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Source: Acta Ornithologica, 36(2) : 153-160

Published By: Museum and Institute of Zoology, Polish Academy of Sciences

URL: <https://doi.org/10.3161/068.036.0208>

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Barn Owl *Tyto alba* predation on small mammals in relation to the Mediterranean environment (Pisa Province, Italy)

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Varuzza P., Capizzi D., Santini L., Apollonio M. 2001. Barn Owl *Tyto alba* predation on small mammals in relation to the Mediterranean environment (Pisa Province, Italy). *Acta Ornithol.* 36: 153–160.

Abstract. The diet of the Barn Owl was investigated in 13 localities in the Pisa province, Central Italy. In each locality the percentage of forest and cultivated land, and the linear development of roads and rivers were recorded. To estimate the prey availability, the small mammal communities in seven different localities within the same province were sampled during live trapping sessions. Barn Owls preyed mainly upon rodents (79.4%) and insectivores (18.8%), while birds were eaten to a small degree (1.9%). The main prey taxon was *Apodemus* sp. (39.7%), followed by *Microtus savii* (26.1%). The relative frequencies of these two prey items were negatively correlated. Statistically significant differences in the mean prey weight in the thirteen localities were detected. The mean prey weight was positively associated with the wood surface and negatively with the area of cultivated fields. A positive relationship between prey diversity and cultivation was recorded. This indicates that Barn Owls which forage in cultivated habitats tend to prey on smaller species, mainly shrews and voles, and to have a more diversified prey spectrum. On the contrary, owls foraging in wooded areas were more specialized and preyed on larger animals.

Key words: Barn Owl, *Tyto alba*, feeding ecology, owl pellets, small mammals

Received — July 2001, accepted — Sept. 2001

INTRODUCTION

The Barn Owl is a cosmopolitan strigiform, especially widespread in tropical and subtropical region, with a distribution range expanding towards north only in Europe and North America. Therefore, studies on its feeding habits are available from many countries of the world (e.g. Uttendorfer 1952, Reed 1957, Thiollay 1968, Glue 1974, Herrera 1974, Marti 1974, Marks & Marti 1984; for reviews see Mikkola 1983, Cramp 1985). In general, food habits of the Barn Owl are well known from several literature sources throughout its European range of distribution (Mikkola 1983, Taylor 1994), and the basic idea is that it does not exhibit pronounced differences from a country to another, especially when compared with other strigiform species. Furthermore, studies performed in climatically and environ-

mentally completely divergent areas (e.g. the Nigerian savannah, Lekunze et al. 2001), clearly demonstrates that Barn Owl is quite constant in its prey preferences.

It is known to feed mainly on voles, which often constitute the main part of the diet, but also shrews and mice are an important part of its food intake. Birds, reptiles, amphibians and insects are only occasionally preyed. The high proportion of shrews in its diet suggests that this species is a non-selective small mammal predator, especially if compared with the Long-eared Owl *Asio otus* and the Tawny Owl *Strix aluco* (Mikkola 1983, Riga & Capizzi 1999, Capizzi 2000). In addition, these species are known to be selective towards age and sex classes of its small mammal prey (Saint Girons 1973, Jędrzejewski et al. 1996, Zalewski 1996). Therefore, basing on the assumption that the Barn Owl forages on the prey in relation to its

availability, studies on the composition of small mammal assemblages are frequently done by investigating Barn Owl diet.

In this study we aim to investigate the influences of some environmental parameters and prey (small mammals) availability on the diet of the Barn Owl.

STUDY AREA, MATERIAL AND METHODS

The research was carried out in the Pisa province, Central Italy, an area of 244.825 ha in the central part of the Italian peninsula between 43°06' and 43°50' N and between 1°26' and 2°14' W (Fig. 1).

