Turkish Journal of Zoology
http://journals.tubitak.gov.tr/zoology/
Research Article

Turk J Zool
(2015) 39: 1151-1159
© TÜBİTAK
doi:10.3906/zoo-1411-22

Factors affecting the diet of the red fox (*Vulpes vulpes*) in a heterogeneous Mediterranean landscape

Dimitrios E. BAKALOUDIS[1,*], Vasileios A. BONTZORLOS[2], Christos G. VLACHOS[1], Malamati A. PAPAKOSTA[1], Evanggelos N. CHATZINIKOS[3], Sotirios G. BRAZIOTIS[1,2], Vasileios J. KONTSIOTIS[1]
[1]School of Forestry and Natural Environment, Laboratory of Wildlife and Freshwater Fish, Aristotle University of Thessaloniki, Thessaloniki, Greece
[2]Hellenic Hunters Confederation, Athens, Greece
[3]Hunting Federation of Sterea Hellas, Athens, Greece

Received: 12.11.2014 • **Accepted/Published Online:** 24.04.2015 • **Printed:** 30.11.2015

Abstract: The diet of the red fox (*Vulpes vulpes*) has been well studied in Europe, but limited information exists about its feeding habits in Greece and in other Mediterranean landscapes. We studied the diet variation of the red fox by analyzing contents from 219 red fox stomachs in central Greece from 2003 to 2005. We used canonical correspondence analysis (CCA) and quasi-distribution generalized linear model (GLM) response curves to investigate whether the trophic groups of the red fox diet varied temporally and/or spatially with environmental factors. Mammals, arthropods, and plants were the most important trophic groups in the diet; in particular, the European brown hare (*Lepus europaeus*) was consumed significantly more within hunting areas. The CCA produced a significant model for the response (trophic groups) and predictor datasets (environmental, spatial, and temporal variables). In addition, GLM response curves resulted in 13 best-fitted complexity models, which were evaluated with the Akaike information criterion. The results demonstrated 4 basic predation patterns. First, the red fox showed an opportunistic exploitation of food resources according to seasonal appearance, with temporal gradients being the main drivers affecting predation. Second, the red fox had a generalist diet, consuming cold-blooded vertebrates, arthropods, birds, and small-sized carnivores in a highly seasonal way. Third, the diet showed uniform predation on small mammals in all habitat types during the study. Finally, the red fox relies on hares within hunting areas, irrespective of habitat type or temporal gradients. Additional and long-term studies are needed to understand in depth the mechanisms involved in those observed high predation rates on hares.

Key words: Habitat, hunting, predation, temporal variables, Greece

1. Introduction

The red fox has been referred to as a generalist with temporal and spatial diet variation due to its wide distributional range and food adaptability (Cavallini and Volpi, 1995; Baker et al., 2006; Kidawa and Kowalczyk, 2011). Its diet composition in variable environments has been frequently studied in Europe (see Sidorovich et al., 2006 for a review; Hartová-Nentvichová et al., 2010). The diet variation among age classes (see Artois, 1989 for a review) and associations between prey density and fox diet (Cavalini and Lovari, 1991; Dell'Arte et al., 2007; Delibes-Mateos et al., 2008; Panek, 2009; Jankowiak and Tryjanowski, 2013) have also been studied. Feeding patterns of the red fox are more complex within multifunctional and human-dominated Mediterranean landscapes (Blondel and Aronson, 1999; de Aranzabal et al., 2008). Heterogeneous Mediterranean landscapes support spatial interactions and temporal changes in prey assemblages, which are reflected in the fox's and other medium-sized predators' diets (Delibes-Mateos et al., 2008; Mangas and Rodríguez-Estival, 2010; Ferreras et al., 2011; Bakaloudis et al., 2012; Díaz-Ruiz et al., 2013).

Within this complex Mediterranean context, information concerning the red fox's diet in Greece is limited (Papageorgiou et al., 1988). Therefore, there is a gap in knowledge about its feeding habits in the country and the effect of its predation upon game species, small mammals, and other prey groups. In the present study, we investigated the variation of animal and/or plant communities (trophic groups hereafter) in the diet across a range of environmental conditions. Thus, large differences in species composition were expected to be detected, along with some predictability of this variation (Panzacchi et al., 2008b). This gradual change is often related to demands

---

* Correspondence: debakaloudis@for.auth.gr

of individual species for different environmental factors (Díaz-Ruiz et al., 2013), and in a landscape context, this variation can be ordered along 1, 2, or 3 imaginary axes. Sometimes these axes are identified with a specific studied environmental condition. On large spatial scales, a visible spatial gradient cannot be found, nor can one be identified with a particular measurable environmental factor in nature; this study tries to offer insight in that direction as well. Through that process we tried to define in both seasonal and habitat terms (a) if the red fox diet varies significantly along spatial (habitat types, hunting and nonhunting areas) and temporal (season, year) gradients, and (b) which feeding groups vary along each one of the aforementioned gradients.

