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# TEMPORAL AND SPATIAL DIETARY SHIFTS OF A GENERALIST TOP PREDATOR: LONG-TERM STUDY OF AN EAGLE OWL *BUBO BUBO* POPULATION

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## Abstract

Changes in land use practices such as livestock rearing and crop farming are crucially important for conserving biodiversity in the modern world. This study characterizes the shifts in the diet of the Eagle Owl *Bubo bubo* population in SE Bulgaria mainly as a result of agro-economic changes and depopulation of settlements. The share of predominant prey species in preferred weight classes from urban and open (mainly gallinaceous birds) habitats decreased significantly after the collapse of traditional livestock husbandry and local abandonment of agricultural land. These species were replaced by wetland ones when available and small rodents especially during population eruptions. The Northern white-breasted hedgehog *Erinaceus roumanicus* and the European hare *Lepus europaeus* contributed more as prey for Eagle Owls. Other significantly increased replacement prey species in the Eagle owl diet consisted of predatory mammals and birds as well as many smaller species typical of open and wood-shrubby habitats. High proportions of the latter prey groups characterized the annual diets of the studied population after resumption of farming operations and indicated at least temporary food shortages for Eagle Owls. The characteristic direction of diet shifts at the subpopulation level in the particular breeding clusters responded to the agro-economic changes and the landscapes of hunting territories. Despite diet changes, the average prey weight and the food niche breadth of successfully breeding Eagle Owl pairs differed insignificantly at a population level over the time series, except during two years with vole outbreaks.

**Key words**: birds' diet characteristics, feeding ecology, food stress, superpredation.

## Introduction

The Eagle Owl *Bubo bubo* (Linnaeus, 1758) is a highly eclectic predator with preferences for mammals and birds. Its diet is driven, however, by local composition of the food supply, temporal fluctuations in prey abundance, and accessibility of potential prey species in diverse hunting habitats (Mebs and Scherzinger 2008, Penteriani and Delgado 2019). The number of preferred prey mostly between 200 and 2000 g in the hunting territory reflect the dominance of a prey species in the Eagle Owl diet (Korpimäki et al. 1990, Marchesi et al. 2002, Schweiger and Lipp 2011, Shin et al. 2013). Reduced supplies of preferred prey lead to increasing Eagle

Owl predation on less frequently used alternative species, with greater prevalence of variety of smaller prey as food niches necessarily expand (Dalbeck 2003, 2005; Obuch and Karaska 2010; Demay et al. 2015; Tobajas et al. 2015). Meanwhile, the Eagle Owl is adapting to urbanized areas by hunting common urban species such as rats (*Rattus* spp.) and feral pigeons (*Columba livia f. dom*., Gmelin, 1789) (Marchesi et al. 2002, Cugnasse 2017). This top predator plays an important role in sustaining prey populations by hunting selectively substandard individuals (Mebs and Scherzinger 2008, Penteriani and Delgado 2019) and affects top-down the community of mesopredators (Lourenço et al. 2011, 2018). The Eagle Owl can serve as an indicator of the high biodiversity and the comparative importance of areas for protection (Sergio et al. 2006, Milchev and Menzel 2017). Therefore, changes in its food spectrum and the fluctuations in diet indicate local environmental changes and the effectiveness of conservation strategies.

Policy changes in Bulgaria since 1990 have restored private land ownership, leading to progressive abandonment locally of agricultural land when agricultural production was no longer economically viable under changed market conditions. Farming was reactivated with agricultural subsidies after the accession of Bulgaria to the European Union in 2007. The livestock sector, especially traditional extensive pasture livestock husbandry, collapsed and never substantively recovered (Milchev et al. 2012). Species from open agricultural lands, pastures, and from urban habitats were expected to be strongly affected by the transformation of economic processes (Plieninger et al. 2014, van der Zanden et al. 2017). The Eagle Owl diet in the Strandzha Mountains had included important prey from the urban species (rats, feral pigeons, 26.5 % by prey number) and open area species (voles, gallinaceous birds, 26 %) before the politico-economic changes in 1988–1989 (Simeonov et al. 1998). Therefore, the traditionally agricultural and livestock grazing region area of south eastern Bulgaria including Strandzha Mountains was chosen for studying the changes in Eagle Owl diet at population and subpopulation levels.

## Material and Methods

The study area of approximately 10,000 km² in south eastern Bulgaria has predominantly hilly or flat relief, from which ridges of Strandzha and Sakar mountains and several hills rise averaging 300–400 m a.s.l. (Fig. 1, see also Milchev et al. 2019). The eight clusters with Eagle Owl localities were defined mainly by similar landscapes and existing economic conditions (Table 1). Thirteen characteristics of the main part of Eagle Owl hunting territories within a 2-km radius around occupied rocks (Penteriani and Delgado 2019) indicate the predominant types of habitats in each clusters. Clusters 7 and 8 stand out the most; the first one is the most wooded cluster with small portions of open and urbanized areas, while the second is the richest in wetlands and urbanized areas. Oaks (*Quercus* spp.) dominate the prevalent deciduous forests, and field crops of grain, sunflower, and rape and vineyards comprise the agricultural lands. The towns and villages in cluster 8 along the seacoast suffered the least from the progressive human depopulation of the study area while the most negatively affected area was the border with Turkey.

