

A COMPARATIVE STUDY OF THE VARIABILITY OF OWL DIETS IN THREE LOCALITIES OF CENTRAL ITALY

Dario CAPIZZI* & Luca LUISELLI**

INTRODUCTION

The Barn Owl (*Tyto alba*), the Tawny Owl (*Strix aluco*) and the Long-eared Owl (*Asio otus*) are found to coexist in some habitats of central Italy. The sympatry among these species can usually occur in farmlands mixed with hedgerows and forested areas, where they often use grasslands and cultivated fields as foraging habitats (Capizzi & Luiselli, 1996a). All the three species are nocturnal (Mikkola, 1983; Cramp & Simmons, 1985) and feed mainly on small mammals, but *T. alba* and *S. aluco* are resident, whereas *A. otus* is partially migrant (Mikkola, 1983).

Despite the fact that dietary habits of these owls have been studied quite in detail in several localities of their distribution ranges (e.g. see for *S. aluco*: Uttendorfer, 1952; Southern, 1954; Jedrzejewski *et al.*, 1996; for *A. otus*: Glue & Hammond, 1974; Nilsson, 1981; for *T. alba*: Herrera, 1974; Lovari *et al.*, 1976; reviews in Thiollay, 1968; Cramp, 1985; Mikkola, 1983; Mead, 1987; Taylor, 1994), relatively little is known on the trophic relationships among these raptors where two or more species coexist (but see Herrera & Hiraldo, 1976; Contoli & Sammuri, 1978; Goszczynski, 1981; Nilsson, 1984; Capizzi & Luiselli, 1995, 1996a), despite simple lists of prey were presented in several local studies (e.g. see Gerdol *et al.*, 1982; Bertarelli *et al.*, 1992).

On the whole, comparative studies which have been conducted on bird communities in different localities (e.g. see Wiens & Rotenberry, 1979; Edwards, 1988; Petit *et al.*, 1990; Fasola, 1994) indicated that birds do not use the trophic resources with an exclusive strategy, i.e. selective or opportunistic (see Morse, 1971). Furthermore, the importance of food competition has generated some remarkable controversies (Connell, 1980; Wiens, 1989). In fact, although in last years it has been ascertained that (i) food is not always the limiting factor in organizing bird communities (Wiens, 1977, 1989; Rotenberry, 1980), and (ii) some forms of interference may produce similar patterns than exploitation competition

* Istituto Nazionale per la Fauna Selvatica, Via Ca' Fornacetta 9, I-40064 Ozzano Emilia (Bologna, Italy); e-mail: me3176 @mclink.it

** Institute of Ecology, CNF, No 4 Adak Uko Street, Calabar, Cross River State (Nigeria), and: Department of Biological Sciences, The Rivers State University of Science and Technology, P.M.B. 5080, Port Harcourt, Rivers State (Nigeria).

in birds of prey and owls (Kostrzewa, 1991; Hakkarainen & Korpimaki, 1996), food competition is generally accepted as having an important role in these birds (see Schoener, 1982, 1984; Korpimaki, 1987).

In this paper, for the first time to our knowledge, we examine the trophic relationships occurring among these three sympatric owl species in different localities. Our aims are: (i) to compare the inter- and intra-specific variations of the main dietary parameters of the three owl species in three localities of central Italy with different habitat features (two localities characterised by wood patches interspersed with wide cultivations, and another locality characterized by extended and well managed high forest); and (ii) to verify by means of small mammal trapping, whether, in the various localities, each owl species fed upon the prey in relation to its relative abundance in the field.

MATERIALS AND METHODS

STUDY AREAS

The research was carried out in three localities situated in the central part of the Italian peninsula, each one with different environmental characteristics.

The first locality (ROME) was situated on the left bank of the river Tiber (100 km² surface, 30-70 m a.s.l. elevation) near the village of Monterotondo, about 15 km northeast of Rome. Wood was coppiced once every 12-18 years and covers about 15 % of the total surface (Capizzi & Luiselli, 1996b). *Quercus cerris* was the dominant tree species, but also *Q. robur*, *Q. pubescens* and *Q. frainetto* were present in the woods. Holm oaks (*Quercus ilex*), maples (*Acer campestris*), elms (*Ulmus minor*), ashes (*Fraxinus ornus*) and laurels (*Laurus nobilis*) were also present. Wide parts of the study area were covered by grassy pastures and cultivations, mainly olive, wine groves and wheat plantations. Data on both owl pellets and small mammals assemblages were drawn from Capizzi & Luiselli (1996a).

The second locality (VITERBO) was situated in a hilly territory of northern Latium surrounding the Cimini mountains (about 80 km² surface, 200-500 m a.s.l.), situated at about 50 km north of Rome, near Viterbo town. The wood, covering 21 % of the total surface, was fragmented in several woodlots and coppicing occurred once every 12-15 years (Capizzi, 1993). Coppice composition was quite diversified depending on the elevation of the site: it was generally constituted by chestnut (*Castanea sativa*) and deciduous oaks (*Quercus cerris* and *Q. robur*), but maples (*Acer campestris*) and elms (*Ulmus minor*), ashes (*Fraxinus ornus*) were also present. Cultivations, which covered about 65 % of the territory, were constituted mainly by hazelnuts and wheat plantations. Data on small mammal assemblages were drawn from Capizzi (1993) and Caroli (1989), while data on owl pellets are given in Guidoni *et al.* (submitted).

