DIET OF THE EGYPTIAN VULTURE *(NEOPHRON PERCNOPTERUS)* IN BULGARIA AND GREECE (2005-2013)

TECHNICAL REPORT UNDER ACTION A5

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ABOUT THE PROJECT
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Contents

Summary

The Egyptian vulture (*Neophron percnopterus*) is the smallest and most threatened European vulture species with an opportunistic and diverse diet. In Eastern Europe, the Egyptian vulture population is declining more rapidly than elsewhere but there is little information on diet composition and the relationship between diet and demographic parameters to inform conservation management. We examined whether Egyptian vulture population decline on the Balkan Peninsula may have been associated with dietary changes that affected breeding productivity by monitoring breeding success and collecting dietary remains from 51 breeding territories with a total of 63 different nest sites in the period 2005–2013. We found that the diet of the Egyptian vulture on the Balkans is very diverse and has not changed significantly over the last 9 years. Diet diversity did not differ between countries, but it was significantly higher in northern Bulgaria compared to southern Bulgaria and Greece. We found no relationship between dietary diversity or composition and productivity. However, diet diversity and the proportion of wild animals in the diet were higher in territories with a lower occupancy rate, and the proportion of livestock in the diet was positively related to occupancy rate. We conclude that it is unlikely that dietary limitations on reproductive output are a critical threat to Egyptian vultures on the Balkan Peninsula. The negative relationship between dietary diversity and territory occupancy rate may be due to a higher susceptibility of adults to poisoning, and more information on the effect of diet availability on adult and juvenile survival would be useful to inform and improve conservation management actions. Providing safe food for Egyptian vultures in the short term, seems an urgent and effective conservation measure for decreasing the risk of poisoning and increasing the persistence of the population in the core areas.

List of abbreviations

CAP – European Union Common Agricultural Policy
EU - European Union
GLMM - generalised linear mixed model
MNI - minimum number of individuals
NMNHB - National Museum of the Natural History in Bulgaria

Introduction

The Egyptian vulture (*Neophron percnopterus*, Linnaeus 1758) is a medium sized opportunistic scavenger with a broad distribution throughout the southern Palearctic and North Africa (Cramp & Simmons 1980, del Hoyo et al. 1994, Baumgart 2001). The populations of the species are declining throughout its range: West African populations declined by about 86% between 1969 and 2004 (Thiollay 2006, 2007, Virani et al. 2011), the population in India declined by 80% between 1999 and 2003 (Cuthbert et al. 2006). In Europe the Egyptian vulture has declined by 50% over the last 50 years and has disappeared from Austria, Hungary, Moldova and Ukraine in the early 20thcentury (Iñigo et al. 2008). The population on the Balkans declined by 80% over the last 30 years (Velevski et al. 2015) and went extinct in several countries such as Bosnia and Herzegovina (Marinković et al. 2007), Croatia (Sušić 1993), and probably Serbia (Grubač 1999). Because of consistent and steep declines throughout its range, the status of the Egyptian vulture was changed from Least Concern to Endangered on the IUCN Red List in 2007 (BirdLife International 2008) with a global population estimated at 20,000 – 61,000 individuals (BirdLife International 2014). The main factors leading to this decline are considered to be large-scale threats like accidental poisoning, electrocution and direct persecution on breeding grounds as well as along their migration routes and wintering areas (Thiollay 2006, Hernández & Margalida 2009, Virani et al. 2011, Angelov et al. 2013, Wacher et al. 2013).

Compared to the large vultures, the Egyptian vulture has a much wider diet spectrum. It feeds on carcasses and excrement of vertebrates, human refuse, eggs, invertebrates and small vertebrates that are captured alive (Cramp & Simmons, 1980, Ceballos & Donázar 1990, Nergo et al. 2002). It is one of only a few bird species that uses tools, throwing stones at eggs to break their shell or lifting tortoises and dropping them to crack them (van Lawick-Goodall & van Lawick-Goodall 1966, Stoyanova & Stefanov 1993). Despite the dietary plasticity of the species, food shortages through changes in land use, pastoral systems, veterinary and sanitary practices have likely contributed to population declines in western Europe (Tucker & Evans 1997, Baumgart 2001, Gallaro & Penteriani 2001, Iñigo et al. 2008, Donázar et al. 2009) and in the Balkans (Kurtev et al. 2008, Velevski et al. 2015). Although the species' diet has been studied in detail in relation to productivity, density and habitat selection of the species in Western Europe (Donázar & Ceballos 1988, Margalida & Boudet 2003, Margalida et al. 2012, Navarro et al. 2003, Sara & Di Vittorio 2003, Zabala & Zuberogoittia 2003), the diet of the Egyptian vulture on the Balkan peninsula is still poorly studied (Helmer & Scholte 1985, Simeonov et al. 1990, Vlachos et al. 1998, Stoyanov & Boev 2009, Milchev et al. 2012).

This study aims to examine whether the population decline of the Egyptian vulture on the Balkans may have been associated with changes in the diet. For this, we investigated the composition and diversity of Egyptian vulture's diet in Bulgaria and Greece over the last nine years and studied their relation to demographic parameters such as productivity and territory occupancy rate. We also tested for regional differences in the diet and if it has changed over time. Such information is valuable to inform effective conservation actions such as adequate supplementary feeding and agri-environmental measures.

Materials and methods

Collection of food remains

During the period 2005–2013 a total of 148 nest content samples were collected from 51 breeding territories with a total of 63 different nest sites (47 nests in Bulgaria and 16 nests in Greece; for the number of sampled nests per year see Table 1), only from nests of pairs that have made a breeding attempt. The fieldwork was conducted during the period October – March (after the end of the breeding season) in order to avoid disturbance on the breeding pairs and their chicks. If some of the pairs failed during the breeding season food remains were collected immediately after the pair abandoned the nest. We accessed all nests using climbing equipment and collected all organic food remains from the nest cavity, which represented the cumulative food remains from a given pair over the preceding breeding season (Figures 1 a, b and c). Nest content samples were stored in plastic bags labeled with a unique code for each nest, the year of the breeding season, the date of collection, and the name of the person who collected the food remains. Samples were stored in freezers until analysis.

Table 1. Number of nests per year from where the nest content samples were collected in Bulgaria and Greece during the period 2005–2013.

Year	**Number of studied nests per geographical area**			
	Eastern Greece and southern Bulgaria	**Northern Bulgaria**	**Central Greece**	**Total**
2005	1	0	0	1
2006	10	10	0	20
2007	16	5	0	21
2008	18	6	0	24
2009	4	3	0	7
2010	9	1	0	10
2011	20	3	1	24
2012	15	4	1	20
2013	17	2	2	21
Total	**110**	**34**	**4**	**148**

Figure 1a. Photos illustrating field work in northern Bulgaria. *Fieldwork in this region started in 2006, covering four main areas (Rusenski Lom Natural Park, Provadiysko-Royaksko Plateau, Eastern Balkan Mountains and northwestern Bulgaria) and 34 nests. The number of visited nests decreased rapidly along the study period because many territories were abandoned and the difficult access at some of the nests (e.g. falling rocks, crumbly cliffs, nest access by swaying with more than a range of 3 m which could cause fraying and splitting of the alpine ropes, etc.).*

Figure 1b. Photos illustrating field work in southern Bulgaria and eastern Greece. *In southern Bulgaria, the field work started in 2005 and until 2013 a total of 93 nests were covered in two main areas: Eastern Rhodopes and south-western Bulgaria. Almost all of the sampled nests refer to the Eastern Rhodopes (where most of the nests were sampled through the whole period of the study), as she last pair in southwestern Bulgaria has extinct in 2006. In Trace, Greece, in 2011 out of seven active nests, five were accessed in order to collect pellets and food remains. In 2012 out of five active nests, four were accessed and one old nest (last active in 2009) was accessed as well. In 2013 out of six active nests, five were accessed and one old nest (with unknown status of occupation) was accessed as well. The not sampled nests were considered as difficult to access that time.*

Figure 1c. Photos illustrating field work in central Greece. *Fieldwork in this region was limited to three nests in the area of Meteora. Access to these nests is difficult due to the height and morphology of the cliffs as well as the composition of the rocks in the area. In addition, the presence of moss again complicates and limits the period when the nests are accessible by the climbers under safe conditions. As a result, only three of the four active nests were accessed.*

Territory and productivity monitoring

Egyptian vulture nests were monitored every year in Bulgaria in the period 2006–2013, and in Greece between 2010–2013. Several visits were made to a breeding territory in each breeding season to confirm if the territory is occupied, to detect the exact nesting place and to register the number of the raised fledglings. A territory was considered occupied if a pair or a single bird was observed displaying, marking territory or building a nest in the beginning of the breeding season (end of March and the begining of April). All territories were visited again in May to confirm which of the occupied territories have started incubation, and which left the territory or failed in breeding. All territories were checked at least once more in June-July to monitor the breeding success and the last visit is during the post-fledgling period in August to confirm the number of the successfully fledged juveniles. For the purpose of the analysis, only those territories where birds initiated a nesting attempt and where food remains were collected were considered (not all successful nests could be accessed to collect dietary remains so the number of the monitored nests is higher than the number of the nests that were visited to collect dietary remains). We considered productivity as the number of fledglings produced by a pair in a given year. Because pairs can use different nest sites within the same territory in different years, we considered the territory as the unit of replication in all analyses, rather than individual nest sites.