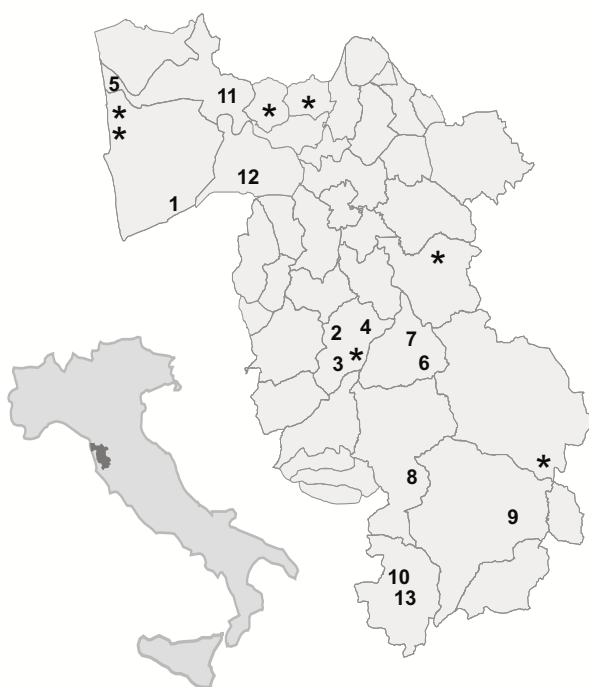


Fig. 1. Location of the pellet collection sites (1–13) and trapping localities (stars) in the study area (Pisa province) and its geographic position in the Italian peninsula.

Pellet collection and analysis

The analysis of Barn Owl pellets included 13 sites with cumulative prey number over 100 items. Pellets were collected between March 1996 and June 1997 on the ground of some abandoned buildings and were easily recognized by their characteristic features (Brown et al. 1987, Bang 1993).

Small mammals were classified to the finest taxon possible by the cranial remains by following the Chaline et al. (1974) and Erome & Aulagnier (1982) keys.

Environmental parameters

Environmental parameters were recorded in two buffer area of 1 km and 2 km of radius respectively from each pellet collection site. In each buffer area, we recorded the amount of woods (WS), cultivated fields (CS) and the total length of roads (KM).

Biomass estimation

Body masses of the small mammals trapped in the study area (Table 1) were used to calculate the mean weight for each prey species. When a given small mammal species was not trapped, to estimate its biomass contribution we used data from literature (Lovari et al. 1976, Santini 1983, Silva & Downing 1995).

Dietary variables

Barn Owl diet was presented in terms of both prey frequency and biomass. Prey frequency was used in most analyses, e.g. when comparing Barn Owl diet with prey availability, and when showing general diet features. Otherwise, the prey biomass was used. To represent the main features of Barn Owl diet in terms of biomass share, six dietary variables were selected. Four of them indicated the main taxonomic groups present in owl diets, i.e. the percentage of biomass of Insectivores (IN), *Muridae* (MU), *Arvicolidae* (AR) and *Gliridae* (GL). Furthermore, mean prey weight (MPW) and taxonomic diversity (DT), estimated for each study locality by means of Simpson's (1949) diversity index, were also included in the analyses.

Live trapping

The main prey (i.e. small mammals) availability was studied performing live-trapping sessions in 7 localities widespread in the Pisa province but not connected by their location with the 13 sites of pellet collection. This was done in order to obtain a representative sample of small mammal assemblages living in the territory of the Pisa province. In each locality, two different trapping sessions were carried out, one in March–April and another in July–August. Data were grouped in two different environmental types, i.e. cultivated fields (2 localities) and woodlands (5 localities). Since the trapping effort was not homogeneous, only the percentages of occurrence of the various small mammal species are used in the analyses.

In each localities two different trapping sessions were carried out (spring and autumn 1996). Three transects, composed of 10 trap-stations (spaced 10

Table 1. Diet of the Barn Owl in 13 sites (1–13) studied. “Positive” — data from localities where the prey was recorded in the diet.