2. Materials and methods

2.1. Study area

The study area, covering 495,181 ha, is situated in central Greece (38°44′N–38°59′N, 22°02′E–22°37′E). Elevation ranges from 180 m to 1826 m a.s.l. Mean annual precipitation ranges between 543 mm to 1100 mm, and mean annual temperatures over most of the study area average 6–17 °C. The area presents high variation in its topographic relief. The forested area (14.59%) occurring on undulating terrain is dominated by several oak species (*Quercus* spp.) with an herb-rich vegetation layer. Shrublands (28.33%) occur on low hills and contain kermes oak (*Quercus coccifera*) and juniper (*Juniperus* sp.). Agricultural crops (56.17%) occur mainly on flat terrain, but also on low hills, and include cotton, corn, cereals, vineyards, orchards, and olive groves. Various wildlife species occupy the study area, with the European brown hare (*Lepus europaeus*), the wild boar (*Sus scrofa*), the European roe deer (*Capreolus capreolus*), the wolf (*Canis lupus*), the rock partridge (*Alectoris graeca graeca*), the common wood pigeon (*Columba palumbus*), and the Eurasian woodcock (*Scolopax rusticola*) having the most representatives.

In the study area, there are 10 wildlife refuges (15,000 ha in total) where hunting is forbidden. Most of the study area has experienced heavy livestock grazing all year round.

2.2. Field procedures and laboratory analyses

We analyzed the contents of 219 stomachs during 2003–2005. Samples (n) were collected in the 3 representative habitat types (agricultural crops [n = 67], shrublands [n = 77], oak forests [n = 75]), according to hunting status (hunting is allowed [n = 115], wildlife refuges [n = 104]), for 3 consecutive years, and they were also seasonally distributed (spring [n = 61], summer [n = 40], autumn [n = 58], and winter [n = 60]). All samples were collected from extensive and distinguishable habitat types by game wardens with the help of hunters. Thus, we considered a sample to belong in a certain habitat type when the distance from the nearest extensive habitat type was farther than 3–4 km. Collections were avoided in areas with a patchy distribution of different habitat types (Lucherini and Lovari, 1996).

We kept each stomach in a plastic bag to prevent loss of stomach contents. Each sample had an identity card with the date of collection, the area, and the habitat type. We filtered each stomach's contents with sieves with metallic wire mesh of different diameters (2.00, 1.25, and 0.5 mm), which we washed with hot water in order to remove very small food parts, fat, and digestive materials (Litvaitis, 2000).

The contents of each stomach were sorted into the following food categories: mammals, birds, reptiles, amphibians, fishes, arthropods, fungi, mollusks, plants, and various (e.g., paper, plastic, gravel). Mammals were identified with stereomicroscopic examination of the specific medulla characteristics (Stains, 1958) and the structure of the cuticle scales of the hair (Teerink, 1991). Furthermore, we identified mammals from their skulls, teeth, and bones. We identified birds from their skulls and feathers (Brown et al., 1987), and reptiles from their scales (Papageorgiou et al., 1993). The identification of plants was conducted by using a reference collection. The minimum number of an identifiable prey item was determined by counting all materials (mammal hairs, skulls, mandibles, teeth, and bones; bird beaks, feathers, and feet; reptile and amphibian scales and bones; snail shells) belonging to the same animal species, and by counting all fragments or seeds belonging to the same plant species.

Diet composition was expressed as the percentage of frequency of occurrence (%F = number of stomachs containing prey *i* / total number of stomachs × 100), and the percentage of numerical occurrence (%N = number of prey *i* / total number of prey items × 100). The second (%N) was used in multivariate statistical analyses. For statistical purposes, we defined 10 trophic groups: Lagomorpha, Rodentia, Soricomorpha, Carnivora, Artiodactyla, birds, cold-blooded vertebrates (reptiles and amphibians), invertebrates, plants, and various. We did not include fishes, fungi, or mollusks in the analyses due to their small representation in the diet.

2.3. Statistical analyses

Multivariate statistical analysis was based on 3 steps (CANOCO v. 5.0; ter Braak and Šmilauer, 2012). First, an indirect gradient analysis, detrended correspondence analysis (DCA), was applied only on the response variables' matrix (feeding groups), indicating the next appropriate statistical step (type of constrained ordination).

We next used an eigenvector ordination technique for multivariate direct gradient analysis, namely canonical correspondence analysis (CCA). The produced canonical eigenvalues measure the amount of variation in the data (feeding groups) that is explained by the explanatory variables. The total variation in the species matrix is called "total inertia" and is measured by the chi-square statistic of the plot-by-species table divided by the table's total (Lepš and Šmilauer, 2003; ter Braak and Šmilauer, 2012). Unrestricted Monte Carlo permutations were used to test the statistical significance and the relation between red fox feeding groups and the produced ordination axes, which was visualized with an ordination biplot.

Finally, in order to explore in greater depth the effect of each one of the explanatory gradients upon the way red fox preys on each feeding group in space and time, response curves were additionally constructed with the use of generalized linear models (GLMs) (Lepš and Šmilauer, 2003; ter Braak and Šmilauer, 2012). Poisson distribution was used in the modeling with GLMs (Quinn and Keough, 2006), with a "quasi-distribution approach" in order to deal with possible under-/overdispersion and allow estimation of the dispersion parameter as part of the model fitting (ter Braak and Šmilauer, 2012). All assumptions for the use of GLMs (independence of observations, specification of variance function, dispersion parameter, link function, and form of explanatory variables) were met (McCullagh and Nelder, 1989; Quinn and Keough, 2006).