Taxonomic analysis of food remains

A total of 3,237 food remains (bones, scales, feathers, hides or tissue, carcass parts and pellets in various states of decomposition) were collected from nests and identified by comparison to collections of the NMNHB to three taxonomic levels: species (n = 1938 individuals), order (n = 2,010 individuals) or class (n = 2,023 individuals; Figure 2). Each sample (remains collected from a single nest in a single year) was analysed separately. For each taxonomic group we determined the MNI based on skeletal elements following standard guidelines (Bokonyi 1970).

Sample collected on 20.11.2011 in Eastern Rhodopes, Bulgaria.

Sample collected on 08.11.2012 in Thrace, Greece.

Figure 2. Photos of analysed food remains (Photographs by Z. Boev).

Statistical analysis

We used similar methods as other studies of vulture diet to facilitate direct comparison of the results (Donázar & Ceballos 1988, Ceballos & Donázar 1990, Tella 1991, Litvaitis 2000, Zubergotia et al. 2001, Donázar et al. 2010, Margalida et al. 2012, Milchev & Georgiev 2012).

Calculation of dietary composition

The analysis of diet composition was based on all nest content samples collected during the period 2005-2013 (Table 1). Diet composition was calculated as the proportion of individuals belonging to a taxonomic order divided by the minimum number of individuals from all remains collected in a nest. In addition, we also classified the source of prey items into domestic animals (e.g. domestic cats, dogs, livestock, etc.) and wildlife (e.g. tortoises, wild cats, wolves, foxes, hedgehogs, etc.) following Hidalgo et al. (2005) (for more details see Appendix).

Calculation of dietary diversity

The dietary diversity was calculated using the Shannon-Wiener diversity index which has been used in other studies of vulture's diet (Donázar et al. 2010, Margalida et al. 2012, Milchev & Georgiev 2012), and is defined as (Fisher et al. 1943, Heck et al. 1975, Hurlbert 1971):

$$H = -\sum_{1}^{species\ i} p_i \times \log(p_i)$$

where p_i is the proportional abundance of species *i* in a sample (based on the minimum number of individuals). This index was calculated using the function 'diversity' in the R package 'vegan'.

Relationship between diet, productivity and territory abandonment

To examine whether dietary diversity or composition explained variability in Egyptian vulture productivity, we used GLMM with the number of fledglings as a response variable and a Poisson error distribution (Margalida et al. 2012). For this analysis we used the data set for productivity monitoring and diet collected in the period 2006-2013, by not considering 2 nests from Greece which had a single piece of food ramain and therefore were not representative diet samples. Because we collected food remains from some territories in several years, and productivity of these nesting attempts may not have been independent, we accounted for serial correlation within territories by including the identity of the territory as random intercept in the model (Bolker et al. 2009). For each analysis we constructed two models: one containing dietary diversity, or the proportional contribution of a given diet category as fixed effect, and a corresponding model without the respective effect, but with the same random intercept. We then compared the two corresponding models using a likelihood-ratio test (Lewis et al. 2011), and concluded that an effect was significant if $P < 0.05$. We fitted all models using the Laplace approximation in R 3.1.1 (R Development Core Team 2014) with the package 'lme4'.

Food availability may not only affect productivity, but also adult condition, survival, and territory retention (Carrete et al. 2007, Grande et al. 2009). We therefore examined whether diet diversity or composition was related to the proportion of years during which a territory was occupied, hereafter termed the territory occupancy rate (Sergio & Newton 2003). For this analysis, we only used territories that had been occupied for at least 5 years, and we calculated the occupancy rate as the number of years in which a territory was occupied divided by the number of years the territory was monitored (Sara & Di Vittorio 2003). We used a similar GLMM as above, but with dietary diversity or composition as Gaussian response variable and occupancy rate as a fixed effect.

Geographic differences in diet

Most Egyptian vulture nests in Bulgaria and Greece can be grouped into discrete population clusters (Velevski et al. 2015), of which we sampled three clusters (i.e. regions): (1) northern Bulgaria, (2) eastern Greece and southern Bulgaria, and (3) central Greece (Figure 3). Because Bulgaria and Greece joined the EU at different times, and the CAP started to operate in Greece much earlier, we hypothesized that diet diversity and composition may vary between these two countries. Habitat and livestock husbandry practices vary between these regions, and we therefore examined whether diet diversity and composition varied at the national or, alternatively, at the regional level. We used the same GLMM as described above for productivity with a two-level (country) or three-level (region) categorical variable to test for significant differences in diet diversity between countries or regions. To avoid this geographic comparison being confounded by variation in sampling intensity over time, we used only nest remains collected after 2009 for this analysis, as no nest remains were collected in Greece before 2010.