The third locality (PISA) was a large forested area situated in the coastal part of the Pisa Province in the northern Tuscany (about 30 km² surface, 0-10 m a.s.l.). It consisted of a wide forested territory covered by Mediterranean vegetation, mainly pine high forests. Main tree species were pines (*Pinus pinea* and *P. pinaster*), oaks (*Quercus ilex*, *Q. cerris* and *Q. robur*) and ashes (*Fraxinus ornus* and *F. oxyphilla*). Other common trees were maples (*Acer campestris*) and elms

(*Ulmus minor*). The forested area was limited in the eastern side by wide cultivations and open fields and in the western side by the Thyrrhenian sea. Data on both small mammal assemblages and owl pellet were drawn from Capizzi *et al.* (submitted).

DISTANCES AMONG THE STUDY AREAS

Two of the above localities were quite close (Rome-Viterbo: linear distance 49 km) while the third one was relatively distant from each other (Pisa-Viterbo: 218 km; Pisa-Rome: 266 km).

OWL PELLET COLLECTION

Data concerning owl pellets became from both published accounts (Rome: Capizzi & Luiselli, 1995 and 1996a) and submitted papers (Viterbo: Guidoni *et al.*, submitted; Pisa: Capizzi *et al.*, submitted). *T. alba* pellets were collected on the ground of some abandoned buildings and were easily recognized by their characteristic features (see Brown *et al.*, 1987; Bang, 1993). *A. otus* pellets were collected in proximity of large trees used by these birds as perches. *S. aluco* pellets were randomly collected on the wood litter as well as in abandoned buildings. Due to the similarity of pellets of these two species, they were considered only when the birds or their distinctive signs of presence (i.e. plumage, cf. Brown *et al.* 1987) were observed.

In all the three study areas the pellets of each owl species were collected in at least three perches.

SYMPATRY OF THE OWLS

The reliability of such comparative studies is strongly biased if the presence of some assumptions is not verified (see Connell, 1980), i.e. in this case the effective sympatry of the studied species. In fact, despite the presence of the three owls in a relatively small area, this sympatric living could be not obvious. Nevertheless, with regard to our study areas, such a sympatry can be reasonably assumed. In fact, spatial segregation was not observed in any study area: for example, in all the study areas, the collection sites of the three species' pellets were situated at less than 250 m linear distance from one another.

OWL PELLET ANALYSIS

To classify the animal components of the various pellets to the lowest taxon possible the collected material was then analysed in the laboratory by using the standard procedures (Chaline *et al.*, 1974). Small mammals and birds were recognized by the cranial, mandibular, skull and bone remains by following the Chaline *et al.* (1974) and Erome & Aulagnier (1982) keys.

BIOMASS ESTIMATION

Body mass of the various small mammals trapped in different studies in the three localities (Caroli, 1989; Capizzi, 1993; Capizzi & Luiselli, 1996b) were

employed to calculate the mean weight for each prey species. When a given small mammal species was not trapped during the above cited field studies, to estimate its biomass contribution we employed data coming from other authors (Toschi & Lanza, 1959; Toschi, 1965; Lovari *et al.*, 1976; Santini, 1983).

PERCENTAGE COMPOSITION OF SMALL MAMMAL COMMUNITIES

As previously indicated, data deriving from different field studies (for Pisa: Capizzi *et al.*, submitted; for Viterbo, Caroli, 1989; Capizzi, 1993; for Rome: Capizzi *et al.*, 1995; Capizzi, 1997) were used to estimate the availability of small mammals in the three study areas. Custom-made WEB live-traps were placed in only two environmental types of each study area: (i) wooded habitats and (ii) grasslands and cultivated fields. Every trapping session lasted five nights. The first trapping session was carried out during early spring, the second during early autumn. Traps were baited with oats mixed into mackerel fillets, a mixture that proved very effective in attracting rodents and shrews (Capizzi *et al.*, 1995; Capizzi & Luiselli, 1996; Capizzi, 1997). The numbers of employed traps ranged from 100 (both in Viterbo and Pisa) to 81 in every trapping session (Rome). Due to the different trapping procedures employed in the above studies, only the percentage composition of the small mammal communities was considered for the analysis.

DIETARY VARIABLES

Seven dietary variables were selected to be analysed by means of multivariate procedures. Four of them represented the main taxonomic groups present in owl diets: they were percentage of occurrence (in terms of biomass share) of (i) Insectivorous (IN), (ii) Murids (MU), (iii) Arvicolids (AR) and (iv) Myoxids (MY). Furthermore, (v) mean prey size (MPS) was also included in the analysis. Finally, (vi) taxonomic diversity (DT) and (vii) prey size diversity (DS) were estimated for each study locality by means of Simpson's (1949) diversity index. The latter parameter (DS) was obtained by splitting the prey in seven classes of size: I) body mass (BM) < 5 g; II) BM < 10 g; III) BM < 20 g; IV) < 40 g; V) BM < 80 g; VI) BM < 160 g; VII) BM > 160 g.

BUILDING OCCUPATION

The occupation of the abandoned building by owls was checked by visiting them in two different years (1995 and 1996). Each building was visited to detect recent owl sign of presence (cf. Bang, 1993). Considering that this survey method is recommended for censusing *T. alba* (cf. Bibby *et al.*, 1993), the obtained information will be considered mainly in this light.

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. Statistics used are described in Sokal and 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. If we failed in obtain a normal distribution, non-parametric Kruskal-Wallis one-way ANOVA was used. Principal component analysis (PCA) was used to explore the eventual similarities among predator diets and small mammal assemblages in the three sites. Hence, discriminant analysis was performed to discriminate among owl diets grouped by (i) study areas and (ii) owl species. Values of food niche breadth were measured by Simpson's (1949) diversity index, while the food niche overlap among predator species was calculated by Pianka's (1973) symmetric equation with values ranging from 0 (no overlap) to 1 (total overlap).

TABLE I

Percent occurrence of the various prey types in dietary habits (expressed in terms of prey frequency) of three coexisting owl species in three different localities of central Italy.