Model selection was based on Akaike's information criterion (AIC) values, in the sense of choosing the best model not by comparing different models between them, but by comparing the particular complexity of the same model (linear, quadratic, or cubic) (Lepš and Šmilauer, 2003; ter Braak and Šmilauer, 2012). The model with the lowest AIC value (highest parsimony) was chosen. The F-statistic for a deviance-based test of the chosen model-significance was also calculated, along with the type I error estimate (P-value) corresponding to the F-statistic value (Lepš and Šmilauer, 2003; ter Braak and Šmilauer, 2012).

3. Results

The most important trophic group in the red fox diet was mammals, particularly the European brown hare, followed by arthropods and plants (Table 1). Once the indirect gradient analysis (DCA) was performed on the "trophic groups" matrix, a value of 3.7 was derived for the largest gradient. Although both linear and unimodal models could be applied in the continuation, the follow-up direct gradient analysis that was chosen was CCA, since that value was between 3 and 4.

The application of CCA on the response and predictor datasets produced a significant model for both the first and all the constrained axes that were constructed, and the explanatory variables of the model, which are summarized in the produced constrained axis, explain 25.9% of the feeding groups' variability (Table 2). The species-predictor variable correlations suggested that the first 2 constrained ordination axes are well correlated with the predictor

Table 1. Percentage of numerical abundance (%N) (n = 1336 prey items) and percentage of frequency of occurrence (%F) of prey items (n = 219 stomachs) identified in the red fox's diet in central Greece (2003–2005).

Prey items	%N	%F
MAMMALS	20.81	
Lagomorpha	5.09	
Lepus europaeus	5.09	31.05
Rodentia	4.79	
Apodemus flavicollis	0.45	2.74
Apodemus mystacinus	0.82	5.02
Glis glis	0.22	0.91
Micromys minutus	0.07	0.46
Mus musculus domesticus	0.30	1.83
Rattus rattus	2.77	14.16
Sciurus vulgaris	0.15	0.91
Soricomorpha	1.65	
Crocidura leucodon	0.97	5.94
Crocidura suaveolens	0.67	4.11
Carnivora	5.84	
Felis silvestris	0.22	1.37
Martes foina	2.02	12.33
Meles meles	0.07	0.46
Mustela nivalis	2.10	12.79
Mustela putorius	1.34	8.16
Vulpes vulpes	0.07	0.46
Artiodactyla	3.44	
Capreolus capreolus	0.90	5.48
Cervus elaphus	0.37	2.28
Ovis aries	0.15	0.91
Sus scrofa	2.02	12.33
Unknown	1.05	5.94
AVES	3.22	
Aves	3.14	18.72
Eggs	0.07	0.46
REPTILIA	1.65	
Lacerta viridis	0.30	1.83
Lizard, unknown	0.90	4.57
Snake, unknown	0.22	1.37
Testudo sp.	0.07	0.46
Unknown	0.15	0.91
AMPHIBIA	0.15	
Rana sp.	0.15	0.91
OSTEICHTHYES	0.15	
Unknown fish	0.15	0.91
ARTHROPODA	34.73	
Araneae	0.07	0.46
Coleoptera	2.92	14.61
Diptera	0.22	1.37
Embioptera	0.90	5.48
Hemiptera	0.07	0.46
Hymenoptera	0.82	2.74
Isopoda	2.40	14.61
Lepidoptera	18.4	20.55
Mecoptera	0.07	0.46
Neuroptera	0.14	0.91

Table 1. (Continued).

Prey items	%N	%F
ARTHROPODA (Continued)		
Orthoptera	3.29	20.09
Polydesmidae	5.69	20.09
Unknown	0.70	0.46
MOLLUSCA	0.07	
Helix spp.	0.07	0.46
PLANTS	30.39	
Achyranthus sp.	0.22	1.37
Actinidia polygama	0.07	0.46
Amydgalus communis	0.22	1.37
Fycus sp.	0.15	0.91
Hordeum sp.	0.07	0.46
Morus alba	0.6	1.37
Pyrus amygdaliformis	10.03	31.05
Pyrus pyraster	4.12	3.2
Triticum laevissimum	0.22	1.37
Plant remains	13.92	84.93
Vitis vinifera	0.15	0.91
Zea mays	0.52	3.2
Unknown fruit	0.07	0.46
FUNGI	0.52	
Mushroom	0.52	3.2
VARIOUS	7.26	
Paper	0.22	1.37
Plastic	0.45	2.74
Gravel	3.37	20.55
Shoes	0.07	0.46
Sponge	0.07	0.46
Rubber	0.07	0.46
Plastic bag	0.15	0.91
Unknown	2.84	13.70

gradients of the model ($r_1 = 0.719$ and $r_2 = 0.673$). In addition, both constrained axes together explained 65.2% of the species dataset variability. Consequently, the constrained ordination biplot, which includes both response and predictor variables (Figure), visualizes the CCA results of the produced constrained model and depicts how the 10 main trophic groups are positioned in ordinational space in relation to the environmental spatial and temporal gradients.

