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DIETARY PATTERNS AND OVERLAP IN AN AMPHIBIAN ASSEMBLAGE AT A POND IN MEDITERRANEAN CENTRAL ITALY

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AMPHIBIAN
NICHE PARTITIONING
FOOD
MEDITERRANEAN
NULL MODELS

ABSTRACT. – The trophic niche characteristics of an amphibian assemblage were studied at a pond locality in Canale Monterano, province of Roma, Central Italy. The assemblage consisted of six species, four anurans (*Bufo bufo, Hyla intermedia, Rana dalmatina, Pelophylax* skl. *esculentus*), and two salamanders (*Triturus carnifex, Triturus vulgaris*). Food contents were obtained by stomach flushing. Stomach vacuity index varied substantially among species, and the species spending longer timespan within the reproductive site were also those with lower vacuity index values. Correspondence analysis discriminated two groups of species: one feeding mainly on terrestrial prey and the other on aquatic prey. Pseudo-community analysis revealed that the terrestrial guild of species was non-randomly structured when analysed by RA2 algorithm for volume of prey but neither for number of prey, nor for both number and volume of prey analysed by RA3. The aquatic subset of species appeared to be randomly assembled according to both RA2 and RA3 algorithms, either for number or for volume of prey. These results indicate that for terrestrial species, micro-habitat resource partitioning and body size discrepancy among species could be the factors influencing dietary patterns and facilitating species coexistence, whereas for aquatic species the observed high overlap in diet spectrum is mainly due to both generalist feeding habits of newts and the superabundance of food resources occurring at the study pond.

INTRODUCTION

Most of the observational and experimental studies of species interactions focus on relatively small subsets of species that are taxonomically or ecologically related, in an attempt to simplify the problem of determining the assembly rules within natural assemblages of species (e.g., Findley 1976, Toft 1985, Wiens 1989, Morton *et al*. 1994, Polis 1994, Kot 2001, Luiselli 2006, 2008a, b). Since Hutchinson's (1957) hypervolume niche theory, community ecologists have oriented their investigations towards the empirical and experimental analyses of single niche dimensions (spatial, temporal, trophic, etc.) or of a combination of them (e.g., Pianka 1973, 1974). Analogously, patterns of resource use along one or more niche axes have been used to investigate the limiting similarity among coexisting species (MacArthur & Levin 1967). It has been suggested that spatial, trophic, and temporal axes (listed in decreasing importance order) are the main niche dimensions (Schoener 1974). This generalized pattern of niche importance has been later confirmed in several animal groups, from protozoa (i.e., Hairston 1958) to higher vertebrates (Brown 1964, Luiselli 2008a), although some groups did not conform at all to this decreasing order of importance. For instance, the trophic niche axis is the most important for snake communities worldwide (Luiselli 2006).

Within amphibian assemblages, population structure of the interacting species is regulated primarily at the larval rather than adult stages (Istock 1967, Heyer 1976, Wilbur 1984, Diaz-Paniagua *et al*. 1988, Cortwright & Nelson 1990, Griffiths & Foster 1998, Brady & Griffiths 2000, Lane & Mahony 2002). However, interspecific interactions at the adult stage could be significant forces in determining qualitative and quantitative aspects of communities as well (Berven 1990, Pechmann 1994, Bardsley & Beebee 1998). For instance, phenology and density traits of adults may strongly influence the outcome of other life stages in a cyclic feedback regulation system (i.e., Pechmann *et al*. 1989, Berven 1990, Walls 1990, Vignoli *et al*. 2007a).

Overall, there are several studies on trophic niche partitioning by sympatric amphibians (e.g., Avery 1968, Toft 1980, 1981, Griffiths 1986, McAlpine & Dilworth 1989, Jaeger *et al*. 1998, Caldwell & Vitt 1999, Parmelee 1999, Cogalniceanu *et al*. 2001, Eniang *et al*. 2003). In amphibian community studies there has been confusion in the interpretation of the concepts of 'sympatry' *vs*. 'syntopy'. Indeed, several studies have examined species interactions at inappropriate spatial scales, merging organisms living in distinct habitats (e.g., Lizana *et al*. 1990, Eterovick & Sazima 2000) that, therefore, could not interact at all. In these cases it may be trivial to analyse interspecific relationships, and generalizations of observed patterns in such otherwise hard-to-compare systems may be difficult. Moreover, community studies examining interactions between genuinely syntopic amphibians are often based on low numbers of interacting species and they are usually restricted to Caudates (maximum 3 species, e.g., Avery 1968, Griffiths 1986, Fasola & Canova 1992, Joly & Giacoma 1992, Fasola 1993, Macale *et al*. 2008). Since the complexity and stability of most natural communities is clearly linked to the number of interacting species, with species-rich assemblages being more likely regulated by deterministic 'competitive' rules than species-poor assemblages (Rohde 1992), it is inappropriate to use only species-poor assemblages to highlight ecological community patterns in syntopic amphibians. Hence, it is necessary to extend studies on genuinely syntopic species also to systems with high or relatively high numbers of species.

In this paper, we examine dietary patterns of six syntopic amphibians at a Mediterranean pond area in central Italy, whose spatial (macro- and micro-habitat use; Vignoli *et al*. 2007a, b) and temporal (phenology; Vignoli *et al*. 2007a) niche dimensions are well known. Amphibian species are arthropophagous generalists at intermediate levels in the trophic chains. Recently, Luiselli (2008b) showed that in insectivorous species a community structure based on interspecific competition can be revealed by pseudocommunity analysis using Lawlor's (1980) RA2 algorithm rather than other algorithms. Hence, we used pseudocommunity analysis (Gotelli 2000, 2001) to investigate whether our amphibian community is structured by competition processes. We aim to explore whether this pattern is confirmed in our amphibian community. The dietary patterns and assembly rules were analysed by using descriptive statistics (univariate and multivariate) and Costello graphic visualization (Amundsen *et al*. 1996, Vignoli *et al*. 2007c).

