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Lesser Kestrel Falco naumanni diet during different phases of breeding and post breeding periods in central Greece

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Abstract - The Lesser Kestrel Falco naumanni is a small migratory falcon, foraging in areas covered by relatively low vegetation. In the Thessalian Plain, Central Greece, it feeds mainly on large Orthoptera and Coleoptera, and is characterized by an opportunistic feeding strategy. The purpose of this study was to investigate the composition of the Lesser Kestrel diet in the Thessalian plain. Systematic visits to two large representative colonies of the Lesser Kestrel in the study area were performed, in order to collect pellets during 2014 and 2015 breeding and post breeding periods of the species. Pellet analysis indicated that Orthoptera and Coleoptera were the main prey categories, which seem to have been the most specialized and dominant feeding choices of the species in the study area, while all other prey categories were rare and not specialized. Lesser Kestrel relied its diet on Orthoptera (Tettigoniidae and Acrididae), mainly during the breeding and post breeding phases, while the feeding strategy of the species during these two phases can be characterized as opportunistic. On the contrary, prior to the breeding phase, main prey category of the species in the study area was Coleoptera (Carabidae and Scarabaeidae). Moreover, a narrower niche breadth of the species based on Levins' index, was recorded during the breeding phase for both years of the study, indicating that the species restricted the variety of the diet during this phase. Conclusively, the species during its whole breeding season made different prey choices, depending on the breeding phase and its specialized needs during each phase.

Keywords: Lesser Kestrel, Thessaly, diet composition, feeding strategy, pellet analysis

INTRODUCTION

The Lesser Kestrel *Falco naumanni* is a small migratory falcon. Even if it was one of the most abundant birds of prey in Europe, it suffered a dramatic population decline during the second half of the 20th century (Cramp et al. 1992, Donazar et al 1993, Parr et al. 1995, BirdLife International 2004, Perez et al. 2011). The population decline reached up to 95% for the European population (Tella & Forero 2000). This is the reason why the species was classified as a "globally endangered species" by Collar & Andrew (1998) and as "vulnerable" by the IUCN. Therefore, Lesser Kestrel was a species of high priority for conservation in Europe (De Frutos et al. 2010) and considered as a potential indicator of agricultural biodiversity (Biber 1996, Rodriguez & Wiegand 2009). From the

1990s onwards, populations of the species were recovering in southwestern and central Europe (Birdlife International 2004, Inigo & Barov 2010), so that, the species has been characterized as "Least Concern" since 2011 (BirdLife International 2015). The Greek population remains in the "Vulnerable" category of endangered species (Legakis & Maragou 2009).

The causes for the reported population decline are generally attributed to the reduced availability of nesting sites (caused by restoration of old buildings and interspecific competition), the increased use of agricultural inputs, which are likely to reduce egg fertility, and agricultural land use change, which reduces the extent and/or quality of the species feeding habitats and the agricultural intensification and the use of pesticides, which affected feeding habitats and food availability (Donazar et al. 1993, Parr et al. 1995, Bustamante 1997, Tella et al. 1998, Tella & Forero 2000, BirdLife International 2004). Regarding the Thessaly plain (central Greece), Sfougaris et al. (2004) reported that the changes of the agricultural land were a possible reason for population decline of the species, where gradual increase of intensive cotton cultivations in the 1980s and 1990s has been recorded.

During its breeding season, the Lesser Kestrel inhabits the pseudo-steppes (open cultivated areas) of the Western Palearctic (Bustamante 1997) and forages in open areas of relatively low vegetation (Cramp et al. 1992, Negro 1997). Its feeding strategies may include selection of larger prey, thus shorter handling time, or selection of prey where it is more easily accessible (Catry et al. 2014). The species captures its prey in the air or on the ground, after hover-fluttering for prey detection (Garcia et al. 2006) or hunt directly from perching sites. Lesser Kestrel diet mainly consists of large arthropods (a large percentage of insects) and to a lower extent on small mammals (Tella et al. 1996). Orthoptera and Coleoptera are the main insect orders, while Dermaptera, Hymenoptera (mainly Formicidae family), Isoptera (mainly in the wintering areas) and other arthropods, such as Chilopoda (mainly Scolopendridae) and Galeodes (order Solifugae), are also preyed upon in a lesser extent by the species (Negro 1997, Rodriguez et al. 2010). In Thessaly, a study of the Lesser Kestrel diet during the breeding season, showed a relative abundance of Insects (98.3%), of which 56.2% were Orthoptera (mainly of the families Acrididae and Tettigoniidae), 32.3% Coleoptera (mainly of the families Carabidae and Scarabaeidae), as well as Formicidae, Dermaptera and Cicadidae in lower percentages (Sfougaris et al. 2004). In addition, Parr et al. (1997) have also reported small lizards as important prey of the species in Turkey. During the whole breeding season, studies from Spain and Portugal have reported high percentages (94.2-99.6%) of arthropods in the diet of the species, while a small part of the diet consisted of small mammals (4.5%), birds and reptiles. Specifically, Orthoptera constituted 38.5% to 85.8% of the species prey items, while Coleoptera 2.8% to 36.2% (Ortego 2010).

During the winter, in sub-Saharan Africa, the diet of the Lesser Kestrel consists mainly of Orthoptera, Coleoptera, Solifugae and a few small mammals, while Dermaptera, Scolopendridae and Isoptera are recorded to a lesser extend (Kopij 2002, Kopij 2007). On the other hand, Pietersen & Symes (2010) recorded Coleoptera as the main prey category of the species in wintering areas, while the species fed upon all aforementioned prey species to a lesser extent.

The feeding habits of the Lesser Kestrel are affected by the available categories of prey, the time of the year and the phase of their biological cycle. Studies conducted in France, recorded differences in the species diet, during the different periods within the species breeding season. Mole Crickets *Gryllotalpa gryllotalpa* were the dominant prey species during pair formation (Choisy et al. 1999), but *Decticus albifrons* (Tettigoniidae) was the dominant one during the rest of the breeding season. Furthermore, Rodríguez et al. (2010) in Spain also noted similar differentiation in the species diet. They recorded Mole Crickets as the main prey during lesser Kestrel's pair formation, the Bush Cricket *Ephippiger ephippiger* during incubation, and the Locust *Locusta migratoria* and the Bush

Cricket *Decticus albifrons* during nestling. In addition, as Hernández-Pliego (2014) and Ramellini et al. (2022) highlighted, the diet of the species is affected by the Lesser Kestrels modulation of their foraging movements according to the phenological phase. Moreover, in Thessaly the species was recorded to select different foraging habitats in the different phenological phases (Christakis & Sfougaris, 2021), suggesting changes in the species feeding preferences, among phases.