The Poisson-distribution GLMs fitted the way red fox specifically preyed upon each feeding group in respect to each explanatory gradient. In each instance, the models' parsimony was indicated through the AIC, whose values demonstrated linear models for the 13 cases which, according to the F-statistic and the P-value, had a significant response (Table 3). According to the significant models of the response curves, the red fox preyed less frequently on invertebrates in agricultural habitats during the third year (2005) of the study, whereas it preyed more on this group during the first year (2003). In agricultural habitats, plant and Insectivora consumption was also less significant. During the third year of the study, the red fox preyed less on Carnivora and Artiodactyla, whereas the coldblooded trophic group was more frequent in its diet. Coldblooded prey inclusion in the diet reached a higher proportion during spring, whereas it decreased during summer. During autumn, birds decreased in the red fox diet. Lagomorpha and Artiodactyla were consumed more within hunting areas irrespective of the habitat type, since they did not present significant response to any environmental gradient.

Table 2. Results of direct gradient analysis (CCA) taking into account the variability of both "response" (trophic groups) and "predictor" (environmental, spatial, and temporal variables) matrices. All 4 eigenvalues reported below are canonical and correspond to axes that are constrained by the explanatory variables, for a total of 999 permutations.

Axes	1	2	3	4	Total inertia
Eigenvalues	0.057	0.032	0.020	0.013	0.524
Pseudocanonical correlations	0.719	0.673	0.590	0.435	
Cumulative percentage variance of response data	10.8	16.9	20.7	23.2	
Cumulative percentage variance of fitted response data	41.7	65.2	80.1	89.5	
Sum of all eigenvalues					0.5243
Sum of all canonical eigenvalues					0.1357
Test of significance of first canonical axis	Eigenvalue				0.0566
	F-ratio				4.8400
	P-value				0.013
Test of significance of first canonical axis	Trace				0.1357
	F-ratio				1.7464
	P-value				0.001

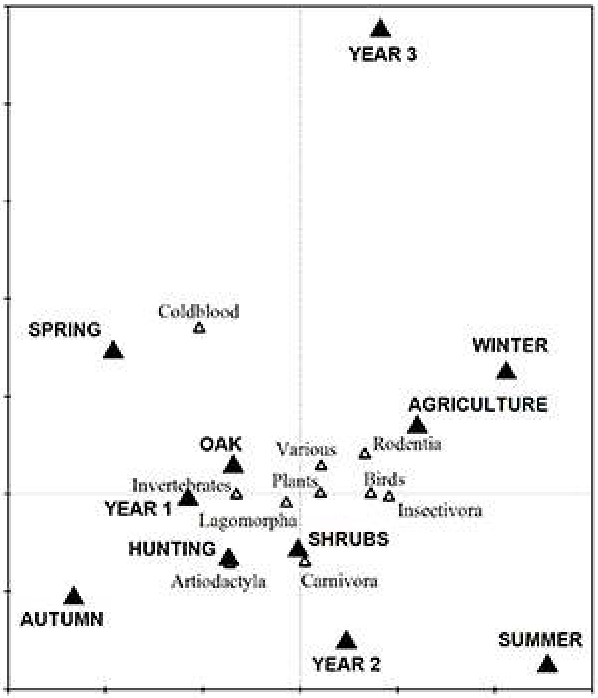

Figure. Constrained ordination plot as produced from canonical correspondence analysis (CCA). The variability of environmental variables is summarized on Axis 1 and Axis 2 of the constrained biplot, explaining the variability of the trophic groups included in the red fox's diet. Trophic groups are shown with black line (unfilled) pyramids, whereas environmental variables are shown with black filled pyramids. Proximity and distance of response centroids to predictor centroids indicate positive and negative correlations between them, respectively.

Table 3. Response of each trophic group included in the red fox diet from each explanatory gradient separately. With the use of Poisson-distribution GLMs and the AIC, the most parsimonious models were chosen in each instance. Only 13 significant response curves were produced according to the deviance-based F-statistic and the model's significance P-value, which according to AIC values were all of linear complexity, while models which were rejected through "null model" hypothesis or non-significant responses are not included in the table.

Response variables (trophic groups)	Explanatory gradients	AIC values	AIC model weights	Model complexity	Coefficient of determination r^2	Dispersion parameter	F-statistic	P-value model significance
Artiodactyla	Year 3	62.90	0.635	Linear	10.5	1.19	5.7	0.021
	Hunting	64.71	0.712	Linear	7.6	1.17	4.2	0.046
Birds	Autumn	49.00	0.612	Linear	7.3	0.80	4.4	0.040
Carnivora	Year 3	61.94	0.699	Linear	17.5	1.09	11.2	0.001
Cold-blooded	Spring	43.15	0.623	Linear	9.5	0.85	4.9	0.032
	Summer	40.83	0.486	Linear	12.4	0.87	6.2	0.016
	Year 3	43.04	0.617	Linear	9.6	0.83	5.0	0.029
Insectivora	Agriculture	43.25	0.529	Linear	7.9	0.79	4.4	0.041
Invertebrates	Agriculture	160.37	0.847	Linear	9.7	3.12	5.2	0.026
	Year 1	165.97	0.780	Linear	8.3	2.89	4.8	0.032
	Year 3	163.12	0.938	Linear	10.1	2.94	5.8	0.020
Lagomorpha	Hunting	51.51	0.618	Linear	19.0	0.84	13.4	<0.001
Plants	Agriculture	87.70	0.471	Linear	9.4	1.59	5.3	0.026