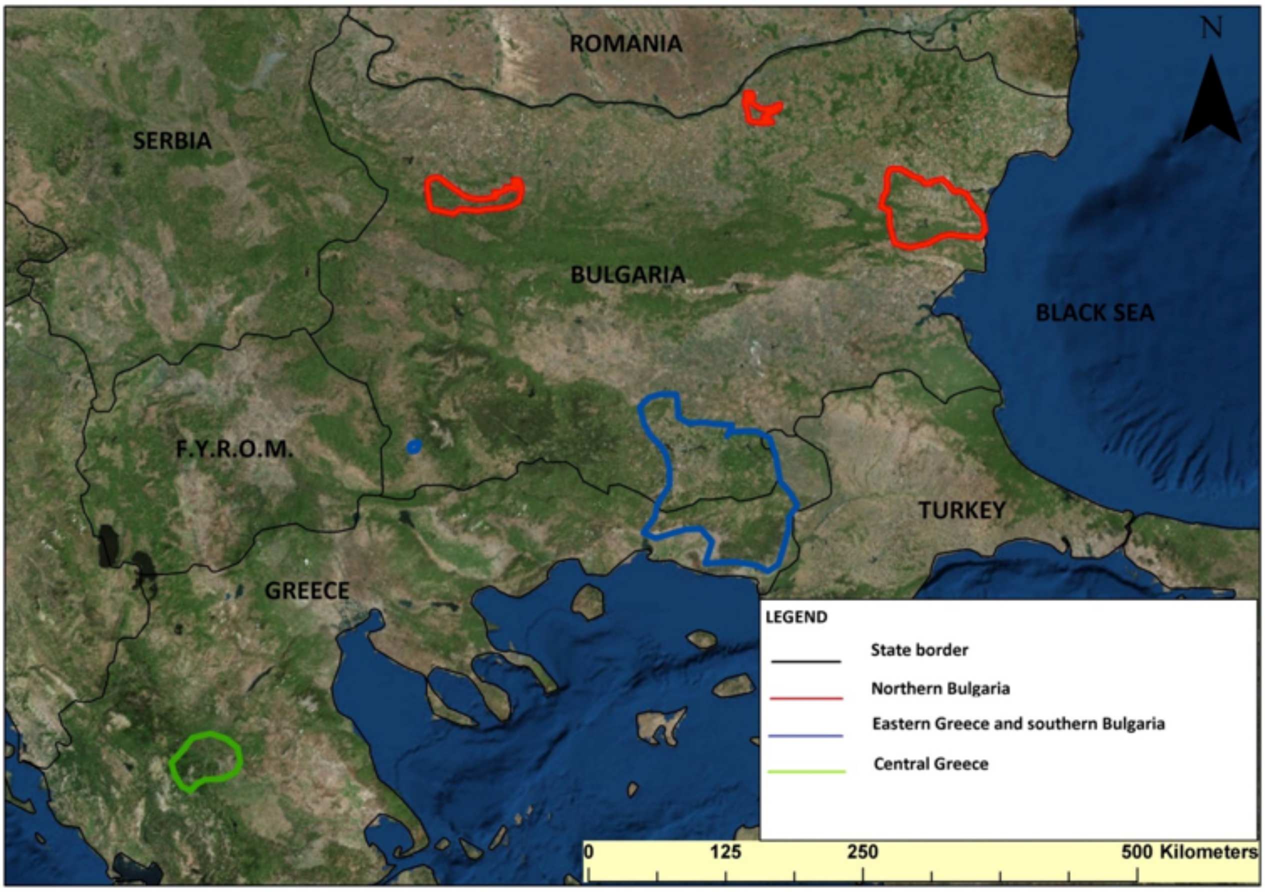

Figure 3. Map of the study area.

Changes in diet over time

EU agricultural policies have transformed landscapes in Europe with widespread consequences for bird populations (Donald et al. 2006, Sanderson et al. 2009). We therefore examined whether Egyptian vulture diet diversity and composition in Bulgaria changed over time since the country joined the EU in 2007. We tested for a continuous year effect in GLMMs with dietary diversity index or the proportional contribution of important prey taxa as response variables in an identical framework as described above for productivity.

Results

Diet composition

A total of 136 species from 32 orders and 8 classes were identified in the food remains (Annex 1). Mammals represented the highest proportion in the diet (48.9%), followed by reptiles (28.3%) and birds (21.5%), while all other animals were presented with a total of 1.3% (Figure 4).

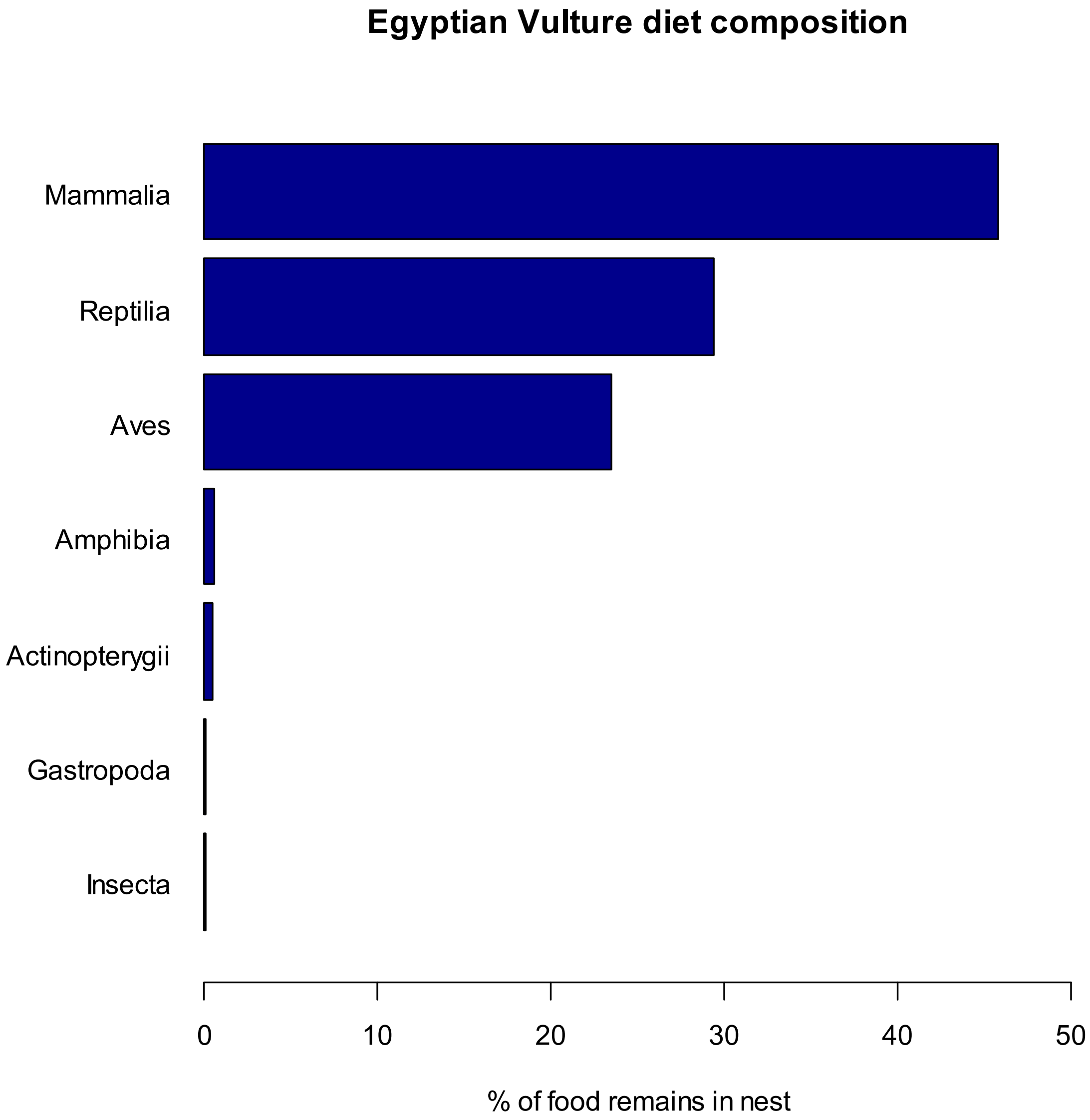

Figure 4. Egyptian vulture diet composition by classes.

There were 16 species (ca. 12% of all identified species) of mammals, reptiles and birds in the diet representing about 71% of the composition of food remains in all the Egyptian vulture's nests (Figure 5). Overall, wild animals contributed approximately 70% to the species diet in Bulgaria and 73% in Greece. The commonest species in the Egyptian vulture's diet were the Greek tortoise (Testudo graeca), and the Hermann's tortoise (Eurotestudo hermanni) represented by 13.2% and 11.4% respectively, and the domestic chicken (Gallus gallus f. domestica) represented by 7.1%.