The purpose of this study was to investigate the composition of the Lesser Kestrel diet in the Thessalian plain during the different phases of breeding and post breeding periods. As the species status in Greece is still “vulnerable”, the study of its foraging ecology under the current changing conditions and agricultural practices at the Thessaly plain, which hosts almost 70% of the total Greek Lesser Kestrel population, was necessary for implementation of effective conservation and management practices.

MATERIALS AND METHODS

Study area

The study area is located in the Thessalian plain and is a representative agricultural ecosystem with intensive cultivation systems of arable crops which occupies an area of about 150 km^2. It includes the villages of Stefanovikeio (39°27’50.62” N, 22°44’32.02” E) and Rizomylos (39°25’43.11” N, 22°44’47.29” E). The villages adjacent and inside the study area, support relatively large colonies of the species — about 2,500 breeding pairs within a radius of 20km from Stefanovikio village according to LIFE11NAT/GR/001011 project [Conservation and management of the Lesser Kestrel (*Falco naumanni*) in three Special Protection Areas (SPAs) of Greece] population survey. The present study was carried out within the framework of the project (Fig. 1).

Diet composition based on pellet analysis

Pellets are the result of compression and extraction

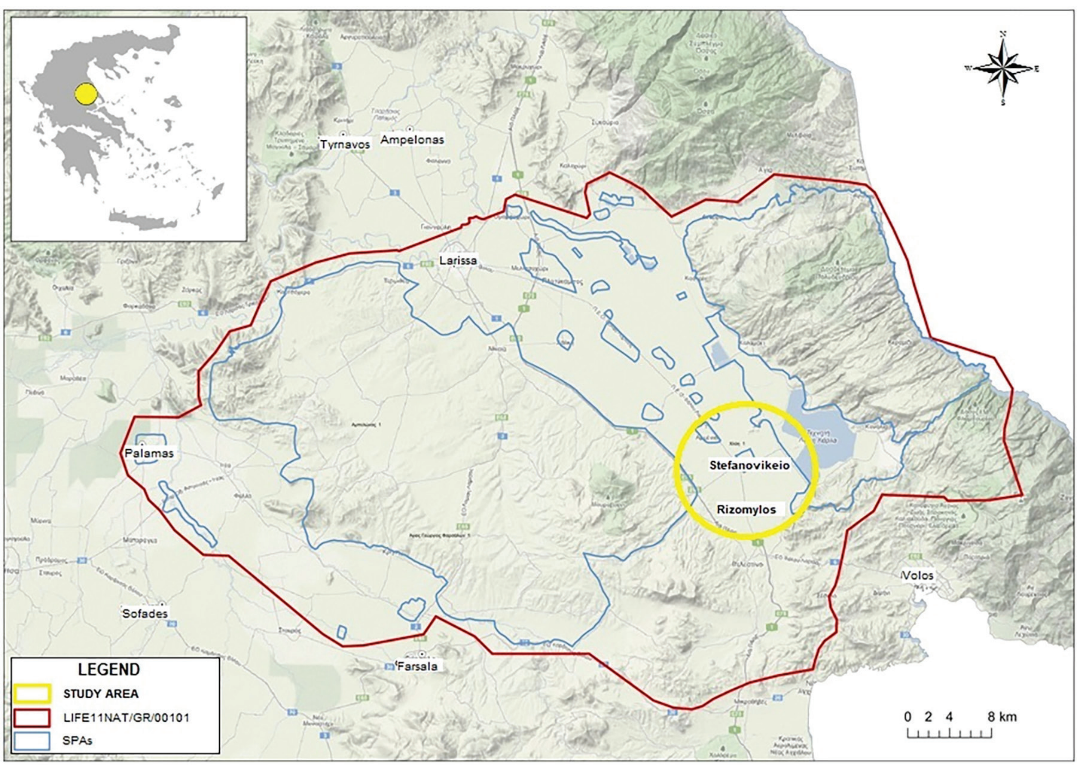

Figure 1. The study Area.

throughout the upper digestive tract of the indigestible residues of prey items of raptors and other bird species and they are usually produced daily. Identification of the prey residues in pellets can produce qualitative and quantitative estimates related to the composition of prey, without directly disturbing the targeted species (Marti et al. 2007). Disadvantage of the method is the decrease of its reliability, due to dismemberment of the prey during capture and consumption. Furthermore, the degradation of bones and chitinous components of insects due to digestion and breakage, could render them non-recognizable. However, the method of pellet collection and analysis is widely accepted by researchers and utilized in several diet studies of predators in general and of the Lesser Kestrel in particular (Kopij 2002, Sfougaris et al. 2004, Rodriguez et al. 2006, Kopij 2007, Perez-Granados 2010, Rodriguez et al. 2010, Catry et al. 2012, Kopij & Liven-Schulman 2012, Sara et al. 2014). Collection of pellets should be representative in terms of number and independence of samples, spatially and temporally, in order to ensure robust conclusions, depending on the research objectives (Sara et al. 2014). It is usually carried out near and inside nests and under perching and roosting sites of predators, while the collected samples must be relatively fresh. In addition, the inadvertent collection of similar sized pellets of other non-targeted species must be avoided (Marti et al. 2007).

Fieldwork took place from the beginning of April until September 2014 and 2015, thus, including the entire breeding and post breeding periods of the Lesser Kestrel for two consecutive years. The methodology included systematic visits to the two large colonies of the Lesser Kestrel in the study area, in villages Rizomylos and Stefanovikeio, to collect pellets on consecutive sampling dates. Pellets were collected under perching and roosting sites, nests and also under electric poles and cables near nests, trying to compensate pellets for the different contributions of sexes and juveniles to pellet production, since there are significant changes in the species population along the breeding season. At the beginning of the breeding season both males and females are roosting. However, when female Lesser Kestrels start incubating, male individuals roost more frequently. These different behavioral patterns between sexes, and furthermore the introduction of new juveniles later in season, may produce bias in data. The researchers also made sure to avoid the collection pellets of non-targeted species. Fresh and intact pellets were collected and packed in small plastic containers separately and later frozen for preservation. The sampling points were cleaned out of old pellets after each sampling. Each individual pellet was later crushed, and the prey item residues were identified using identification key resources (Willemse 1985, Chatenet 1986, Chinery 1993, Willemse 1993, McGavin 2000) and recorded. The rule of “pairs of parts” was followed to count prey items. Parts of exoskeletons were used to identify insects, while bones, teeth and hair were used to identify mammals. The majority of individuals found in each pellet were classified at family level.

