

Diet of the Barn Owl (*Tyto alba*) and Little Owl (*Athene noctua*) in wetlands of northeastern Greece

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ABSTRACT. The diets of the Barn Owl (*Tyto alba*) and Little Owl (*Athene noctua*) were studied through pellet analysis in four northeastern Greek wetlands. Results from the months February-September showed that in all areas, the most important prey for the Barn Owl were small mammals (mainly *Mus* spp., *Microtus rossiaemeridionalis*, *Crocidura* spp. and *Apodemus* spp.) The mammalian prey composition showed winter-summer and among-areas differences. Except in the Evros Delta, where small mammals were dominant by both numbers and biomass, the most numerous prey of the Little Owl were insects (mainly Orthoptera and Coleoptera), but small mammals (mainly *M. rossiaemeridionalis* and *Mus* spp.) dominated the diet by biomass. Significant seasonal differences in prey composition occurred in the Evros Delta, while the summer diets were also different among wetlands. Barn Owl median prey biomass (MPB) was significantly higher than Little Owl MPB in summer, whereas prey diversity and evenness values were higher in the latter species as a consequence of considerable amounts of insects in its diet. In both owl species, MPB differed significantly among the wetlands in the year of study, while seasonal differences occurred occasionally in some of the wetlands. The total prey overlap (Pianka's symmetric equation) of the two owl species in the summer (range 27%-53%) was lower than the mammalian prey overlap (60%-97%) and both were greater than those found by other authors in most parts of the Mediterranean.

KEY WORDS : Barn Owl *Tyto alba*, Little Owl *Athene noctua*, diet, wetland, Greece.

INTRODUCTION

The Barn Owl (*Tyto alba* (Scopoli, 1769)) and the smaller-sized Little Owl (*Athene noctua* (Scopoli, 1769)) are sympatric in most of continental Europe and partly around the Mediterranean (CRAMP, 1985), belonging to common trophic guilds (that is groups of coexisting species with more or less dietary overlap, HERRERA & HIRALDO, 1976). The food habits and prey relationships of the Barn Owl have been much more widely studied but considerable geographical variation has been observed in prey composition of both species (BUNN et al., 1982 ; MIKKOLA, 1983 ; CRAMP, 1985 ; TAYLOR, 1994). The diet of both owl species is different from that of the central European populations (HERRERA & HIRALDO, 1976). Across the Mediterranean, which is characterized by drier and warmer climate than continental Europe, most studies on both species have been carried out in inland or island areas while information is lacking from coastal wetlands. Such areas, widely occurring in northeastern Greece, have been greatly transformed into cultivations but still include natural habitat of great conservation importance (MEHPW¹). Nowadays, despite delineation and managed wetland projects, adequate habitat conservation is still lacking.

The aims of this study were : a) to describe and compare the diets of the Barn Owl and the Little Owl in coastal wet-

lands of northeastern Greece b) to compare the owls' diet composition between winter and summer in each wetland and among wetlands studied and, c) to compare the results of this study with others carried out in Greece and in other Mediterranean countries. The study of the diets of these and other owl species is being continued in Greece, thus the results of this study have a preliminary character.

MATERIAL AND METHODS

Pellets of Barn Owl and Little Owl were collected on successive dates from February to August 1987, in known roosts. The study areas were in four wetlands in northeastern Greece, (described briefly below). The distances between them ranged from 15 to 92 km.

The Evros Delta (40°84' N, 26°07' E), is the easternmost Greek wetland. This area includes a high diversity of habitats, such as extensive saltmarshes and salty grounds, lagoons, sand dunes and sandy islands, reed beds, tamarisk and riverine forest, temporary and permanent freshwater marshes and extensive cultivation areas (BABALONAS, 1979 ; BRITTON & HAFNER, 1979 : unpublished report).