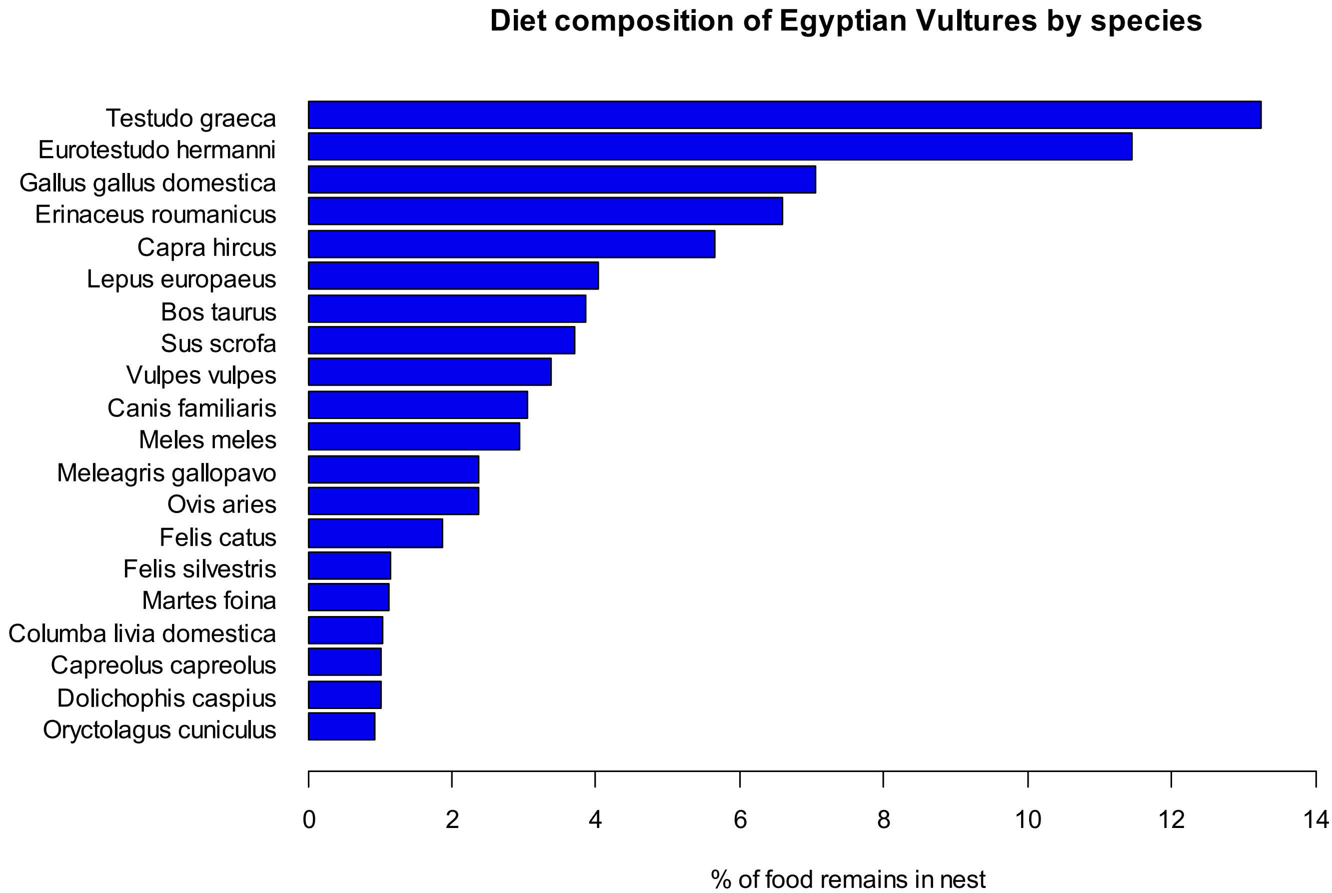

Figure 5. Diet composition of Egyptian vultures by species (only those species with an average contribution of>1% to dietary remains are shown)

Diet diversity and productivity

There was no significant relationship between dietary diversity and productivity (n = 137 nests; $\chi 2=1.17$, P = 0.28; Figure 6). Although territories with a higher dietary diversity appeared to raise more fledglings, the uncertainty around this effect (b = 0.19, 95% confidence interval -0.16 – 0.54) was very large (Figure 6). We also found no relationship between the number of fledglings produced by Egyptian vultures and the overall proportion of wild animals ($\chi 2= 0.05$, P = 0.81), or the proportion of livestock ($\chi 2= 0.86$, P = 0.35), chicken ($\chi 2= 0.42$, P = 0.52), carnivores ($\chi 2= 0.65$, P = 0.42), or tortoises ($\chi 2= 0.77$, P = 0.38) in the diet.

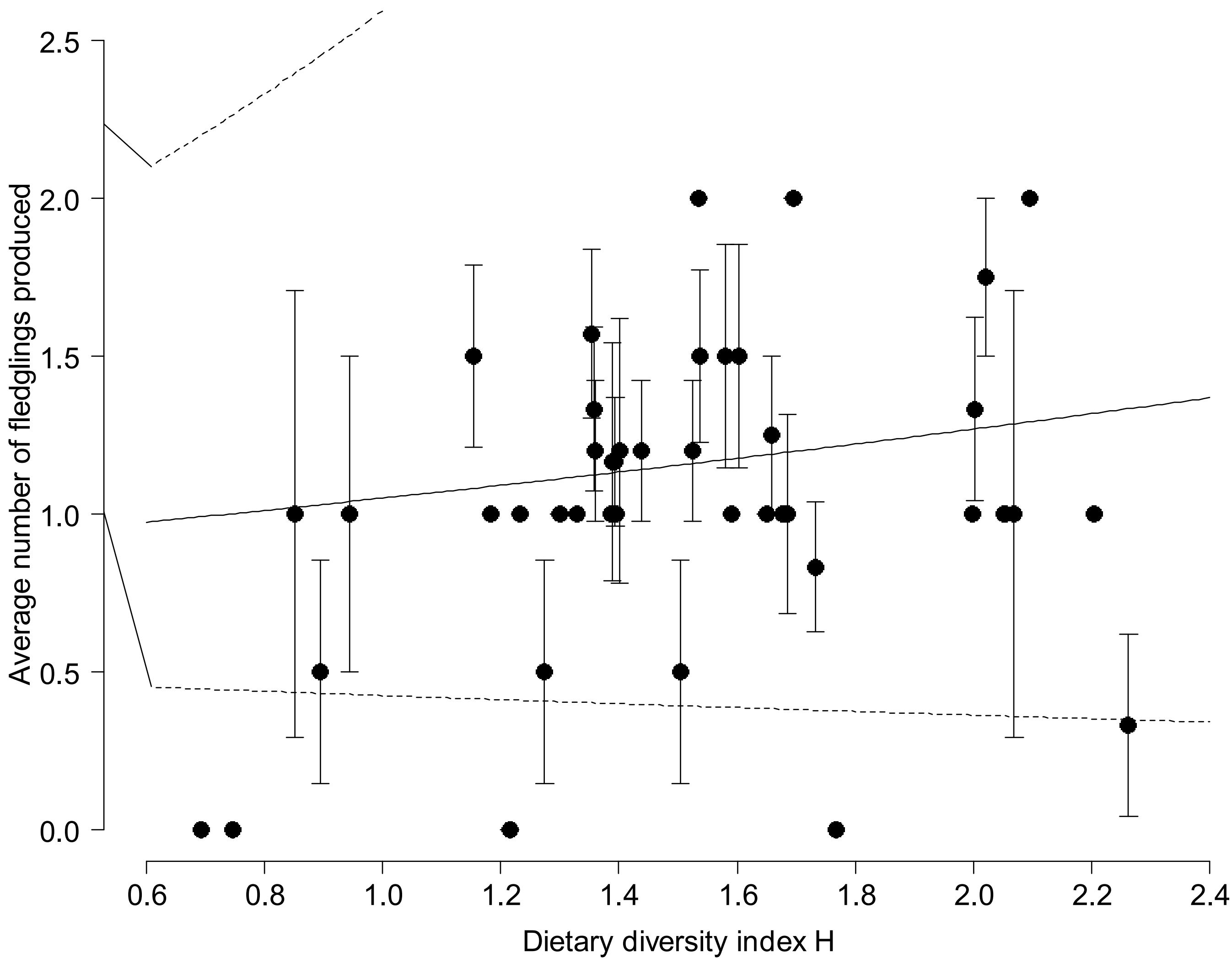

Figure 6. Mean (± standard deviation) productivity in 45 Egyptian vulture territories in Bulgaria and Greece in relation to the average dietary diversity calculated from food remains collected at nests in these territories between 2006 and 2013. Lines are mean fitted response (solid) and 95% confidence interval (dashed) of a GLMM.

Diet diversity and territory occupancy

Egyptian vulture dietary diversity was negatively related to occupancy rate across territories, indicating that birds nesting in territories that were abandoned earlier had a broader diet ($b = -0.57 \pm 0.22$; $\chi 2 = 6.24$, $P = 0.012$, Figure 7). This relationship was also reflected in the composition of the diet: we found an increasing proportion of wild animals in the diet of territories with lower occupancy rate ($b = -0.22 \pm 0.09$; $\chi 2 = 5.83$, $P = 0.016$), and a positive relationship between occupancy rate and the dietary proportion of livestock ($b = 0.23 \pm 0.07$; $\chi 2 = 10.63$, $P = 0.001$). There was no relationship between occupancy rate and the dietary proportion of chicken ($\chi 2 = 0.28$, $P = 0.60$), carnivores ($\chi 2 = 0.07$, $P = 0.79$), or tortoises ($\chi 2 = 1.67$, $P = 0.20$).