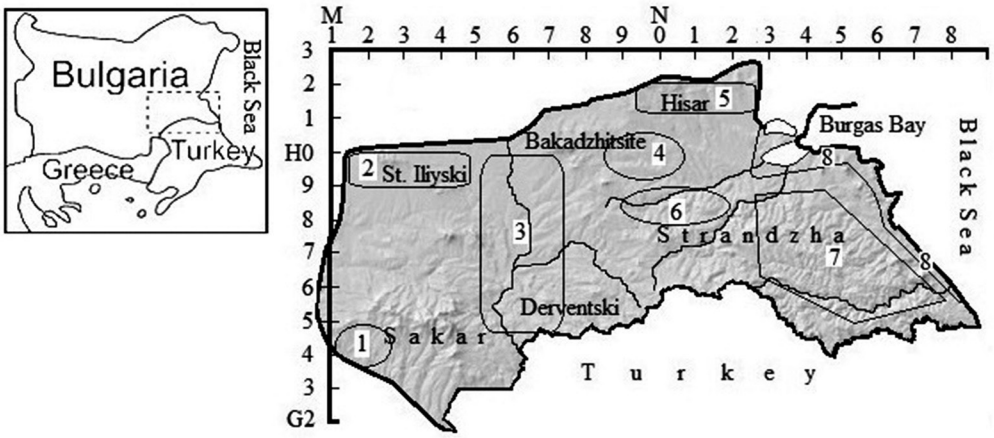


**Fig. 1. The eight clusters with Eagle Owl *Bubo bubo* localities in SE Bulgaria with marked 10-km UTM grid.**

**Table 1. Landscape characteristics (average value) of the main Eagle Owl *Bubo bubo* hunting territories (2 km radius around the 53 occupied localities) in 8 clusters of SE Bulgaria.**

| Landscape characteristics | 1 (*n* = 2) | 2 (*n* = 2) | 3 (*n* = 9) | 4 (*n* = 7) | 5 (*n* = 5) | 6 (*n* = 7) | 7 (*n* = 11) | 8 (*n* = 10) |
|---|---|---|---|---|---|---|---|---|
| Open, % | 72.3 | 58.7 | 61.6 | 81.3 | 77.6 | 51.0 | 28.5 | 35.2 |
| Urban, % | 2.0 | 4.5 | 5.1 | 4.0 | 6.9 | 4.4 | 1.4 | 8.1 |
| Wood-shrub, % | 22.1 | 32.7 | 30.6 | 13.8 | 13.9 | 43.1 | 67.9 | 35.0 |
| Wetland, % | 1.3 | 0.6 | 1.5 | 0.6 | 1.1 | 1.0 | 1.4 | 21.4 |
| Rock, % | 2.3 | 3.5 | 1.2 | 0.4 | 0.4 | 0.5 | 0.8 | 0.3 |
| Habitat heterogeneity | 39.0 | 21.0 | 33.6 | 34.9 | 22.2 | 37.0 | 31.5 | 25.9 |
| Topographic relief | 19.0 | 11.0 | 16.9 | 12.4 | 14.6 | 19.4 | 32.2 | 14.6 |
| Altitude, m | 177 | 228 | 171 | 96 | 204 | 92 | 123 | 64 |
| To building, m | 1867 | 1803 | 1945 | 1235 | 1458 | 1348 | 2383 | 1156 |
| To road, m | 960 | 725 | 1581 | 1116 | 788 | 1167 | 1524 | 666 |
| To water body, m | 35 | 871 | 387 | 59 | 380 | 58 | 113 | 575 |
| To open areas, m | 67 | 44 | 51 | 33 | 16 | 102 | 116 | 63 |
| Farmland | 1 | 0 | 1 | 1 | 0 | 2 | 3 | 2 |

Abbreviations and symbols: *n* – number of Eagle Owl localities in brackets; Landscape characteristics: 1) Open (%) – percentage of open areas (pastures, agricultural, and arable lands); 2) Urban (%) – percentage of urban areas (settlements, detached buildings, and main road networks); 3) Wood-shrub (%) – percentage of woodlands and shrub lands; 4) Wetland (%) – percentage of wetland habitats (open water area and areas covered with aquatic vascular vegetation); 5) Rock (%) – percentage of rocky areas; 6) Index for habitat heterogeneity – number of borderlines between the 5 main groups of habitats described above cut by the 2

diagonals in the cardinal directions N, S, E, and W; 7) Index for variability in topographic relief – number of 25-m contour lines cut by the 2 diagonals in the cardinal directions N, S, E, and W; 8) Altitude (m a.s.l.) of the occupied site; 9) To building (m) – distance (m) to the nearest building; 10) To road (m) – distance (m) to the nearest paved road; 11) To water (m) – distance (m) to the nearest wetland; 12) To open (m) – distance (m) to the nearest open area; 13) Farmland use at a cluster level: 0 – without abandoned farmland, 1 – partially abandoned farmland, but the majority has been re-cultivated since 2007, 2 – completely abandoned farmland and re-cultivated in a minor part since 2007, 3 – completely abandoned farmland.

