

Diet shifting of tortoise-eating Golden Eagles (*Aquila chrysaetos*) in southeastern Bulgaria

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Top predators may adapt their diets to changes in prey availability where human-induced environmental changes are intense. This long-term study of the breeding-season diet of Golden Eagle (*Aquila chrysaetos*) in the Strandzha Mountains analyzed shifts in diet caused by the population decline in principal prey species, the tortoises (*Testudo hermanni* and *T. graeca*). Tortoises comprised 50.0% of the eagle diet by prey number in the 1990s, but that share collapsed to 5.8% in 2014–2021. During this later interval, Golden Eagles preyed more intensively on lighter-weight prey such as Northern White-breasted Hedgehog (*Erinaceus roumanicus*, an increase of 28.2% by number) and Edible Dormouse (*Glis glis*, an increase of 14.9% by number). Hedgehogs predominated in the diet of an individual eagle nest site for the first time in 1998 and became the principal prey in 2014–2021. Differences in food niche breadth and proportions of mesopredators between tortoise- and hedgehog-dominated individual annual diets were not significant, corresponding to a low level of food stress. The only eagle with an annual diet dominated by Squamata (snakes and lizards) was an exception, having the widest food niche. Young domestic ungulates have almost completely disappeared from eagle diets at the same as the reduction of tortoises, corresponding to a concurrent decline of livestock farming. The results obtained here have relevance to conservation management of both predator and prey populations.



1. Introduction

Adaptability of predators to changes in food supply and accessibility to prey largely determine the degree of plasticity of predator populations in a changing environment. A shift in diet to alternate prey species when preferred prey populations decrease is a common response of opportunistic birds of prey including owls (Newton 1979, Mebs

& Schmidt 2014, Scherzinger & Mebs 2020). In this way predators survive periods of scarce supply of favored prey (Steenhof & Kochert 1988, Taylor 1994, Rutz & Bijlsma 2006, Penteriani & Delgado 2019). Some opportunistic top predators even occupy new territories and improve the condition of their populations by adjusting their diet to locally available food supplies (Tofft 2002, Clouet *et al.* 2015, Horváth *et al.* 2018).

The Golden Eagle (*Aquila chrysaetos*) hunts a large variety of prey across its vast range in the Northern Hemisphere, but its diet depends on mostly medium-size mammals and birds weighing 0.5–4 kg (review in Watson 2010). The local populations of rabbits and hares (Lagomorpha), marmots and squirrels (Rodentia), young ungulates including domestic livestock (Cetartiodactyla) and gallinaceous birds (Galliformes) comprise the principal prey, in varying proportions according to the specific food supply (Watson 2010, Mebs & Schmidt 2014). Carrion can be significant in winter (Haller 1996, Watson 2010). The predominance of tortoises is one of the exceptions to the breeding-season diet of the Golden Eagle typical of the Balkan Peninsula (Fischer *et al.* 1975, Grubač 1987, Miltschew & Georgiewa 1992, Georgiev 2009, Sidiropoulos *et al.* 2022). Tortoises (Hermann's Tortoise *Testudo hermanni*, Common Tortoise *T. graeca*) comprised 70.5% of the prey ($n = 227$) in the Strandzha Mountains, SE Bulgaria, in the late 1980s (Miltschew & Georgiewa 1992). Both tortoise species are currently listed as “endangered” in the Bulgarian Red Data Book due to the marked reduction in their number and distribution in recent decades (Golemanski 2015). Consumption of tortoises by local residents and fires set in pastures, forests and abandoned arable lands are among the main negative factors still relevant today (Petrov *et al.* 2004, Popgeorgiev 2008, Tzankov & Milchev 2014). Adaptation by Golden Eagles to the declining supply of their former main prey, tortoises, is expected to transition opportunistically to alternative prey and a wider food niche (Fernández 1993, Sulkava *et al.* 1998, Collins & Latta 2009, Clouet *et al.* 2015, Bedrosian *et al.* 2017, Heath *et al.* 2021). A hypothesized change would be to more mesopredator mammals and birds in the top predator's diet as an adaptive strategy to reduced supply of the principal prey in response to an increased food stress (Lourenço *et al.* 2011).

This study (i) describes the breeding-season diet of Golden Eagle during the shift in principal prey and (ii) investigates the fluctuations of dietary breadth within the study population as the main prey categories change.

2. Material and methods

2.1. Study area

The study area covers the Bulgarian part of the Strandzha Mountains, a landscape with strongly folded hill relief up to 300–400 m a.s.l. (2950 km², N42°11' S27° 26'; Fig. 1). The climate is continental-Mediterranean characterized with hot and dry summers, mild winters and annual rainfall of 600–800 mm. Deciduous forests dominated by oaks (*Quercus* spp.) and less often beech (*Fagus orientalis*) characterizes the forested landscape. Scattered open areas on flattened ridges especially at the northern and western periphery of the mountain range diversify the landscape. The Strandzha Mountains are sparsely inhabited by an aging population living in scattered villages. Malko Tarnovo municipality (747.4 km²) in the central Strandzha Mountains averages 5.1 people/km². Economic activity in the area was historically based on logging, extensive livestock husbandry and farming (see also Milchev & Georgiev 2014). Arable land was abandoned with the restitution of private land ownership after 1991/1992. Agricultural subsidies attempted but failed to restore farming after Bulgaria's accession to the EU in 2007. At the same time, the number of grazing livestock declined by more than 90% and has not recovered. The last remnants of traditional grazing pig farming disappeared following the spread of African swine fever in 2019.



Fig. 1. Study area in southeastern Bulgaria.