MATERIALS AND METHODS

Study Area: The field work was carried out at Canale Monterano (190 m a.s.l.; N46.8107°, E6.7181°) in the Regional Natural Reserve of Monterano (Province of Rome, Italy). Samples were taken over an area of five hectares within a tuff quarry abandoned for about 30 years. Over that time several lentic aquatic habitats developed due to the impermeability of tuffaceous ground. These ponds were fed predominantly by annual rainfall that varied approximately from 900 to 1100 mm annually and was more intense during the winter and early spring (Mantero 2006). Two main independent aquatic systems were detected: one permanent and one temporary, both constituted by two ponds connected after major rainfalls. Water temperature varied among seasons (winter: 04-13°C; spring: 13-24°C; summer: 26-32°C), and pH range was 7.1-8.6. Aquatic vegetation consisted of *Chara* sp., *Juncus* sp., *Carex* sp., *Ranunculus aquaticus,* and the riparian vegetation surrounding the ponds consisted of *Salix* sp., *Rubus* sp., various shrub species and pastures (Vignoli 2003).

The study area was surveyed periodically over two years (from January 2001 to December 2002) with a minimum survey effort of once a month during late summer and autumn, and a maximum frequency of 4 visits per week in late winter and Spring when most species had their activity peaks (Vignoli *et al*. 2007a). The various ponds were surveyed for different periods, with efforts varying from 25 to 69 sample-days.

Study species: Six syntopic species of amphibians are found in the study area (Vignoli 2003), constituting an assemblage of two salamanders and four anurans. These species are: *Triturus carnifex* (Laurenti, 1768), *Triturus vulgaris* (Linnaeus, 1758), *Bufo bufo* (Linnaeus, 1758), *Hyla intermedia* Boulenger, 1882, and the green frogs *Pelophylax lessonae* (Camerone, 1882), *Pelophylax klepton esculentus* (Linnaeus, 1758) (analysed together as a single unit, *Rana* skl. *hispanica*, because of their extreme morphological similarity which prevented identification in the field), and *Rana dalmatina* Bonaparte, 1838. Three additional amphibian species (*Salamandrina perspicillata* (Savi, 1821), *Bufo viridis* Laurenti, 1768, and *Rana italica* Dubois, 1987), occasionally found in the same or in neighbouring areas, were not considered in the analysis because, unlike the species studied, they did not use the ponds for feeding (Vignoli *et al*. 2007a, b). Monthly activity and habitat choice of the various amphibian species of the study area was studied elsewhere (Vignoli *et al*. 2007a, b). In this paper, waiting for a definitive nomenclatural assessment of the various taxa, we intentionally adopted the more widely accepted nomenclature.

Protocol and statistical procedures: For this study only adult individuals were considered. The field work was more intense during the specific peaks of activity (e.g. January and February for *Rana dalmatina*, March and April for *Hyla intermedia* and the green frogs). We sampled all the amphibian species when they were at the pond and when they were active. Non-active specimens (e.g. specimens found under stones or out of their usual phenology) were excluded from the analysis. Amphibian species were sampled by the Visual Encounter Survey method with 60 minutes of dipnetting. Newts were also sampled by using aquatic funnel traps (self made; Vignoli 2003).

Immediately after capture, the amphibian individuals were stomach flushed, repeating this procedure until no further content came out (Legler & Sullivan 1979, Joly 1987, Leclerc & Courtois 1993). Food items still present in the oral cavity after flushing were carefully removed by entomological forceps. Newts and frogs were released in the pond approximately 30 min after flushing, once their normal activity was verified. No mortality was observed during or after stomach flushing. Taxonomic identification of stomach contents was made using a stereomicroscope (Olympus SZX 12. Range of magnification 9-55X). Food items were identified to the lowest taxonomical level possible, then photographed with a digital camera (Olympus C3030). Pictures of items were analysed by Image Tool 3.00 software (University of Texas Health Science Center - San Antonio) and measured for prey volume. Prey volume was estimated using the volume of a prolate spheroid used for most adult insects and other arthropods. The volume of a prolate spheroid is as follows:

$$V = 4/3\pi\,(\text{prey length}/2)\cdot(\text{prey width}/2)^2$$

For insect larvae, instead, we used the volume of a cylinder, calculated as follows:

$$V = 2r\pi\,(\text{prey length}).$$

Cumulative-diversity curves (prey diversity plotted against the number of stomachs) were produced for each species to test whether the collected data were representative of the dietary spectrum and to avoid sample size bias in intra-specific comparisons (Kovács & Török 1997). The index of vacuity, calculated as the percentage of empty stomach out of the total analysed, was estimated for all six species. In the text, prey items are reported by frequency of occurrence (FO: number of stomachs containing one item divided by the total number of stomachs containing food) and relative abundance (RA: number and volume of individuals belonging to a single prey item divided by the total number and volume of individuals belonging to all prey items). The identified prey taxa were grouped in some more comprehensive categories defined by both systematic and ecological traits (see captions of Figs 1 and 2 for details), in order to maximize either the variance in multivariate statistical analyses or the clarity in graphic representation.