Data analysis

To quantify the prey categories in the pellet analysis, the frequency of occurrence of the prey category in pellets was calculated (% F = number of pellets in which a prey category appears / number of total pellets x 100), and the specific abundance of each prey category (%P = percentage of prey category in relation to all prey categories, only in pellets containing that category).

For the estimation of the species richness and the evenness of prey categories and consequently the species feeding niche breadth, the Levins’ index $B = 1/\Sigma p_j^2$ was calculated (Levins 1968), where B is the Levins’ index, p_j the percentage of j prey category items consumed (Levins 1968). Levins’ index is maximized when there is an equal number of individuals in each prey category, i.e. the prey species are not classified to different prey categories and the maximum possible niche breadth is reached. In contrast, the index becomes minimum when all prey items belong to the same prey category, thus, minimum niche breadth and maximum specialization is calculated. The index values range from 1 to n, where n is the total number of prey categories. To have a better perspective of the niche breadth between phases we also calculated the standardized version of the index [Bsta = (B-1)/(n-1)], estimating the Levins' index in the scale of 0 to 1. In addition, the modified Costello method (Costello 1990, Amundsen et al. 1996) was used to assess the feeding strategy of the Lesser Kestrel in the study area, plotting the frequency of occurrence of each prey category (%F) and the specific abundance of each prey category (%P), as seen in Fig. 2 (Amundsen et al. 1996).

In the Amundsen diagram, the relative abundance of each prey category among the diagonal axis from the lower left to the upper right corner gives an estimate of the importance of that prey category in the species' diet. The distribution along each axis represents how specialized or generalized the bird's feeding strategy is. Prey categories in the upper right quadrant of the diagram demonstrate specialization of the population in the prey category, while in the upper left quadrant demonstrate specialization of individuals within the population in this prey category. The upper left quadrant or lower right quadrant represent prey categories that overall have the same contribution the diet of the species population yet are indicative of completely different feeding strategies. Prey with high relative abundance and low frequency of occurrence have been consumed by a few individuals, who show specialization in that prey, while prey with low relative abundance but high frequency of occurrence is consumed by most individuals in the population. The concept of the diagonal axes from the upper left to the lower right of the diagram is a measure of niche breadth. Furthermore, a high between-phenotype component (high BPC) reflects a population in which different individuals are specialized in different prey types, while a high within-phenotype component (high WPC) reflects a population in which most individuals consume many types of prey at a given time.

The pellet data were tested for normality and homogeneity. One-way ANOVA was used to compare the means of the distributions. When lack of normali-

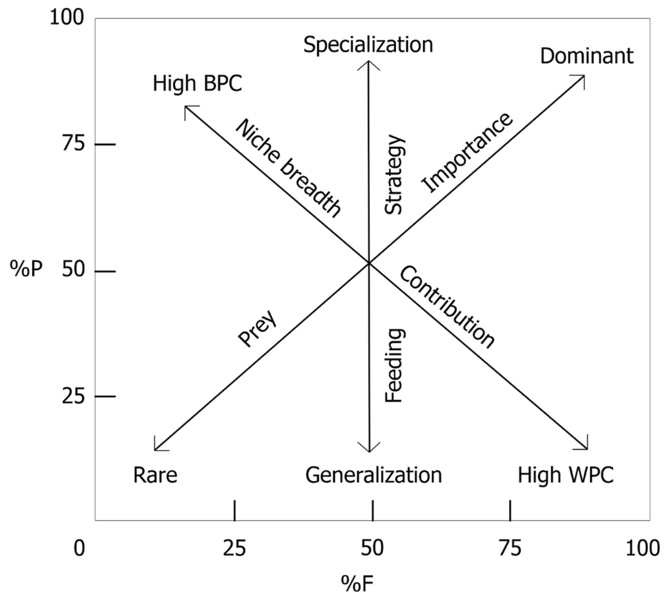

Figure 2. Explanatory diagram of the modified Costello method (Amundsen et al. 1996) (BPC: between-phenotype component; WPC: within phenotype component).

ty, Kruskal-Wallis non-parametric analysis of variance was used. In addition, χ^2 test was used to check for independence of the study variables. Tables, figures and statistical analysis of the pellet data were created and performed using Microsoft Excel 365, IBM SPSS Statistics 25 and PAST (v.4.02).

RESULTS

Diet composition

From April to September 2014 and 2015, 457 and 516 pellets of Lesser Kestrels were collected respectively, a total of 973 pellets for the whole study period. After behavioral observations of the species, the collected pellets were divided into three distinct phases, covering the breeding and post breading periods of the species in Thessaly, modifying Rodriguez & Bustamante (2003) methodology, as follows: 1st phase (pre): Pair formation phase, pre-breeding (late March to early May), 2nd phase (bre): Breeding phase, egg incubation and chick rearing (mid May to late June), 3rd phase (post): Post Breeding, pre-migratory phase (July and August). In 2014, 114 pellets were collected in pre breeding phase, 248 in breeding and 95 in post breeding phase. During 2015, 234, 147 and 135 pellets were collected for each phase respectively.

After pellet analysis, a total of 4,362 prey items were recorded (2,116 items in 2014 and 2,246 in 2015) and were systematically classified at family or a higher taxon level. During the first year, 555 prey items were recorded during the pre-breeding phase (4.87 ± 0.353 mean items per pellet), 1,127 during the breeding phase (4.54 ± 0.132 mean items per pellet), and 434 during the post-breeding phase (4.57 ± 0.190 mean items per pellet). Similarly, during the second year of the study, 1,178 prey items, (5.03 ± 0.264 mean items per pellet), 611 (4.16 ± 0.175 mean items per pellet) and 457 (3.39 ± 0.128 mean items per pellet) were recorded during the three phases, respectively.

Eight orders of insects were identified, namely four families of Orthoptera, 12 families of Coleoptera, some unidentified Coleoptera individuals, one family of Hymenoptera, two families of Dermaptera, one family of Hemiptera, as well as individuals of Neuroptera, Diptera and Lepidoptera. The rest of the arthropods recorded, were belonging to Chilopoda class (Tab. 1).

For further analysis, prey items were categorized into 9 prey categories: Orthoptera, Coleoptera, Formicidae, Dermaptera, Hemiptera, Other insects, Scolopendridae, Mammalia and Other taxa (Fig. 3). It seems that the Lesser Kestrel diet consisted mainly of Orthoptera, Coleoptera and Formicidae, whereas all other prey categories accounted for about 10% of the total. In 2014, 50% of the total number of prey items were Orthoptera, 32.1% Coleoptera and 10.7% Formicidae, while all other prey categories accounting for much smaller percentages. In 2015, Orthoptera constituted 29.0% of the total number of prey items, while Coleoptera was the prey category with the highest percentage of items recorded (36.4%). Formicidae were accounting for 21.0%, while all other categories smaller percentages.