Tortoise populations in the Strandzha Mountains were in good condition, according to a questionnaire circulated throughout Bulgaria in the 1980s (Beshkov 1984). Both species are only slightly impacted in the study area by otherwise major negative factors at the national level such as intensification in agriculture, fires and replacement of native deciduous forests and shrubs by conifer plantations (Stojanov *et al.* 2011, Golemanski 2015). Human consumption continues to be the negative factor (Tzankov & Milchev 2014, Golemanski 2015) that has affected the tortoises in the Strandzha Mountains (Petrov *et al.* 2004, author's unpubl. data). People's unrestricted access to the Strandzha Mountains was allowed after the democratic changes of the 1990s and appears to have increased the human consumption of tortoises.

2.2. Data collection

Data on Golden Eagle diets were collected over two periods: (1) 1991–2005 with two visits in late June to early July, and again in late August to early September each year; and (2) 2014–2021 with a third intervening visit in late July. To minimize disturbance to nest sites, the visits occurred after the young eagles were over 45–50 days old. This delayed first visit probably led to the omission of some prey that could be important in the early nestling period (Collopy 1983). Eagle pairs nesting unsuccessfully in June–July were usually dropped from subsequent visits. Golden Eagles nested only in trees in about ten nesting territories (terminology follows Steenhof *et al.* 2017) in the Strandzha Mountains (Miltschew & Georgiewa 1992). Diet data were collected from eight nesting territories, and occupied nests were found in six of them during the first study period. Their number decreased to five territories with three known occupied nests in the second period; two territories were excluded as unoccupied and one pair built a nest in a densely wooded valley that precluded the possibility of tracking the eagles. The lack of open sites with visibility to the nests in the heavily wooded, rugged landscape made it difficult to find occupied nests in all nesting territories. Food remains (parts of prey, skin, feathers, bones, 312 intact and disintegrated pellets, *etc.*)

were collected beneath occupied nests and at sites where eagles were resting, feeding, or consuming prey. One nest was climbed to collect food remains in 1994–2003 and nine fallen nests were inspected; Golden Eagles leave relatively few remains in their nests (Whitfield *et al.* 2009, Preston *et al.* 2017, and author's observation). Clearly recognizable remains, such as a tortoise shell and a leaf-filled stomach left next to it by the Golden Eagle, skinned hedgehog hides or legs of a hare, were described on the spot and removed so that they would not be counted again on the next visit. Other food remains were examined more closely in the laboratory to determine prey to the lowest taxonomic level possible using the published technical references (Görner & Hackethal 1987, März 1987, Peshev *et al.* 2004, Stojanov *et al.* 2011), comparative material from the National Museum of Natural History, Sofia, and the author's own reference collection. A minimum number of individuals was estimated for each taxon based on the number of the most frequent anatomical part in food remains or the pairing of anatomical parts. Bird feathers identified to species were compared to the list of bone determinations from the same sample, and the missing species from bone samples were added to the species list. The number of snakes and lizards corresponded to the number of pellets with their scales (Seguin *et al.* 1998).

Food niche breadth (FNB) was computed after Levins (1968):

$$FNB = 1/\sum p_i^2 \quad (1)$$

where p_i is the proportion of prey category i by number in the actual diet. The larger values indicate a higher dietary diversity. To obtain results comparable to those of Watson (2010), mammals and birds were classified by family, reptiles by order. Birds unidentified at the family level were excluded from the prey lists.

The large number of prey taxa is categorized for the analyses into seven main prey categories. The dominant prey species, (1) tortoises and (2) hedgehog, are in separate categories. The other four categories include at least one species with significant variations in its diet proportions: (3) hare (*Lepus europaeus*) and all small mammals; (4) ungulates; (5) birds; (6) lizards

and snakes, Squamata. The last prey category (7) mesopredators incorporates predatory mammals (Carnivora) and birds (Accipitriformes and Strigiformes), whose share in the diet of top predators is an indicator of the level of food stress (Lourenço *et al.* 2011).

2.3. Statistical analysis

Differences between the diets of the Golden Eagle populations from the two study periods were tested with a chi-square contingency table. The annual diets (food caught by a successfully breeding pair raising at least one fledgling during one breeding season) in individual nesting territories with at least 25 prey specimens presented the dietary range within the study population. The Product Moment Correlation Coefficient measured the relations between proportions (arcsine-transformed data) of the main prey categories in the annual diets and FNB. The significance level was $p < 0.05$. All means are reported as the arithmetic mean \pm standard deviation. The analyses were carried out with PAST 3.01 software (Hammer *et al.* 2001). Principal component analysis was used for studying the pattern of distribution of the prey categories in annual diets (CANOCO v. 4.5; ter Braak 1995). The samples were the annual diets, while the variables were the proportions of

the main prey categories (% by number) in the respective diets. The variables are represented by arrows and the annual diets by circles on the ordination chart. The arrows show the weightings of the variables in the first two principal components. The angles between the arrows approximate the correlations among variables. Most important in the analysis with the ordination axes were species with longer arrows and sharper angles (ter Braak 1995, Lepš & Šmilauer 2003)

3. Results

3.1. Food composition

The feeding range includes 1417 prey specimens distributed among 56 identified vertebrate taxa (Supplementary Table S1). Mammals and reptiles dominated the diet in number (cumulative 87.5% by number), and birds were the most diverse class with 23 prey species. Six prey species accounted for 81.8% of the total prey number (Northern White-breasted Hedgehog *Erinaceus roumanicus* 33.6%, tortoises 23.6%, Edible Dormouse *Glis glis* 12.7%, Aesculapian Ratsnake *Zamenis longissimus* 5.7%, Common Woodpigeon *Columba palumbus* 3.1% and European Hare 3%).