Food categories were graphically represented by Costello's method modified by Amundsen *et al.* (1996) interpreting the feeding attitude of a predator (Costello 1990, Vignoli 2003, Bombi *et al.* 2005, Vignoli *et al.* 2006, 2007c) by dividing the diet into its constituent components, providing insight about feeding patterns that might not be inferred from single diet indices. Three important aspects of the diet were evaluated: 1) feeding strategy (specialized *vs.* generalist), 2) prey importance (dominant *vs.* rare) and 3) niche width (resource use changing from BPC [between phenotype component – high diversity among individuals of population] to WPC [within phenotype component – tending towards the same resource use]). These components were graphed plotting frequency of occurrence (FO) on the X-axis and prey-specific abundance on the Y-axis. Prey-specific abundance (P_i) is defined as the proportion a prey item (*i*) comprises of all prey items in only those individuals in which prey *i* occurs (Amundsen *et al.* 1996).

Prey niche overlap was calculated applying Pianka's (1973) index:

$$O_{xy} = \frac{\sum_{i=1}^{n} p_{xi}\; p_{yi}}{\left(\sum_{i=1}^{n} p_{xi}^{2} \sum_{i=1}^{n} p_{yi}^{2}\right)^{1/2}}$$

where p_{xi} is the proportional utilization of prey *i* by form *x* and p_{yi} the proportional utilization of prey *i* by form *y*. The index ranges from 0 (no prey in common in the diet spectrum) to 1 (same diet spectrum).

Because the evaluation and comparison of niche overlap indexes are affected by the limitation of arbitrary cut-offs (Feinsinger *et al.* 1981), we compared the observed overlap values to an appropriate null model. The distribution of the null model was created using EcoSim software (version 7.0; Gotelli & Entsminger 2001, 2003) running two simulations each with 1000 randomised replications of the data set. The simulations were generated using two randomisation algorithms: RA2 (Niche breadth relaxed/Zero States retained) whereby every cell in the matrix is replaced with a randomly chosen, uniforming number between zero and one but maintaining the zero structure in the matrix; and RA3 (the 'scrambled-zeros' randomisation algorithm proposed by Winemiller & Pianka 1990) whereby the entries in each row of the utilization matrix were randomly reshuffled for each iteration retaining the niche breadth of each species but randomising which particular resource states are utilized. Due to the impossibility of reliably assessing food resource availability in the study area (Vignoli 2003), we constrained our null models into an equiprobable resource availability state. In this model, the different resource states are assumed to be equally abundant (or usable) by all species. When the number of independent food categories preyed upon by species is high (as in our study case), this assumption is likely untrue. Thus, null model analysis will tend to over-estimate niche overlap because species will tend to use common resource states even if there is niche segregation (Gotelli & Entsminger 2003). In order to reduce this weakness, we excluded from the analysis those food resources that are marginal dietary components for our species (i.e., accounting for less than 5 % of occurrence). In this way, we reduced the total number of food resources from 35 to 11. This procedure reduces the probability of over-estimating interspecific overlaps. An observed overlap either greater or lower than 95 % of the simulated overlaps indicates a significant deviation from random use of the resources by the two species (Winemiller & Pianka 1990), with community structure compatible with interspecific competition rules requiring that the observed index value should be significantly smaller ($p < 0.05$) than expected (e.g., Gotelli & Entsminger 2003).

Statistical analyses were performed to compare food habits among the species studied. Prior to any analyses, data distribution was assessed for normality and homogeneity of variance by Levene's test. We used parametric tests when data fitted normal distribution or when data were successfully transformed (logarithmic and arc-sin transformations); otherwise non-parametric tests were used. A Kruskal-Wallis test was used to compare the average stomach content volume and the average number of prey found in non-empty stomachs in the studied species. Due to the strongly unequal sample analysed (e.g: 31 *T. vulgaris* versus 111 *T. carnifex*), a bootstrap procedure was performed to avoid sample-dependent biases; for this purpose we randomly selected five subsets of, respectively, 5, 7, 10, 12, and 15 individuals, and defined niche breadth for each sub-sample, and then compared by chi-square the observed niche breadth with the one calculated for the whole sample size (expected value). If there was no difference between the observed and expected values, we concluded that unequal sample size did not affect the analyses. Correspondence analysis was used to evaluate how the species exploit the food resources. Multi Response Permutation Procedure (MRPP) was used to evaluate the significance of interspecific differences generated by the correspondence analysis. MRPP allowed to compare the observed intra-group average distances with the average distances that would have resulted from all the other possible combinations of the data under the null hypothesis (Mielke *et al.* 1976). In the Costello's graphic representation and in the Correspondence analysis, food items were grouped in homogeneous assemblages based on taxonomical and ecological characteristics. All statistical analyses were performed by Statistica (Statsoft, version 6.0), with two tailed test and alpha set at 5 %.

Table I. – Numeric and volumetric data of 36 prey categories eaten by the six amphibian species at the study site (388 analysed specimens). Frequency of occurrence (FO) and relative abundances of prey based on numeric (Num) and volumetric (Vol) data are shown. Prey categories are listed along a terrestrial-aquatic gradient.