During the first year of the study (2014), in the pre-breeding phase, the species hunted mainly Coleoptera (43.4%). The second most important prey category was Formicidae (31.9% of the total number of prey items). During the breeding phase, the Lesser Kestrel preyed mainly upon Orthoptera (68.7%). The second most important prey category was Coleoptera, which constituted 24.5% of the total prey items. During post-breeding phase, the species preyed mainly on Orthoptera (52.5%). Coleoptera category estimated at 37.6% of the total prey items.

During the second year of the study (2015), in pre-breeding phase, Coleoptera (49.2%) and Formicidae (36.5%) were the most abundant prey items in pellets. In the breeding phase, the species preyed mainly upon Orthoptera (59.6%) and Coleoptera (25.5%), and in the post-breeding phase, the species hunted mainly Orthoptera (47.5%). Other important prey categories were Formicidae and Coleoptera with 27.6% and 17.9% of the total number of prey items respectively.

Calculation of the frequencies of occurrence

Table 1. The taxa identified by pellet analysis and number of items identified in the different phases of the breeding seasons for both years of the study.

	Taxa	**Breeding phases**						
		1st year			**2nd year**			
		Number of items						
		pre	bre	post	pre	bre	post	Total
1	Acrididae	50	62	74	53	31	18	288
2	Tettigoniidae	1	693	152	×	329	199	1374
3	Gryllidae	2	5	×	×	×	×	7
4	Gryllotalpa spp.	4	14	2	18	4	×	42
5	Carabidae	147	187	99	354	94	47	928
6	Scarabaeidae	58	401	43	111	35	29	317
7	Geotrupidae	2	6	×	3	1	1	13
8	Silphidae	12	12	1	26	1	×	52
9	Staphylinidae	1	3	1	1	×	×	6
10	Buprestidae	11	5	1	14	7	1	39
11	Elateridae	3	2	3	4	1	2	15
12	Tenebrionidae	×	×	1	9	2	×	12
13	Cerambycidae	1	×	1	4	×	×	6
14	Curculionidae	×	5	1	3	3	×	12
15	Meloidae	1	×	×	×	×	×	1
16	Dytiscidae	1	×	×	5	×	×	6
17	Unidentified Coleoptera	4	15	12	45	12	2	90
18	Formicidae	177	44	6	430	31	11	699
19	Forficulidae	36	7	×	18	25	1	87
20	Lambiduridae	7	3	7	17	1	5	40
21	Cicadidae	×	×	24	0	1	126	151
22	Unidentified Hemiptera	×	×	×	×	2	×	2
23	Myrmeleontidae	×	×	×	2	1	×	3
24	Other Neuroptera	2	×	×	×	×	×	2
25	Diptera	3	×	×	1	×	×	4
26	Lepidoptera	×	4	2	×	2	×	8
27	Scolopendra spp.	26	5	1	16	6	×	54
28	Mammalia	4	13	3	31	20	12	83
29	Passer sp.	×	1	×	×	×	×	1
30	Gastropoda	2	×	×	8	2	2	14
31	Unidentified Ranidae	×	×	×	2	×	1	3
32	Lacertidae	×	×	×	2	×	×	2
33	Julidae	×	×	×	1	×	×	1

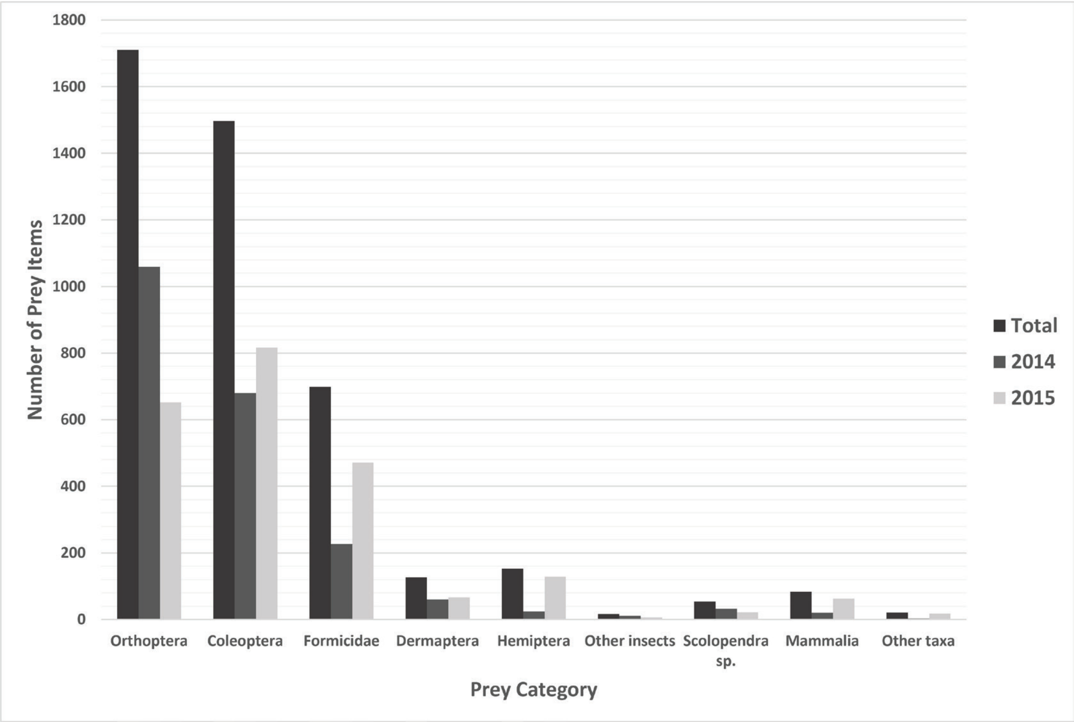

Figure 3. Number of prey items per prey category for 2014, 2015 and in total.

Table 2. Frequencies of occurrence of the prey categories in the pellets, during the breeding period and post breeding period in both years of the study (pre-breeding, breeding, and post breeding phase).