	Pisa			Viterbo			Rome		
	<i>Tyto alba</i>	<i>Strix aluco</i>	<i>Asio otus</i>	<i>Tyto alba</i>	<i>Strix aluco</i>	<i>Asio otus</i>	<i>Tyto alba</i>	<i>Strix aluco</i>	<i>Asio otus</i>
	(n = 183)	(n = 64)	(n = 181)	(n = 177)	(n = 92)	(n = 135)	(n = 673)	(n = 169)	(n = 201)
	%	%	%	%	%	%	%	%	%
<i>Apodemus</i> sp.	48.6	7.8	51.4	29.4	46.7	11.1	28.7	43.2	8.5
<i>M. domesticus</i>	13.1	6.3	3.3	5.6	2.2	5.9	6.8	4.7	1.5
<i>R. rattus</i>	3.3	51.6	1.7	—	2.2	0.7	0.3	1.2	1.0
<i>M. savii</i>	9.3	1.6	40.9	42.4	27.2	76.3	38.6	30.2	84.1
<i>C. glareolus</i>	—	—	—	1.1	5.4	—	2.4	10.1	—
<i>A. terrestris</i>	—	9.4	—	—	—	—	—	—	—
<i>M. avellanarius</i>	—	—	—	4.0	5.4	—	3.3	3.6	—
<i>M. glis</i>	1.1	3.1	—	—	1.1	—	—	—	—
<i>Crociodura</i> sp.	18.0	3.1	0.6	9.0	4.3	—	10.7	—	—
<i>S. etruscus</i>	4.9	1.6	—	4.5	1.1	—	4.9	—	—
<i>Sorex</i> sp.	—	—	—	1.7	—	—	1.5	—	—
Chiroptera	—	—	—	—	—	—	0.4	—	—
Aves	1.1	7.8	2.2	2.3	4.3	5.9	2.4	7.1	5.0
Invertebrata	0.5	7.8	—	—	—	—	—	—	—

RESULTS

A total of 967 owl pellets were collected, 497 out of which (51.4 %) came from *T. alba*, 296 (30.6 %) from *A. otus* and 174 (18.0 %) from *S. aluco*. Considering the study areas, 251 (26.0 %) pellets came from Pisa, 197 (20.4 %) from Viterbo, 519 (53.7 %) from Rome. The diet compositions of the three owl species in the three study localities are given in Table I (taxonomic prey frequency) and Table II (biomass shares of the various prey types), while the number of pellets collected in the four seasons is indicated in Table III.

TABLE II

Percent occurrence of the various prey types in dietary habits (expressed in terms of biomass share) of three coexisting owl species in three different localities of central Italy.

		Pisa			Viterbo			Rome		
		<i>Tyto alba</i>	<i>Strix aluco</i>	<i>Asio otus</i>	<i>Tyto alba</i>	<i>Strix aluco</i>	<i>Asio otus</i>	<i>Tyto alba</i>	<i>Strix aluco</i>	<i>Asio otus</i>
	biomass (g)	(g = 4 188)	(g = 5 754.5)	(g = 4 531)	(g = 3 634)	(g = 2 369.5)	(g = 3 280.5)	(g = 13 791)	(g = 4 219)	(g = 4 996.5)
		%	%	%	%	%	%	%	%	%
<i>Apodemus</i> sp.	23.5	49.9	2.0	48.2	33.6	42.6	10.7	32.9	40.7	8.0
<i>M. domesticus</i>	17	9.7	1.2	2.3	4.7	1.4	4.1	5.7	3.2	1.0
<i>R. rattus</i>	120	17.2	68.8	7.9	—	10.1	3.7	1.7	5.7	4.8
<i>M. savii</i>	24	9.7	0.4	39.2	49.5	25.3	75.4	45.2	29.0	81.2
<i>C. glareolus</i>	29.5	—	—	—	1.6	6.2	—	3.4	11.9	—
<i>A. terrestris</i>	200	—	20.9	—	—	—	—	—	—	—
<i>M. avellanarius</i>	17	—	—	—	3.3	3.6	—	2.7	2.4	—
<i>M. glis</i>	120	5.7	4.2	—	—	5.1	—	—	—	—
<i>Crocidura</i> sp.	7.5	5.9	0.3	0.2	3.3	1.3	—	3.9	—	—
<i>S. etruscus</i>	2.5	0.5	0.0	—	0.6	0.1	—	0.6	—	—
<i>Sorex</i> sp.	8	—	—	—	0.7	—	—	0.6	—	—
Chiroptera	15	—	—	—	—	—	—	0.3	—	—
Aves	25	1.2	2.2	2.2	2.8	4.2	6.1	2.9	7.1	5.0
Invertebrata	0.5	0.0	0.0	—	—	—	—	—	—	—

TABLE III

Total number of pellets of the three coexisting owl species collected in the four seasons in the three study areas.

Season	<i>T. alba</i>		<i>S. aluco</i>		<i>A. Otus</i>	
	n	%	n	%	n	%
Spring	174	35.0	51	29.3	120	40.5
Summer	67	13.5	32	18.4	38	12.8
Autumn	118	23.7	41	23.6	34	11.5
Winter	86	17.3	50	28.7	104	35.1
Undetermined	52	10.5	0	0.0	0	0.0
Total	497		174		296	

Values of taxonomic and prey size diversities of the diets of the three owl species in the three study areas are given in Table IV. Kruskal-Wallis ANOVA was performed among these indexes of each owl species (grouping variable, in all cases $n = 9$) in the various localities. The values of *T. alba* and *S. aluco* were significantly higher than those of *A. otus* in terms of prey frequency (PF: $H_2 = 7.20$, $p = 0.03$), while for biomass share (BS: $H_2 = 4.36$, $p = 0.11$) and prey size (PS: $H_2 = 5.42$, $p = 0.07$) the same trend was evident but fell short of statistical significance. No statistically significant difference among owls emerged when data are grouped by locality (BS: $H_2 = 0.36$, $p = 0.84$; PF: $H_2 = 0.27$; $p = 0.88$; PS: $H_2 = 1.87$, $p = 0.39$).