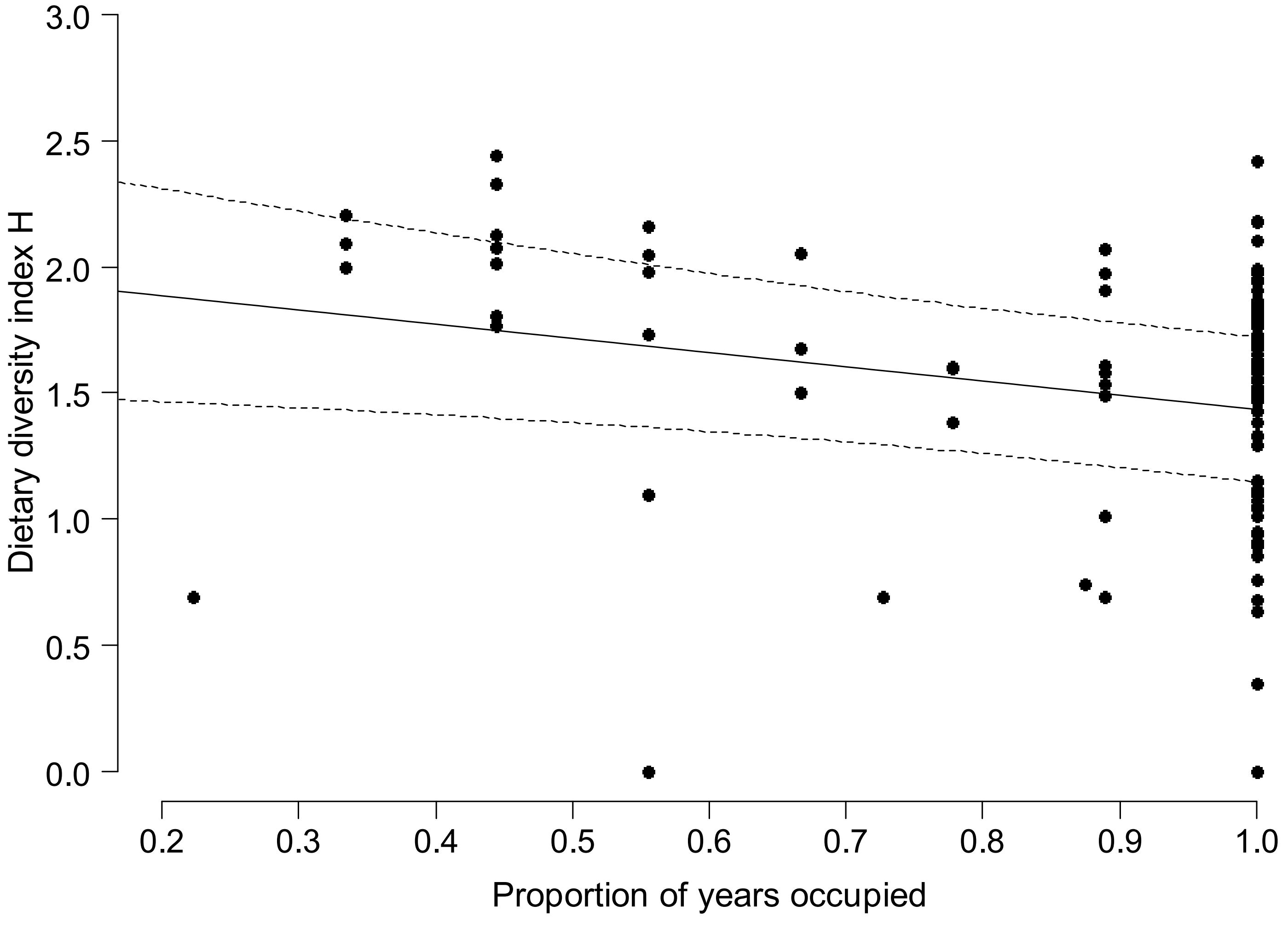

Figure 7. Dietary diversity index H calculated on the basis of the food remains in 133 nest content samples in 45 Egyptian vulture territories in Bulgaria and Greece in relation to the proportion of years during which the territories were occupied between 2006 and 2013. Lines are mean fitted response (solid) and 95% confidence interval (dashed) of a GLMM.

Geographic differencies in diet

Diet diversity did not differ between countries (n = 73; $\chi2$= 2.42, P = 0.12), but was significantly higher in northern Bulgaria (H = 1.68, n = 10) than in southern Bulgaria and Greece (H = 1.34, n = 63; $\chi2$=4.92, P = 0.03). This regional difference was due to a much lower proportion of tortoises in the diet in northern Bulgaria (12.6%) than in southern Bulgaria and Greece (29.8%; $\chi2$= 4.73, P = 0.03), which appeared to be offset by a marginally higher proportion of carnivores and chickens in northern Bulgaria (Table 2). The proportion of livestock (cows, sheep, goats, pigs) was variable and did not differ between countries or regions ($\chi2$= 2.39, P = 0.30, Table 2).

Class	**Order**	**northern Bulgaria (*n* = 33)**	**southern Bulgaria and Greece (*n* = 112)**
Mammalia	Carnivora	22.5 ± 18.0	14.6 ± 13.4
Mammalia	Artiodactyla	12.4 ± 12.3	19.6 ± 16.6
Aves	Galliformes	10.7 ± 12.6	6.2 ± 9.4
Reptilia	Testudines	10.1 ± 11.4	31.2 ± 20.9
Mammalia	Erinaceomorpha	6.9 ± 7.8	7.2 ± 13.7
Mammalia	Lagomorpha	6.9 ± 7.7	4.2 ± 7.1
Mammalia	Rodentia	6.8 ± 9.1	0.1 ± 1.1
Aves	Passeriformes	4.6 ± 6.6	7.1 ± 13.8
Reptilia	Squamata	3.1 ± 5.3	1.6 ± 4.2
Aves	Columbiformes	2.5 ± 4.0	1.0 ± 3.2
Mammalia	Soricomorpha	2.0 ± 4.9	0.2 ± 2.0
Aves	Accipitriformes	1.5 ± 3.9	1.2 ± 4.3

Table 2. Relative frequency (in %, ± standard deviation) of the most important prey categories in the Egyptian vulture diet assessed on the basis of the food remains in 145 nest content samples from Bulgaria and Greece between 2006 and 2013.

Dietary changes over time

The diversity of Egyptian vulture diet did not change significantly in Bulgaria between 2006 and 2013 (b = -0.029 ± 0.018; χ^2= 2.52, P = 0.11, n = 124 nests). However, we found a small decrease of 1.5% per year in the proportion of tortoises (χ^2= 4.13, P = 0.04, Figure 8), and an increase of 1.3% per year in the proportion of livestock (χ^2= 5.62, P = 0.02, Figure 8). There was no distinct trend in the proportion of carnivores (χ^2= 2.63, P = 0.11), the proportion of chicken (χ^2= 2.86, P = 0.09, Figure 8), or the proportion of all wild animals in the diet over time (χ^2= 1.08, P = 0.30).