Taxa	g		Sites studied													Total		Positive	
			1	2	3	4	5	6	7	8	9	10	11	12	13	n	%	n	%
<i>Sorex minutus</i>		4.5	-	2.9	-	-	0.4	1.9	0.8	-	6.2	-	-	-	0.6	34	0.8	6	46.2
<i>Sorex</i> sp.		6.5	0.6	-	-	-	-	-	-	0.7	-	-	-	0.6	0.2	12	0.3	4	30.8
<i>Neomys fodiens</i>		13	-	-	-	-	-	-	-	-	0.4	-	-	-	-	1	0.0	1	7.7
<i>Suncus etruscus</i>		2	3.1	3.9	-	2.9	5.1	4.7	1.6	4.8	8.0	1.3	0.8	5.2	3.0	150	3.7	12	92.3
<i>Crocidura suaveolens</i>		3.5	8.1	2.9	2.5	4.9	11.4	7.9	3.9	2.5	3.3	3.5	5.4	19.9	2.3	239	5.8	13	100
<i>Crocidura leucodon</i>		8	8.7	1.5	1.7	6.9	3.4	5.1	3.1	3.2	6.2	2.6	2.3	11.6	1.9	204	5.0	13	100
<i>Crocidura</i> sp.		5.75	1.8	9.3	-	1.0	3.8	1.0	2.3	6.5	2.9	0.3	1.5	0.6	5.5	131	3.2	12	92.3
Total Insectivora	n		225	42	5	16	57	65	15	100	74	24	13	64	71	771		13	
	%		22.3	20.6	4.2	15.7	24.1	20.5	11.7	17.7	26.8	7.7	10.0	37.9	13.4		18.8		100
<i>Glis glis</i>		120	0.1	-	-	-	1.3	-	-	-	0.4	-	0.8	-	-	6	0.1	4	30.8
<i>Muscardinus avellanarius</i>		27.5	-	2.5	11.7	-	-	1.3	-	2.1	1.8	7.0	-	-	1.1	68	1.7	7	53.8
<i>Clethrionomys glareolus</i>		29	-	3.4	6.7	-	-	0.3	-	0.7	5.8	2.2	-	-	4.5	67	1.6	7	53.8
<i>Microtus savii</i>		21	53.6	5.4	12.5	42.2	9.8	41.6	27.3	21.9	21.0	2.9	29.2	22.7	0.2	1070	26.1	13	100
<i>Arvicola terrestris</i>		200	0.3	-	-	-	-	-	-	-	-	-	-	-	-	3	0.1	1	7.7
<i>Rattus norvegicus</i>		300	-	-	-	1.0	-	-	-	-	-	-	-	-	-	1	0.0	1	7.7
<i>Rattus rattus</i>		180	0.8	2.0	3.3	-	3.4	-	0.8	-	1.1	0.6	5.4	-	0.8	44	1.1	9	69.2
<i>Apodemus</i> sp.		27	16.7	53.9	57.5	24.5	46.6	19.9	50.8	49.7	35.1	65.5	19.2	18.6	71.8	1631	39.7	13	100
<i>Mus domesticus</i>		19	4.4	8.8	3.3	16.7	13.6	14.8	7.0	6.7	6.5	9.9	30.0	19.2	7.2	368	9.0	13	100
Total Rodentia	n		767	155	114	86	176	247	110	459	198	279	110	104	453	3258		13	
	%		75.9	76.0	95.0	84.3	74.6	77.9	85.9	81.1	71.7	88.2	84.6	60.5	85.6		79.4		100
Total Aves	n		19	7	1	-	3	5	3	7	4	13	7	2	5	76		12	
	%		1.9	3.4	0.8	-	1.3	1.6	2.3	1.2	1.5	4.2	5.4	1.2	1.0		1.9		92.3
Total			1011	204	120	204	236	317	128	566	276	316	130	170	529	4105			

m apart), were performed in all locality. Transect number was higher in the localities 2 and 6, where five transects were performed, and lower in the locality 7, with only two transects. Each trap-station consisted of two WEB live-traps (Le Boulengé & Le Boulengé-Nguyen 1987), baited with oats and fillet of mackerel. Thus, 20 traps per trap line were used. This method provides a reliable index of the presence for small mammals (Hansson 1967). In all localities, each session lasted five nights, and the traps were visited every morning. A removal method was employed: captured mammals were weighed, sexed, classified to the lowest taxon possible and released in a distant place.

Statistical analyses

Statistical analyses were performed by an SPSS computer package (Norusis 1993), with all tests being two tailed and alpha set at 0.05. However, when multiple tests were performed, the a level was adjusted by using the Bonferroni correction.