Diet differed very significantly in the frequency of prey across the main categories

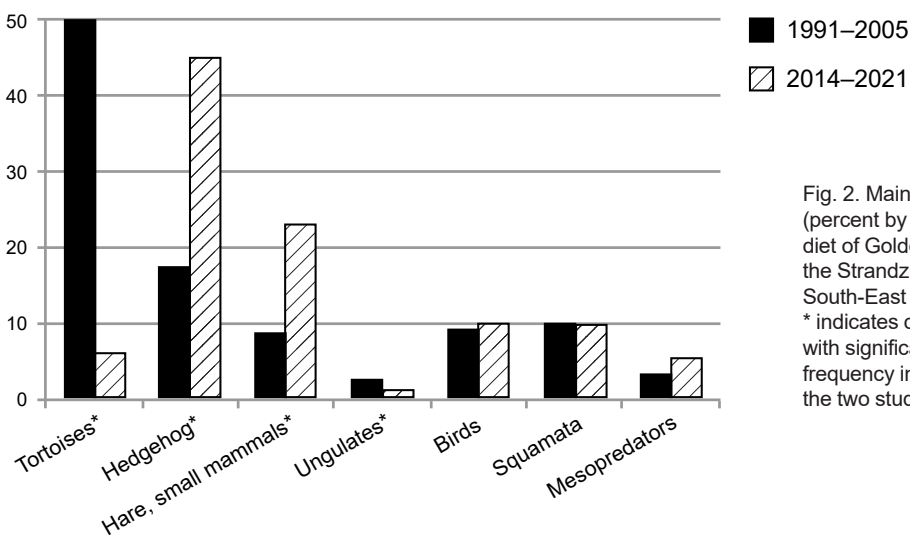


Fig. 2. Main prey categories (percent by number) in the diet of Golden Eagles in the Strandzha Mountains, South-East Bulgaria: * indicates categories with significantly different frequency in the diet during the two study periods.

between the two study periods ($\chi^2 = 420.9$, $df = 6$, $p < 0.001$; Fig. 2). Tortoises were predated much less frequently in the second period, when their proportions in the diet collapsed to 5.8% by number ($n = 845$; a decrease of 44.2%). The ratio between the two tortoise species in the diet also changed, but with a similar proportion of unidentified tortoises to species (Supplementary Table S1): the number of Hermann's Tortoise versus Common Tortoise was 1.6 : 1 in the first period and 5.3 : 1 in the second one. Ungulates significantly decreased to a few items (0.5% by number, $n = 845$). The resinous black color of the fur from the birth of local domestic pigs showed that they were the only ones present in the food with one exception. The prey list included wild boar (*Sus scrofa*) according to a hole from a gunshot wound in a scapula of a subadult specimen.

Frequency of Northern White-breasted Hedgehog as the eagle prey increased and this species became the dominant prey with an increase in 28.2% by number in the second period. A similar change occurred in the frequency of the category "hare, small mammals" (an increase of 14% by number). Edible Dormice in this category were responsible for the increase (a growth of 14.9% by number). Thus, species not traditionally consumed by local people accounted for 40.9% ($n = 572$) of the prey number in the Golden Eagle diet in the first study period but reached 86% (n

= 845) of the diet after 2014. The shift to hunting White-breasted Hedgehogs and Edible Dormice corresponded to a slight widening of the food niche (3.40 in 1991–2005, 3.84 in 2014–2021).

3.2. Analysis of individual diets of eagles

The 22 analyzed annual diets of successful pairs comprised 86% of the total number of prey collected ($n = 1417$). Tortoises were the most numerous prey in 11 diets (50%, $n = 22$), while Northern White-breasted Hedgehogs predominated 10 diets (45%, Table 1). Snakes and lizards, category "Squamata", were the most frequent prey in one diet (5%). Tortoise-dominated and hedgehog-dominated diets differed significantly in median prey numbers ($U = 1.5$, $p < 0.001$), being higher in hedgehog-dominated diets. The proportions of the three dominant categories varied greatly in annual diets, but hedgehogs were the only prey among them represented in all diets.

The proportions of the three dominant prey categories and the categories "ungulates" and "hare, small mammals" correlated significantly with each other in the annual diets (Table 2). The strongest correlations were negative between the proportions of tortoises and those of "hare, small mammals" ($r = -0.815$, $p < 0.001$) and hedgehogs

Table 1. Variations of diet characteristics in 22 individual annual diets of Golden Eagles in the Strandzha Mountains, SE Bulgaria: n = number of annual diets; %N = percent by prey number; FNB = food niche breadth; average \pm standard deviation (minimum–maximum).

Prey categories		Tortoise-dominated diets ($n = 11$)	Hedgehog-dominated diets ($n = 10$)	Squamata dominated diet ($n = 1$)
Tortoises	%N	53.7 \pm 12.5 (38.7–79.2)	8.2 \pm 9.9 (0–34.6)	5.8
Hedgehog	%N	15.4 \pm 6.5 (8.0–30.2)	47.3 \pm 13.5 (34.1–68.4)	19.2
Hare, small mammals	%N	4.0 \pm 3.9 (0–14.0)	21.0 \pm 11.3 (6.6–35.1)	28.8
Birds	%N	9.4 \pm 5.3 (3.0–18.5)	9.0 \pm 2.2 (6.7–12.7)	13.5
Squamata	%N	10.4 \pm 4.8 (0–15.2)	9.1 \pm 3.3 (3.8–13.3)	30.8
Ungulates	%N	3.0 \pm 3.3 (0–8.3)	0.8 \pm 1.2 (0–3.8)	0
Mesopredators	%N	4.0 \pm 4.0 (0–11.1)	4.6 \pm 2.7 (0–8.6)	1.9
Prey number		31 \pm 7 (25–44)	83 \pm 25 (43–135)	53
FNB		3.12 \pm 0.94 (1.57–4.31)	3.46 \pm 1.01 (2.01–4.69)	5.28

Table 2. Significant correlations between the proportions of the prey categories (% by number) and the food niche breadth (FNB) in the individual annual diets of Golden Eagles in the Strandzha Mountains, SE Bulgaria: * $p < 0.05$, ** $p < 0.01$, *** $p < 0.001$, ns = not significant.