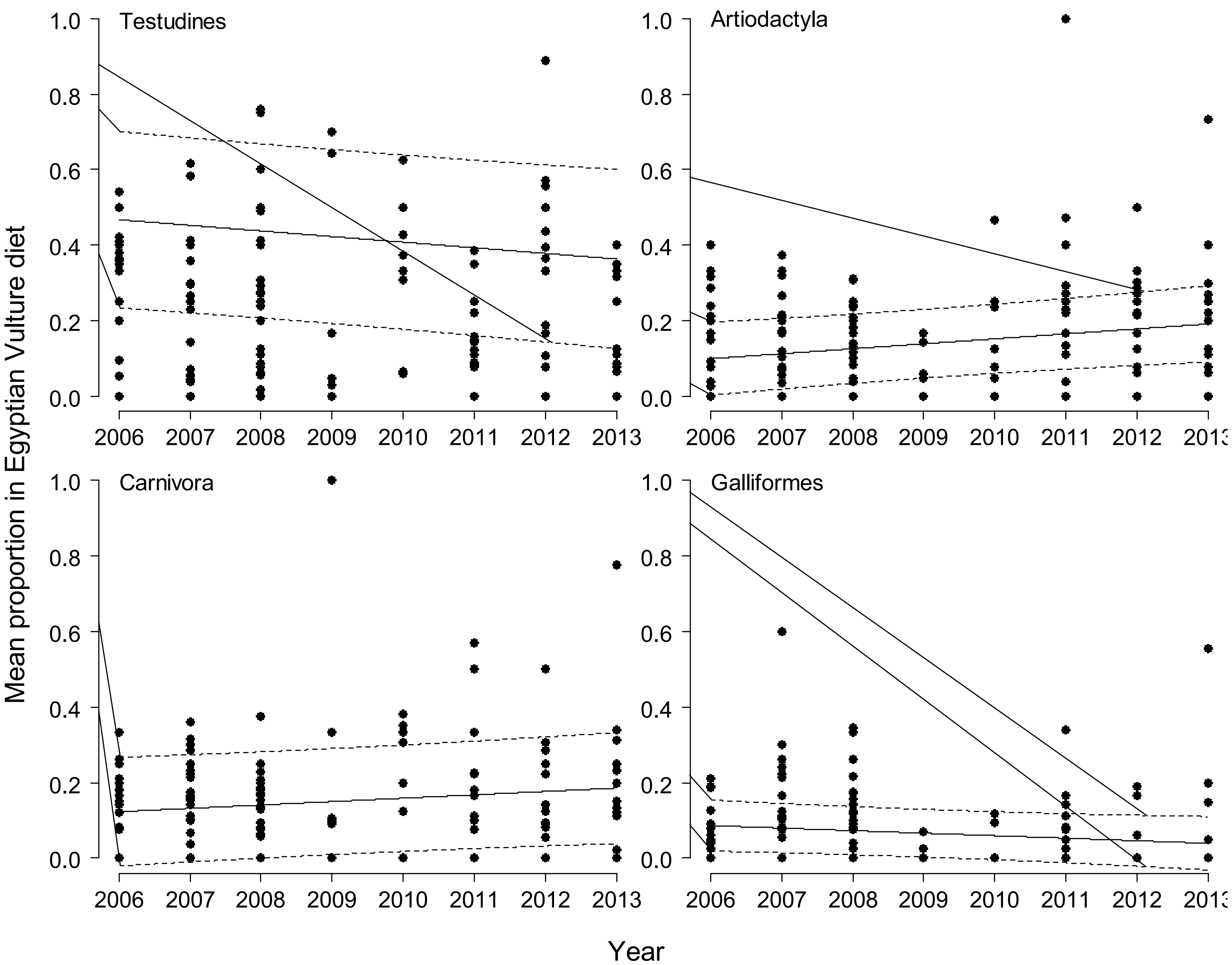

Figure 8. Proportion of the four most common taxonomic orders in the diet of Egyptian vulture in Bulgaria calculated from nest remains collected between 2006 and 2013 (n = 124 nest content samples). Lines are mean fitted response (solid) and 95% confidence interval (dashed) of a GLMM with year as a continuous predictor variable.

Discussion

This study provides the first quantitative assessment of Egyptian vulture diet composition on the Balkan Peninsula. We found that the diversity of Egyptian vulture diet did not change significantly since 2006 and that there is not significant relationship between dietary diversity and productivity. Therefore, our study does not provide any evidence that the diet of Egyptian vulture is an important contributor for low breeding performance and for population declines in Bulgaria and Greece (Velevski et al. 2015).

Diet composition

It is known that the Egyptian vulture has the ability to use a wide range of food sources in different parts of the species' range (Cramp & Simmons 1980, del Hoyo et al. 1994). The results from the present study confirm that the species has a very broad diet composition in Bulgaria and Greece and a broader dietary diversity than was found in previous studies from the Balkans (Milchev et al. 2012, Stoyanov & Boev, 2009, Kirilov 1983).

Mammals were the most common group of vertebrates in the Egyptian vulture's diet composition in Bulgaria and Greece which is consistent with previous studies from the two countries (Michev 1968, Yankov 1977, Kirilov 1983, Baumgart 1991, Miltschew & Georgiewa 1994, Vlachos et al. 1998, Kurtev et al. 2008, Milchev et al. 2012) and also from southern Spain (Margalida et al. 2012, Donázar et al. 2010). In our study, the other groups of vertebrates with significant proportions in the diet were reptiles (mostly as a consequence of the dominance of land tortoises) followed by birds. In the Strandzha mountains, south-eastern Bulgaria (Milchev et al. 2012), and southern Spain (Margalida et al. 2012), birds were more common than reptiles in the diet, and in northern Spain (Hidalgo et al. 2005) they were found to dominate the dietary composition of the species.

On a species level, we found that approximately 32% of all remains of animals in the nests were from 3 species: the Greek tortoise, the Hermann's tortoise and the domestic chicken. Both tortoise species represented 25% of the diet of the Egyptian vulture, and in agreement with other studies from the Balkans (Michev 1968, Yankov 1977, Baumgart 1991, Miltschew & Georgiewa 1994, Vlachos et al. 1998, Kurtev et al. 2008, Milchev et al. 2012), they appear to be one of the main food resoure utilized by the species especially in areas where tortoises are abundant - such as Eastern Greece and southern Bulgaria;. Miltschew and Georgiewa (1994) suggested that a probable source of tortoises could be the rocky areas where Golden Eagles (Aquila chrysaetos) drop tortoises to break them. While the high tortoise consumption may reflect a genuine prey preference, we need to interpret this result with due caution because tortoises and chickens are animals with very conspicuous and persistent prey remains and their proportion to the Egyptian vulture's diet may be overestimated by our methods (Simmons et al. 1991).

Regarding the source of food, wild animals dominated in our data set (represented by approximately 70%). In northern Spain most of food remains originated from wild birds (41%) and domestic mammals (29%) with smaller proportion of wild mammals (14%) and domestic poultry (10%) (Hidalgo et al. 2005). However, in another study from northern Spain, most remains were associated with domestic livestock (Donázar et al. 2010) in contrary with Hidalgo et al. (2005), most likely due to different methodological approaches and different sources of food available to the species in both studies. So far, domestic animals (cattle, horse, donkey, pig, goat, sheep, dog, cat, rabbit, etc.) were reported as the main prey for the species in Bulgaria, but the importance of tortoises for the diet had been recognised in some parts of the country (Michev 1968, Yankov 1977, Simeonov et al. 1990, Miltschew & Georgieva 1994, Kurtev et al. 2008).

Geographic differences in the diet

We found a higher dietary diversity in northern Bulgaria in comparison with southern Bulgaria and Greece and eastern Greece. In a local dietary study in south-eastern Bulgaria, Milchev et al. (2012) found that when the livestock numbers decreased in the region, the species shifted to other main food sources (in their case - on reptiles). It is known that birds may use a greater variety of food resources when the abundance of their favorable prey declines (Bell & Ford 1990) which could be the case with northern Bulgaria. Because there are no big livestock farms in northern Bulgaria, the Egyptian vulture in that region feeds mainly on road kill, some small prey in the fields and domestic chickens. On the other hand tortoises were most common in the diet in southern Bulgaria and eastern Greece, which is likely a consequence of regional differences in availability (Margalida et al. 2012), because tortoises are abundant in the dry and warm hills of that region, but considerably scarcer in northern Bulgaria (Petrov 2007). These geographic patterns therefore provide further support that Egyptian vultures are opportunistic foragers whose diet is closely linked to local availability of various prey animals (Hidalgo et al. 2005, Milchev et al. 2012).

Diet diversity and productivity

This study demonstrates no direct correspondence between dietary diversity and productivity. This result is in contrast to previous assessments of vultures, which generally found higher productivity with a more diverse diet (Margalida et al. 2009, Margalida et al. 2012). Two hypotheses exist that link individual breeding performance with dietary breadth (Whitfield et al. 2009): the diet specificity hypothesis predicts that species whose preferred diet decreases in availability will be forced to broaden their diet and suffer lower productivity (Katzner et al. 2005); conversely, the prey availability hypothesis suggests that a broader diet reflects a higher availability of prey and thus leads to an increase in productivity (Steenhof & Kochert 1988, Arroyo & Garcia 2006, Whitfield et al. 2009). Our study indicates that the productivity of Egyptian vultures in Bulgaria and Greece is not closely linked to the overall diversity or the proportion of certain prey taxa in the diet. Because we found no effect of diet on productivity, and productivity had a relatively small effect on population viability in theoretical models for the species (Garcia-Ripolles & Lopez-Lopez 2011, Velevski et al. 2014), we conclude that it is unlikely that dietary limitations on reproductive output are a critical threat to Egyptian vultures on the Balkan Peninsula. Similar results were found in a case study in south-eastern Bulgaria where the changes in the food abundance and subsequent changes in diets were reported as not the decisive factor for the extinction of the species from the Strandzha Mountains (Milchev et al. 2012).