	Food categories	*Rana dalmatina*			*Pelophylax* kl. *esculentus*			*Hyla intermedia*			*Bufo bufo*			*Triturus carnifex*			*Triturus vulgaris*		
		FO	NUM	VOL	FO	NUM	VOL	FO	NUM	VOL	FO	NUM	VOL	FO	NUM	VOL	FO	NUM	VOL
TERRESTRIAL	Oligochaeta		-	-	0.01	0.002	0.034		-	-		-	-	0.01	-	-		-	-
	Gastropoda ter	0.17	0.143	0.14	0.14	0.026	0.106		-	-	0.67	0.08	0.055	0.03	0.003	0.008		-	-
	Isopoda		-	-	0.11	0.087	0.026	0.06	0.028	0.162	0.50	0.15	0.077	0.03	0.0014	0.006	0.06	0.005	0.018
	Aranea		-	-	0.47	0.09	0.014	0.33	0.194	0.056	0.50	0.12	0.028	0.01	0.0004	0.0001	0.09	0.009	0.008
	Miriapoda	0.17	0.143	0.263	0.10	0.018	0.002		-	-	0.67	0.13	0.114	0.02	0.001	0.0013	0.06	0.005	0.008
	Collembola		-	-	0.07	0.093	0.0006	0.11	0.056	0.003		-	-	0.01	0.0004	0.0001	0.03	0.002	0.0001
	Orthoptera		-	-	0.02	0.003	0.009		-	-		-	-		-	-		-	-
	Dermaptera		-	-	0.06	0.008	0.0009		-	-	0.17	0.01	0.002		-	-		-	-
	Homoptera		-	-	0.02	0.002	0.0001		-	-		-	-	0.02	0.003	0.004		-	-
	Heteroptera ter		-	-	0.14	0.02	0.002	0.06	0.028	0.0324		-	-	0.01	0.0004	0.001		-	-
	Neuroptera L		-	-		-	-	0.06	0.028	0.009		-	-		-	-		-	-
	Lepidoptera L	0.50	0.57	0.585	0.15	0.024	0.127	0.22	0.139	0.58		0.02	0.039	0.04	0.002	0.02		-	-
	Lepidoptera		-	-	0.01	0.002	0.001		-	-		-	-		-	-		-	-
	Coleoptera ter	0.17	0.143	0.011	0.57	0.2	0.099	0.28	0.139	0.08	0.67	0.17	0.535		-	-		-	-
	Coleoptera ter L		-	-	0.01	0.002	0.0001		-	-		-	-	0.02	0.0007	0.0009		-	-
	Hymenoptera		-	-	0.10	0.015	0.004	0.11	0.056	0.01		-	-	0.01	0.0004	0.0001		-	-
	Formicidae		-	-	0.37	0.22	0.01	0.17	0.083	0.028	0.83	0.19	0.026	0.02	0.0007	0.0004		-	-
	Nematocera		-	-	0.10	0.021	0.001	0.06	0.028	0.003		-	-	0.01	0.0004	-		-	-
	Brachycera		-	-	0.07	0.009	0.0004		-	-		-	-		-	-	0.03	0.002	0.001
	Brachycera L		-	-	0.03	0.01	0.009		-	-		-	-		-	-	0.03	0.002	0.002
	Hexapoda n.d.		-	-	0.24	0.06	0.01	0.22	0.167	0.017	0.50	0.06	0.004	0.09	0.005	0.003	0.13	0.013	0.001
	Vertebrata		-	-	0.05	0.009	0.357		-	-		-	-	0.01	0.0004	0.0026		-	-
AQUATIC	Gastropoda acq		-	-	0.03	0.006	0.006		-	-		-	-	0.31	0.134	0.186	0.09	0.009	0.021
	Copepoda		-	-		-	-		-	-		-	-	0.03	0.014	0.0004	0.38	0.082	0.015
	Cladocera		-	-	0.25	0.084	0.0002					-	-	0.25	0.462	0.053	0.63	0.532	0.205
	Ostracoda		-	-		-	-		-	-		-	-	0.09	0.005	0.0007	0.38	0.094	0.018
	Zygoptera L		-	-	0.02	0.003	0.0003		-	-		-	-	0.09	0.007	0.005	0.13	0.011	0.015
	Anisoptera L		-	-	0.36	0.08	0.154	0.06				-	-	0.63	0.11	0.43	0.31	0.09	0.43
	Ephemeroptera L		-	-		-	-		-	-		-	-	0.21	0.013	0.01	0.19	0.016	0.029
	Heteroptera acq		-	-	0.08	0.014	0.002		-	-		-	-	0.13	0.01	0.013		-	-
	Coleoptera acq		-	-	0.07	0.01	0.015		-	-	0.33	-	-	0.16	0.0004	0.001	0.22	-	-
	Coleoptera acq L		-	-	0.06	0.01	0.001		-	-		0.07	0.122	0.01	0.013	0.056	0.16	0.046	0.08
	Trichoptera L		-	-	0.01	0.002	0.0003		-	-		-	-		-	-		-	-
	Plecoptera L		-	-		-	-		-	-		-	-	0.01	0.002	0.0014		-	-
	Nematocera L		-	-	0.08	0.012	0.006		-	-		-	-	0.44	0.194	0.183	0.44	0.058	0.098
	Amphibia ova		-	-		-	-		-	-		-	-	0.09	0.016	0.01	0.09	0.025	0.052

RESULTS

Descriptive analysis of the diets

A total of 388 individuals were analysed: 131 *T. carnifex*, 38 *T. vulgaris*, 62 *H. intermedia*, 40 *R. dalmatina*, 104 green frogs, and 13 *B. bufo*.