4. Discussion

The red fox is an opportunistic and generalist predator (Macdonald, 1980, 1983), which never preys upon more at low than at high densities of its main prey (Dell'Arte et al., 2007). Throughout its range, the importance of different trophic groups varies depending on the region, habitat, and season (Jedrzejewski and Jedrzejewska, 1992; Baltrūnaitė, 2006; Díaz-Ruiz et al., 2013). Moreover, in most studies a broader trophic niche was observed during the warm season when diverse food was available, whereas a narrower niche breadth was recorded during the colder months, when food resources were less abundant (Sidorovich et al., 2000).

In our study, the red fox showed a strong temporal exploitation of cold-blooded vertebrates (Table 3). Their increased consumption during spring is possibly due to the increased activity of cold-blooded vertebrates in April and May (Cavallini and Lovari, 1991). On the other hand, their decreased consumption in summer, when they are still active (Díaz-Ruiz et al., 2013), is not easily explained. It could probably be due to the ending of late summer mating season (Bartelt et al., 2010). It could also be explained by the seasonal availability of abundant alternative food resources, such as grapes and wild pears. The trend of consumption of cold-blooded vertebrates confirms a strong temporal-seasonal predation, regardless of habitat type.

The consumption of invertebrates varied annually, probably due to the seasonal peaks of arthropod populations that occur periodically (Ricci et al., 1998). They are mostly captured in oak forests and less in agricultural areas. This could be explained by the application of insecticides in agricultural crops, which eradicates invertebrate populations (Otto et al., 2009).

Carnivores represented a small percentage in the red fox diet (Table 1), indicating that they are an alternative prey, as reported in other studies (Cavallini and Lovari, 1991; Lucherini et al., 1995; Palomares and Caro, 1999). A strong habitat trend is observed for the Carnivora prey group, comprising mostly mustelids, which are mainly preyed upon in shrublands (Figure). These species are mainly associated with shrublands (Fournier et al., 2007; Virgos et al., 2010). The same predation trend on carnivores has also been recorded in other recent studies, but mainly by female red foxes (Viranta and Kauhala, 2011). In addition, carnivores have been reported in the literature as an alternative food resource for the red fox (Cavallini and Lovari, 1991; Lucherini et al., 1995), depending on habitat type, seasonal abundance, and abundance of other more important prey (see Palomares and Caro, 1999).

It has been repeatedly noted that small mammals such as voles, rats, and shrews always form a substantial part of the red fox's diet (Jedrzejewski and Jedrzejewska, 1992; Ferrari, 1995; Dell'Arte et al., 2007; Jankowiak and Tryjanowski, 2013). They were preyed upon consistently in all habitats and seasons (Figure). This pattern has also been reported by Papageorgiou et al. (1988) in a study covering the whole of Greece. That could happen due to the complexity of Mediterranean ecosystems (Blondel and Aronson, 1999), in comparison to ecosystems of central and northern Europe with less complex habitats and simpler and clearer spatial predation patterns (Myers et al., 2000). An exception in this pattern is the decrease of consumption of shrews in agricultural habitats. Although various studies have recorded a generally poorer biodiversity spectrum in agricultural areas (Duelli, 1997; Kleijn et al., 2001; Tscharntke et al., 2005), this tendency cannot give a satisfactory explanation for the decrease of shrews in the diet, since their capture has been repeatedly recorded in agricultural areas (Jedrzejewski and Jedrzejewska, 1992; Dell'Arte et al., 2007). It could be possible that the agricultural habitat matrix sustains assemblages of mice, rats, and voles, which are more territorial than shrews, resulting in poorer shrew assemblages, as has also been indicated in the diet of other top predators in similar Mediterranean agroecosystems (Bontzorlos et al., 2005, 2009).

Plants were also a dominant food type in the red fox's diet, especially wild pears (*Pyrus amygdaliformis*) (Table 1). The position of the group near the center of the constrained ordination plot, without proximity to any specific temporal or spatial gradient (Figure), probably suggests that the overall participation of emerging vegetation and fruits in different periods merged any existing spatial or temporal trends in the diet. On the other hand, the significant decreased consumption of plants within agricultural habitats is explained by extensive single crops and intensive agricultural practices.

Birds were preyed on uniformly across seasons and habitats, probably due to hunting energy costs and shifts to other more abundant alternative food resources. No spatial trend was revealed in our study, but others showed that habitat plays a significant role (Prudnicki et al., 2000; Goldyn et al., 2003). The unique significant response is the decrease of avian prey during autumn. During this season, avian communities consist of more experienced individuals than during spring and summer when nestlings are learning to fly, and thus are less vulnerable to predation risk (Cavallini and Lovari, 1991).