Diet diversity and territory occupancy

In contrast to productivity, we found a negative relationship between dietary diversity and territory occupancy rate. Territory occupancy is generally a good indicator of the quality of a territory (Sergio & Newton 2003), and for Egyptian vultures the lower occupancy rate may indicate low adult survival either due to a poor diet or the risk of consuming poisoned carcasses (Carrete et al. 2007, Grande et al. 2009, Hernandez & Margalida 2009). The negative relationship between occupancy rate and diet diversity and the proportion of wild animals in the diet therefore conforms more with the diet specificity hypothesis and is in contrast with the apparent positive effect of a more diverse diet found in Spain (Margalida et al. 2012). Although our study is correlational and therefore unable to resolve whether dietary diversity is a cause or a consequence of lower territory occupancy, a potential mechanism of diet-mediated territory abandonment is that lower food availability may force individuals to consume a wider variety of wild animals and thus increase the risk of mortality from accidental ingestion of poisoned carcasses. The use of illegal poisoning to control livestock predators is ubiquitous in Greece (Mazaris et al. 2008, Kalpakis et al. 2009), and recent questionnaire surveys found that many livestock owners and hunters still use illegal poison substances to protect their livestock, cultivations, or game animals from dogs, foxes, or wolves (Skartsi et al. 2014). The risk of consuming a poisoned carcass may be especially high in areas with low availability of livestock, which may explain the positive relationship we found between occupancy rate and the proportion of livestock in the diet. Similar seems the situation in northern Bulgaria, where the dietary diversity was found to be higher compared to the other studied regions and the availability of livestock is lower, in the same time, there is a high rate of abandonment territories in the recent years (Kurtev et al. 2007, Velevski et al. 2015) and the main reason for this is suspected to be the uncontrolled use of pesticides (Gradinarov & Difova 2014).

Providing safe food for breeding vultures in regions with high risk of poisoning incidents may increase survival of adult and juvenile birds by reducing the risk of ingesting poisoned carcasses (Blanco et al. 2009, Oro et al. 2008). If provision of unlimited safe diet was considered to reduce mortality of juvenile and adult birds, this management had a large positive effect on Egyptian vulture populations in theoretical models (Garcia-Ripolles & Lopez-Lopez 2011). Territories in which we found a high dietary diversity may be suitable candidates for supplementary feeding to avoid poisoning incidents. Although supplementary feeding may reduce mortality risk and slow population declines, this approach may risk conserving qualitatively inferior territories and individuals (Garcia-Heras et al. 2013), and a more thorough evaluation of the long-term consequences of this management technique would be useful.

Temportal changes in the diet

Despite ongoing population declines (Velevski et al. 2015), we found no temporal trends in Bulgaria that suggested that population declines were associated with a decrease in dietary diversity. There was a slight decline in the proportion of tortoises in the Egyptian vulture diet in Bulgaria, which may be related to population declines of tortoises (Petrov 2007, Zivkov et al. 2007). In contrast, the proportion of livestock in the Egyptian vulture diet increased since Bulgaria joined the EU, although agricultural intensification was expected to lead to a decrease in small livestock farms and the overall availability of livestock carcasses. The apparent increase in livestock consumption may have been a consequence of drastic declines in the number of livestock herds after the collapse of socialist cooperative farming structures in the 1990s (Robinson & Milner-Gulland 2003, Kamp et al. 2011). Following this reduction of livestock, EU subsidies to livestock farmers are likely to have resulted in an increase of livestock in several rural areas of Bulgaria, including some of the areas inhabited by Egyptian vultures (e.g. eastern Rhodopes). Another possible factor is the increase of vulture restaurants and intensity of supplementary feeding in Bulgaria in the last 15 years (Dobrev & Stoychev 2013).

Methodological limitations

We used prey remains in nests as an indication of the diet consumed by Egyptian vultures, and it is widely known that indices based on prey remains may be biased because soft tissues that can be consumed and digested without leaving any remains will not be detected by this approach (Redpath et al. 2001, Simmons et al. 1991). Thus, the approach that we adopted may overestimate certain animals with hard exoskeletons (e.g. tortoises), and underestimate the contribution of animals which may not leave any remains or are not consumed entirely. For example, the carcass of a large animal (cow, sheep, etc.) may provide large amounts of soft tissue, without leaving any prey remains at the nest, and it is possible that the contribution of large livestock is therefore underestimated in our study. In addition, our approach relies on the number of individuals to estimate dietary diversity, but arguably the contribution of individuals from species of different size is not equal: the amount of energy derived from the consumption of an entire fox will be larger than the energy derived from consuming a hedgehog or another small animal. Moreover, the carcasses of small animals brought to nests often dry up and become unfit for feeding which may further decrease the energetic value of small animals (Baumgart 2001). The problem of unequal biomass of different prey animals is further compounded by the fact that we were unable to estimate what proportion of an individual is actually consumed. Prey remains from a fox do not necessarily indicate that the entire fox was consumed by a pair, and the actual energetic contribution of the various dietary items is impossible to assess with non-intrusive methods. Despite these limitations our approach allows valid comparisons among geographic regions, abandoned and occupied nests, and successful and unsuccessful nests (Margalida et al. 2012), and the majority of our conclusions are therefore not affected by uncertainties about the precise contribution of various animal groups to the diet of Egyptian vultures.

Recommendations for further research

Because we found no relationship between diet and productivity, further research is urgently needed to better understand the links between dietary diversity, food availability and territory occupancy, which will require studies relating food availability and consumption to the susceptibility to poisoning and ultimately to survival probabilities of adult and juvenile birds. In addition, testing the accuracy of the method we used to assess diet by examining food remains may be useful, for example by comparing prey remains to an independent control data set derived from nest cameras (Simmons et al. 1991). If any relationships between survival and dietary diversity can be found, then further investigations that relate dietary diversity to the availability of different prey animals in the landscape, or other landscape characteristics in the territory would be useful to identify high priority territories for management. Last but not least, the relationship between diet composition and bioaccumulation of contaminants (heavy metals, VMPs, etc.) might provide useful insights to explain any demographic effects of dietary diversity in Egyptian vulture.

Conclusions

As opportunistic scavengers, Egyptian vultures have an extremely variable diet, but our work did not provide any evidence that dietary diversity or the proportional contribution of a certain taxonomic order affects reproductive output. However, the dietary diversity was negatively related to occupancy rate across territories and we found an increasing proportion of wild animals in the diet of territories with lower occupancy rate and a positive relationship between occupancy rate and the dietary proportion of livestock.

In this project we were unable to explore the consequences of dietary composition or diversity on adults and their survival. For a long-lived species such as the Egyptian vulture, the survival of juveniles and especially adult birds will have a much larger effect on population trends than productivity. Although we found no effect of diet on productivity, the provision of safe food by means of supplementary feeding (as opposed to poisoned animals as a consequence of the illegal practice of poison baits) may increase survival of adult and juvenile birds by reducing the risk of consuming poisoned carcasses (Blanco et al. 2009, Oro et al. 2008, García-Ripollés & López-López 2011). However, it should be taken into account that supplementary feeding alone could not be considered as a factor that eliminates completely the risk of poisoning as two of the last breeding territories of the species in north-eastern Bulgaria were abandoned during the LIFE project when they have been subject of supplementary feeding and nest guarding and the most probable reason was non-intentional poisoning because of agricultural use of pesticides in the area (Gradinarov & Difova 2014). Based on the result that occupancy rate increases with the proportion of livestock in the diet, the promotion of extensive livestock breeding could be a beneficial practice for the persistance of the population in the core areas.

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Appendix

List of all species identified in food remains collected from Egyptian Vulture nests in Bulgaria and Greece between 2006–2013. The source describes whether a species is considered domestic or wild. For some species (e.g. pig, cat) both wild and domestic animals exist, and source reflects the origin of the majority of remains.