Porto Lagos (40°01' N, 25°08' E), is a small village situated within a wide wetland complex including the shallow, polluted, brackish Lake Vistonis on the north, surrounded by reed beds and forest remnants. Extensive coastal lagoons fringed marginally with saltmarshes, sandy beaches and livestock grazing fields extend to the southwest.

Lafres (39°05' N, 25°00' E) comprises a complex of two coastal lagoons close to each other named "Lafri" and

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¹ MEHPW: Ministry of Environment, Housing and Public Works. Project for delineation of Ramsar Convention wetlands. Wetland: Evros Delta (1985; 1986a; 1986b), Athens (in Greek).

“Lafrouda” surrounded by rocky cliffs with *Quercion ilicis* vegetation (MEHPW, 1986b). Extensive grasslands, saltmarshes, sandy beaches and cultivation areas occur mainly to the north of the lagoons.

Lake Mitrikou (hereafter Mitrikou) (40°99' N, 25°32' E) is a shallow freshwater lake extending over 2.3 km², surrounded by extensive reed beds and cultivation areas, situated in the vicinity of a coastal wetland complex (MEHPW, 1986a).

Samples from February to March were combined in a category hereafter called “winter”, whereas samples collected from April to August comprised a category that will be called “summer”.

The analysis of food from pellets may involve biases, especially in the case of the Little Owl, which captures invertebrates, such as annelid worms, that are difficult to recover from pellets. Nevertheless, analysis of pellets is still the most suitable method of studying the diet of owls. Pellets were analysed using reference books (Mammals : LAWRENCE & BROWN, 1973 ; CHALINE, 1974. Birds : BROWN et al. (1987). Reptiles : ARNOLD & BURTON (1980). Insects : CHINERY (1981). Mean weight of each prey was taken from the literature (Reptiles : HELMER & SCHOLTE (1985 : unpublished report). Birds : PERRINS (1987). Mammals : MACDONALD & BARRET (1993)). Due to uncertainties in the taxonomic position of mice *Mus* sp. in our area and the impossibility of reliably distinguishing mice *Apodemus* sp. by cranial characters alone (VOHRALIK & SOFIANIDOU, 1992), we did not separate them by species. The diets of each owl species were analysed separately for the winter and summer periods (where samples were available) in terms of numerical and biomass proportions, and

were compared between winter and summer and between species within common periods. The trophic diversity (NB) was estimated on a prey class level by using the antilog of the Shannon-Wiener index (SHANON & WEAVER, 1963), while in order to standardize the trophic diversity for comparison within and among the areas we calculated evenness index (MARTI, 1987). The diet overlaps (based on prey classes) between species in each wetland were estimated by PIANKA's symmetric equation (PIANKA, 1973 ; ALATALO, 1981 ; MARTI, 1987). These indices have been widely used in similar studies and were suitable for comparing our results with other studies.

In comparing the diet of Barn Owls among wetlands, due to the importance of mammals in their diet, we presented data on only mammalian prey to the species level, whereas other prey types were presented to a class level. Numerical proportions were compared by the χ^2 test. While for statistical reasons median prey weights were estimated and compared (by Mann-Whitney U-test or Kruskal-Wallis test), average prey weights were also estimated for comparisons with the literature. Cluster analysis was also performed to investigate whether dietary compositions were clumped by geographical area or by owl species.

RESULTS

Barn Owl

The diet of the Barn Owl in all studied areas consisted mainly of mammals, although birds, amphibians and arthropods were also included in lower proportions (Table 1). Of

TABLE 1
Diet of the Barn Owl in wetlands of northeastern Greece. W: winter; S: summer.