Prey categories	Tortoises	Hedgehog	Hare, small mammals	Squamata	Birds
Hedgehog	-0.790***		0.475*	ns	ns
Hare, small mammals	-0.815***	0.475*		ns	ns
Ungulates	0.477*	-0.457*	-0.465*	-0.543**	ns
FNB	ns	ns	0.593**	0.457*	0.483*

($r = -0.790$, $p < 0.001$). FNB correlated positively with the proportions of “hare, small mammals”, “birds” and “Squamata” (Table 2) and peaked at 5.28 for the Squamata-dominated diet. Mean FNB values did not differ significantly between tortoise- and hedgehog-dominated diets.

Principal component analysis determined the main regularities in the food composition of 22 annual diets. The first and second ordination axes explain 80.1% and 12.0% of the total variation in the data. The first gradient distributes diets according to the proportions of tortoises versus proportions of hedgehogs and “hare, small mammals” (Fig. 3). The categories “Squamata” and “hare, small mammals” correlate with the positive part of the second axis, while the categories “hedgehog”, “ungulates” and “mesopredators” respectively with the negative part of the axis. Tortoise-dominated diets fall in the left half of the chart and form a group of diets from all nesting territories in 1991–1999. Only diets from the nesting territory 1 from 1994, 1996 (both tortoise-dominated) and 1998 (hedgehog-dominated) displayed the gradual transition to a diet with decreasing tortoise proportion. Mostly the prey categories “ungulates”, “mesopredators” and “hedgehog” replaced the tortoises in these diets. The 1996 and 1998 diets in territory 1 included 83% of the smallest tortoises as Golden Eagle prey ($n = 6$ Hermann’s Tortoises, carapace length 11.2 ± 2.3 cm, range 8.5–14.4 cm).

The squamata-dominated diet (4-00, Fig. 3) in 2000 stood out from the rest by the high share of snakes, small mammals, and birds (cumulative 73.1% by number) and a drop of tortoises to 5.8% by number. All hedgehog-dominated diets since 2016 are positioned in the right half of the chart in two groups. One group included diets in nesting

territory 3 with the highest hedgehog dominance ($62.1 \pm 7.2\%$ by number). The category “hare, small mammals” complemented these diets the most with $10.7 \pm 7.2\%$ by number at FNB 2.4 ± 0.5 . More diverse prey replaced the tortoises in the second group with diets at FNB 4.5 ± 0.2 of territories 4 and 5 ($37.2 \pm 2.3\%$ hedgehogs, $31.1 \pm 3.9\%$ “hare, small mammals” and $10.6 \pm 3.8\%$ “Squamata”). The diet of territory 4 in 2019 was the only one without tortoises.

4. Discussion

Data from breeding-season Golden Eagle diets confirmed the expected change with the replacement of tortoises as the most numerous prey by the Northern White-breasted Hedgehog. This new dominant prey occupied the second position by number in previous Bulgarian studies (Miltshew & Georgiewa 1992, Georgiev 2009) and in the non-breeding diet in Greece (Sidiropoulos *et al.* 2022). Hedgehogs dominated as an exception the Golden Eagle food in Estonia (Zastrov 1946, in Watson 2010) and Gotland, Sweden (Högström & Wiss 1992). The third numerical position of the Edible Dormouse in the eagle diets in the Strandzha Mountains has an analogue only in the forested Italian pre-Alps (Pedrini & Sergio 2002). The uniqueness of the present study’s diets was reinforced by the substantial share of snakes that were important in some diets in southern Europe (Clouet 1981, Seguin *et al.* 1998), Kazakhstan (Karyakin *et al.* 2011) and Japan (Takeuchi *et al.* 2006). Ungulates were the final category with a significantly changed frequency in eagle diets during the second study period. The observed decline corresponds to the collapse of grazing

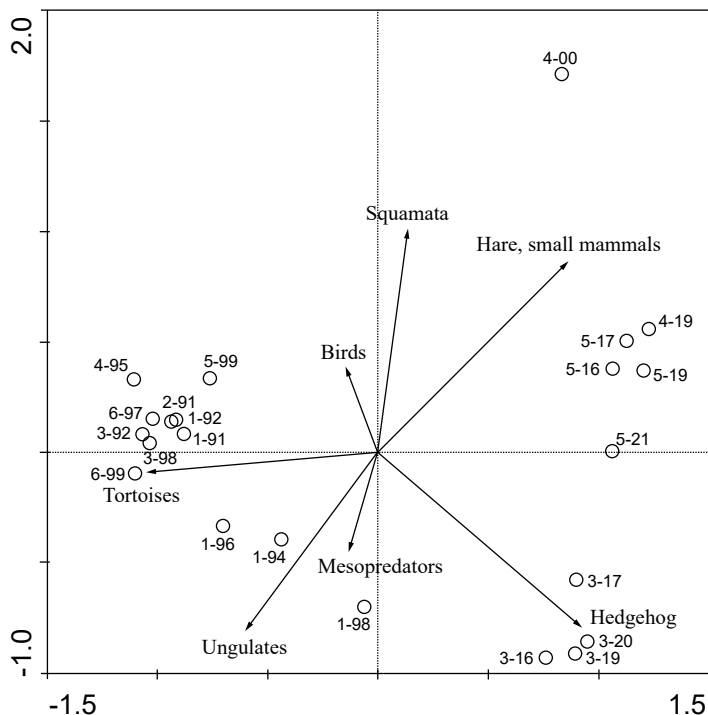


Fig. 3. PCA ordination of seven main prey categories (arrows) and 22 annual diets (circles) of Golden Eagle pairs in the Strandzha Mountains, SE Bulgaria: the category names are given at the arrowheads; individual diets are marked with a combination of two numbers, where the first is a serial number on the nesting territory according to Miltschew, Georgiewa (1992), and the latter are the last two digits of the year of the diet collection.

livestock in recent decades and the complete ban on pig farming in 2019.