Prey category	**Frequencies of occurrence (%)**								
				Breeding Phase					
	Total	**Year**		**1st year**			**2nd year**		
		1°	2°	pre	bre	post	pre	bre	post
Orthoptera	58.2	71.3	46.5	37.7	85.9	73.7	26.1	71.4	54.8
Coleoptera	70.4	73.1	68.0	93.0	63.7	73.7	91.9	53.1	43.0
Formicidae	17.1	13.6	20.2	32.5	8.5	4.2	36.8	7.5	5.2
Dermaptera	6.0	6.3	5.6	17.5	2.8	2.1	6.4	6.1	3.7
Hemiptera	7.7	1.3	13.4	0.0	0.0	6.3	0.0	2.0	48.9
Other insects	1.6	2.2	1.2	3.5	1.6	2.1	1.3	2.0	0.0
Scolopendridae	4.4	5.9	3.1	19.3	1.6	1.1	5.6	2.0	0.0
Mammalia	8.4	4.4	12.0	3.5	5.2	3.2	13.2	12.9	8.9
Other taxa	1.8	0.4	3.1	0.9	0.4	0.0	5.1	1.4	1.5

(F%) of the main prey categories in the phases of the breeding and post breeding period in both years of the study (Table 2), revealed that overall, Orthoptera and Coleoptera accounted for the highest frequency of occurrence in the Lesser Kestrel pellets (58,2% and 70,4% respectively), followed by the Formicidae family (17,1%), which occurred mainly in the pre-breeding phase each year, while the rest of the prey categories had lower frequency of occurrence.

Orthoptera and Coleoptera

Considering the percentage of each Orthoptera family in the total number of Orthoptera prey items identified in the pellets (Fig. 4), it seems that Tettigonidae family constituted the vast majority of Orthoptera in the Lesser Kestrel diet during breeding and post-breeding phase for both years of the study, and Acrididae family during the pre-breeding phase of each year. On the contrary, Gryllidae family and the genus *Gryllotalpa*, contributed a small part of the Lesser Kestrel diet consisted of Orthoptera species. Furthermore, *Gryllotalpa sp*. had a relative increased contribution during the pre- breeding phase of both years of the study.

Concerning Coleoptera (Fig. 5), Carabidae family constituted more than 60% of this order in the Lesser Kestrel diet, in all phases for both years of the study, with an exception at the post-breeding phase of the second year when a lower percentage was recorded. The second most important Coleoptera family was Scarabaeidae, with slightly higher percentages during the two post-breeding phases of the study. All other families accounted for the rest 10% of the Lesser Kestrel Coleoptera diet.

The overall Orthoptera and overall Coleoptera prey items portion of the species diet differed significantly among the study phases (H_{orth} = 312.5, $p < 0.05$ and H_{col} = 221.4, $p < 0.05$ respectively). In contrast, comparing the percentages in the diet composition of Orthoptera and Coleoptera families, no statistically significant differences were found (F_{orth} = 0.4836, df = 23, $p > 0.05$ and F_{col} = 1,529, df = 83, $p > 0.05$).

Chi-squared, χ^2 test was performed to check for independence among the phases of the breeding and post breeding period of the Lesser Kestrel and the frequencies of occurrence of the four most important categories of prey items recorded in pellets. The null hypothesis supposed that the variables “breeding phase” and “prey category” were independent, meaning that the feeding habits of the Lesser Kestrel are not affected by the three biological phases of the species. The result of the test led to the rejection of the null hypothesis (χ^2= 190.3 d.f.= 15 and $p<0.001$) and consequently, the three phases of breeding and post breeding period affected the composition of the diet of the Lesser Kestrel.

Niche breadth

The values of the Levins’ index (B) based on the prey taxa (Table 1) and its stabilized version (Bsta) ranging from 0-1, reflect the niche breadth of the species, during the three phases of the breeding and post breeding periods. In 2014, the species niche breadth (B=5.04, Bsta=0.13) was broader during the pre-breeding phase in comparison to the other phases, demonstrating a wider variety of diet. The narrower value of the species’ niche breadth (B=2.43, Bsta=0.04) was recorded during the breeding phase, when the diet of the lesser kestrel was limited to variety and some categories of prey prevailed in the diet compared to others in relation to the other phases. During post breeding phase, the Levins’ index was calculated B=4.59, and the standardized one was Bsta=0.11. Similarly, during the following year (2015), the broader niche breadth of the species (B=4.20, Bsta=0.10) was recorded in the pre-breeding phase, thus highlighting a wider variety of diet during this phase, compared to the other phases. The narrower value niche breadth of the species (B=3.07, Bsta=0.06) was calculated for the breeding phase and an intermediate one (B=3.53, Bsta=0.08) for the post breeding phase, narrower than the respective one for the same breeding phase of the previous year.

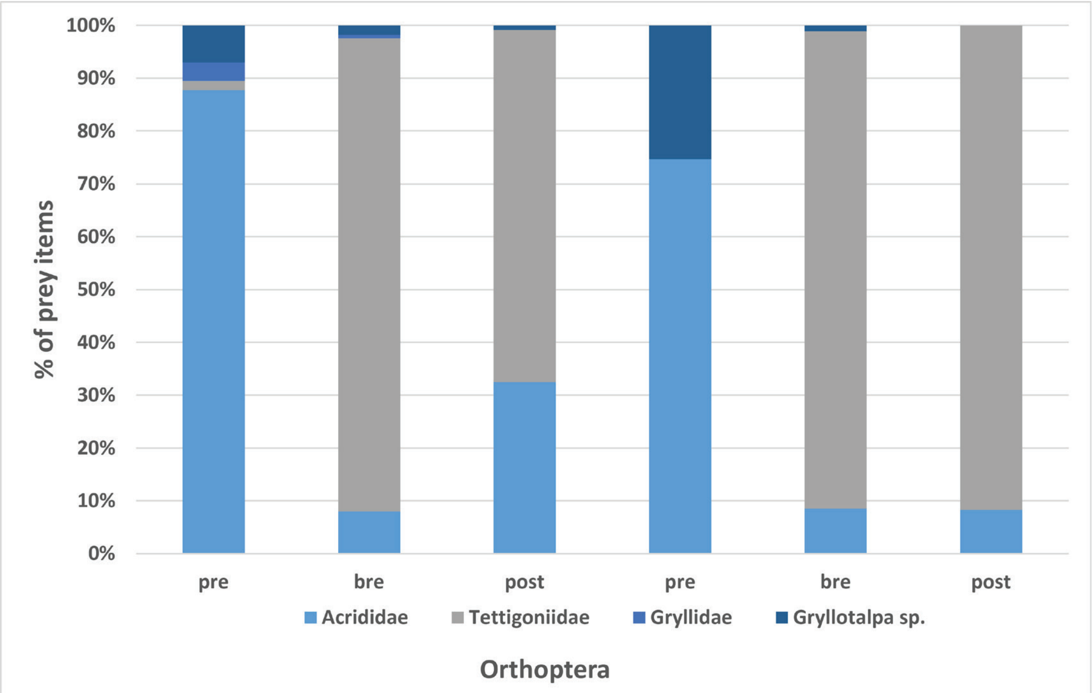

Figure 4. Percentage of Orthoptera families in the total number of Orthoptera prey items in the pellets analyzed.