Two game species occurred in the red fox's diet: the European hare and the wild boar. European hares (Table 1) were captured equally in all habitats and seasons. That was quite unexpected since subadult hares have been repeatedly recorded to be preyed upon from April to June. During this period, the red fox prefers to prey upon species with higher biomass compensation in order to feed its cubs (Lindström, 1994; Reynolds and Tapper, 1995a, 1995b; Kauhala and Helle, 2000), while Lovari and Parigi (1995) found that although adult foxes preyed on bigger species, they tended to feed their cubs with smaller prey. In addition, hares are usually captured in pastures, meadows, and open agricultural land (Webbon et al., 2006; Hartová-Nentvichová et al., 2010). Wild boar was preyed upon similarly across habitats and seasons, showing only a significant temporal decrease in the red fox's diet during the third year of the study.

The red fox preyed significantly more upon hares and wild boars within hunting areas during all seasons and in all habitat types (Table 3; Figure). This pattern for the wild boar's appearance in the red fox's diet could have resulted from the consumption of hunting remnants during autumn and winter (Lovari et al., 1994), but during spring and summer this could be related to predation on newborn wild boars (Panzacchi et al., 2008a). However, the latter should be further studied. The occurrence of hares in the stomachs (Table 1), particularly within hunting areas, may be due to exposure to predation due to injuries from hunting activity, as suggested by Angerbjörn (1989) and Reynolds and Tapper (1995a). In central Greece, predation on hares occurs all year long and does not decrease during spring and summer (February to August) when hunting is not allowed. This pattern could also be related to food provisioning for their cubs (Lindström, 1994; Lovari and Parigi, 1995).

In conclusion, the findings of this study could support 4 basic patterns concerning the red fox's predation in a typical Mediterranean landscape of central Greece. First, the red fox hunts in a variety of different habitats; the season was the main variable affecting predation. Temporal gradients (season and year) seem to mainly explain variability of trophic groups. Second, the main trophic groups in the red fox diet, which support its generalist behavior, were cold-blooded vertebrates, invertebrates, plants, carnivores, and birds. Third, red fox preyed on small mammals and hares without following any habitat or temporal pattern. Although a habitat composition and fragmentation analysis with prey abundances could outline the importance of a prey class, it is not feasible in complex Mediterranean environments, and specifically in large spatial scale studies. Finally, the fourth basic predation pattern is the higher consumption of hares in hunting areas, irrespective of habitat type or temporal gradients. This pattern poses the question of a possible negative effect of red fox predation upon one of the most important game species in Greece, despite no restocking program for hares being applied in the region during the study period. Therefore, both additional studies from other places in Greece and long-term studies in the study area would increase understanding of the underlying mechanisms for the observed high predation on hares.

Acknowledgments

We are grateful to G Liagas, P Panagitsas, J Psomas, and G Kourelas for their help in the fieldwork during the sample collection. In addition, the authors are thankful to Prof S Lovari for his insightful suggestions, and for his constructive comments on an earlier draft of the manuscript. We also thank two anonymous reviewers for their useful comments on our manuscript. The study was supported by the Hunting Federation of Sterea Hellas. We also thank the Greek Ministry of Agricultural Development and Food, Department of National Parks, Aesthetic Forests, and Hunting for permission to collect samples during the 3-year study. The authors declare that the experiments comply with Greek and EU laws.

References

Angerbjörn A (1989). Mountain hare populations on islands: effects of predation by red fox. Oecologia 81: 335–340.

Artois M (1989). Le Renard Roux (*Vulpes vulpes* Linnaeus 1758). Encyclopédie des Carnivores de France, vol. 3. Puceul, France: Société Francaise pour l'etude et la protection des mammifères (in French).

Bakaloudis DE, Vlachos CG, Papakosta MA, Bontzorlos VA, Chatzinikos EN (2012). Diet composition and feeding strategies of the stone marten (*Martes foina*) in a typical Mediterranean ecosystem. ScientificWorldJournal 2012: 163920.

Baker P, Furlong M, Southern S, Harris S (2006). The potential impact of red fox *Vulpes vulpes* predation in agricultural landscapes in lowland Britain. Wildlife Biol 12: 39–50.

Baltrūnaitė L (2006). Diet and winter habitat use of the red fox, pine marten and raccoon dog in Dzukija National Park, Lithuania. Acta Zool Lituan 16: 46–53.

Bartelt EP, Klaver PW, Porter WP (2010). Modelling amphibian energetics, habitat suitability, and movements of western toads, *Anaxyrus* (*Bufo*) *boreas*, across present and future landscapes. Ecol Model 221: 2675–2686.

Blondel J, Aronson J (1999). Biology and Wildlife of the Mediterranean Region. Oxford, UK: Oxford University Press.

Bontzorlos AV, Peris JS, Vlachos CG, Bakaloudis DE (2005). The diet of Barn owl in the agricultural landscapes of central Greece. Folia Zool 54: 99–110.