The study is based on 62,314 prey specimens from 367 taxa collected in 53 Eagle Owl localities studied between 1994 and 2013 (Milchev and Georgiev 2019). Mammals and birds were most frequently hunted, while other vertebrates and arthropods were negligible with total 7.8 % by number and 0.8 % by biomass respectively. Voles (*Microtus* spp.) 18.2 %, typical mice (*Mus* spp.) 8.2 % and Northern white-breasted hedgehog (*Erinaceus roumanicus*, Barrett-Hamilton, 1900) 5.9 % were the most numerous prey species by number. The greatest contribution to food biomass was supplied by Northern white-breasted hedgehogs 22.9 %, European hare (*Lepus europaeus*, Pallas, 1778) 8.9 %, Norway rat (*Rattus norvegicus* (Berkenhout, 1769) 6.5 % and Common Moorhen (*Gallinula chloropus* (Linnaeus, 1758) 5.5 %.

The comparisons of diet samples (a breeding period diet per breeding locality per year) between years were based on the following estimators: *i*) average prey weight: total biomass divided by total prey number; *ii*) food niche breadth as computed: FNB = $1/\Sigma\ p_i^2$, where $p_i$ is the proportion of prey category *i* by number (FNBn) or by biomass (FNBb) in the actual diet sample (Levins 1968). The larger values indicate a higher dietary diversity.

The large number of prey taxa was categorized for the analyses into 8 main prey species/groups (Fig. 2A-H). The grouping was based on the prey predominance in the annual diets (a breeding period diet of the study population per year) in combination with taxonomic affinity and habitat similarity between species. The generalized linear model and polynomial regression tested the relationship between the proportions of prey species/groups (dependent variable) in the annual diets versus years (independent variable). Differences in the means of average prey weight and of FNB of the successful pairs between years were computed with one-way ANOVA. Tukey *post hoc* test was used to test the differences between years when ANOVA results were significant. Arcsine-transformed values were tested in statistical analyses when the variables were proportions, while logarithmic transformations were applied for the count data. A chi-square test computed the differences between the diets in Strandzha Mountains before (Simeonov et al. 1998) and after the start of the economic transformation. The significance level was $p < 0.05$. All means are reported as an arithmetic mean ± standard deviation. The analyses were implemented with the PAST 3.01 software (Hammer et al. 2001).

Principal component analysis was used for studying the pattern of distribution of the prey groups in annual diets of the population and in diets of the clusters during five-year periods (CANOCO v. 4.5; ter Braak 1995). The samples were the separate annual diets or cluster diets,