Diets of Golden Eagles respond to the local supply and availability of prey from the preferred weight group. Diet changes follow Schluter's (1981) optimal diet theory (Bedrosian *et al.* 2017, Preston *et al.* 2017, Roemer & Collins 2019). Northern White-breasted Hedgehog (about 750 g, Glutz von Blotzheim & Bauer 1994) falls within the favorable weight group for Golden Eagle prey. Edible Dormouse (about 125 g, Glutz von Blotzheim & Bauer 1994) is a night climber on trees and shrubs, much lighter than the preferred prey weight group. Both prey species are significantly lighter than the predominant size group in the Bulgarian tortoise populations with 20–25 cm carapace length (Stojanov *et al.* 2011) and a biomass of about 2100 g (Jackson 1980). The Golden Eagles likely compensate for the lighter-weight alternative prey by increasing

the total prey number in annual diets. No data on the populations of the Golden Eagle prey in the Strandzha Mountains have shown estimates that the Northern White-breasted Hedgehog and the Edible Dormouse are the most profitable prey. But indirect confirmation of flourishing populations of both mammals could explain their dominance in the opportunistic diet of a sympatric top predator such as the Eagle Owl (*Bubo bubo*) (cluster 7 in Milchev & Georgiev 2020). The Northern White-breasted Hedgehog was also the principal prey of the Eastern Imperial Eagle (*Aquila heliaca*), another opportunistic top predator breeding in neighboring more open landscapes to the west and southwest of the Golden Eagle population studied here (Demerdzhiev *et al.* 2014).

The food niche expanded slightly after the decline of tortoises in the diet, but remained below the average of 4.03 ± 2.07 in Eurasia ($n = 24$ diets, Watson 2010). Large birds such as

two young Great Cormorants (*Phalacrocorax carbo*) and White Storks (*Ciconia ciconia*) were found in the food subsequently. Neither species breed in the nesting territories of the predator eagles (author's unpub. data). Golden Eagles have benefited little from the dispersal of young Great Cormorants in the Strandzha Mountain River Network and from White Storks migrating over the mountains on the main western Black Sea Flyway. Migratory bird predation was as low as that found by Clouet *et al.* (2015) for trans-Pyrenean migrants, although the migration of the numerous White Storks largely coincides with the nesting period of the Golden Eagles in the Strandzha Mountains (Milchev & Kovachev 1995).

Proportion of mesopredators also rose insignificantly and remained below the average $6.6 \pm 5.6\%$ in Europe ($n = 21$ diets, Lourenço *et al.* 2011). The predominance of owls (3.3% by number in the second period) among eaten predators in the present study was atypical for Golden Eagles ($0.5 \pm 0.6\%$ owls, Lourenço *et al.* 2011) and included resident and vagrant forest owls (Menzel & Miltshev 2001). The food niche breadth and the share of mesopredators did not show extreme values nor a high level of food stress after changes in the breeding-season diet of the study population.

The analysis of annual diets between and within nesting territories shows that populations of preferred tortoises were large enough in the 1990s. Tortoise-dominated diets had a very similar structure in all territories during this period. The exception was the westernmost territory 1, where the first data on mass consumption of tortoises by humans in 1991 and 1992 were obtained (author's data, Petrov *et al.* 2004). This territory was the only one with a gradual transition to a hedgehog-dominated diet and compensatory predation of ungulates and mesopredators over the years. The collection of large adult tortoises for food by humans in the post-1990 economic crisis was the most likely explanation for the appearance of smaller young tortoises in the eagles' diet. The two tortoise species differ in their habitat preferences. Hermann's Tortoise prefers forest-shrub habitats, and the Common Tortoise inhabits mainly open grasslands (Stojanov *et al.* 2011). Hermann's Tortoise predominated over the

Common Tortoise in the eagle's diet in the forested Strandzha Mountains in both periods, but three times more in the second period. I speculate that easier collection of tortoises by humans in open habitats has more strongly reduced the population of Common Tortoises and has been reflected in the Golden Eagle diet. Tortoise populations have dropped below some threshold level and have been replaced by alternative prey in all diets since 2000.

The shift in Golden Eagles' specialization to a new main prey, hedgehogs, has not led to significant differences in the food niche breadth within the study population over the years. Additional prey from the categories of small mammals, birds, and Squamata correlated positively with the width of the niche. Snakes have dominated the most diverse annual diet, but they do not seem to have furnished a stable enough supply over the years to be a diet alternative equivalent to hedgehogs and Edible Dormice. The observed transition with diversification of the diet is similar to the processes that took place in the diet of other Golden Eagle populations (Fernández 1993, Nyström *et al.* 2006, Bedrosian *et al.* 2017, Preston *et al.* 2017) including even subsequent specialization in new principal prey (Collins & Latta 2009, Watson & Davies 2015, Heath *et al.* 2021). Seasonal changes in food supply and availability cause usually alterations in the non-breeding-season diet of Golden Eagles (Watson 2010, Mebs & Schmidt 2014). Sidiropoulos *et al.* (2022) reported such seasonal dietary changes in neighboring northern Greece as the first in the Balkans. The Golden Eagles in the Strandzha Mountains have to change their diet during the cold half of the year much more markedly than in Greece, due to the obligatory hibernation of their main prey, hedgehogs, Edible Dormice and reptiles. The nonbreeding-season diet is important for overwinter survival and its study is needed for developing a complete Golden Eagle conservation strategy in the context of both global climate and socio-economic changes.