The index of vacuity was nearly 9 % (n = 12) in *T. carnifex*, 18 % (n = 7) in *T. vulgaris*, 71 % (n = 44) in *H. intermedia*, 81 % in *R. dalmatina* (n = 34), 16 % in green frogs (n = 17), and 54 % in *B. bufo* (n = 7). A total of 4173 prey items was identified and classified into 36 prey taxonomic groups (Table I). Four of the study species (*T. carnifex*, *T. vulgaris*, *H. intermedia*, green frogs) reached the plateau phase in the cumulative-diversity curves (Vignoli *et al*., unpublished data), thus showing that prey composition was reliably assessed. The other species (*B. bufo, R. dalmatina*) were excluded from com-

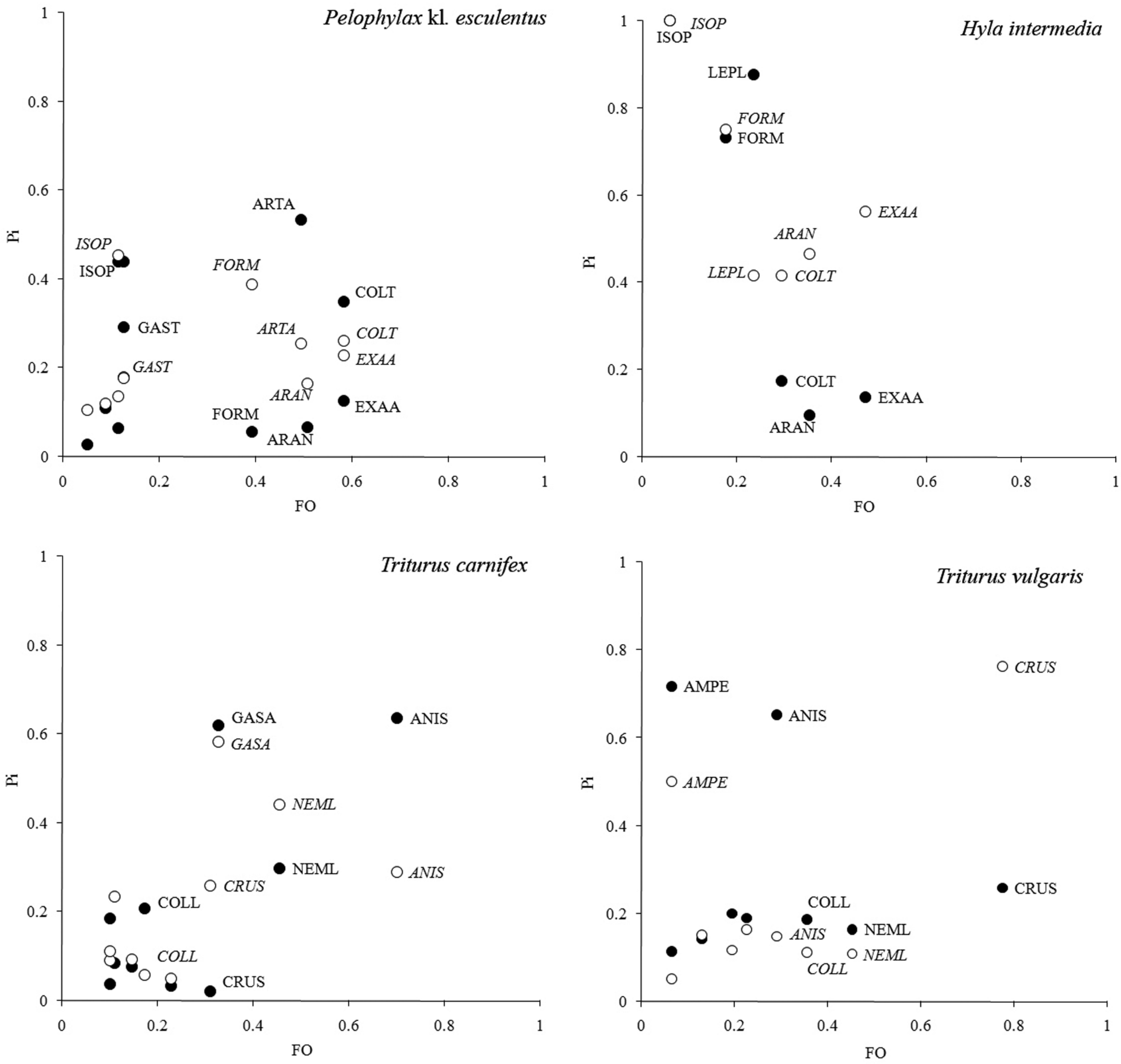

Fig. 1. – Modified Costello graphic visualization by Amundsen *et al.* (1996), showing trophic strategies of the amphibian species at the study site. Analyses performed on number of prey (white circles and italic labels) and volume (black circles and roman labels). Pi = prey relative importance; FO = frequency of occurrence. Food categories with low frequency of occurrence or Pi were not shown for clarity. Aquatic prey labels are in italics. Symbols: AMPE = amphibian eggs; ANIS = Anisoptera larvae; ARAN = Araneae; ARTA = aquatic Arthropoda (Anisoptera larvae, aquatic Coleoptera); ARTT = terrestrial arthropods (Collembola, terrestrial Coleoptera); COLL = aquatic Coleoptera larvae; COLT = terrestrial Coleoptera; CRUS = Cladocera, Copepoda, Ostracoda; EPHL = Ephemeroptera larvae; EXAA = winged insects (Anisoptera, Zygoptera, Homoptera, terrestrial Heteroptera, Lepidoptera, Hymenoptera, Nematocera, Brachyicera); FORM = Formicidae; GASA = aquatic Gastropoda; GAST = terrestrial Gastropoda; ISOP = Isopoda; LEPL = Lepidoptera larvae; NEML = Nematocera larvae.

putations because the plateau phase was not reached.