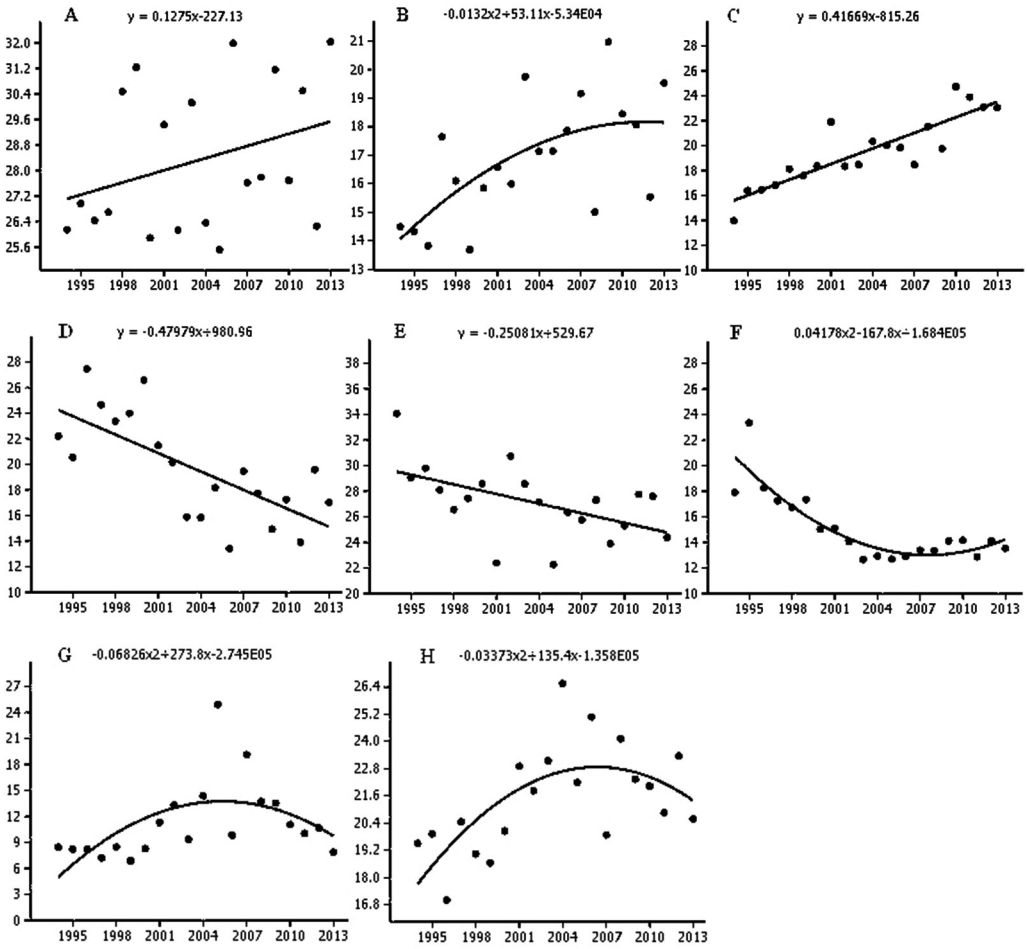


**Fig. 2. Relationship between proportion of the main prey species/groups (% by biomass) in annual diets of the Eagle Owl *Bubo bubo* population in SE Bulgaria and study years.**

Note: A – *Erinaceus roumanicus* – generalized linear model (GLM), $G = 0.38$, $P = 0.537$; B – *Lepus europaeus* – polynomial regression (PR), $F = 5.943$, $P < 0.05$; C – Superpredation – GLM, $G = 5.89$, $P < 0.05$; D – Urban species – GLM, $G = 8.1$, $P < 0.01$; E – Wetland species – GLM, $G = 7.06$, $P < 0.01$; F – Open area non-passerines – PR, $F = 30.991$, $P < 0.001$; G – *Microtus*, *Apodemus*, *Mus* – PR, $F = 4.224$, $P < 0.05$; H – 'other animals' – PR, $F = 6.574$, $P < 0.01$. Abbreviations and symbols: abscissa, years; ordinate, % by biomass (arcsine-transformed).

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

## Results

The shares of three main prey species/groups increased during the study, Northern white-breasted hedgehog, European hare and superpredation (predatory mammals and birds), but the increase of hedgehogs was not statistically significant (Fig. 2A-C). Urban and wetland species and open areas non-passerines were predated in decreasing proportions (Fig. 2D-F). Predation on voles with mice and 'other animals' after an initial increase has declined during the most recent five-year period studied (Fig. 2G, H). The proportions of some individual species within the main prey groups have changed even in the opposite pattern. Adult European hares were hunted in decreasing proportion, while the proportions of smaller species within 'other animals' of open habitats (larks, buntings, shrikes, grasshoppers, field mice and Günther's vole (*Microtus guentheri* (Danford and Alston, 1880) and forest-shrub land habitats (thrushes, finches and longhorn beetles) increased significantly. The house rat (*Rattus rattus* (Linnaeus, 1758) with an increasing proportion over the last five-year period was an exception in the group of urban species. Important wetland species such as Common Moorhens and Common Coots (*Fulica atra* Linnaeus, 1758) supplied varying proportions for the food biomass over the years, but without statistically significant trend.

Figure 3 displays changes in the importance of main prey species/groups for Eagle Owl diets over the years. The first axis (eigenvalues 0.528) distributes the annual diets and prey in two groups. The positive part of the axis corresponds to the annual diets between 1994 and 2000 and higher level of hunting on reported prey species/groups mostly with significant decreases in proportions during the study period (urban and wetland species, open areas non-passerines). The majority of prey with significant increases in diet proportions over time and the later annual diets fall into the opposite part of the chart. The second axis (eigenvalues 0.224) distributes the annual diets according to the predominance by biomass of voles and mice along its positive part and Northern white-breasted hedgehog in combination with superpredation, European hare and 'other animals' along its negative part. The diets in 2005 and 2007 were exceptions, resulting in peaks in hunting on voles and mice (17.8 % and 10.8 % by biomass, respectively). Most annual diets at the end of the study and prey with significant increases in diet proportions correlated with the negative part of the second axis.

Average prey weight of the successful breeding pairs was 224.7 ±79.0 g (range 70.1 – 562.3 g) with significant difference in the means between years ($F_{19, 206} = 7.63$, $p < 0.001$). The smallest values for average prey weight corresponded with the two years of hunting on abundant voles (132.3 ±70.2 g in 2005, 138.8 ±55.9 g in 2007). Tukey tests calculate significant differences exclusively between the average prey weights in these two years with almost all other years.