One of the most troubling findings from this study is the indirect confirmation of the ineffectiveness of conservation for tortoises in the Strandzha Mountains. Both tortoise species have been strictly protected under national law since

1961 (Golemanski 2015). The Strandzha Natural Park established in 1995 covers nesting territories 4 and 5, while the other Golden Eagle territories with analyzed annual diets remain outside park boundaries. However, the Natura 2000 protected-area network has covered most of the mountain range since 2007 and only nesting territory 3 has remained unprotected. Tortoises are the only reptiles with a national conservation action plan (Petrov *et al.* 2004). Nevertheless, the tortoises diminished as a prominent prey source for the Golden Eagle both in protected and unprotected territories. Both tortoise species are now among the ineffectively protected and managed wildlife populations in the Strandzha Mountains, joining extirpated and declining breeding birds (Milchev & Georgiev 2014, 2021, Demerdzhiev *et al.* 2019). The adaptive abilities of the Golden Eagle population in this study to adapt to new food sources could guide future actions to preserve both the predator and its prey.

Ruokavaliomuutos kilpikonniin erikoistuneissa maakotkissa (*Aquila chrysaetos*) Bulgarian lounaisosassa

Huippusaalistajat saattavat muokata ruokavaliotansa saalistarjonnan mukaan ympäristön muuttuessa. Tässä pitkäaikaistutkimuksessa analysoimme maakotkan (*Aquila chrysaetos*) ruokavaliomuutoksia Strandzhan vuoristossa, jossa pääsaaliin eli kilpikonniin (*Testudo hermanni* ja *T. graeca*) populaatiokoot ovat pienentyneet. Kilpikonniin osuus maakotkan saalistamasta ruokavaliosta oli 50.0% 1990-luvulla, mutta tämä osuus on pienentynyt 5.8% 2014–2021 tutkimusjaksolla. Tällä myöhemmällä tutkimusjaksolla maakotkat saalistivat voimakkaammin kevyempiä saaliita, kuten siilejä (*Erinaceus roumanicus*), joiden osuus kasvoi 28.2%, ja unikekoja (*Glis glis*), joiden osuus kasvoi 14.9%. Siilit olivat tärkeimpiä saaliita yhdessä maakotkapesässä ensimmäisen kerran 1998, ja vuosina 2014–2021 siitä tuli vallitseva saalistaji maakotkien pesissä. Ruokavaliion laajuuden ja piensaalistajien osuuden vaihtelu kilpikonni- ja siilivaltaisissa pesissä ei eronnut, mikä viittaa siihen, että ravinnon saataisuus ei ole rajoittava tekijä. Ainoastaan yksi

käärmeihin ja liskoihin (Squamata) erikoistunut maakotka erottui joukosta muita selvästi laajemmalla ruokavaliolla. Nuorten kotieläimienä pidettyjen sorkkaeläinten osuus saaliista on vähentynyt samaan aikaan kilpikonniin kanssa, mikä johtuu karjanhoidon vähenemisestä kyseisessä maanosassa. Tutkimuksen tulokset ovat tärkeitä sekä peto- että saalistajien suojelussa.

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References

- Bedrosian, G., Watson, J., Steenhof, K., Kochert, M., Preston, C., Woodbridge, B., Williams, G., Keller K. & Crandall, R. 2017: Spatial and Temporal Patterns in Golden Eagle Diets in the Western United States, with Implications for Conservation Planning. — *Journal of Raptor Research* 51: 347–367. <https://doi.org/10.3356/JRR-16-38.1>
- Beshkov, V. 1984: On the distribution, relative abundance and protection of tortoises in Bulgaria. — *Ecology, Sofia* 14: 14–34. (In Bulgarian)
- Clouet, M. 1981: L’Aigle Royal *Aquila chrysaetos* dans les Pyrénées Françaises. Résultats de 5 ans d’observations. — *La Revue française d’ornithologie* 51: 89–100. (In French)
- Clouet, M., Gonzalez, L., Laspreses, F. & Rebours, I. 2015: Le régime alimentaire de l’Aigle royal *Aquila chrysaetos* en période de reproduction dans le nord du Pays Basque. — *Alauda* 83: 1–6. (In French)
- Collins, P. & Latta, B. 2009: Food habits of nesting Golden Eagles (*Aquila chrysaetos*) on Santa Cruz and Santa Rosa islands, California. — In *Proceedings of the 7th California Islands Symposium*. (ed Damiani, C. & Garcelon D.): 255–268. Institute for Wildlife Studies, Arcata, CA.
- Collopy, M. 1983: A comparison of direct observations and collections of prey remains in determining the diet of Golden Eagles. — *The Journal of Wildlife Management* 47: 360–368. <https://doi.org/10.2307/3808508>
- Demerdzhiev, D., Dobrev, D., Isfendiyaroglu, S., Boev, Z.,