Prey	Evros Delta				P. Lagos				Lafres				Mitrikou			
	% Nr		% Biomass		% Nr		% Biomass		% Nr		% Biomass		% Nr		% Biomass	
	W	S	W	S	W	S	W	S	W	S	W	S	W	S	W	S
CRUSTACEA	-	-	-	-	-	-	-	-	-	0.2	-	0.1	-	-	-	-
CHILOPODA	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-
INSECTA	-	-	-	-	2.3	0.6	0.2	0.1	1.7	0.2	0.1	0.0	0.6	1.2	0.0	0.2
AMPHIBIA	-	-	-	-	-	-	-	-	0.3	0.5	0.7	0.8	-	-	-	-
AVES	-	-	-	-	5.8	4.2	14.7	9.9	2.8	2.2	9.0	4.1	12.9	11.1	39.6	43.4
MAMMALIA	100	100	100	100	92.0	95.3	85.1	90.0	95.1	96.8	90.2	95.0	86.5	87.7	60.4	56.3
<i>Neomys</i> spp.	0.0	2.0	0.0	1.5	-	-	-	-	-	-	-	-	-	-	-	-
<i>Suncus etruscus</i> (Savi, 1822)	0.9	0.0	0.1	0.0	0.6	2.0	0.1	0.3	1.4	1.0	0.2	0.1	3.2	12.3	0.4	1.6
<i>Crocidura suaveolens</i> (Pallas, 1811)	28.2	31.3	12.3	13.8	19.3	16.2	7.9	6.6	21.5	14.1	10.0	5.5	18.7	8.6	7.4	3.4
<i>Crocidura leucodon</i> (Hermann, 1780)	1.4	0.0	0.8	0.0	1.9	1.7	1.1	0.9	8.7	6.7	5.4	3.5	21.9	25.9	11.5	13.6
<i>Crocidura</i> spp.	1.4	-	0.7	-	-	-	-	-	1.0	0.7	0.6	0.3	-	-	-	-
Soricidae unidentified	0.0	1.0	0.0	0.4	-	-	-	-	-	-	-	-	-	-	-	-
<i>Pipistrellus</i> spp.	-	-	-	-	0.3	0.3	0.1	0.1	-	-	-	-	-	-	-	-
<i>Microtus rossiaemeridionalis</i> Ognev, 1924	37.7	22.2	54.9	32.7	20.3	22.1	27.6	29.9	22.2	42.3	34.4	55.5	8.4	8.6	11.0	11.4
<i>Arvicola terrestris</i> (Linnaeus, 1758)	-	-	-	-	0.3	-	1.3	-	-	-	-	-	-	-	-	-
<i>Rattus rattus</i> (Linnaeus, 1758)	-	-	-	-	1.0	1.1	3.9	4.5	-	-	-	-	-	-	-	-
<i>Apodemus</i> spp.	7.3	22.2	10.6	32.7	7.4	11.2	10.1	15.2	3.5	9.4	5.4	12.3	5.8	3.7	7.6	4.9
<i>Micromys minutus</i> (Pallas, 1771)	-	-	-	-	0.6	1.4	0.2	0.5	-	0.2	-	0.1	-	-	-	-
<i>Mus</i> spp.	22.7	21.2	19.9	18.8	40.2	38.8	32.9	31.6	36.1	22.0	33.5	17.3	27.7	27.2	21.8	21.4
Muridae unidentified	-	-	-	-	-	-	-	-	0.7	0.2	0.8	0.2	0.6	1.2	0.6	1.2
Rodentia unidentified	0.5	0.0	0.7	0.0	-	-	-	-	-	-	-	-	-	-	-	-
Number of prey items	220	99			311	358			288	404			155	81		

1916 prey items of the Barn Owl in the four wetlands studied (both seasons, 1987), 95% were mammals, 4% birds and 1% amphibians and arthropods. The mammalian prey, including at least 11 species, consisted mainly of *Mus* spp. (31% numerically), *Microtus rossiaemeridionalis* (26%), *Crocidura* spp. (26%) and *Apodemus* spp. (8%) but there were differences between seasons depending on the species and area. These species also were the most important in terms of biomass in both seasons. The total proportions of mammalian prey both by numbers and biomass were similar in each wetland be-

tween winter and summer. Birds, being a much less important diet constituent, varied more in proportions among areas but differences between winter and summer were not considerable. The evenness values and median prey weights (except in Lafres) were similar between winter and summer (Table 2). The median prey biomasses (with an overall average of 14.4 g), (Table 2), differed significantly among the four wetlands due to differences in the ranges of individual prey weights (winter : $\chi^2 = 20.081$, $df = 3$, $P = 0.0002$; summer : $\chi^2 = 32.874$, $df = 3$, $P < 0.001$, Kruskal-Wallis χ^2 tests).