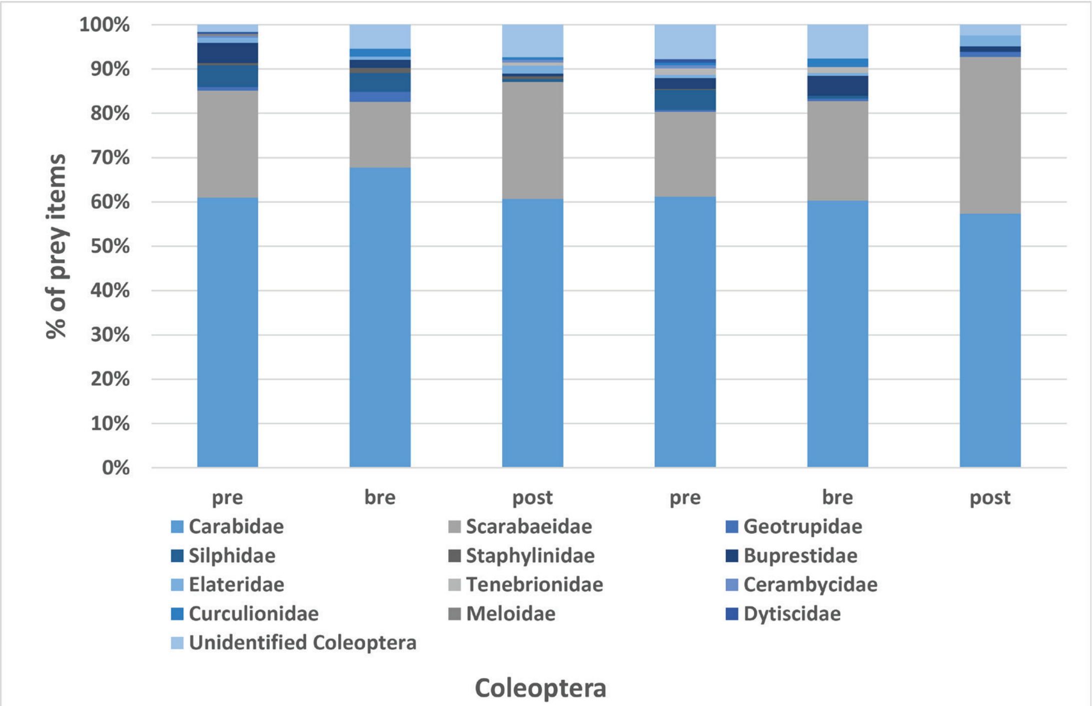

Figure 5. Percentage of Coleoptera families in the total number of Coleoptera prey items in the pellets analyzed.

Feeding strategy

To evaluate the feeding strategy of the species, the modified Costello method (Costello 1990, Amundsen et al. 1996) was applied, plotting the relative frequency of occurrence of each food category in the pellet containing each prey category (% P =% prey specific abundance) and the frequency of occurrence of each food category in all pellets (% F =% frequency of occurrence). Examining the distribution of points in the Amundsen diagrams generated, along the diagonals and axes of the diagrams, leads to highlighting the importance of each prey category, according to the method's explanatory figure (Fig. 2). Overall Coleoptera and Orthoptera seem to have been the most specialized and dominant feeding choices of the species in the study area, while all other prey categories were rare and not specialized (Fig. 6).

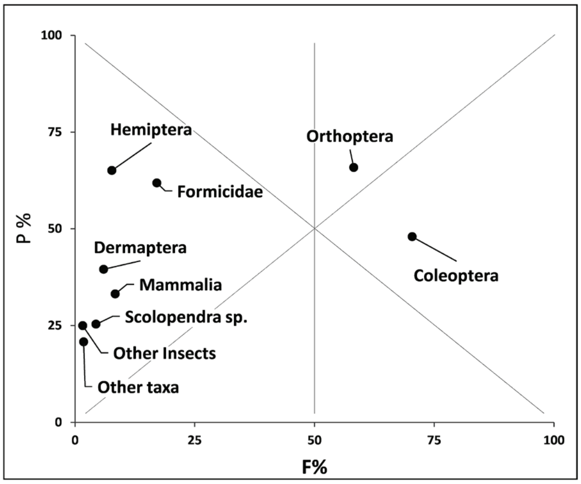

Figure 6. Feeding strategy of the species based on the total pellet data.

Lesser Kestrels, during the pre-breeding phase in both years of the study showed a similar pattern of feeding strategy, as shown in the respective graphs (Fig. 7). No prey category is found in the upper right quadrant, therefore the population does not seem to have been specialized in any prey category, while the species niche breadth appeared increased. Individual specialization was observed with respect to Formicidae, whereas a general preference was observed for Coleoptera. Orthoptera and the rest of the prey categories during this phase were less important.

A similar feeding strategy was shown by the graphs concerning the breeding and the post-breeding phase (Fig. 7), with the exception of post-breeding phase of 2015. During these phases, Orthoptera were the dominant and most important prey category, however in post-breeding phase of 2014, Coleoptera were of increased importance and specialization in the species diet. Formicidae in these phases were a non-significant and non-specialized prey category in relation to pre-breeding phase. Only some individuals of the population seemed to have a specialized choice during the breeding phase of 2014 and to a lesser extent during the post-breeding phase of 2015. Based on Amundsen diagrams, Coleoptera during these phases were the choice of most individuals of the species population in the study area. The other prey categories remained unimportant and rare diet choices.

The diagram pattern referring to post-breeding phase of 2015, reveals no prey category in the upper right quadrant. The species diet at this phase seems to have been based mainly on Orthoptera and Hemiptera and less on Coleoptera, whereas the other prey categories were insignificant and rare.

