galerida cristata* [nb]
Thrushes and pigeons		Passeriformes	Turdidae	22	2.7	*Turdus philomelos* 8, *T merula* 5, *Turdus sp*[nb] (5), *T viscivorus* 3, *T pilaris 1*
Birds all other		Passeriformes	Paridae	1	0.1	*Cyanistes caeruleus* [nb]
Birds all other		Passeriformes	Sturnidae	7	0.8	*Sturnus vulgaris*
Corvids		Passeriformes	Corvidae	18	2.2	*Garrulus glandarius* (15), *Corvus cornix* [nb] (2), *Pica pica* (1)
Birds all other		Passeriformes	Fringillidae	2	0.2	
Snakes and lizards	*Reptilia*	Squamata	Anguidae	24	2.9	*Pseudopous apodus*
Snakes and lizards		Squamata	Lacertidae	6	0.7	*Lacerta* spp. 6, Podarcis spp 1
Snakes and lizards		Serpentes	-	3	0.4	
Snakes and lizards		Ophidia	Colubridae	7	0.8	*Elaphe situla* [b] (2), *Dolichophis caspius* (4), *Platyceps najadum* [nb] (1)
Snakes and lizards		Ophidia	Psammophilidae	3	0.4	*Malpolon insignitus*
Tortoises		Chelonia	Testudinidae	511	61.8	*Eurotestudo hermanni* (133), *Testudo graeca* (56), *Testudo* spp. (322)
				827		

Appendix B

Table A2. Summary of the observation dataset. N of instances refers to all behavioral interactions including unsuccessful attacks, N of successes to instances where eagles were seen successfully capturing prey or feeding in prey already captured or scavenged.

Prey Category	N of Instances	N of Successes	Breeding Season	Non–Breeding Season
Corvids	4	0	3	1
Raptors and owls	3	0	2	1
Thrushes and pigeons	1	1	0	1
Waterbirds	1	0	1	0
Other birds	4	2	4	0
Carnivores	7	7	2	5
Glirids and Sciurids	1	1	1	0
Hedgehogs	2	2	1	1
Hares	1	1	1	0
Ungulates	7	5	1	6
Other mammals	1	1	2	2
Snakes and lizards	12	12	9	3
Tortoises	57	57	53	4
Ungulates (carrion and offal) left on designated sites		96	21	75

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