Values of interspecific and intraspecific food niche overlaps (in terms of both prey frequency and biomass share) are given respectively in Table V and VI. Three different pairs of Kruskal-Wallis ANOVAs were performed on overlap values computed between owl dietary habits represented in terms of both prey frequency (PF) and biomass share (BS). A first pair of analyses was performed on intraspecific overlap values, i.e. grouped by species. The analyses proved that there were no intraspecific statistically significant difference (PF: $H_2 = 1.77$, $p = 0.413$; BS: $H_2 = 1.16$, $p = 0.56$). A further pair of analyses was performed on interspecific overlap values, i.e. grouped by locality. These analyses showed that there were statistically significant differences in terms of prey frequency (PF: $H_2 = 5.70$, $p = 0.058$; BS: $H_2 = 3.23$, $p = 0.19$). However, the three pairs of species compared in the various localities did not differ significantly (PF: $H_2 = 0.72$, $p = 0.19$; BS: $H_2 = 0.63$, $p = 0.73$).

Kruskal-Wallis ANOVA was performed on intraspecific and interspecific overlap values, but in all cases the differences were not statistically significant (PF: $n = 18$, $H_1 = 0.008$, $p = 0.93$; BS: $n = 18$, $H_1 = 0.125$, $p = 0.73$).

Means and dispersion measures of the prey size eaten by the three owl species in each locality are given in Figure 1. The mean prey size of *T. alba* was significantly lower than that of both *S. aluco* and *A. otus* in both Rome (one-way ANOVA: $F_{2, 1040} = 27.001$, $p < 0.00001$) and Viterbo ($F_{2, 401} = 8.62$, $p < 0.0003$), but *S. aluco* preyed upon prey significantly heavier than *T. alba* and *A. otus* ($F_{2, 481} = 161.73$, $p < 0.000001$) in Pisa.

TABLE IV

Taxonomic diversity (in terms of both prey frequency and biomass shares) and prey size diversity, assessed by Simpson's (1949) diversity index, of the diets of three sympatric owls in the three study areas of central Italy.

a) prey frequency		b) biomass share		c) prey size	
<i>A. otus</i>		<i>A. otus</i>		<i>A. otus</i>	
Pisa	2.31	Pisa	2.54	Pisa	1.23
Rome	1.39	Rome	1.49	Rome	1.12
Viterbo	1.66	Viterbo	1.71	Viterbo	1.17
<i>S. aluco</i>		<i>S. aluco</i>		<i>S. aluco</i>	
Pisa	3.34	Pisa	1.92	Pisa	1.73
Rome	3.37	Rome	3.66	Rome	1.26
Viterbo	3.30	Viterbo	3.76	Viterbo	1.56
<i>T. alba</i>		<i>T. alba</i>		<i>T. alba</i>	
Pisa	3.35	Pisa	3.28	Pisa	2.29
Rome	3.96	Rome	3.12	Rome	1.38
Viterbo	3.55	Viterbo	2.75	Viterbo	1.29

Interestingly, intraspecific differences in prey size among the three localities were also present. The mean prey size of *T. alba* at Pisa was significantly heavier than that of conspecifics at Rome (one-way ANOVA: $F_{2, 1086} = 8.62, p < 0.05$); mean prey size of *S. aluco* at Pisa was significantly heavier than that of conspecifics at both Rome and Viterbo (one-way ANOVA and post-hoc Tukey HSD test: $F_{2, 322} = 122.2, p < 0.000001$); but mean prey size of *A. otus* did not vary significantly among the study areas (one-way ANOVA: $F_{2, 514} = 0.201, p > 0.81$).

TABLE V

Values of food niche overlap (measured by Pianka's (1973) symmetric equation) among the three coexisting owl species in the three study areas.

biomass share			prey frequency		
Pisa	<i>S. aluco</i>	<i>A. otus</i>	Pisa	<i>S. aluco</i>	<i>A. otus</i>
<i>T. alba</i>	0.334	0.852	<i>T. alba</i>	0.243	0.817
<i>S. aluco</i>		0.148	<i>S. aluco</i>		0.164
Viterbo	<i>S. aluco</i>	<i>A. otus</i>	Viterbo	<i>S. aluco</i>	<i>A. otus</i>
<i>T. alba</i>	0.878	0.894	<i>T. alba</i>	0.896	0.876
<i>S. aluco</i>		0.616	<i>S. aluco</i>		0.616
Rome	<i>S. aluco</i>	<i>A. otus</i>	Rome	<i>S. aluco</i>	<i>A. otus</i>
<i>T. alba</i>	0.925	0.855	<i>T. alba</i>	0.910	0.826
<i>S. aluco</i>		0.639	<i>S. aluco</i>		0.639

TABLE VI

Values of intraspecific food niche overlap (measured by Pianka's (1973) symmetric equation) of the three coexisting owl species in the three study areas.

biomass share			prey frequency		
<i>T. alba</i>	Viterbo	Rome	<i>T. alba</i>	Viterbo	Rome
Pisa	0.670	0.702	Pisa	0.719	0.752
Viterbo		0.998	Viterbo		0.997
<i>S. aluco</i>	Viterbo	Rome	<i>S. aluco</i>	Viterbo	Rome
Pisa	0.222	0.134	Pisa	0.194	0.178
Viterbo		0.979	Viterbo		0.986
<i>A. otus</i>	Viterbo	Rome	<i>A. otus</i>	Viterbo	Rome
Pisa	0.731	0.704	Pisa	0.730	0.698
Viterbo		0.996	Viterbo		0.997

Cluster analysis (single linkage system, standardized to 100 %) on percent diet composition in terms of eaten biomass of the three predator species in the different study areas showed that the diets of *S. aluco* were very similar in both Rome and Viterbo, the same diet similarities being present even in *T. alba* of Rome and Viterbo, and in *A. otus* of Rome and Viterbo (see Fig. 2).