TABLE 2

Prey size parameters and prey diversity indices of the Barn Owl and Little Owl in northeastern Greek wetlands. Statistics between adjacent median prey weight values were performed using Mann-Whitney U tests.

Sample	N	Median (g)	Average (g)	Range (g)	Significance*	Diversity	Evenness
<i>Tyto alba</i>							
Evros Delta, winter	220	12.0	13.7	2-20	n. s.	0.00	0.00
Evros Delta, summer	99	12.0	13.6	6-20		0.00	0.00
Porto Lagos, winter	311	12.0	14.9	1-80	n. s.	1.39	0.46
Porto Lagos, summer	358	12.0	15.2	2-100		1.23	0.43
Lafres, winter	288	12.0	12.9	0.5-100	$P < 0.0001$	1.27	0.39
Lafres, summer	404	20.0	15.1	2-30		1.19	0.36
Mitrikou, winter	155	12.0	15.7	0.5-100	n. s.	0.42	0.59
Mitrikou, summer	81	12.0	15.4	2-70		0.41	0.55
<i>Athene noctua</i>							
Evros Delta, winter	428	20.0	14.3	0.2-70	$P < 0.0001$	1.89	0.58
Evros Delta, summer	361	12.0	10.3	0.1-70		2.48	0.83
Porto Lagos, summer	105	2.0	4.8	0.1-25		2.20	0.55
Lafres, summer	118	0.5	6.9	0.1-25		2.91	0.72

Little Owl

In the study areas, the Little Owl preyed mainly on small mammals and insects, but also, to a lesser extent, on other invertebrates, birds, reptiles and fish (Table 3). In total insects were the most numerous prey, making up 52% of 1012 prey items, followed by mammals (41%, at least eight species) being the most important biomass, with *Microtus* and *Mus* sp. predominating (17% and 11% respectively). The remaining prey types (birds, reptiles, fish and various invertebrates) made up 7% of the total by number.

In the Evros Delta, insect proportions increased in the summer whereas mammal proportions dropped. This resulted in a significantly greater median prey weight and a lower evenness in winter (Table 2). Median prey weight was significantly different in the summer among the three wetlands, being considerably highest in the Evros Delta (Kruskal-Wallis $\chi^2 = 22.781$, $df = 2$, $P < 0.0001$) reflecting differences in the use of prey types. Diversity indices had relatively high values (Table 2) reflecting the considerable diversity in prey use by the Little Owl.

TABLE 3

Diet of the Little Owl in wetlands of northeastern Greece. W: winter, S: summer of 1987.

Prey	Evros Delta		Porto Lagos		Lafres		
	% Nr	% Biomass	% Nr	% Biomass	% Nr	% Biomass	
	W	S	W	S	S	S	
MOLLUSCA	-	0.6	-	0.2	-	0.8	0.1
CRUSTACEA	-	0.3	-	0.1	-	-	-
ARACHNIDA	-	-	-	-	-	0.8	0.1
DIPLOPODA	-	-	-	-	1.9	0.2	0.2
ANNELIDA	0.2	0.0	-	-	-	-	-

TABLE 3
Diet of the Little Owl in wetlands of northeastern Greece. W: winter, S: summer of 1987.