Statistics used are described in Sokal & Rohlf (1969) and Zar (1984).

Normality in the distribution of the variables was assessed by Kolmogorov-Smirnov test. When appropriate, they were transformed by using Arcsin (square root) (for percentages) or Ln (x + 1) transformation. Otherwise, if we failed in obtaining a normal distribution, non-parametric tests were used.

RESULTS

In the thirteen study sites (Fig. 1), a total of 4105 prey were recorded (Table 1), 4029 (98.1%) of these being mammals and only 76 (1.9%) birds. Barn Owls preyed mainly upon rodents (79.4%) and insectivores (18.8%). The main prey were the wood mice *Apodemus* sp., followed by *Microtus savii*. The frequencies of these two prey, which globally accounted for over 65% of the whole diet

intake, were negatively correlated ($n = 13$, Spearman's $\rho = -0.819$, $p < 0.0007$). Only five taxa were preyed in all the sites, three rodents (*Apodemus* sp., *Microtus savii*, *Mus domesticus*) and two insectivores (*Crociodura suaveolens* and *C. leucodon*). On the contrary, two rodents (*Arvicola terrestris* and *Rattus norvegicus*) and one insectivorous (*Neomys fodiens*) were recorded in only one site.

Patterns in Barn Owl diet

As expected, there was a positive correlation between the frequency of the various prey types in the field as estimated by trapping sessions and their frequency in Barn Owl diet (Spearman's $\rho = -0.98$, $n = 8$, $p < 0.00004$). We correlated also the frequency of different prey species separately in both cultivated fields and woodlands with their frequency in Barn Owl diet, and the statistical significance was obtained only for cultivated fields (Bonferroni-corrected alpha level: 0.025; cultivated fields: Spearman's $\rho = 0.79$, $n = 8$, $p < 0.02$, woodlands: Spearman's $\rho = 0.43$, $n = 8$, $p < 0.29$).

One-way ANOVA detected statistically significant differences in the mean prey weight (MPW) in the thirteen localities (one-way ANOVA: $F_{12,4091} = 8.82$, $p < 0.00001$).

MPW was positively associated with the wood surface and negatively with the amount of cultivated field (Table 2; in all cases, $n = 13$, analyses for each parameter: 4; Bonferroni-corrected alpha level: 0.013). DT was negatively correlated with wood perimeter and surface only in the 1 km buffer, but the statistical significance fell short after Bonferroni correction.

Within 1 km radius from each collection site significant correlations between the frequency of

Table 2. Correlations between dietary parameters of the Barn Owl versus environmental parameters measured in 1 km and 2 km buffers around the 13 pellet collection sites (alfa level after Bonferroni correction: 0.013)

R — Spearman's correlation coefficient; MPW — mean prey weight; DT — taxonomic diversity; WS — surface of woods; CS — surface of cultivated fields

Pairs of variables			R	P
1 km buffer				
MPW	vs	WS	0.725	0.005
MPW	vs	CS	-0.709	0.007
DT	vs	WS	-0.632	0.02
DT	vs	CS	0.615	0.03
2 km buffer				
MPW	vs	WS	0.676	0.01
MPW	vs	CS	-0.670	0.01

Table 3. Correlations between frequencies of main prey species in the diet of the Barn Owl and environmental parameters measured in 1 km and 2 km buffers around the 13 pellet collection sites. Alfa level after Bonferroni correction: 0.013, KM — total lenght (in km) of roads. Other symbols — see Table 2.

Pairs of variables			R	P
1 km buffer				
<i>C. leucodon</i>	vs	WS	-0.758	0.003
<i>C. leucodon</i>	vs	CS	0.720	0.006
<i>S. etruscus</i>	vs	KM	-0.685	0.01
2 km buffer				
<i>C. leucodon</i>	vs	WS	-0.758	0.003
<i>M. savii</i>	vs	CS	0.742	0.004
<i>M. savii</i>	vs	WS	-0.742	0.004
<i>C. glareolus</i>	vs	WS	0.720	0.006
<i>Apodemus</i> sp.	vs	WS	0.714	0.006
<i>C. leucodon</i>	vs	CS	0.687	0.01
<i>M. avellanarius</i>	vs	WS	0.685	0.01
<i>Apodemus</i> sp.	vs	CS	-0.676	0.01

the various prey taxa and the habitat parameters were recorded only for insectivorous species. Statistically significant trends for rodents were noted in the 2-km buffer (Table 3). The correlations between the main taxonomic prey groups and environmental parameters confirmed results from previous analyses (Table 4). For glirids and murids positive relationships were recorded with wood surface, and negative with cultivated fields, while an opposite trend was noted for arvicolidids.