Percentage composition of small mammal assemblages in two environmental types is given in Table VII.

By using the percentage of occurrence of small mammals in the field, we tried to estimate the habitat where the various predators conducted their predatory activity. To do this, we performed PCA analyses. In all PCAs the variables were prey types and the cases were both predator types and habitat categories (woodlands and grasslands). We excluded from the analyses all the birds, small mammals, and invertebrates which were neither captured in traps nor eaten by any

TABLE VII

Percent composition of the small mammal assemblages in two different environmental types (woodland and grassland) in the three study areas. For more detail, see text.

	Pisa		Viterbo		Rome	
	woodland (n = 142)	grassland (n = 30)	woodland (n = 128)	grassland (n = 60)	woodland (n = 485)	grassland (n = 96)
	%	%	%	%	%	%
<i>Apodemus</i> sp.	46.48	6.67	45.31	5.00	67.22	8.33
<i>Mus domesticus</i>	23.94	10.00	6.25	1.67	2.47	9.38
<i>Rattus rattus</i>	11.97	—	5.47	—	3.92	—
<i>Microtus savii</i>	—	76.67	3.91	88.33	—	82.29
<i>Clethr. glareolus</i>	—	—	25.00	—	19.38	—
<i>Crocridura</i> sp.	17.61	6.67	14.06	5.00	7.01	—

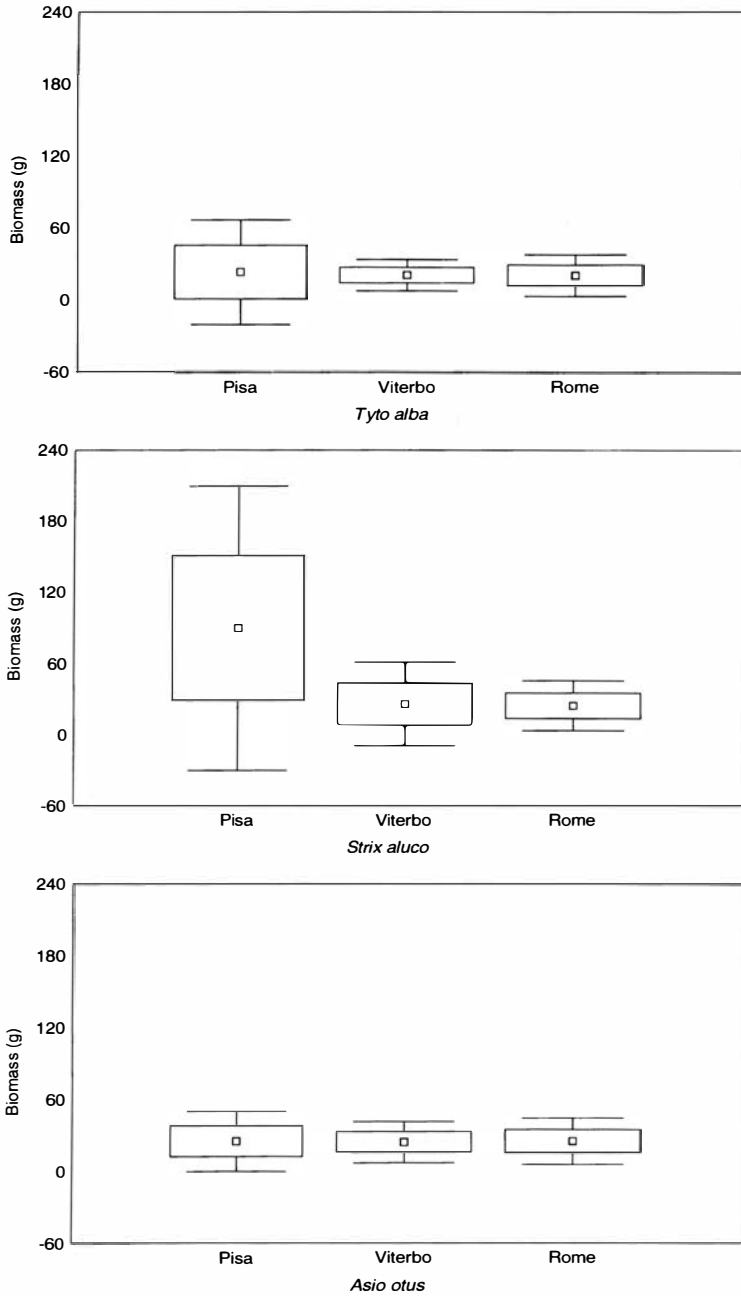


Figure 1. — Box and whisker plots showing averages and dispersion measures (mean, standard deviation and 1.96 standard deviation) of the prey size eaten by the three owl species in the three study areas. Note that values recorded for both *T. alba* and *S. aluco* at Pisa significantly exceeded those of the other two localities (one-way ANOVA, at least $p < 0.05$). None significant difference was found for *A. otus*. For more details and statistics, see text.