Prey	Evros Delta				Porto Lagos		Lafres	
	% Nr		% Biomass		% Nr	% Biomass	% Nr	% Biomass
	W	S	W	S	S	S	S	
INSECTA	17.3	44.6	0.8	3.9	75.5	23.1	53.4	4.4
Orthoptera	2.1	9.4	0.3	1.8	46.7	20.5	0.8	0.2
Dermaptera	0.5	3.9	-	0.1	2.9	0.1	9.3	0.6
Coleoptera	14.7	31.3	0.4	2.0	24.9	2.5	41.5	3.6
Hymenoptera	3.7	3.6	-	-	1.0	-	1.7	0.0
PISCES	-	0.6	-	0.3	-	-	-	-
REPTILIA	1.2	1.9	1.1	5.7	-	-	0.8	0.5
AVES	1.9	1.9	3.9	7.0	5.8	26.5	5.1	16.1
MAMMALIA	79.2	49.9	94.3	82.7	17.3	50.2	36.4	78.6
<i>Neomys anomalus</i> Cabrera, 1907	-	-	-	-	-	-	0.8	1.2
<i>Crocidura leucodon</i> (Hermann, 1780)	0.2	0.3	0.1	0.2	-	-	0.8	1.0
<i>Crocidura suaveolens</i> (Pallas, 1811)	2.8	1.9	1.2	1.1	2.9	3.6	1.7	1.4
<i>Crocidura</i> spp.	-	0.6	-	0.4	-	-	-	-
<i>Suncus etruscus</i> (Savi, 1822)	0.2	-	-	-	-	-	-	-
<i>Pipistrellus pipistrellus</i> (Schreber, 1774)	-	0.6	-	0.3	-	-	-	-
<i>Microtus rossiaemeridionalis</i> Ognev, 1924	42.1	25.5	59.2	49.7	4.8	19.9	3.4	9.6
<i>Apodemus</i> spp.	3.5	4.4	4.9	8.7	-	-	12.7	35.9
<i>Mus</i> spp.	21.5	11.4	18.1	13.3	6.7	16.7	16.1	27.2
Muridae indetermined	0.9	0.6	1.0	0.8	1.9	6.0	-	-
Rodentia indetermined	3.7	2.8	5.3	5.4	1.0	4.0	0.8	2.4
Mammalia indetermined	4.2	1.9	4.4	2.8	-	-	-	-
Number of prey items	428	361			105		118	

In all areas mammals were more numerous in the diet of the Barn Owl and insects in the diet of the Little Owl. Total prey overlap in the summer ranged from 27% to 53%, while the overlap in mammal prey was much higher ranging from 60% to 97%. Both prey diversity and evenness were considerably higher in the diet of the Little Owl than in the diet of the Barn Owl (Table 2). In the cluster analysis of biomass dietary proportions for all samples and areas, most prey samples of each owl species were clumped together despite the fact that they originated from different areas.

DISCUSSION

Seasonal variation in the owls' diets

From our samples we could conclude that there were differences in the composition of mammalian prey of the Barn Owl between summer and winter in most areas. Seasonal dietary differences have also been found in some other studies (e.g. CAMPBELL et al., 1987; TAYLOR, 1994) but have not been clear in others (SMITH et al., 1972; PARKER, 1988). Such differences have been attributed to seasonal fluctuation in abundance and behavioural changes of mammalian prey (WEBSTER, 1973; BROWN, 1981; GOSZCZYNSKI, 1981; TAYLOR, 1994). BUNN et al. (1982) attributed seasonal variations in the predation of shrews to differences between habitat types in the different areas.