Table 4. Correlations between frequencies of taxonomic main groups in the diet of the Barn Owl and environmental parameters measured in 1 km and 2 km buffers around the 13 pellet collection sites. Alfa level after Bonferroni correction: 0.013. Other symbols — see Table 2.

			R	P
1 km buffer				
Murids	vs	WS	0.714	0.006
Murids	vs	CS	-0.709	0.007
Glirids	vs	WS	0.691	0.009
Glirids	vs	CS	-0.663	0.01
Arvicolidids	vs	CS	0.643	0.02
Arvicolidids	vs	WS	-0.637	0.02
2 km buffer				
Glirids	vs	WS	0.862	0.0002
Glirids	vs	CS	-0.818	0.001
Murids	vs	WS	0.747	0.003
Arvicolidids	vs	CS	0.731	0.005
Murids	vs	CS	-0.731	0.005
Arvicolidids	vs	WS	-0.731	0.005

Live trapping

On the whole, 261 small mammal specimens belonging to nine taxa were captured during the live trapping sessions (Table 5). We correlated the

Table 5. Relative frequencies of small mammals captured with live traps. x — mean values, % — percentage for localities where the prey was recorded.

Taxa	Woodland n = 225		Cultivation n = 36		Total n = 261	
	x	%	x	%	x	%
<i>Apodemus</i> sp.	60.1	71.4	3.3	50.0	43.8	85.7
<i>Clethrionomys glareolus</i>	5.2	14.3	-	-	3.7	14.3
<i>Mus domesticus</i>	6.0	28.6	5.0	50.0	5.7	42.9
<i>Rattus rattus</i>	7.3	42.9	-	-	5.2	42.9
<i>Microtus savii</i>	-	-	80.0	100.0	22.9	28.6
<i>Eliomys quercinus</i>	0.7	14.3	-	-	0.5	14.3
<i>Glis glis</i>	1.2	14.3	-	-	0.8	14.3
<i>Crocidura leucodon</i>	4.6	57.1	-	-	3.3	57.1
<i>Crocidura suaveolens</i>	15.0	71.4	11.7	100.0	14.0	100.0
Simpson's index	2.46		1.52		2.19	

data obtained in each environmental type with those relative to Barn Owl diet. We excluded from the analyses those species that were preyed by Barn Owl but not captured with live traps. The percentage of positive localities of the various prey species in the two habitats were correlated with those in Barn Owl diet, but the relationship was statistically significant only for cultivated fields (number of tests: 2; alpha level: 0.025; cultivated fields: Spearman's $\rho = 0.727$, $n = 9$, $p = 0.025$; woodland: Spearman's $\rho = 0.504$, $n = 9$, ns). The same trend was recorded for the mean percentage of occurrence of small mammals in the two environmental types, which were both positively correlated with that in Barn Owl diet. However, only the relationship relative to the cultivated fields was statistically significant (number of tests: 2; alpha level: 0.025; cultivated fields: Spearman's $\rho = 0.785$, $n = 9$, $p = 0.012$; woodland: Spearman's $\rho = 0.383$, $n = 9$, ns).