Food niche breadth varied with significant differences in the mean FNBn (13.34 ±6.70, range 1.98 – 34.04) between years ($F_{19, 206} = 3.76$, $p < 0.001$) but insignificant ones in the mean FNBb (8.79 ±3.61, range 1.90–20.38, $F_{19, 206} = 0.85$, $p = 0.65$). Tukey tests indicate 10 significant differences only between FNBn in the two years with vole predation, respectively with the narrowest niches (6.66 ±5.10 in 2005, 6.90

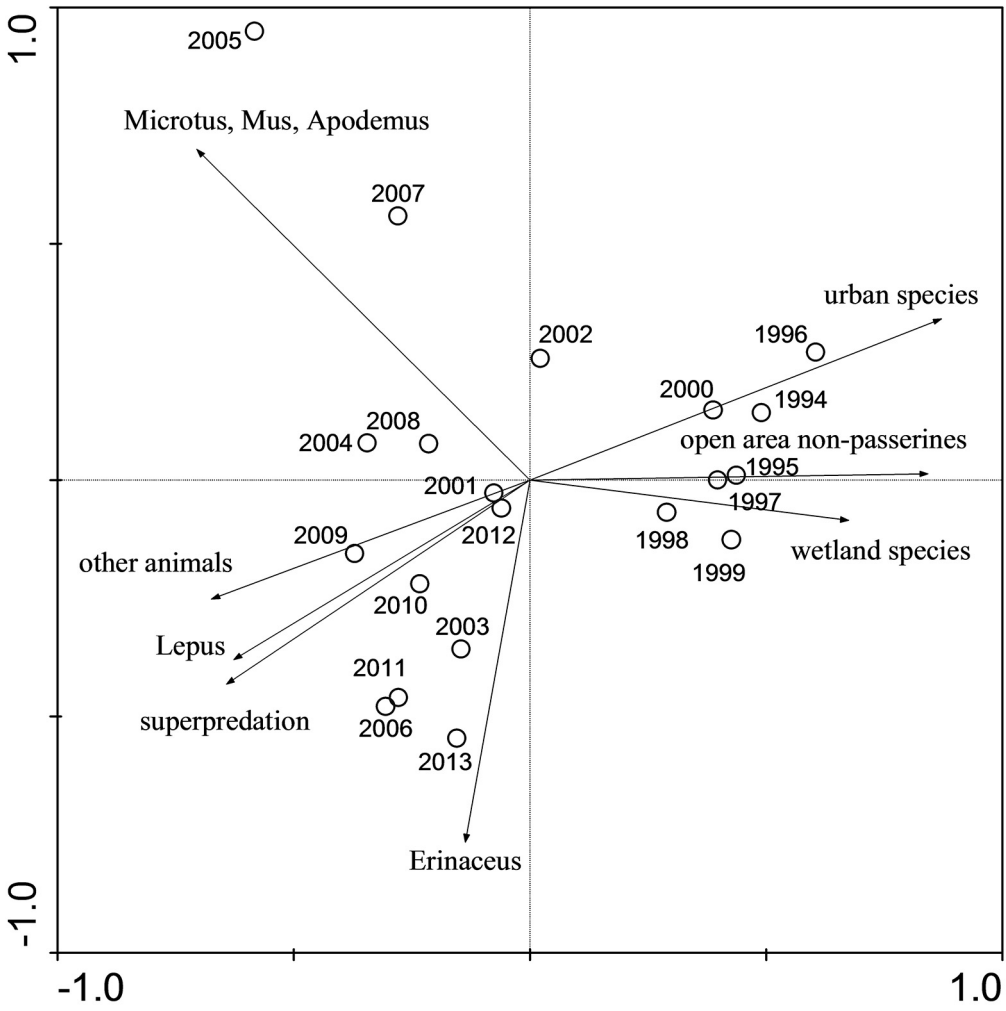


**Fig. 3. PCA ordination of main prey species/groups (% by biomass) and annual diets of the Eagle Owl *Bubo bubo* population in SE Bulgaria, 1994–2013.**
Note: arrows – prey species/groups; open points – annual diets.

±3.38 in 2007) and FNBn in the other years.

The Eagle Owl diet in the Strandzha Mountains (clusters 6, 7 and a locality from cluster 8) changed significantly after 1990 ($\chi^2 = 678.8$, $N = 8$, $p < 0.001$, Table 2). The frequency of urban species and voles with mice decreased significantly and their proportions collapsed by 20.9 % and 12.7 % by number, respectively. Wetland species and the diverse group 'other animals' were hunted significantly more frequently (increase by 11.9 % and 18.4 % by number, respectively). Thrushes (*Turdus* spp.) increased most among the 'other animals' by 7.6 % by number. The level of superpredation doubled to 5.4 % by number of prey individuals.