DISCUSSION

Diet composition

Raptor populations are affected by the availability of their prey (Bonal & Aparicio 2008), therefore studies concerning their diet composition are considered crucial for their conservation, especially for the Lesser Kestrel (Kopij 2002), a locally endangered species. Raptor ecology is well understood with the contribution of diet studies, conclusions of which are applied in their population management programs (Rodriguez et al. 2010). Data on the abundance of prey items at each phase of the breeding season of the species are considered necessary, as the possible scarcity of food can reduce its breeding success. Based on these data, it is possible, through manage-

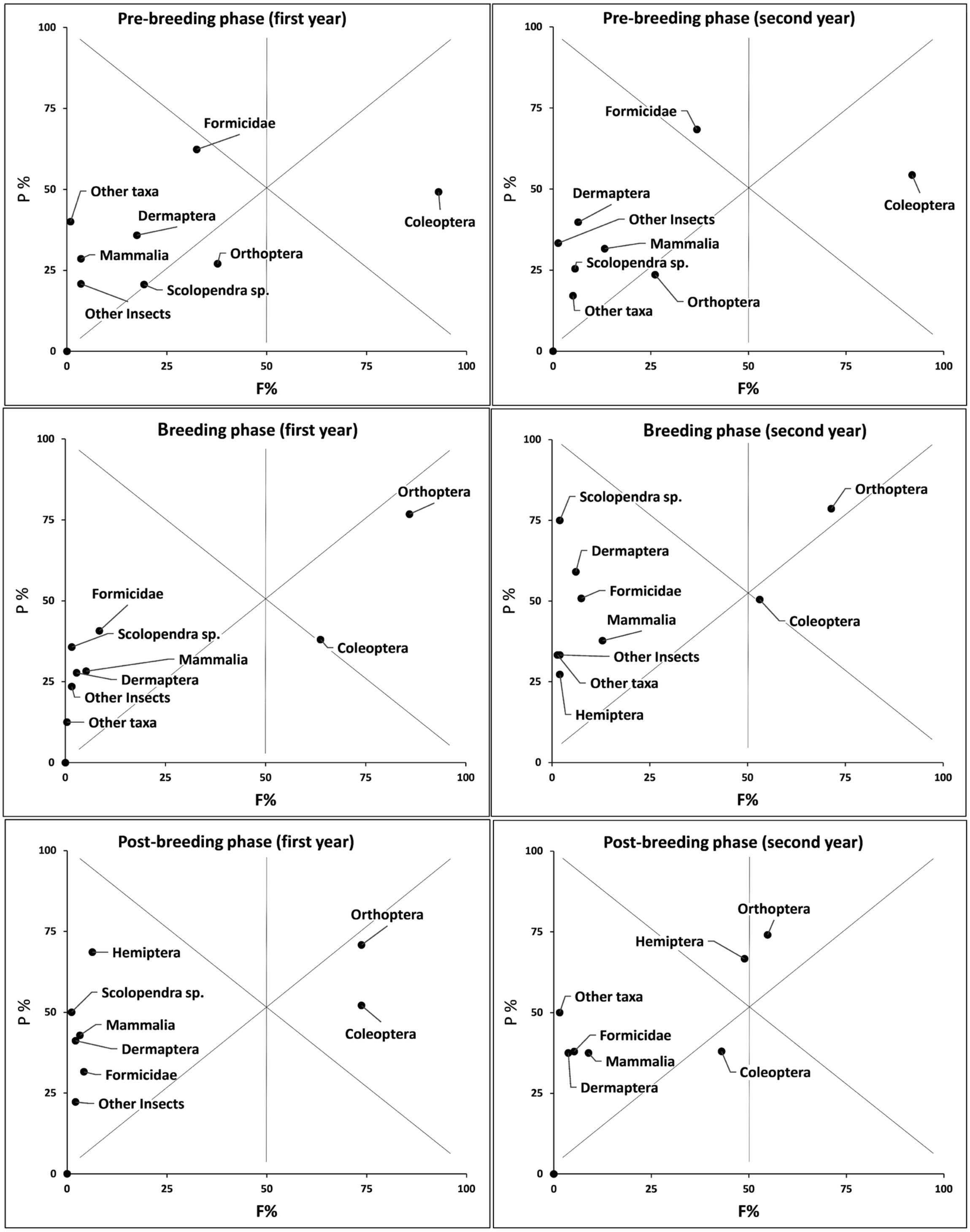

Figure 7. Feeding strategy of the species based on the pellet data of the different breeding and post-breeding phases.

ment of agroecosystems – foraging habitats, to increase the availability and accessibility of prey for the Lesser Kestrel during the breeding season (Franco & Sutherland 2004).

Based on the present data, Lesser Kestrel preyed mainly on arthropods (97.98%) throughout its breeding and post breeding period during the two years of the study, thus confirming its insectivorous nature. All diet studies concerning the species, have recorded high rates of arthropod consumption (Negro 1997, Cramp et al. 1992, Sfougaris et al. 2004, Rodriguez et al. 2010, Bounas & Sotiropoulos 2017, Ganbold et al. 2017, Di Maggio et al. 2018). Ortego (2010) in particular, reports variations from 94.2% to 99.6% in the consumption of arthropods during the breeding season of the species in areas of Spain and Portugal. Lesser Kestrel winter diet also consists of arthropods, as recorded in a twelve-year study of the species food preferences in South Africa (Kok et al. 2000). In the present study, other prey species, as small mammals, constitute a very small part of the Lesser Kestrel diet.

The diet of the species in the study area included mainly Orthoptera and Coleoptera and secondarily Hymenoptera (mainly Formicidae family), Dermaptera, other insects and arthropods, such as Chilopoda (mainly Scolopendridae). These results are consistent with those of a previous study from the region of Thessaly (Sfougaris et al. 2004). Ortego (2010), listed Orthoptera, Coleoptera, Hymenoptera, Dermaptera and arachnoids as the main prey species of the Lesser Kestrel. In various wintering areas of the species, where Solifugae residues were found in the pellets, arachnoids were a significant part of its diet (Kok et al. 2000, Kopij 2002). In the pellets analyzed during the present study, arachnoid species remains were not recorded, perhaps due to the high degree of digestion of this soft prey, while their population in the foraging area of the Lesser Kestrel was adequate (Christakis et al. unpublished data). The same is probably true for other prey species, e.g. insect larvae. The absence of such prey residues recorded in the pellets, may lead to underestimation of these types of prey. On the contrary, prey species with hard exoskeletons, bones and hairs, the remnants of which remain and are easily traceable in pellets, can be overestimated. This is a possible bias of the pellet analysis methodology (Pietersen & Symes 2010). Furthermore, in this study, mammals were a small part of the species diet. However, there are studies, such as Perez-Granados (2010), which report significant contribution of mammals, in terms of biomass, to the diet of the Lesser Kestrel, as well as Rodriguez et al. (2010), who have recorded significant consumption of mammals by the species during the first weeks of chick rearing. This is not confirmed in the Thessaly plain.