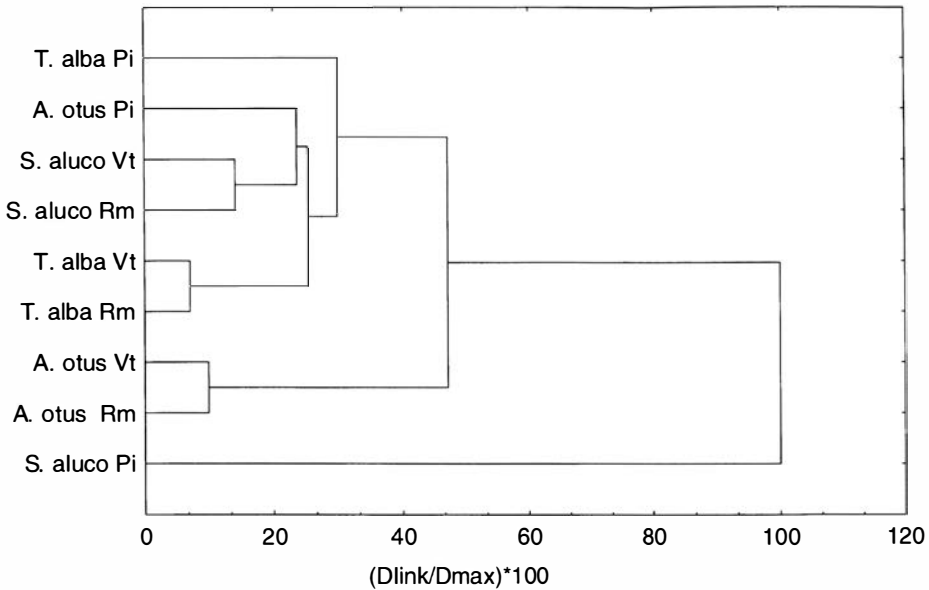


Figure 2. — Cluster analysis (single linkage system, linkage distance standardized to 100 %) performed on percent diet composition (in terms of eaten biomass) of the three predator species in the different study areas. Note that dietary habits of each owl species at Rome and Viterbo were very similar, while at Pisa they varied depending on the species.

owl species. Factor scores of the analyses are shown respectively in Figure 3. PCA analyses confirmed that the diets of the three owl species were relatively similar at both Rome and Viterbo, while they exhibited remarkable differences at Pisa. Moreover, (i) in all the study areas (and mainly at Pisa) there was a remarkable similarity between small mammals preyed by *A. otus* and small mammal community composition of grasslands; (ii) diets of *T. alba* were similar to small mammal communities present in grasslands at both Rome and Viterbo, but not at Pisa, where it appeared to prey mainly in the forest, and (iii) diet of *S. aluco* was not similar to any of the small mammal assemblages as recorded in live-trapping studies.

Discriminant analysis was used to check whether the diet of each owl species was similar throughout the three study areas or, conversely, whether a local characterization was recognizable. To do this, two different sets of discriminant analyses were performed on data grouped (i) by species and (ii) by locality. The analyses provided a good discrimination of the data grouped by species (*Function 1*: eigenvalue: 117.536; Wilks'λ: 0.0008; canonical correlation: 0.996; $\chi^2 = 28.618$; $df = 10$, $p = 0.001$. *Function 2*: eigenvalue: 9.798; Wilks'λ: 0.093; canonical correlation: 0.953; $\chi^2 = 9.518$; $df = 4$, $p = 0.05$) but not by locality (*Function 1*: $\chi^2 = 13.579$; $df = 10$; $p = 0.19$. *Function 2*: $\chi^2 = 0.754$; $df = 4$; $p = 0.75$).

On the whole, 120 visits in abandoned buildings were performed during 1995 and 1996. Signs of recent owl presence were found in 64 (53 %) of them. Detailed