Species	Order	Class	Source
Cyprinus carpio	Cypriniformes	Actinopterygii	wild
Hypophthalmichthys molitrix	Cypriniformes	Actinopterygii	domestic
Rutilus rutilus	Cypriniformes	Actinopterygii	wild
Silurus glanis	Siluriformes	Actinopterygii	wild
Bufo bufo	Anura	Amphibia	wild
Pelophylax ridibundus	Anura	Amphibia	wild
Pseudopidalea viridis	Anura	Amphibia	wild
Rana sp.	Anura	Amphibia	wild
Accipiter gentilis	Accipitriformes	Aves	wild
Accipiter nisus	Accipitriformes	Aves	wild
Buteo buteo	Accipitriformes	Aves	wild
Buteo rufinus	Accipitriformes	Aves	wild
Gyps fulvus	Accipitriformes	Aves	wild
Pandion haliaetus	Accipitriformes	Aves	wild
Anas platyrhynchos	Anseriformes	Aves	wild
Anser anser domesticus	Anseriformes	Aves	domestic
Cairina moschata	Anseriformes	Aves	domestic
Mergus merganser	Anseriformes	Aves	wild
Bos taurus	Artiodactyla	Aves	domestic
Caprimulgus europaeus	Caprimulgiformes	Aves	wild
Larus michahellis	Charadriiformes	Aves	wild
Numenius arquata	Charadriiformes	Aves	wild
Vanellus vanellus	Charadriiformes	Aves	wild
Ardea cinerea	Ciconiiformes	Aves	wild
Ciconia ciconia	Ciconiiformes	Aves	wild
Ciconia nigra	Ciconiiformes	Aves	wild
Columba livia domestica	Columbiformes	Aves	wild
Columba oenas	Columbiformes	Aves	wild
Columba palumbus	Columbiformes	Aves	wild
Streptopelia turtur	Columbiformes	Aves	wild
Coracias garrulus	Coraciiformes	Aves	wild
Merops apiaster	Coraciiformes	Aves	wild

Upupa epops	Coraciiformes	Aves	wild
Cuculus canorus	Cuculiformes	Aves	wild
Falco tinnunculus	Falconiformes	Aves	wild
Gyps fulvus	Falconiformes	Aves	wild
Alectoris chukar	Galliformes	Aves	wild
Alectoris graeca	Galliformes	Aves	wild
Coturnix coturnix	Galliformes	Aves	wild
Gallus gallus domestica	Galliformes	Aves	domestic
Meleagris gallopavo	Galliformes	Aves	domestic
Perdix perdix	Galliformes	Aves	wild
Phasianus colchicus	Galliformes	Aves	wild
Gallinula chloropus	Gruiformes	Aves	wild
Rallus aquaticus	Gruiformes	Aves	wild
Acrocephalus arundinaceus	Passeriformes	Aves	wild
Aegithalos caudatus	Passeriformes	Aves	wild
Alauda arvensis	Passeriformes	Aves	wild
Carduelis carduelis	Passeriformes	Aves	wild
Carduelis chloris	Passeriformes	Aves	wild
Coccothraustes coccothraustes	Passeriformes	Aves	wild
Corvus corax	Passeriformes	Aves	wild
Corvus cornix	Passeriformes	Aves	wild
Corvus corone	Passeriformes	Aves	wild
Corvus frugilegus	Passeriformes	Aves	wild
Corvus monedula	Passeriformes	Aves	wild
Delichon urbicum	Passeriformes	Aves	wild
Garrulus glandarius	Passeriformes	Aves	wild
Hirundo rustica	Passeriformes	Aves	wild
Lanius collurio	Passeriformes	Aves	wild
Lanius minor	Passeriformes	Aves	wild
Lanius senator	Passeriformes	Aves	wild
Miliaria calandra	Passeriformes	Aves	wild
Muscicapa striata	Passeriformes	Aves	wild
Oenanthe oenanthe	Passeriformes	Aves	wild
Parus major	Passeriformes	Aves	wild
Passer domesticus	Passeriformes	Aves	wild
Passer hispaniolensis	Passeriformes	Aves	wild
Passer montanus	Passeriformes	Aves	wild
Pica pica	Passeriformes	Aves	wild
Ptyonoprogne rupestris	Passeriformes	Aves	wild

Riparia riparia	Passeriformes	Aves	wild
Saxicola torquata	Passeriformes	Aves	wild
Sturnus vulgaris	Passeriformes	Aves	wild
Sylvia sp.	Passeriformes	Aves	wild
Turdus merula	Passeriformes	Aves	wild
Turdus philomelos	Passeriformes	Aves	wild
Egretta garzetta	Pelecaniformes	Aves	wild
Dendrocopos major	Piciformes	Aves	wild
Jynx torquilla	Piciformes	Aves	wild
Podiceps grisegena	Podicipediformes	Aves	wild
Asio otus	Strigiformes	Aves	wild
Athene noctua	Strigiformes	Aves	wild
Bubo bubo	Strigiformes	Aves	wild
Strix aluco	Strigiformes	Aves	wild
Phalacrocorax pygmaeus	suliformes	Aves	wild
Helix pomatia	Helicidae	Gastropoda	wild
Cepaea vindobonensis	Helicoidea	Gastropoda	wild
bos taurus	Artiodactyla	Mammalia	domestic
Bos taurus	Artiodactyla	Mammalia	domestic
Capra hircus	Artiodactyla	Mammalia	domestic
Capreolus capreolus	Artiodactyla	Mammalia	domestic
Cervus elaphus	Artiodactyla	Mammalia	wild
Dama dama	Artiodactyla	Mammalia	wild
Ovis aries	Artiodactyla	Mammalia	domestic
Sus scrofa	Artiodactyla	Mammalia	domestic
Canis familiaris	Carnivora	Mammalia	domestic
Canis lupus	Carnivora	Mammalia	wild
Felis catus	Carnivora	Mammalia	domestic
Felis silvestris	Carnivora	Mammalia	wild
Martes foina	Carnivora	Mammalia	wild
Martes martes	Carnivora	Mammalia	wild
Meles meles	Carnivora	Mammalia	wild
Mustela nivalis	Carnivora	Mammalia	wild
Mustela putorius	Carnivora	Mammalia	wild
Ursus arctos	Carnivora	Mammalia	wild
Vormela peregusna	Carnivora	Mammalia	wild
Vulpes vulpes	Carnivora	Mammalia	wild
Erinaceus roumanicus	Erinaceomorpha	Mammalia	wild
Lepus europaeus	Lagomorpha	Mammalia	wild

Oryctolagus cuniculus	Lagomorpha	Mammalia	wild
Equus asinus	Perissodactyla	Mammalia	domestic
Equus caballus	Perissodactyla	Mammalia	domestic
Glis glis	Rodentia	Mammalia	wild
Mesocricetus newtoni	Rodentia	Mammalia	wild
Microtus arvalis	Rodentia	Mammalia	wild
Muridae	Rodentia	Mammalia	wild
Nannospalax leucodon	Rodentia	Mammalia	wild
Rattus norvegicus	Rodentia	Mammalia	wild
Rattus rattus	Rodentia	Mammalia	wild
Sciurus vulgaris	Rodentia	Mammalia	wild
Spermophilus citellus	Rodentia	Mammalia	wild
Sylvaemus flavicollis	Rodentia	Mammalia	wild
Talpa europaea	Soricomorpha	Mammalia	wild
Colubridae	Squamata	Reptilia	wild
Dolichophis caspius	Squamata	Reptilia	wild
Elaphe sauromates	Squamata	Reptilia	wild
Lacerta viridis	Squamata	Reptilia	wild
Malpolon insignitus	Squamata	Reptilia	wild
Natrix natrix	Squamata	Reptilia	wild
Pseudopus apodus	Squamata	Reptilia	wild
Serpentes	Squamata	Reptilia	wild
Vipera ammodytes	Squamata	Reptilia	wild
Zamenis longissimus	Squamata	Reptilia	wild
Emys orbicularis	Testudines	Reptilia	wild
Eurotestudo hermanni	Testudines	Reptilia	wild
Mauremys rivulata	Testudines	Reptilia	wild
Testudo graeca	Testudines	Reptilia	wild