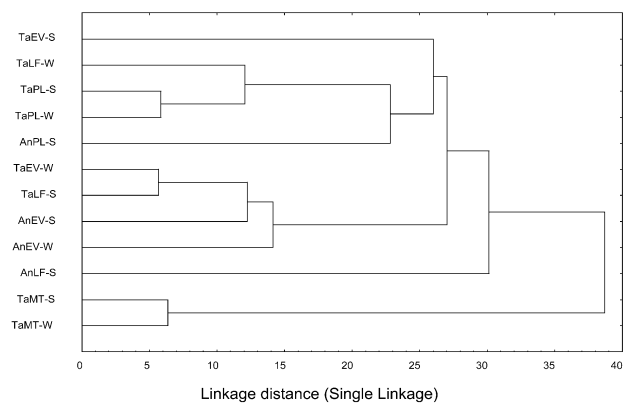


Fig. 1.—Dendrogram showing linkage distance of dietary similarity of Barn Owl and Little Owl in northeastern Greek wetlands. Ta: *Tyto alba*. An: *Athene noctua*. EV: Evros Delta. MT: Lake Mitrikou. PL: Porto Lagos. LF: Lafres. S: summer. W: winter.

Regarding the Little Owl, a seasonal change in prey diversity and evenness indices (as in the Evros Delta), denotes an opportunistic exploitation of food resources. Other studies have also revealed seasonal changes in the Little Owl's diet (CRAMP, 1985; ZERUNIAN et al., 1982; MIKKOLA, 1983). The highest prey diversity at Lafres suggests that prey was taken from a more diverse spectrum of habitats, probably because the relative transformation of this area by man is low. Certainly, more information on the

seasonal behaviour of small mammals in our study areas would throw more light on the variation of the owls' diet.

Interspecific prey variation

In each area, differences in the diet of the two owl species were found a) in the general prey composition, containing more invertebrates in the Little Owl (as in BUNN et al., 1982; CAPIZZI & LUISELLI, 1995). b) in the relative composition of mammalian prey and c) in the median prey weight, being lower in the Little Owl (as a consequence of invertebrate predation). Differences in hunting techniques and different morphology and digestive efficiency of the two owl species may partly account for a different representation of prey remains in pellets (BUNN et al., 1982). The different average prey weight seems to be the result of different energetic demands of each species, with the larger species (the Barn Owl) generally taking larger prey (MARTI, 1974). The cluster analysis, which revealed a considerable dietary clumping by owl species, i.e. dietary differentiation of the two species in the study area, possibly suggests a degree of prey selection by both species. This is also supported by the low total prey overlap of the two species. However, the suggestion of selection of a kind of prey is speculative unless supported by experimental evi-

dence. In Spain, the owls' dietary overlap was even lower (5%, HERRERA & HIRALDO, 1976; DELIBES et al., 1984) and in parts of Europe these owls do not co-exist in the same areas, therefore they exist in different trophic guilds (JAKSIC, 1988). In contrast, there was a considerable mammalian prey overlap found both in this study and other Mediterranean studies (94%, GOTTA & PIGOZZI, 1997) suggesting that the situation of the trophic guilds in the Mediterranean countries is more complex than originally believed and needs further investigation.

Geographical variation in prey use

In our area the differences between areas in the composition of main mammalian prey in the diet of both owls probably reflect geographical particularities in prey composition. Geographical variation in prey use by the Barn Owl has been attributed to various factors that influence the prey, such as habitat (including human-induced changes), geographical location, altitude, rainfall and temperature (HERRERA, 1974a; 1974b; DUENAS & PERIS, 1985; MARTI, 1988; TORRE et al., 1996; YOM-TOV & WOOL, 1997). Dietary variation of the Little Owl in different areas was reported by ZERUNIAN et al. (1982) and attributed to different habitat use.