- Stoychev, S., Terziev, N. & Spasov, S. 2014: Distribution, abundance, breeding parameters, threats and prey preferences of the eastern Imperial Eagle (*Aquila heliaca*) in European Turkey. — Slovak Raptor Journal 8: 17–25. <https://doi.org/10.2478/srj-2014-0004>
- Demerdzhiev, D., Dobrev, D., Arkumarev, V., Terziev, N. & Georgiev, G. 2019: Distribution, abundance and breeding performance of Lesser Spotted Eagle *Clanga pomarina* Brehm, 1831 (Aves: Accipitridae) in Southeast Bulgaria. — Acta Zoologica Bulgarica Suppl. 14: 15–33.
- Fernández, C. 1993: Effect of the viral haemorrhagic pneumonia of the wild rabbit on the diet and breeding success of the Golden Eagle *Aquila chrysaetos* (L.). — Revue d'Ecologie (La Terre et la Vie) 48: 323–329.
- Fischer, W., Zenker, D. & Baumgart, W. 1975: Ein Beitrag zum Bestand und zur Ernährung des Steinadlers (*Aquila chrysaetos*) auf der Balkanhalbinsel. — Beiträge zur Vogelkunde 21: 275–287. (In German)
- Georgiev, D. 2009. Diet of the Golden Eagle (*Aquila chrysaetos*) (Aves: Accipitridae) in Sarnena Sredna Gora mountains (Bulgaria). — Ecologia Balkanica 1: 95–98.
- Glutz von Blotzheim, U. & Bauer, K. 1994: Handbuch der Vögel Mitteleuropas. vol. 9. — Wiesbaden, Germany: Akademische Verlagsgesellschaft. (In German)
- Golemanski, V. (ed.) 2015: Red Data Book of Bulgaria. 2nd ed. — Bulgarian Academy of Sciences and Ministry of Environment and Waters of Bulgaria, Sofia, Bulgaria.
- Görner, M. & Hackethal, H. 1987: Säugetiere Europas. — Neumann Verl., Leipzig-Radebeul. (In German)
- Grubač, R. 1987: L'Aigle Royal en Macedone. — In L'Aigle Royal en Europe. (ed. Michel S.): 37–39. Actes du Premier Colloque International, Arvieux. (In French)
- Haller, H. 1996: Die Steiadler in Graubünden. Langfristige Untersuchungen zur Populationsökologie von *Aquila chrysaetos* im Zentrum der Alpen. — Der Ornithologische Beobachter, Beiheft 9: 1–167. (In German with English summary)
- Hammer, Ø., Harper, D. & Ryan, P. 2001: PAST: Paleontological Statistics software package for education and data analysis. — Paleontologia Electronica 4: 1–9.
- Heath, J., Kochert, M. & Steenhof, K. 2021: Golden Eagle dietary shifts following wildfire and shrub loss have negative consequences for nestling survivorship. — Ornithological Applications. 123: 1–14. <https://doi.org/10.1093/ornithapp/duab034>
- Högström, S. & Wiss L.-E. 1992: Diet of the Golden Eagle *Aquila chrysaetos* (L.) in Gotland, Sweden during the breeding season. — Ornis Fennica 69: 39–44.
- Horváth, M., Solti, B., Fátér, I., Juhász, T., Haraszthy, L., Szitta, T., Ballók, Z. & Pásztor-Kovács, S. 2018: Temporal changes in the diet composition of the Eastern Imperial Eagle (*Aquila heliaca*) in Hungary. — Ornis Hungarica 26: 1–26. <https://doi.org/10.1515/orhu-2018-0001>
- Jackson, O. 1980: Weight and measurement data on tortoises (*Testudo graeca* and *Testudo hermanni*) and their relationship to health. — Journal of small animal practice 21: 409–416. <https://doi.org/10.1111/j.1748-5827.1980.tb01269.x>
- Karyakin, I., Kovalenko, A., Levin, A. & Pazhenkov, A. 2011: Eagles of the Aral-Caspian Region, Kazakhstan. — Raptor Conservation 22: 92–152.
- Lepš, J. & Šmilauer, P. 2003: Multivariate Analysis of Ecological Data using CANOCO. — Cambridge, UK: Cambridge University Press. <https://doi.org/10.1017/CBO9780511615146>
- Levins, R. 1968: Evolution in Changing Environments. — Princeton, NJ, USA: Princeton University Press. <https://doi.org/10.1515/9780691209418>
- Lourenço, R., Santos, S., Rabaça, J. & Penteriani, V. 2011: Superpredation patterns in four large European raptors. — Population Ecology 53: 175–185. <https://doi.org/10.1007/s10144-010-0199-4>
- März, R. 1987: Gewöll- und Rupfungskunde. — Akademie-Verlag Berlin. (In German)
- Mebs, T. & Schmidt, D. 2014: Die Greifvögel Europas, Nordafrikas und Vorderasiens. Biologie, Kennzeichen, Bestände. 2nd edn. — Franckh-Kosmos Verlag, Stuttgart. (In German)
- Menzel, J. & Miltschev, B. 2001: Ein neues Vorkommen des Habichtskauzes *Strix uralensis* in Bulgarien. — Ornithologische Mitteilungen 53: 280–281. (In German)
- Milchev, B. & Kovachev, A. 1995: A contribution to the migration of the White Stork (*Ciconia ciconia* (L.)) along the Bulgarian Black sea coast. — Annual University of Sofia “St. K. Ohridski” 86/87: 43–48.
- Milchev, B. & Georgiev, V. 2014: Extinction of the globally endangered Egyptian vulture *Neophron percnopterus* breeding in SE Bulgaria. — North-Western Journal of Zoology 10: 266–272. art.141601 <http://biozoojournals.ro/nwyz/index.html>
- Milchev, B. & Georgiev, V. 2020: Temporal and spatial dietary shifts of a generalist top predator: long-term study of an Eagle owl *Bubo bubo* population. — Forestry Ideas 26: 366–379.
- Milchev, B. & Georgiev, V. 2021: The effect of Natura 2000 network on the Eurasian Eagle-owl (*Bubo bubo*) population in Southeast Bulgaria: implications for conservation. — Ornis Hungarica 29: 170–178. <https://doi.org/10.2478/orhu-2021-0013>
- Miltschew, B. & Georgiewa, U. 1992: Eine Studie zum Bestand, zur Brutbiologie und Ernährung des Steinadlers, *Aquila chrysaetos* (L.) im Strandshagebirge. — Beiträge zur Vogelkunde 38: 327–334. (In German)
- Newton, I. 1979: Population ecology of raptors. — T & AD Poyser, Berkhamsted.
- Nyström, J., Ekenstedt, J., Angerbjörn, A., Thulin, L., Hellström, P. & Dalén, L. 2006: Golden Eagles on the Swedish mountain tundra – diet and breeding success in