**Table 2. Eagle Owl *Bubo bubo* diet in the Strandzha Mountains, SE Bulgaria in 1988–1989 (Simeonov et al. 1998) and 1994–1998 (present study).**

| Prey species/groups | 1988–1989 | | 1994–1998 | |
|---|---|---|---|---|
| | ***N*** | **% *N*** | ***N*** | **% *N*** |
| *Erinaceus roumanicus* | 140 | 8.1 | 247 | 8.5 |
| *Lepus europaeus* | 21 | 1.2 | 46 | 1.6 |
| Superpredation * | 42 | 2.4 | 158 | 5.4 |
| Urban species * | 475 | 27.5 | 191 | 6.6 |
| Wetland species * | 324 | 18.8 | 894 | 30.7 |
| Open area non-passerines | 106 | 6.1 | 157 | 5.4 |
| *Microtus, Apodemus, Mus* * | 414 | 24.0 | 329 | 11.3 |
| Other animals * | 207 | 12.0 | 885 | 30.4 |
| Total | 1729 | 100 | 2907 | 100 |

Note: Abbreviations and symbols: *N* – number of specimens; % *N* – percent by number; * – prey with a significantly different frequency between the two periods.

Figure 4 presents the ordination of the eight clusters according to the proportions of the main prey species/groups in diets during the four five-year study periods. The first axis (eigenvalue 0.340) distributes clusters according to the diet proportions of mainly urban species to the positive part of the axis. Higher proportions of Northern white-breasted hedgehog in combination with more 'other animals' and superpredation correlated with the negative part of the second axis (eigenvalue 0.315). The higher proportions of wetland species and more urban species were associated with the positive part of the axis. Urban species were the most important prey in clusters 3, 4 and 5 during the initial two five-year periods. Eagle Owls in cluster 8 along the Black Sea coast depended greatly on wetland species in all four five-year periods. Wetland species were an essential part of the diet also in cluster 1, but in combination with more superpredation and the smallest proportion of urban species. Wetland species dominated the diet in the richest of open habitats cluster 4 during the third five-year period and in the most wooded cluster 7 during the first five-year period. Hedgehogs, 'other animals' and predators became the primary prey in cluster 7 in subsequent periods when the cluster correlated with the negative parts of both axes. Clusters 1, 3 and 4 changed their diet composition drastically in the final five-year period and correlated with the negative parts of both axes like cluster 7. The prey from predators and 'other animals' groups was in line with the share of their main habitat in Eagle Owl hunting territories in these clusters during the last five-year period. Most typical forest species were predated with the highest proportions in the wooded cluster 7, while the diets in clusters 1, 3 and 4 included a larger share of typical inhabitants of open and urbanized landscapes (Table 3).