Bontzorlos AV, Peris JS, Vlachos CG, Bakaloudis DE (2009). Barn owl *Tyto alba* prey in Thessaly, and evaluation of diets throughout Greece. Ardea 97: 625–630.

Brown R, Ferguson J, Lawrence M, Lees D (1987). Tracks and Signs of the Birds of Britain and Europe: An Identification Guide. London, UK: Christopher Helm.

Cavallini P, Lovari S (1991). Environmental factors influencing the use of habitat in the red fox *Vulpes vulpes*. J Zool (Lond) 223: 323–339.

Cavallini P, Volpi T (1995). Biases in the analysis of the diet of the red fox *Vulpes vulpes*. Wildlife Biol 1: 243–248.

de Aranzabal I, Schmitz MF, Aguilera P, Pineda FD (2008). Modelling of landscape changes derived from the dynamics of socio-ecological systems: a case of study in a semiarid Mediterranean landscape. Ecol Indic 8: 672–685.

Delibes-Mateos M, Fernandez de Simon J, Villafuerte R, Ferreras P (2008). Feeding responses of the red fox (*Vulpes vulpes*) to different wild rabbit (*Oryctolagus cuniculus*) densities: a regional approach. Eur J Wildlife Res 54: 71–78.

Dell'Arte GL, Laaksonen T, Norrdahl K, Korpimaki E (2007). Variation in the diet composition of a generalist predator, the red fox, in relation to season and density of main prey. Acta Oecol 31: 276–281.

Díaz-Ruiz F, Delibes-Mateos M, García-Moreno JL, López-Martín JM, Ferreira C, Ferreras P (2013). Biogeographical patterns in the diet of an opportunistic predator: the red fox *Vulpes vulpes* in the Iberian Peninsula. Mammal Rev 43: 59–70.

Duelli P (1997). Biodiversity evaluation in agricultural landscapes: an approach at two different scales. Agr Ecosyst Environ 62: 81–91.

Ferrari N (1995). Influence of the abundance of food resources on the feeding habits of the red fox, *Vulpes vulpes*, in western Switzerland. J Zool 236: 117–129.

Ferreras P, Travaini A, Zapata SC, Delibes M (2011). Short-term responses of mammalian carnivores to a sudden collapse of rabbits in Mediterranean Spain. Basic Appl Ecol 12: 116–124.

Fournier P, Maizeret C, Jimenez D, Chusseau J-P, Aulagnier S, Spitz F (2007). Habitat utilization by sympatric European mink *Mustela lutreola* and polecats *Mustela putorius* in South-western France. Acta Theriol 52: 1–12.

Goldyn B, Hromada M, Surmacki A, Tryjanowski P (2003). Habitat use and diet of the red fox *Vulpes vulpes* in an agricultural landscape in Poland. Eur J Wildlife Res 49: 191–200.

Hartová-Nentvichová M, Šálek M, Červený J, Koubek P (2010). Variation in the diet of the red fox (*Vulpes vulpes*) in mountain habitats: effects of altitude and season. Mamm Biol 75: 334–340.

Jankowiak Ł, Tryjanowski P (2013). Cooccurrence and food niche overlap of two common predators (red fox *Vulpes vulpes* and common buzzard *Buteo buteo*) in an agricultural landscape. Turk J Zool 37: 157–162.

Jedrzejewski W, Jedrzejewska B (1992). Foraging and diet of the red fox *Vulpes vulpes* in relation to variable food resources in Bialowieza National Park, Poland. Ecography 15: 212–220.

Kauhala K, Helle P (2000). The interactions of predator and hare populations in Finland – a study based on wildlife monitoring counts. Ann Zool Fenn 37: 151–160.

Kidawa D, Kowalczyk R (2011). The effect of sex, age, season and habitat on diet of the red fox *Vulpes vulpes* in northeastern Poland. Acta Theriol 56: 209–218.

Kleijn D, Berendse F, Smit R, Gilissen N (2001). Agri-environment schemes do not effectively protect biodiversity in Dutch agricultural landscapes. Nature 413: 723–725.

Lepš J, Šmilauer P (2003). Multivariate Analysis of Ecological Data Using CANOCO. Cambridge, UK: Cambridge University Press.

Lindström ER (1994). Large prey for small cubs – on crucial resources of a boreal red fox population. Ecography 17: 17–22.

Litvaitis JA (2000). Investigating food habits of terrestrial vertebrates. In: Boitani L, Fuller TK, editors. Research Techniques in Animal Ecology. New York, NY, USA: Columbia University Press, pp. 165–190.

Lovari S, Parigi L (1995). The red fox as a gamebird killer or a considerate parent? Mammalia 59: 455–459.

Lovari S, Valier P, Ricci Lucchi M (1994). Ranging behavior and activity of red foxes (*Vulpes vulpes*: Mammalia) in relation to environmental variables, in a Mediterranean mixed pinewood. J Zool (Lond) 232: 323–339.

Lucherini M, Lovari S (1996). Habitat richness affects home range size in the red fox *Vulpes vulpes*. Behav Process 36: 103–106.