- relation to prey fluctuations. — *Ornis Fennica* 83:145–152.
- Pedrini, P. & Sergio, F. 2002: Regional conservation priorities for a large predator: Golden eagles (*Aquila chrysaetos*) in the Alpine range. — *Biological Conservation* 103: 163–172. [https://doi.org/10.1016/S0006-3207\(01\)00116-1](https://doi.org/10.1016/S0006-3207(01)00116-1)
- Penteriani, V. & Delgado, M. 2019: The Eagle Owl. — T & AD Poyser, London, Oxford, New York, New Delhi, Sydney
- Peshev, C., Peshev, D. & Popov, V. 2004: Fauna Bulgarica. Vol. 27 Mammalia. — BAS, Sofia. (In Bulgarian with English summary).
- Petrov, B., Beshkov, V., Popgeorgiev, G. & Plachijski, D. 2004: Action plan for the tortoises in Bulgaria: 2005–2014. — BSPB-NMNH-BFB, Plovdiv. (In Bulgarian)
- Preston, C., Jones, R. & Horton, N. 2017: Golden Eagle diet breadth and reproduction in relation to fluctuations in primary prey abundance in Wyoming's Bighorn Basin. — *Journal of Raptor Research* 51: 334–346. <https://doi.org/10.3356/JRR-16-39.1>
- Popgeorgiev, G. 2008: The effects of a large-scale fire on the demographic structure of a population of Hermann's (*Testudo hermanni boettgeri* Mojsisovics, 1889) and Spur-thighed (*Testudo graeca iberica* Pallas, 1814) tortoises in eastern Rhodopes Mountains, Bulgaria. — *Historia naturalis bulgarica* 19: 115–127.
- Roemer, G. & Collins, P. 2019: Community reorganization revealed by exploring shifts in the diet of an apex predator, the Golden Eagle *Aquila chrysaetos*, with stable isotopes and prey remains. — *Ibis* 66 <https://doi.org/10.1111/ibi.12734>
- Rutz, C. & Bijlsma, R. 2006. Food-limitation in a generalist predator. — *Proceedings of the Royal Society of London, Series B* 273: 2069–2076. doi: 10.1098/rspb.2006.3507
- Scherzinger, W. & Mebs, T. 2020: Die Eulen Europas: Biologie, Kennzeichen, Bestände. — Franckh-Kosmos Verlag, Stuttgart. (In German)
- Schluter, D. 1981: Does the theory of optimal diets apply in complex environments? — *American Naturalist* 118: 139–147. <https://doi.org/10.1086/283810>
- Seguín, J.-F., Bayle, P., Thibault, J.-C., Torre, J. & Vigne, J.-D. 1998: A comparison of methods to evaluate the diet of Golden Eagles in Corsica. — *Journal of Raptor Research* 32: 314–318.
- Sidiropoulos, L., Whitfield, D., Astaras, C., Vasilakis, D., Alivizatos, H. & Kati, V. 2022: Pronounced seasonal diet diversity expansion of Golden Eagles (*Aquila chrysaetos*) in Northern Greece during the Non-Breeding Season: The Role of Tortoises. — *Diversity* 14, 135. <https://doi.org/10.3390/d14020135>
- Steenhof, K. & Kochert, M. 1988: Dietary responses of three raptor species to changing prey densities in a natural environment. — *Journal of Animal Ecology* 57: 37–48. <https://doi.org/10.2307/4761>
- Steenhof, K., Kochert, M., McIntyre, C. & Brown, J. 2017: Coming to terms about describing Golden Eagle reproduction. — *Journal of Raptor Research* 51: 378–390. <https://doi.org/10.3356/JRR-16-46.1>
- Stojanov, A., Tzankov, N. & Naumov, B. 2011: Die Amphibien und Reptilien Bulgariens. — Frankfurt am Main, Germany: Edition Chimaira (in German).
- Sulkava, S., Huhtala, K., Rajala, P. & Tornberg, R. 1998: Changes in the diet of the Golden Eagle *Aquila chrysaetos* and small game populations in Finland in 1957–96. — *Ornis Fennica* 76: 1–16.
- Takeuchi, T., Shiraki, S., Nashimoto, M., Matsuki, R., Abe, S. & Yatake, H. 2006: Regional and temporal variations in prey selected by Golden eagle *Aquila chrysaetos* during the nestling period in Japan. — *Ibis* 148: 79–87. <https://doi.org/10.1111/j.1474-919X.2006.00495.x>
- Taylor, I. 1994: Barn Owls: predator-prey relationships and conservation. — Cambridge, UK: Cambridge University Press.
- ter Braak, C. 1995: Ordination. — In *Data Analysis in Community and Landscape Ecology* (ed. Jongman R., ter Braak C. & van Tongeren O.): 91–173 Cambridge, UK: Cambridge Univ. Press. <https://doi.org/10.1017/CBO9780511525575.007>
- Tofft, J. 2002: Zur Einwanderung und Bestandsituation von Seedler (*Haliaeetus albicilla*) und Steinadler (*Aquila chrysaetos*) in Dänemark. — *Corax* 19: 79–84. (In German with English summary)
- Tzankov, N. & Milchev, B. 2014: Tortoises as prey of three bird species in Bulgaria: Implications for tortoise reintroduction programs. — *Herpetozoa* 26: 173–177.
- Watson, J. 2010: The Golden Eagle. 2nd edn. — London: T. & A.D. Poyser.
- Watson, J. W. & Davies R. 2015: Comparative diets of nesting Golden Eagles in the Columbia Basin between 2007–2013 and the late 1970s. — *Northwestern Naturalist* 96: 81–86. <https://doi.org/10.1898/NWN13-31.1>
- Whitfield, D., Reid, R., Haworth, P., Madders, M., Marquiss, M., Tingay, R. & Fielding, A. 2009: Diet specificity is not associated with increased reproductive performance of Golden Eagles *Aquila chrysaetos* in Western Scotland. — *Ibis* 151: 255–264. <https://doi.org/10.1111/j.1474-919X.2009.00924.x>

Online supplementary material

Supplementary material available in the online version includes Table S1.