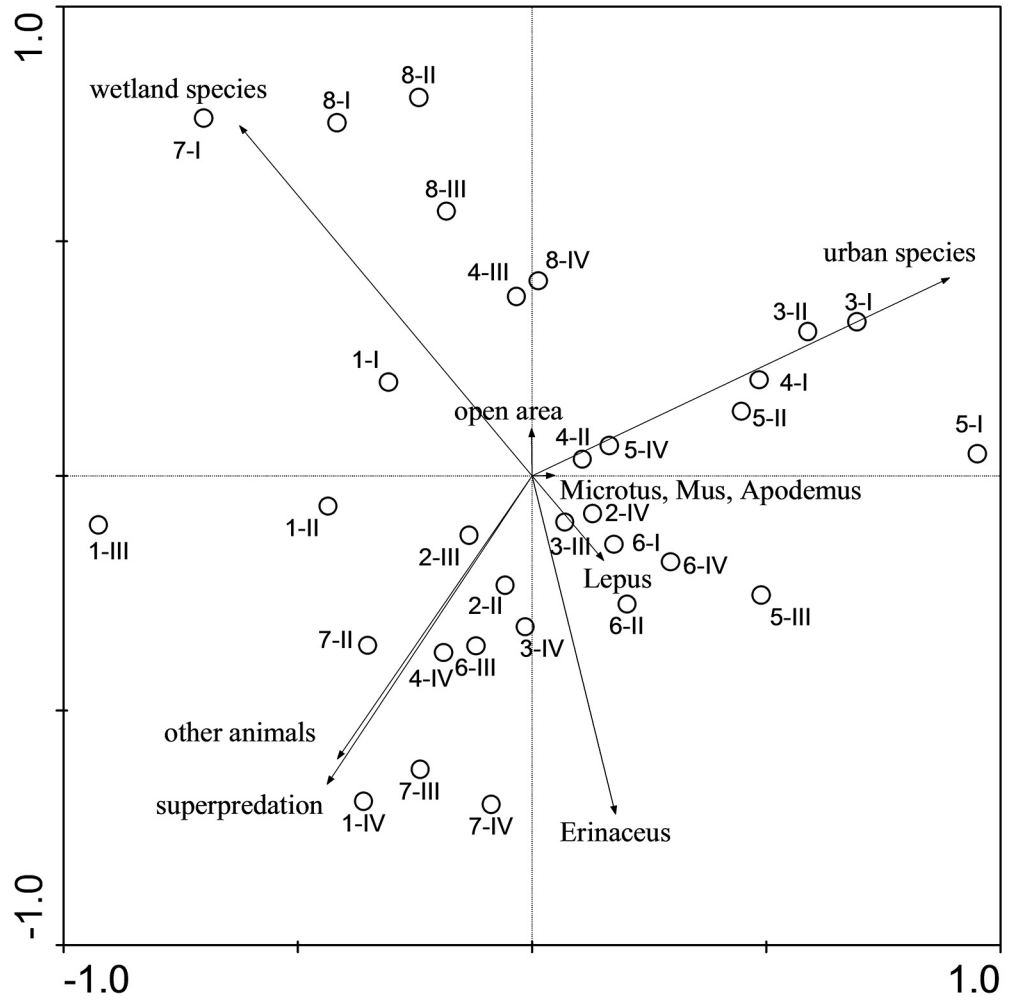


**Fig. 4. PCA ordination of the clusters with Eagle Owl *Bubo bubo* localities in SE Bulgaria during four five-year periods between 1994 and 2013 according to the average proportions (% by biomass) of main prey species/groups.**

Note: arrows – prey species/groups; open points – cluster diets where an Arabic numeral is a cluster number while a Roman numeral is a consecutive five-year period.

**Table 3. Inhabitants (% by biomass) of forest, open and urbanized habitats from the prey groups of predators and 'other animals' in Eagle Owl *Bubo bubo* diets in clusters 1, 3, 4 and 7 of SE Bulgaria during the fourth five-year study period, 2009–2013.**

| Prey | Clusters | | | |
|---|---|---|---|---|
| | 1 | 3 | 4 | 7 |
| Mostly woodland-scrubland inhabitants, subtotal | 6.5 | 7.5 | 9.8 | 24.8 |
| *Glis glis* (Linnaeus, 1766), *Sciurus vulgaris*, Linnaeus, 1758 | 0.1 | 0.3 | 0.5 | 5.6 |
| *Columba palumbus*, Linnaeus, 1758, *C. oenas*, Linnaeus, 1758, *Scolopax rusticola*, Linnaeus, 1758 | 4.3 | 3.0 | 2.8 | 9.8 |
| *Strix aluco*, Linnaeus, 1758 | 0.1 | 0.04 | | 3.5 |
| *Accipiter* spp. | 0.9 | 0.4 | 1.2 | 0.3 |
| *Turdus* spp. | 0.5 | 3.0 | 3.9 | 3.7 |
| *Garrulus glandarius* (Linnaeus, 1758) | 0.7 | 0.8 | 1.4 | 1.9 |
| Mostly open and urban species, subtotal | 19.1 | 7.3 | 8.7 | 1.7 |
| *Tyto alba* (Scopoli, 1769), *Athene noctua* (Scopoli, 1769), *Asio* spp. | 6.2 | 5.0 | 5.9 | 1.6 |
| *Circus* spp. | 0.3 | 0.2 | 0.6 | 0.1 |
| *Falco* spp. | 1.0 | 0.1 | 0.2 | |
| *Pica pica* (Linnaeus, 1758), *Corvus* spp. | 11.6 | 2.0 | 2.0 | |
| Total | 25.6 | 14.8 | 18.5 | 26.5 |

## Discussion

The Eagle Owl is an opportunistic generalist and the variable proportions of prey in its diets are highly dependent on fluctuations in the population of potential prey species (Mebs and Scherzinger 2008, Penteriani and Delgado 2019). The decline in traditional livestock husbandry, along with the progressive depopulation of settlements, was expected to adversely affect populations of urban species and their proportions in its diet. The present study confirms this assumption.

The abandonment of arable land and pastures, and the subsequent restart in agriculture do not correlate with similar changes in the proportions of their main resident species in the Eagle Owl's diet. Open area non-passerines including mainly gallinaceous birds decreased their proportion in the diet while the proportions of European hare increased over the same period. Predation data on Chukar (*Alectoris chukar* (J. E. Gray, 1830) conformed well to data about the extinction of this species as a breeding bird in the study area (Gruychev 2016). The European hare inhabited Bulgarian lowland habitats with an average density of 1.8 hares/100 ha, but clusters 2 and 3 had 2–4.9 hares/100 ha at the end of the study (Zhelev et al. 2013). Despite the low population number of European hares, the Eagle Owls increased significantly the proportions of hares in its food biomass. The European hare was dominant or subdominant prey in 32.3 % of diet samples of successful breeding pairs of Eagle Owls ($n$ = 226 diets; Milchev and Georgiev 2019), but mainly in clusters 3 and 4 (63 %, $n$ = 73) with partially abandoned farmland. Lagomorphs have been exceptionally desirable prey for the Eagle Owl across its entire range (Penteriani and Delgado 2019). However, the local status of the European hare population appears to have increased, benefitting from the

abandonment of pastures and cropland.