The analysis of pellets during the pre-breeding phase of the Lesser Kestrel led to the conclusion that the main prey category of the species in the study area was Coleoptera, especially Carabidae and Scarabaeidae families. In addition, Hymenoptera (mainly Formicidae), Dermaptera and Chilopoda (mainly Scolopendridae) were recorded. The important role of Coleoptera in the diet of the species in early spring has also been recorded by Perez-Granados (2010). Their availability at this time of the year since they depart their nymph shelters is one of the reasons for their importance as prey items. Furthermore, Orthoptera, mainly those of the genus *Gryllotalpa sp.*, have been reported as important prey species for the Lesser Kestrel during the pre-breeding phase (Choisy et al. 1999, Rodriguez et al. 2010, Catry et al. 2012). This was not confirmed in the study area, as pellets of this phase did not contain a high percentage of Orthoptera in general.

During egg laying and chick rearing, Lesser Kestrels in Thessaly hunted mainly Orthoptera. Many researchers, such as Perez-Granados (2010) and Rodriguez et al. (2010), reported significant contribution of mammals during chick rearing, suggesting the foraging of bigger in terms of biomass preys during this phase. Even though mammals were not a big part of the species diet in this study, the adults of Tettigoniidae and Acrididae families that were the main prey items recorded in this phase, also highlight the predation of large-sized prey in the same phase. The increased abundance and high availability of

Orthoptera, as well as their large size of adults during this phase, are the main reasons why the species preys mainly on this prey category (Rodriguez et al. 2006, Perez-Granados 2010, Rodriguez et. 2010). For the same reasons, pellets of the post-breeding phase of the study, during nest abandonment and beginning of autumn migration, consisted of a fairly large percentage of Orthoptera (mainly Tettigoniidae and Acrididae) for the two years of the study. Cicadidae, Carabidae and Scarabaeidae also contributed to the species diet, in this phase during the second year of the study to a lesser extent. This could be due to a late June drought that year affecting Orthoptera population. It must be noted that even though the two years of the study were roughly the same regarding weather conditions, some late raining took place in early April and a small drought period was recorded in late June that may affected prey availability in the post breeding phase 2015. The specialization of the species diet in specific preys, in these two phases of the breeding season is recorded by other authors. Lepley et al. (2000) recorded as the main prey species of Lesser Kestrel in the Crau (Mediterranean France) in chick rearing the *Decticus albifrons* (Tettigoniidae), while Sara et al. (2014) identified *Grylloderes brunneri* (Gryllidae), a small cricket as the main prey item prior to migration. These specializations in diet seem to favor the most abundant prey for each area (Kok et al. 2000), suggestion that is confirmed by Sara et al. (2014) and this study, since the aforementioned prey species recorded were the most abundant in the study area (Christakis et al. unpublished data).

In general, diet composition of the Lesser Kestrel in the study area, seemed to be affected by the different phases of the breeding and post breeding periods and the differences recorded were significant. Food availability significantly affects the breeding success of raptors, especially insectivorous ones, that are greatly influenced by insect populations and their outbreaks (Rodriguez et al. 2010). Birds of prey may adapt their breeding phenology in order to take advantage of the increasing population of the prey species, since successful breeding is highly energy demanding.

Niche breadth and feeding strategy

Lesser Kestrel showed a wide niche breadth during the pre-breeding phase of the study; thus, its diet was characterized by a variety of prey categories. Niche breadth decreased in range as the breeding season progressed and reached its minimum during the main breeding phase of the study. During this phase, the species restricted the variety of the diet, while it seemed to consume mainly specific prey categories, larger in size, thus consuming more biomass with less energy expenditure. The species during chick rearing, when energy demands are raised due to frequent nestling provisioning, increases its foraging efficiency (Ramellini et al., 2022), and as a result niche breadth marked the lowest range in both years of the study. In the post-breeding phase niche breadth had an intermediate range, for both years of the study. While interpreting the results, we must take into account that the variation of the number of pellets collected in the three phases and the number of preys recorded may have a small effect in Levins' index since increasing number of preys (or pellets) may lead to increased diet diversity, and thus overestimating the species niche breadth. However, the results of the study concerning niche breadth seem to suggest that this was not the case.

The variability of the niche breadth of the species during the different phases for the two years of the study could be related not only to prey phenology, but also to agricultural practices and the types of crops that are dominant or scarce in the area, that may allow different densities of specific types of prey. Rodriguez & Bustamante (2008) noted in that regard, that differences in prey availability could be explained by mean size of crop fields, agricultural inputs and practices. The same authors suggested as key role habitat for the species semi-natural and edge habitats, acting as prey reservoirs. These habitats also suggested as important for the species by Christakis & Sfougaris (2021) in the same study area of the Thessaly plain, are quite scarce, thus lesser kestrels take the most advantage of agricultural practices for capturing their prey (Morganti et al. 2021).

The species in Thessaly, in the framework of this study (Fig. 6 and Fig. 7) seem to consume mainly Coleoptera (Carabidae and Scarabaeidae) during pre breeding phase of the study but specialize on Orthoptera (Tettigoniidae and Acrididae) during the breeding and post breeding phases, while its feeding preferences during these phases can be characterized as opportunistic. Formicidae appeared to be consumed by some individuals of the population, with a high frequency in the pre-breeding phase pellets. The preference for a certain prey category in a given phase of the breeding and post breeding periods of the Lesser Kestrel and the absence of the same category from the diet in another phase of the periods, despite its abundance in the foraging habitats, has been observed in the past by Rodriguez et al. (2010). The energy requirements of each phase of the breeding and post breeding period of the species determine the consumption of different types of prey, while the size of the selected prey increases as the breeding season progresses (Rodriguez et al. 2010). The analysis of pellets in the present study confirmed the above conclusion, as at the beginning of the breeding season the Lesser Kestrels consumed different and small prey species, such as Carabidae and Scarabaeidae, Formicidae and Dermaptera, while later in the breeding season, preferred Tettigoniidae and Acrididae, which are larger in size and better fulfil the species energy needs. The increased temperature during the late spring-early summer allows arthropods to grow at an increased rate, so larger prey items are available as prey for the Lesser Kestrel. This delayed availability of larger prey may explain the fact that Lesser Kestrels do not begin egg laying before April, despite arriving in the breeding colonies earlier (Rodriguez et al. 2010). The energy requirements of each phase of the breeding and post breeding period of the species seem to determine the consumption of different types of prey. Finally, based on the pellet analysis results, the species, during its whole breeding season, made specialized and non-specialized prey choices.

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