Costello graphics (based on number and volume of prey; Fig. 1) showed different diet patterns for the studied species. Green frogs were characterized by a generalist pattern in resource use (many prey categories with FO > 0.5 and $P_i < 0.5$) with high diversity within individuals and large niche width (low abundance of a wide variety of prey - within phenotype component pattern). For *H. intermedia*, the distribution of prey (high P_i score and low frequency) suggested a generalist pattern with high diversity among individuals (between phenotype component pattern) in resource use. *Triturus carnifex* presented a mixed feeding strategy with some individuals having a specialized diet towards insect larvae (Anisoptera and Nematocera) and others having a more generalized feeding strategy. *Triturus vulgaris* showed a high specialization towards aquatic crustaceans (particularly Cladocera), and a narrow niche width due to the remaining food categories being preyed only occasionally.

Correspondence analysis was based on 16 comprehen-

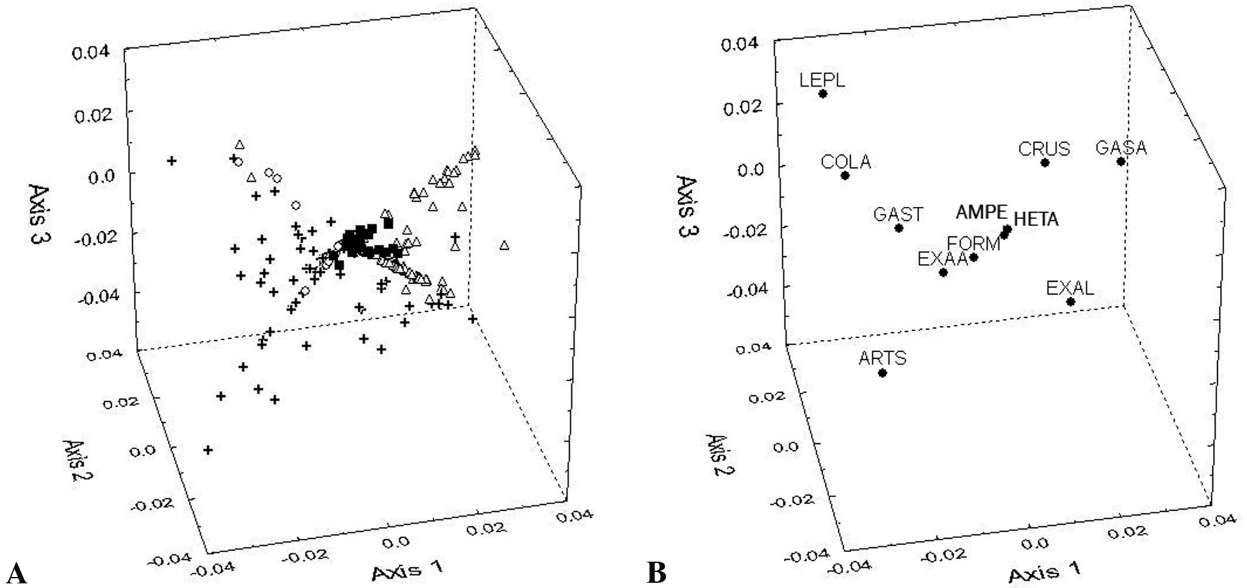

Fig. 2. – Correspondence analysis performed on diet of the amphibian species at the study area. Cases and variables are shown respectively in part A and B. Symbols: circles = *H. intermedia*; crosses = *Pelophylax* kl. *esculentus*; squares = *T. vulgaris*; triangles = *T. carnifex*. Aquatic prey labels are in italic. AMPE = amphibian eggs (anuran eggs); ARTS = Ground arthropods (Araneae, ground beetles, isopods, miriapods); COLA = Aquatic coleoptera; CRUS = Aquatic crustaceans (cladocerans, copepods, ostracods); EXAA = Winged Hexapoda (various winged insect orders); EXAL = Aquatic Hexapoda larvae (aquatic larvae of odonata, nematocera, ephemeroptera, coleoptera); FORM = Formicidae; GASA = Aquatic Gastropoda; GAST = Terrestrial Gastropoda; HETA = Aquatic Heteropetra; LEPL = Lepidoptera larvae.