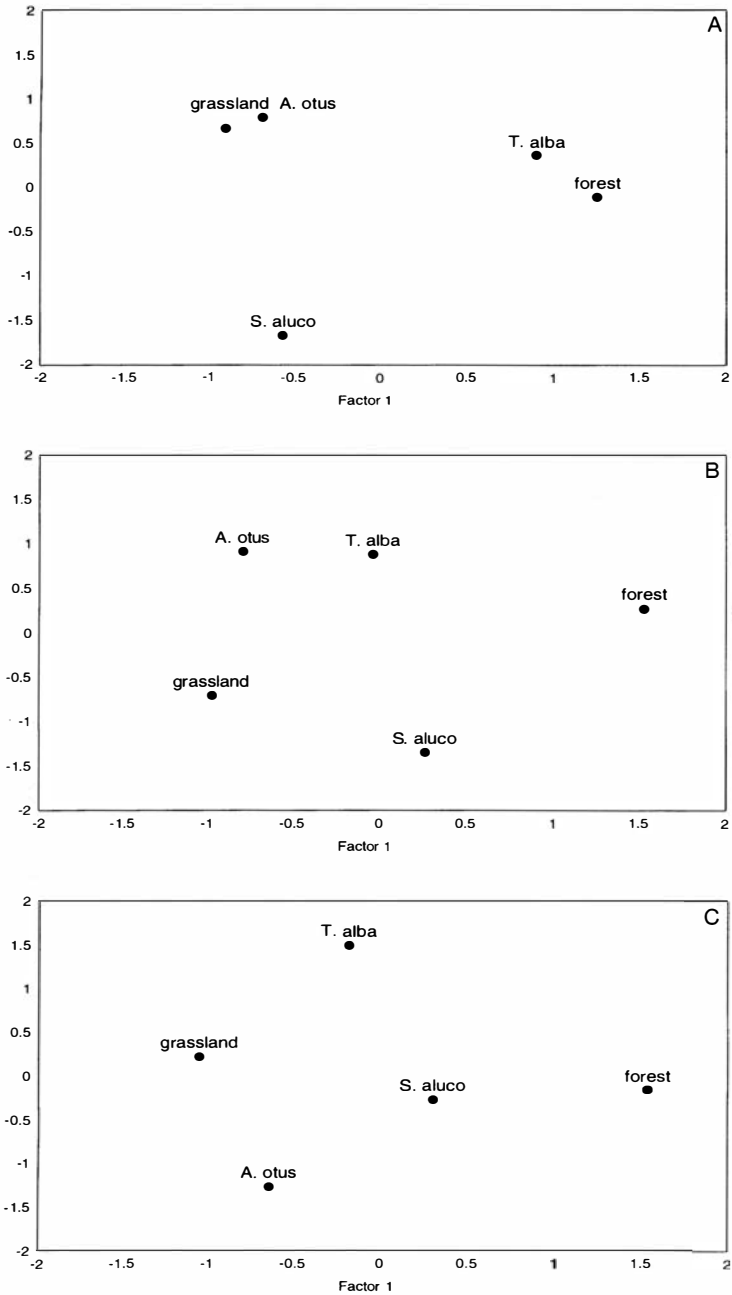


Figure 3. — Scores of the first two factors extracted by a principal component analysis performed on owl dietary habits and the frequency of small mammals in the field (in two environmental types) as recorded in the study area of Pisa (A), Viterbo (B), and Rome (C).

TABLE VIII

Building occupation by owls in the three study areas during two different years of research.

	Visited		Occupied		% Occupied	
	1995	1996	1995	1996	1995	1996
Pisa	17	19	5	4	29.4	21.1
Viterbo	25	19	18	13	72.0	68.4
Rome	23	17	13	11	56.5	64.7

results for each locality are given in Table VIII. To check for the existence of a significant difference in the proportion of occupied buildings in the three localities, χ^2 test (2×2 contingency table) was used. Significant differences were found between Pisa and the other two localities (Pisa vs Viterbo: $\chi^2 = 5.76$, $p = 0.02$; Pisa vs Rome: $\chi^2 = 3.83$, $p = 0.05$) but not between Rome and Viterbo ($\chi^2 = 0.21$, $p = 0.64$).

DISCUSSION

Much international literature has generally recognized that considerable variation in dietary habits could be found among distant bird populations, e.g. insectivorous birds (Petit *et al.*, 1990), herons (Fasola, 1994) and diurnal raptors (Edwards, 1988; Korpimaki & Marti, 1995). Diets of the three owl species were relatively similar at Rome and Viterbo, whereas they were different from the diet exhibited by owls at Pisa. Thus, considering the relative linear distances among the three study areas, our data confirm the expectable trends highlighted by previous authors (Edwards, 1988; Korpimaki & Marti, 1995).

The present study has revealed several dietary patterns for the three owls species at the three study localities. A summary of these patterns is presented in Table IX. Differences in the mean prey size taken by the three owls were recorded in all the three localities, suggesting that this parameter was an important factor in structuring the owl guild in each locality. Some intraspecific differences were also noted: one species (*A. otus*) tended to forage upon similarly sized prey in all the study areas, while in both *S. aluco* and *T. alba* the mean prey size was higher at Pisa than in the other two localities.

Interestingly, some differences in the use of the trophic resource among the three localities were shown by PCAs. Assuming that species selectivity did not vary in a relatively short geographic distance (Ricklefs, 1973), we suggest that the choice of the hunting terrain was responsible for the main differences in diet between the three owls. For instance, the fact that Viterbo and Rome study areas were characterized by a wider surface of open and cultivated fields in comparison with Pisa is in agreement with the higher frequency of occurrence in the owl diets of the field vole *Microtus savii*, a Microtine occurring almost exclusively in cultivated fields. This is in fact not surprising, as prey resources are not only dependent on their local densities but also on the area of their habitats in a landscape (Ricklefs, 1973).

Despite that inter- and intra-specific overlap values were not significantly different, discriminant analysis indicated that species dietary habits maintained their distinctive features even in distant localities. However, the evidences from this study are not consistent with an exclusive use of the trophic resource by sympatric owls, suggesting that predator selectivity may play an important role for *A. otus* and *T. alba*, as their diets (but especially those of *A. otus*) were in agreement with patterns predicted for selective predators (Morse, 1971; Fasola, 1994). Confirming the records from literature (see Mikkola, 1983), our own analyses suggested that *S. aluco* tended to a local specialization, allowing to adapt itself to a wide variety of habitats, ranging from open farmlands to ancient woodlands since to urban areas (Galeotti *et al.*, 1991; Galeotti, 1994; Redpath, 1995; Capizzi & Luiselli, 1995; Jedrzejewski *et al.*, 1996). Conversely, *A. otus* exhibited a relatively homogeneous diet in all the three study areas, allowing it to be less influenced in its predatory activity by local habitat features.

We have so far described the main characteristics of the variability of the owl diets in the three study localities (Table IX). A crucial issue is to address the “ecological determinism” of this variability. To begin with, it should be noted that the relative little number of owl individuals in the studied localities could be responsible for some of the described variability. For instance, the apparent enormous amount of rats in *S. aluco* at Pisa could be caused by a local effect (presence of colonies of rats in the surroundings of the owl perches) and by an individual effect. However, we are led to think that this is not the case. In fact, remains of rats in *S. aluco* pellets were recorded in several places of the study area, thus suggesting that this is a widespread pattern in Pisa’s Tawny Owls. Furthermore, seasonal variations may account for some of the observed differences between and within species. However, our sampling protocol permitted to collect an adequate number of pellets in each season and for each owl species (see Table III), so that we suggest that the observed patterns are truly representative of the field situation. In general, inter- and intraspecific competition could be claimed as an explanation of some of the observed patterns.