Principal component analysis

To reduce the variables to few independent factors, principal component analysis (PCA) was performed between the percentage of occurrence of the various prey in the thirteen sites. In this analysis, variables were prey taxa (Fig. 2a) and cases were the localities (Fig. 2b). In order to facilitate the interpretation of the factors, Varimax rotation was applied. Scores and loadings of the first three factors extracted are plotted (Fig. 2). Factor 1 (eigenvalue 4.22) explained the 38.4% of the total variance, Factor 2 (eigenvalue: 2.41) 21.9% and Factor 3 (eigenvalue: 1.78) 16.2% (cumulative eigenvalue: 8.41, cumulative explained variance 76.5%). Factor loadings and scores were then subjected to further analysis. Scores obtained by the

various prey taxa on Factor 1 tended to be negatively correlated with the respective biomass, but the relationship was not statistically significant (Spearman's $r = -0.536$, $n = 11$, ns). Furthermore, scores obtained by the thirteen localities on both

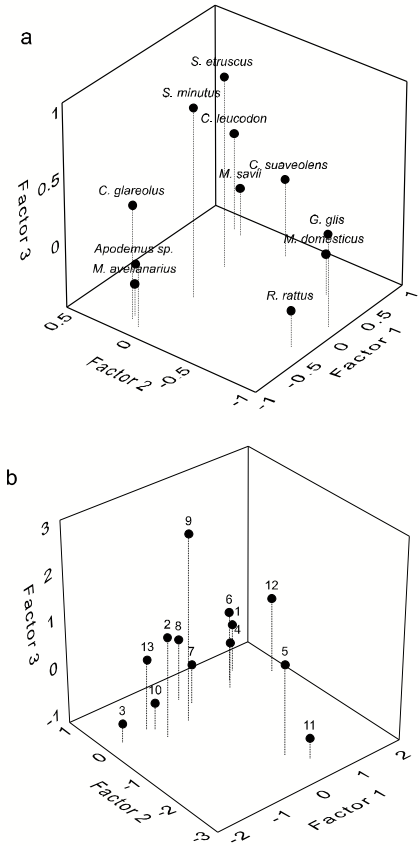


Fig 2. Scores (a) and loadings (b) of the first three factors extracted by a Principal Component Analysis performed on the Barn Owl diet.

Factor 1 and Factor 2 were positively correlated with their wood surface (Factor 1: Spearman's $r_s = 0.769$, $p < 0.003$; Factor 2: Spearman's $r_s = 0.615$, $p < 0.03$.) and negatively with cultivated areas (Factor 1: Spearman's $r_s = -0.829$, $p < 0.0005$; Factor 2: Spearman's $r_s = -0.588$, $p < 0.04$).

DISCUSSION

Food habits of the Barn Owl in the study area were quite similar to those recorded in other Italian Mediterranean localities very close to the study area (e.g. see Lovari et al. 1976, Contoli & Sammuri 1978, Contoli et al. 1983) as well as quite distant (e.g. see Massa & Sarà 1982, Contoli et al. 1993). It was resulted that it based its diet on two main prey types, i.e. the wood mice *Apodemus* sp. and the field vole *Microtus savii*. Although its diet included 16 different taxa, the cumulative frequency of the two main prey types averaged on 63.07 ± 10.37 , and only in two cases this value was lesser than 50%. Moreover, these two food sources appeared to be complementary, as they were negatively correlated. In general, Barn Owl seemed to exploit the locally more abundant prey as in the case of *Microtus savii* and *Apodemus* sp., but also of *Clethrionomys glareolus* and *Muscardinus avellanarius*. All these prey were positively associated to their typical habitat types, i.e. cultivated fields for *Microtus savii* and woods for the latter three prey taxa, which, on the contrary, were also negatively associated to the amount of cultivated fields. The habitat preferences of these rodents, although well known from bibliographic sources (e.g. see Santini 1983, Amori et al. 1986, Capizzi & Luiselli 1996a, 1996b), were confirmed by results of live trapping sessions: *Apodemus* sp. and *Clethrionomys glareolus* were frequently captured in the wood, but disappeared when the traps were placed in the cultivated areas. *Muscardinus avellanarius* was not captured by live-traps placed on the ground, as it is an arboreal species, and is found in woods and hedges. An opposite trend was recorded for *Microtus savii*, which was never captured in the woods, but was the dominant species in the open fields (Caroli et al. 2000). As expected, the occurrence this vole was negatively associated with surface of woods, but positively with cultivated fields, and the same was true for the shrews *Crocidura leucodon* and *Crocidura suaveolens*. However, results from live trappings showed that the vole *Microtus savii* is the most abundant prey in the open areas, but shrews were

captured frequently also in the woods. Thus, it seems that the Barn Owl does not select shrews when hunting in woodland habitats, maybe due to the fact that they are little prey in terms of biomass.