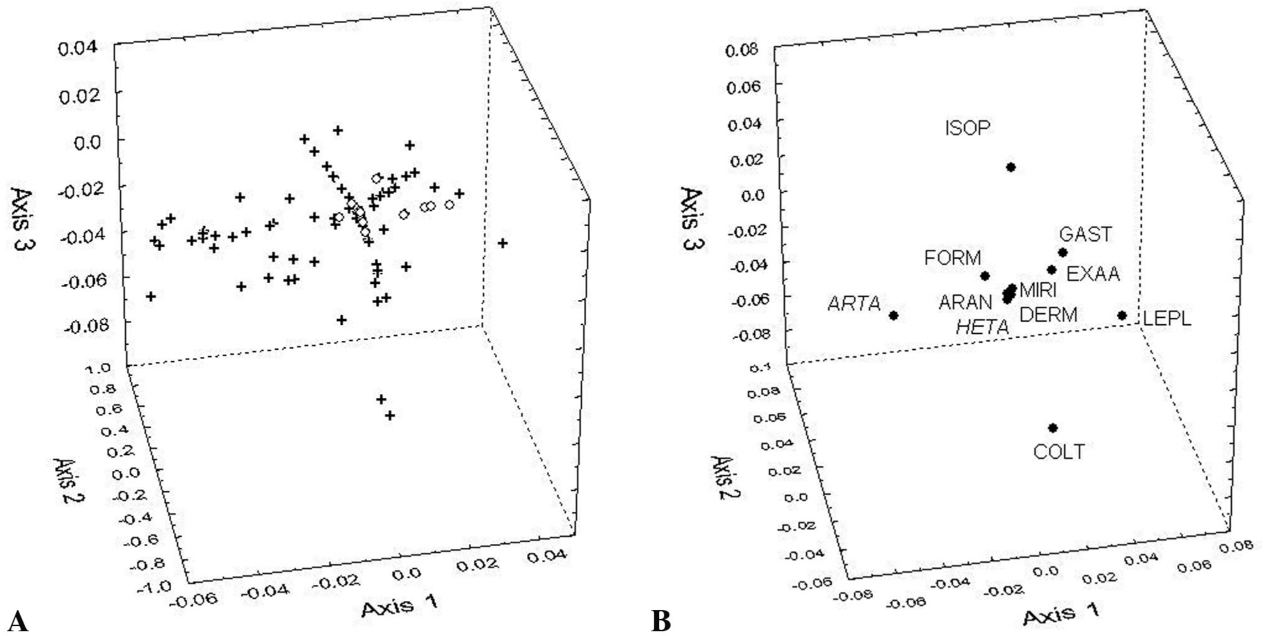

Fig. 3. – Correspondence analysis performed on diet of the terrestrial amphibian species at the study area. Cases and variables are shown respectively in part A and B. Symbols: crosses = *Pelophylax* kl. *esculentus*; circles = *H. intermedia*. Aquatic prey labels are in italic. ARAN = Araneae; ARTA = Aquatic arthropods (aquatic crustaceans; aquatic insect larvae and adults); COLT = Terrestrial Coleoptera; DERM = Dermaptera; EXAA = Winged Hexapoda (various winged insect orders); FORM = Formicidae; GAST = Terrestrial Gastropoda; HETA = Aquatic Heteroptera; ISOP = isopods; LEPL = Lepidoptera larvae; MIRI = miriapods.

sive prey categories, because some prey taxa were grouped and those with FO less than 5 % were not considered in the analysis (to avoid variance overdispersion). This analysis arranged the amphibian species on the basis of their diet spectrum (Fig. 2). We presented only data for prey volume because prey number data also gave similar results. Correspondence analysis (done on three factors to maximize the explained variance; factor1: 11.02 %; fac-

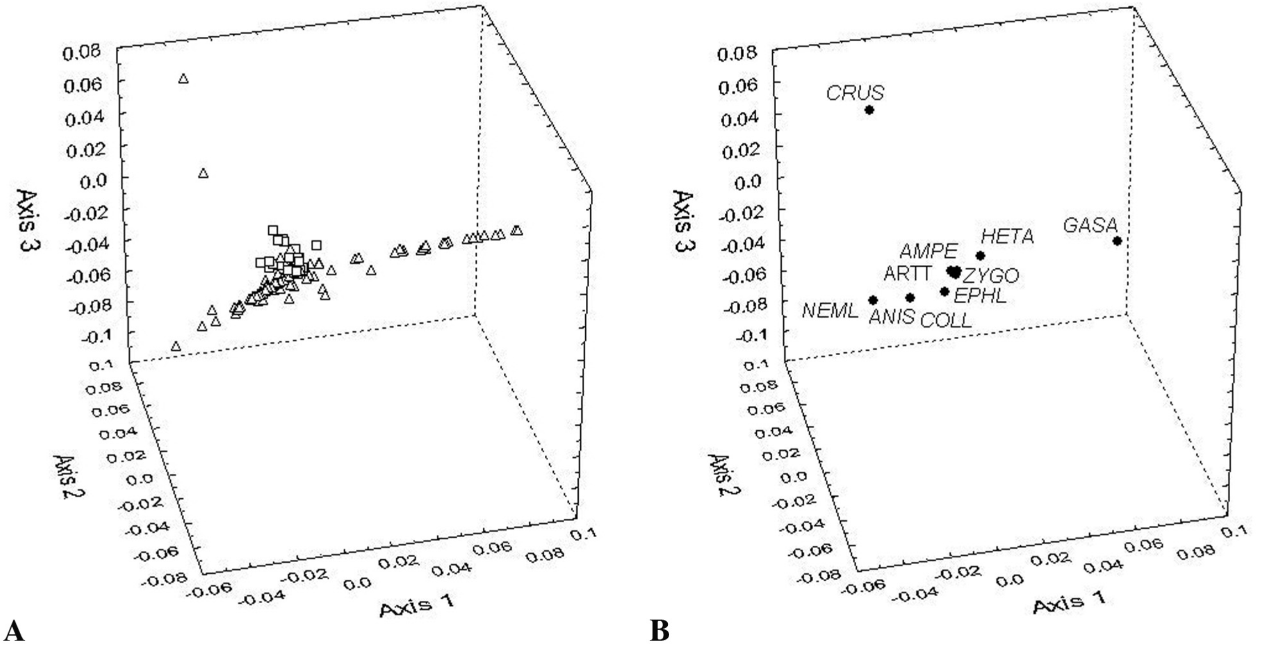

Fig. 4. – Correspondence analysis performed on diet of the aquatic amphibian species at the study area. Cases and variables are shown respectively in part A and B. Symbols: triangles = *T. carnifex*; squares = *T. vulgaris*. Aquatic prey labels are in italic. AMPE = amphibian eggs (anuran eggs); ANIS = Anisoptera larvae; ARTT = Terrestrial arthropods (Araneae, Hexapoda, isopods, miriapods); COLL = Aquatic Coleoptera larvae; CRUS = Aquatic crustaceans (cladocerans, copepods, ostracods); EPHL = Ephemeroptera larvae; FORM = Formicidae; GASA = Aquatic gastropods; HETA = Aquatic Heteroptera; NEML = Nematocera larvae; ZYGO = Zygoptera larvae.