Lucherini M, Lovari S, Crema G (1995). Habitat use and ranging behavior of the red fox (*Vulpes vulpes*) in a Mediterranean rural area: is shelter availability a key factor? J Zool (Lond) 237: 570–591.

Macdonald DW (1980). The red fox, *Vulpes vulpes*, as a predator upon earthworms, *Lumbricus terrestris*. Z Tierpsychol 52: 171–200.

Macdonald DW (1983). The ecology of carnivore social behavior. Nature 301: 379–384.

Mangas JG, Rodríguez-Estival J (2010). Logging and livestock influence the abundance of common mammal species in Mediterranean forested environments. Forest Ecol Manag 260: 1274–1281.

McCullagh P, Nelder JA (1989). Generalized Linear Models. 2nd ed. London, UK: Chapman and Hall.

Myers N, Mittermeier RA, Mettermeier CG, da Fonseca GAB, Kent J (2000). Biodiversity hotspots for conservation priorities. Nature 403: 853–858.

Otto S, Lazzaro L, Finizio A, Zanin G (2009). Estimating ecotoxicological effects of pesticide drift on nontarget arthropods in field hedgerows. Environ Toxicol Chem 28: 853–863.

Palomares F, Caro TM (1999). Interspecific killing among mammalian carnivores. Am Nat 153: 492–508.

Panek M (2009). Factors affecting predation of red foxes *Vulpes vulpes* on brown hares *Lepus europaeus* during the breeding season in Poland. Wildlife Biol 15: 345–349.

Panzacchi M, Linnel JDC, Odden J, Odden M, Andersen R (2008a). When a generalist becomes a specialist: patterns of red fox predation on roe deer fawns under contrasting conditions. Can J Zool 86: 116–126.

Panzacchi M, Linnel JDC, Serrao G, Eie S, Odden M, Odden J, Andersen R (2008b). Evaluation of the importance of roe deer fawns in the spring–summer diet of red foxes in southeastern Norway. Ecol Res 23: 889–896.

Papageorgiou NK, Sfougaris A, Christopoulou OG, Vlachos CG, Petamidis JS (1988). Food habits of the red fox in Greece. Acta Theriol 33: 13–324.

Papageorgiou NK, Vlachos CG, Sfougaris A, Bakaloudis DE (1993). Identification of Reptiles by Scale Morphology. Thessaloniki, Greece: University Studio Press (in Greek).

Prudnicki W, Nowicki W, Jabłoński R, Skoczylaś B (2000). Menu of foxes in autumn and winter in Pomorze and Kujawy. In: Kubiak S, editor. Wloclawskie, Poland: Wloclawskie Towarzystwo Naukowe, pp. 192–199 (in Polish with English summary).

Quinn GP, Keough MJ (2006). Experimental Design and Data Analyses for Biologists. Cambridge, UK: Cambridge University Press.

Reynolds JC, Tapper SC (1995a). The ecology of the red fox *Vulpes vulpes* in relation to small game in rural southern England. Wildlife Biol 1: 105–119.

Reynolds JC, Tapper SC (1995b). Predation by foxes *Vulpes vulpes* on brown hares *Lepus europaeus* in central southern England, and its potential impact on population growth. Wildlife Biol 1: 145–158.

Ricci S, Colombini I, Fallaci M., Scoccianti C, Chelazzi L (1998). Arthropods as bio-indicators of the red fox foraging activity in a Mediterranean beach-dune system. J Arid Environ 38: 335–348.

Sidorovich VE, Polozov AG, Lauzhel GO, Krasko DA (2000). Dietary overlap among generalist carnivores in relation to the impact of the introduced raccoon dog *Nyctereutes procyonoides* on native predators in northern Belarus. Z Saugetierkd 65: 271–285.

Sidorovich VE, Sidorovich AA, Izotova I (2006). Variations in the diet and population density of the red fox *Vulpes vulpes* in the mixed woodlands of northern Belarus. Mamm Biol 71: 74–89.

Stains HJ (1958). Field guide to guard hairs of Middle-Western furbearers. J Wildlife Manage 22: 95–97.

Teerink BJ (1991). Hair of West-European Mammals: Atlas and Identification Key. Cambridge, UK: Cambridge University Press.

ter Braak CJF, Šmilauer P (2012). CANOCO Reference Manual and User's Guide: Software for Ordination (Version 5.0). Ithaca, NY, USA: Microcomputer Power.

Tscharntke T, Klein AM, Kruess A, Steffan-Dewenter I, Thies C (2005). Landscape perspectives on agricultural intensification and biodiversity-ecosystem service management. Ecol Lett 8: 857–874.

Viranta S, Kauhala K (2011). Increased carnivory in Finnish red-fox females: adaptation to a new competitor? Ann Zool Fenn 48: 17–28.

Virgos E, Cabezas-Diaz S, Mangas JG, Lozano J (2010). Spatial distribution models in a frugivorous carnivore, the stone marten (*Martes foina*): is the fleshy-fruit availability a useful predictor? Anim Biol 60: 423–436.

Webbon CC, Baker PJ, Cole NC, Harris S (2006). Macroscopic prey remains in the winter diet of foxes *Vulpes vulpes* in rural Britain. Mammal Rev 36: 85–97.