TABLE 4
Importance of small mammals in the diet of barn owls across the Mediterranean Region

	Diet content (% by number)		Total number of mammal species	Most frequent mammal prey by number		Most important mammal prey by biomass		No. of species forming 80% of diet by		Prey weight (g)		References
	Small mammals	Rodents		Species	% of diet	Species	% of diet	Number	Biomass	Average	Range	
1. Greece												
This study	94.8	66.7	11	<i>Mus spp.</i>	30.9	<i>Mus spp.</i> ^a #	30.4	4	5	14	1-70	this study, 1987
Euboea island	92.8	83.6	8	<i>Mus spp.</i>	32.9	<i>Rattus norvegicus</i>	60.1	4	3	24	2-60	AKRIOTIS, unpubl. data
Korfu island	90.2	74.5	15	<i>Apodemus sylvaticus</i>	50.6	<i>Apodemus sylvaticus</i>	52.2	4	4	19	1-60	BÖHR, 1962
Krete island	96.5	87.6	7	<i>Mus musculus</i>	72.1	<i>Mus musculus</i>	57.0	2	3	15	2-60	CHEYLAN, 1976
Attica (Dafni)	67.6	53.5	6	<i>Apodemus mystacinus</i>	29.6	<i>Apodemus mystacinus</i>	76.5	***	2	15	2-40	CHEYLAN, 1977
Attica (Hymettus)	84.9	81.7	4	<i>Mus domesticus</i>	47.1	<i>Mus domesticus</i>	38.5	3	****	21	6-100	TSOUNIS & DIMITROPOULOS, 1992
2. Elsewhere												
Spain ^{ab}	96.8	79.2	10	<i>Mus spp.</i>	44.4	<i>Mus spp.</i>	37.3	4	4	17	4-30	BRUNET-LECOMTE & DELIBES, 1984
	87.1	68.8	12	<i>Mus musculus</i>	44.9	<i>Mus musculus</i>	37.0	4	4	20	10-30	HERRERA, 1974a
France (Provence)	99.5	84.8	8	<i>Mus musculus</i>	54.1	<i>Mus musculus</i>	41.8	2	3	16	1-30	CHEYLAN, 1976
Italy *	96.1	77.4	12	<i>Apodemus spp.</i>	33.7	<i>Apodemus spp.</i>	49.0	5	3	18	5-80	LOVARI et al., 1976
Italy *	97.6	80.6	13	<i>Microtus savii</i>	38.6	<i>Microtus savii</i>	43.2	7	4	20	2.5-105	CAPIZZI & LUISELLI, 1996
Slovenia	99.0	32.2	18	<i>Neomys anomalus</i>	20.9	<i>Neomys anomalus</i>	19.0	8	9	14	1-70	TOME, 1992
Palestine *	77.7	65.0	11	<i>Microtus socialis</i>	46.1	<i>Microtus socialis</i>	-	3	-	-	-	DOR, 1947
Israel	99.0	97.6	5	<i>Meriones spp.</i>	49.8	<i>Meriones spp.</i>	49.8	2	2	48	20-120	YOM-TOV & WOOL, 1997
Israel	96.2	92.4	7	<i>Gerbillus dasyurus</i>	59.5	<i>Gerbillus dasyurus</i>	-	2	-	-	-	REKASI & HOVEL, 1997
Egypt	45.3	50.0	5	<i>Mus musculus</i>	42.8	<i>Rattus rattus</i>	26.8	**c	***d	35 ^e	9-201	GOODMAN, 1986
Morocco *	99.7	88.7	4	<i>Mus musculus</i>	69.7	<i>Mus musculus</i>	-	4	-	-	-	SAINT-GIRONS & THOUY, 1978

a.# *Microtus rossiaemeridionalis* contributed similarly to biomass, 30.3%.

b.* Compiled by TAYLOR, 1994

c.** Five mammal prey species comprised only 52.6% of the diet by number and c. 50% by biomass.

d.*** Six mammal prey species comprised only 67.6% of the diet by number.

e.**** Four mammal prey species comprised only 75.8% of the diet by biomass.

TABLE 5
Comparison of the main prey categories of Little Owls in Mediterranean countries.