The positive correlation between mean prey weight and wood surface in the various study sites corroborated this hypothesis, suggesting that energetic balances may be involved in the prey choice. Smaller prey seems to be chosen in open habitats, but more frequently ignored in the woods. The same trend was noted for the Tawny Owl throughout the Italian Peninsula (Capizzi 2000). Furthermore, we recorded a positive relationship between prey diversity and cultivated fields, but diversity values of small mammal assemblages recorded by live trapping were higher in the woodlands. The above evidences indicate that Barn Owls when forage in cultivated habitats tend to prey on smaller species, mainly shrews and voles, and to have a more diversified prey spectrum. On the contrary, owls when forage in wooded areas appeared to be more specialised and tended to prey on larger animals.

On the whole, Barn Owl foraged on the prey according to its availability in the field, but its diet was more similar to the small mammal assemblages recorded in cultivated fields than in woodland, suggesting that this strigiform is more selective in the latter habitat. This may be due to the presumptive higher difficulty of hunting in woods that can lead to a lower frequency in predation rate.

Finally, we recorded a negative significant relationships between the frequency of *Suncus etruscus* and the km of roads. The trend is intriguing and confirms Lovari's et al. (1976) findings, but, at the present, it seems quite inexplicable.

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STRESZCZENIE

[Drapieżnictwo płomykówki w stosunku do drobnych ssaków w krajobrazie śródlądowym]

Badania prowadzono w prowincji Piza w środkowych Włoszech (Fig. 1), gdzie w 13 miejscowościach zbierano wypluwki, a w 7 innych dokonywano połowu pułapkami żywołownymi drobnych ssaków, dla określenia dostępności potencjalnych ofiar płomykówki. Wokół każdego miejsca zbioru wypluwek, w strefach o promieniu 1 km i 2 km, określano udział trzech wyróżnionych składników krajobrazu: zadrzewień (WS), pól uprawnych (CS) oraz łączną długość dróg (KM).

Z ogólnej liczby 4105 ofiar stwierdzonych w wyplawkach 98.1% stanowiły ssaki, a ptaki tylko 1.9% (Tab. 1). Zaznaczyła się negatywna korelacja frekwencji między dwoma głównymi grupami ofiar — myszami *Apodemus* sp. i nornikiem *Microtus savii*.

Stwierdzono pozytywną korelację częstości występowania poszczególnych grup ofiar w wyplawkach (Tab. 1) i w materiale z połowów pułapkami (Tab. 5). Korelacja ta była też istotna przy oddzielnym rozpatrywaniu materiału (wypluwki i połowy) ze środowiska polnego, natomiast w przypadku zadrzewień nie była znacząca. Średni ciężar ofiar (MPW) był pozytywnie skorelowany z udziałem zadrzewień w danej okolicy, a negatywnie — z udziałem pól (Tab. 2). Analiza udziału 3 wyróżnionych składników krajobrazu w strefie 1 km od miejsca zbioru wypluwek, w stosunku do udziału poszczególnych taksonów, wykazała istotną zależność tylko w stosunku do gatunków owadożernych. Podobna analiza składu środowiskowego w strefie o promieniu 2 km wykazała zależność dla udziału

gryzoni (Tab. 3 i 4). Głównym czynnikiem zróżnicowania diety płomykówki między 13 miejscami badań był ciężar osobniczy ofiar oraz powierzchnia zadrzewień i pól uprawnych (Fig. 2).

Autorzy wnioskują, że zwyczaje pokarmowe płomykówki na badanym obszarze są podobne jak na innych terenach we Włoszech. Ptak ten na

ogół wykorzystuje gatunki ofiar najliczniej reprezentowane w lokalnej faunie. Jednak w tej pracy stwierdzono, że płomykówki na polach częściej wybierały gatunki o mniejszym ciężarze osobniczym, co zwiększało różnorodność diety, natomiast w lesie skład ich ofiar był zawężony tendencją do wyboru większych zwierząt.



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