Whether interspecific competition for food is really a central feature in structuring Mediterranean owl communities is still questionable, and this problem goes much beyond the aims of the present paper. However, despite our data are not enough to solve this problem, some considerations are possible. Following a traditional view, competition is an important factor especially in presence of a limited food source (e.g. see Giller, 1984; Welder & Slauson, 1986; Wiens, 1989), so that in our case the central question is whether small mammals are really limited resources in the study areas. Capizzi & Luiselli (1996a) showed that mechanisms of resource partitioning in an owls-and-snakes guild were more likely to occur among the former group, according to the fact that snakes, contrary to owls, are predators with low food requirements that could survive on a limited food source. As overlap values among the three species were higher at Rome and Viterbo, and comparatively lower at Pisa, one may expect an higher competition level in the former two localities. However, it has been noticed that high overlap values does not necessarily indicate competition (see Schoener, 1986). It may be hypothesized that the level of food competition was higher at Pisa than at Rome and Viterbo, as (i) shifts in prey size are often associated with an increased food competition level (see Schoener, 1986; Glasser & Price, 1988) and (ii) macro-habitat overlap tends to be inversely related to experimentally demonstrated competition (Schoener, 1983). It may be hypothesized that, at both Rome and Viterbo, food was not the

TABLE IX

Patterns of trophic relationships among three sympatric owls observed in three localities of central Italy.

Trophic niche diversity		Trophic niche overlap			Prey size		Hunting habitat*		Dietary features	
Between species	Within species	Between species	Between pairs of species	Within species	Between species	Within species	Between species	Within species	Between species	Between localities
different	not different	not different	not different	different	differences in each locality	similar for <i>A. otus</i> , different for <i>T. alba</i> and <i>S. aluco</i>	relatively similar at Rome and Viterbo, partitioned at Pisa	similar for <i>A. otus</i> , different for <i>T. alba</i> and <i>S. aluco</i>	different	not different

* As estimated by comparing owl dietary habits with prey frequency in the field.

main limiting resource, but the availability of nesting or roosting sites (see also von Haartman, 1968; Korpimäki, 1986). The high degree of occupation of abandoned buildings suggests that this factor could be a limiting resource, at least for *T. alba*, although in absence of reliable data on owl densities it is impossible to stress any firm conclusion.

However, as the role of competition could be not always easily differentiated from that of predation, it has been noted that predation among owl species is a possible — although not frequent — event (Mikkola, 1983). The suggestion that interspecific aggression occurs essentially in presence of limiting resources has generated controversy (see Case & Gilpin, 1974; Roughgarden, 1979; Maurer, 1984; review in Wiens, 1989). However, observational and experimental studies have shown that interference could have direct fitness effects as well as exploitation competition (Kostrzewa, 1991; Hakkarainen & Korpimäki, 1996). In this regard, we did not record any case of predation among the three owls in any of the study areas, thus confirming that predation is an extremely rare event among these three owl species (Mikkola, 1983).

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SUMMARY

Trophic niches of three coexisting owl species (*Asio otus*, *Strix aluco* and *Tyto alba*) in three localities of central Italy were investigated by using the pellet analysis method. Furthermore, data on small mammal assemblage composition in two different environmental types (i.e. woodland and grassland) were drawn from previous studies performed in the study areas. The three owls preyed chiefly upon small mammals, while birds were occasionally eaten. The trophic niches of *A. otus* in the three study areas were significantly narrower than that of *T. alba* and *S. aluco*. These latter species varied the size of their prey between the three localities, while *A. otus* preyed upon similarly sized prey in the three study areas. By using data on small mammal occurrence we tried to estimate the environmental type where the owls conducted their predatory activity: principal component analysis revealed that *A. otus* was linked to the cultivated fields as foraging habitat, while *S. aluco* and *T. alba* were less selective in the choice of hunting habitat. Furthermore, discriminant analysis indicated that species dietary habits maintained their distinguishing features also in distant localities. However, it appeared that owls did not use foraging resource with an exclusive strategy: evidences from this study are consistent with the hypothesis of a selective use of the trophic resource by *A. otus*, while diets of *T. alba* and *S. aluco* showed differences between the three localities.

RÉSUMÉ

Les niches trophiques de trois espèces de chouettes et hibou (*Asio otus*, *Strix aluco* et *Tyto alba*) coexistant dans trois localités d'Italie centrale ont été étudiées

par analyse des pelotes de réjection. De plus, ont été utilisées des données sur la composition des peuplements de petits mammifères dans deux types d'habitat (i.e. zones boisées et zones herbeuses) obtenues au cours d'études précédentes sur les mêmes zones. Ces trois espèces de rapaces nocturnes capturaient essentiellement des petits mammifères, les oiseaux n'étant qu'occasionnellement consommés. Dans les trois sites d'étude, les niches trophiques d'*A. otus* se sont avérées significativement plus étroites que celles de *T. alba* et de *S. aluco*. Ces deux dernières espèces ont montré des variations de taille de leurs proies entre les localités alors qu'*A. otus* capturait partout des proies de même taille. En utilisant des indices d'occurrence des petits mammifères, nous avons cherché à estimer le type d'habitat dans lequel chassaient ces rapaces nocturnes. Une analyse en composantes principales a révélé que, pour sa chasse, *A. otus* était lié aux terrains cultivés alors que *S. aluco* et *T. alba* étaient moins sélectifs quant à l'habitat dans lequel ils chassaient. Par ailleurs, une analyse discriminante a montré que les caractéristiques des habitudes alimentaires de chaque espèce se maintenaient d'un site à l'autre. Il est toutefois apparu que ces espèces n'exploitent pas les ressources alimentaires selon une stratégie exclusive. Les données de la présente étude sont en accord avec l'hypothèse d'une utilisation sélective des ressources trophiques par *A. otus*, mais pas par *T. alba* et *S. aluco*.

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