Prey	Spain	Spain	Italy	Italy	Egypt	Euboea isl. Greece	Astyp- alea isl. Greece	NE Greece
INVERTEBRATES	95.9	96.2	95.7	88.2	14.3	97.6	99.4	38.3
PISCES	-	-	-	-	-	-	-	0.2
AMPHIBIA	0.2	1.6	-	-	-	-	-	-
REPTILIA	0.5	0.6	0.5	-	12.5	0.1	0.3	1.3
AVES	0.4	0.3	1.1	0.5	16.1	0.3	0.1	2.9
MAMMALIA	2.8	1.3	2.7	11.3	57.1	2.4	0.2	57.3
Insectivora	-	-	0.3	1	1.8	0.4	0.2	3.1
Chiroptera	-	-	-	-	-	-	-	0.2
Rodentia	2.5	1.1	1.2	10.3	55.4	1.6	-	51.6
Other	-	0.2	1.2	-	-	-	-	2.5
Total number of prey items	5018	631	3405	1636	56	1763	1068	1012
Prey Diversity (NB)	1.23	1.27	1.15	1.46	3.19	1.13	1.06	2.36
Evenness (N)	0.39	0.33	0.33	0.57	0.71	0.31	0.33	0.86
References	HERRERA & HIRALDO, 1976	JAKSIC & MARTI, 1981	ZERUNIAN et al., 1982	CAPIZZI & LUIZELLI, 1996	GOODMAN, 1988	AKRIOTIS, unpubl. data	ANGELICI et al., 1997	This study, 1987

In northeastern Greece, habitat differences between study areas are considerable (MEHPW, 1985; 1986a; 1986b), probably accounting for differences in the composition of the small mammals in the diet of both owls. The dominance of mice in the diet of both owls was possibly due to this prey's greater abundance in the study area as a previous trapping study suggested: 42% of a total of 473 small mammals trapped in northeastern Greece were mice (VOHRALIK & SOFIANIDOU, 1992). *Microtus* may actually be abundant, because it also makes up a considerable part of the diet of other raptors in Evros (ALIVIZATOS & GOUTNER, 1997). Thus the highly opportunistic Little Owl, being typically insectivorous in other parts of Europe (see further), exploited this abundant mammalian prey source.

Comparisons with other studies

Mice were the most frequent mammalian prey of the Barn Owl's diet in most Mediterranean areas. The mean proportion of small mammals in this species' diet in our study area (94.8%), fell within the range of the respective proportions in other parts of Greece (84.9% to 96.5%) (Table 4). In northeastern Greece, the total number of mammalian prey species fell within the range of that in other Mediterranean areas (4-18), but the estimated average prey weight was 14.2 g (2.9 g to 15.4 g), being among the lowest in the Mediterranean, the rest of Europe (12.8 g to 25.0 g) and the New World populations (TAYLOR, 1994). The information in Table 4 suggests that Barn Owls, mainly small mammal predators across the Mediterranean countries, seem to exploit locally available and/or abundant prey, probably according to the local situations, without a particular pattern being apparent in regard to geographical location.

Little Owls preyed upon a wide prey spectrum varying among northeastern Greek study areas. In four Italian neighbouring areas such prey variability resulted from hab-

itat differences (ZERUNIAN et al., 1982). The diet of Chilean, American and Spanish *Athene* populations presented discrepancies that reflected differential availability and not selection of prey (JAKSIC & MARTI, 1981; JAKSIC, 1988). Thus, habitat and opportunistic feeding behaviour of Little Owls seems to affect the composition of their diet locally.

In most Mediterranean countries Little Owls prey mainly upon invertebrates (Table 5). It has been suggested that the relative proportions of invertebrates in the diet during the breeding season increase gradually from mid-Europe to the Mediterranean (HERRERA & HIRALDO, 1976; MIKKOLA, 1983). However, in northeastern Greece and Egypt (also in Sicily, LO VERDE & MASSA, 1988), there were considerably higher proportions of mammals; a fact that may have considerable consequences in the biology of these populations of the Little Owl and is worthy of further studies.

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