Exceptions with peaks in proportions of voles and mice were recorded twice when the Eagle Owls switched to hunt the numerous voles. These instances of vole proliferation were the first ones since 1988 (Miltschev and Georgiev 2009). Peaks of the vole population are rare and not cyclical in SE Bulgaria because they are limited by summer droughts (Straka and Gerasimov 1977). Eagle Owls shifted to hunt temporarily numerous voles, as recorded in other parts of its range at higher latitudes (Korpimäki et al. 1990, Schweiger and Lipp 2011, Andreychev et al. 2014). The proportions of voles correlated positively with hunting on typical mice and field mice. Bezzel et al. (1976) and Dalbeck (2003) also reported that field mice were predated as incidental prey in the course of hunting on voles.

The declining share of wetland species such as some ducks could not be attributed solely to the progressive drying up of small ponds previously used mostly as livestock water sources (Milchev and Menzel 2017). Some waterbirds, predominantly Common Moorhens and Common Coot, have remained important prey species in SE Bulgaria.

It turned out that the Eagle Owls did not compensate the reduced hunting on preferred urban and wetland species or gallinaceous birds, principally by predating hedgehogs much more intensively. Northern white-breasted hedgehogs supplied the principal share of food biomass in fluctuating proportions with a non-significant upward trend. The steadily growing share of superpredation, as well as small insect prey and small passerines in SE Bulgaria was considered as indicator of food shortages (Mebs and Scherzinger 2008, Lourenço et al. 2018). The gradual changes in studied population diet led to a stable alteration in the diet structure at the end of the second five-year period. Prey with increased shares in the Eagle Owl diet over time, including the above-mentioned predators and small animals, characterized the population diet over the next two five-year periods.

The Eagle Owl optimizes its diet according to the available food supply in its permanent breeding territory, balancing between the energetic input of the prey and the costs of prey capture, transport to the nest and eating according to the optimal foraging theory (Dalbeck 2003, Mebs and Scherzinger 2008). The large number of prey species in varying proportions in the diets of successful owl pairs explained the variability established in average prey weight and FNBn over the years. Significant changes in these diet characteristics occurred only in both years with peaks in vole populations: the narrowest food niches and low average prey weight. No other prey was so profitable for most breeding pairs simultaneously in one year even though significant changes in the share of a large number of prey species were in evidence over the years.

The differences among hunting territories and among available food supplies in habitats definitely influence Eagle Owl diets of specifics (Dalbeck 2003, Schweiger and Lipp 2011, Shin et al. 2013, Penteriani and Delgado 2019). The localities of Eagle Owl pairs in cluster 8 included the largest urbanized area within the hunting territories and were closest to buildings. The localities were mainly in a coastal resort area with small crop farming and livestock grazing but with the largest wetland of all clusters. Wetland species dominated Eagle Owl food in this cluster. The diets in cluster 1 were also dominated by wetland species, harvested mainly from ponds used for livestock. Draining these aban-

doned small ponds as a measure to avoid local flooding most likely led to the distinct change in diet from waterbirds toward hedgehogs, superpredation and 'other animals' over the last five-year period. Higher shares of the last three prey groups and European hares compensated for the reduced proportion of urban species in clusters 3, 4 and 5. The diet in clusters 1, 3 and 4 approximated that in the wooded clusters 7, where the decline in the share of urban species took place before the beginning of this study. The increased diet share of Northern white-breasted hedgehog, a habitat generalist and the non-homogeneous groups of predators and 'other animals' appeared to eliminate the significance of habitat characteristics on Eagle Owl diets in these several clusters. Eagle Owls hunted prey species in groups of predators and 'other animals' living in forested or open and urbanized habitats in proportions corresponding with the presence of these habitats in each cluster also over the last five years.

The Eagle Owl is an endangered species according to the national Red Data Book (Golemanski 2015). Abandonment of arable land, collapse of traditional livestock farming and depopulation of human settlements in SE Bulgaria did not positively affect the dietary structure of the Eagle Owl breeding population. The highest values of superpredation and hunting otherwise neglected small prey as indicators of a high level of food stress coincided with recovery of intensive farming during the last five-year study period. Many predatory mammals and birds were found in the Eagle Owl diet in a neighbouring geographical area in Central Bulgaria during the same period (Milchev and Gruychev 2015) as an exception in the Balkan Peninsula (Lourenço et al. 2011). Economic changes have taken place with varying intensity and in diverse natural conditions across Bulgaria. Therefore, our results may not be replicable in other parts of the country. However, the negative tendencies in the diet structure of this top predator exist in one eleventh (9 %) of the Bulgarian territory. Combined with high breeding losses from direct and indirect anthropogenic factors (Milchev et al. 2019), the stability of its population is uncertain.

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