tor2: 9.94 %; factor3: 9.72 %) with the first three factors explaining 30.7 % of the total variance allowed to classify the species into two separated units in the multidimensional space (average δ_{obs}-δ_{exp} along the three axes = -0.202; $p < 0.0001$; MRPP analysis): one group feeding on terrestrial prey types (hereafter called TER - negative value of first axis) and the other on aquatic ones (hereafter called AQU - positive values of first axis). Indeed, a same set of correspondence analysis based on number and volume of prey performed respectively on TER (*H. intermedia* and green frogs; *B. bufo* and *R. dalmatina* were not considered in the analysis because of their large proportion of empty stomachs) (with first three factors explaining 41.6 % of the total variance for number of prey and 44.5 % for volume - Fig. 3) and AQU (*T. carnifex* and *T. vulgaris*) (49.0 % and 55.7 % - Fig. 4), clearly arranged the species in separate units. Regarding TER, green frogs and *H. intermedia* were arranged in two distinct groups for volume (average δ_{obs}-δ_{exp} along the three axes = -0.037; $p < 0.01$), but not for number of prey (average δ_{obs}-δ_{exp} = -0.0086; $p > 0.05$) (Fig. 3). With regards to AQU, *T. carnifex* and *T. vulgaris* were also significantly arranged in distinct groups for both number and volume of prey (for both analyses average δ_{obs}-δ_{exp} at least = -0.083 $p < 0.0001$) (Fig. 3). In both two-species-subset plots, one species had a wider and scattered distribution (green frogs average group distance number of prey = 1.692, volume = 1.773; *T. carnifex* group distance number = 1.542, volume = 1.764) and completely overlapped the second species, whose distribution was very narrow in the three-dimensional space (*H. intermedia* average group distance number of prey = 1.172, volume = 0.700; *T. vulgaris* average group distance number of prey = 1.354, volume = 0.652).

The bootstrap procedure on the five subsets of each

Table II. – Values of observed and expected (mean of simulated indices) niche overlap for TER and AQU groups, and associated probability that observed overlap is minor or equal to the expected between real and pseudo-communities applying both RA2 and RA3 algorithms (i.e., community structure ruled by interspecific competition; Gotelli and Entsminger, 2001). RSK = green frogs; HI = *Hyla intermedia*; TC = *Triturus carnifex*; TV = *T. vulgaris*.

	Observed overlap		Mean of simulated indices				p(obs ≤ exp)		p(obs ≤ exp)	
			RA2		RA3		RA2		RA3	
	Num	Vol	Num	Vol	Num	Vol	Num	Vol	Num	Vol
TER (RSK vs. HI)	0.770	0.225	0.536	0.573	0.424	0.250	0.989	0.004	0.990	0.653
AQU (TC vs. TV)	0.905	0.863	0.227	0.717	0.702	0.362	0.993	0.933	0.986	0.970

pair of species (green frogs-*H. intermedia* and *T. carnifex*-*T. vulgaris*) revealed no difference between the observed and expected samples (green frogs: $\chi^2 = 3.37$, $p = 0.498$; *H. intermedia*: $\chi^2 = 1.156$, $p = 0.885$; *T. carnifex*: $\chi^2 = 1.079$, $p = 0.897$; *T. vulgaris*: $\chi^2 = 1.037$, $p = 0.904$. For all tests df = 4).

Pseudocommunity analysis

Null model analyses revealed contrasting patterns for TER and AQU. Concerning TER, the amphibian assemblage appeared to be non-randomly structured by RA2 for volume of prey ($p_{obs \leq exp} < 0.01$) but not for number of prey ($p_{obs \leq exp} = 0.989$) or for both number and volume of prey analysed by RA3 (at least $p_{obs \leq exp} = 0.653$). Concerning AQU, the species appeared to be randomly assembled according to both RA2 and RA3, either for number or for volume of prey (at least $p_{obs \leq exp} = 0.933$) (Table II).

DISCUSSION

Our data revealed in a clear way that the studied assemblage consisted of two groups (TER and AQU) that are separated in terms of (i) pattern of vacuity index, (ii) use of the trophic resources, and (iii) assembly forces organizing the various species' interactions.

The bootstrap procedure did not reveal any difference between observed and expected samples for each pair of species from the groups TER and AQU, and allowed us to analyse them despite the discrepancy of sampled individuals.

Examination of vacuity index provided evidence of the activity time span of each species within the wetland, and allowed us to define species constituting a genuinely syntopic assemblage. For the vacuity index, TER species showed high values apart from the green frogs, whereas AQU species showed lower values. This pattern may depend on the different activity timespan at the reproductive site of the studied species (Vignoli *et al.* 2007a), with species spending longer timespan at the reproductive site in foraging (*T. carnifex*, *T. vulgaris*, and the green frogs) being characterized by lower vacuity index compared to species widely dispersing for foraging in the surroundings after a relative short period at the reproductive site (*B. bufo*, *H. intermedia* and *R. dalmatina*). Among these latter species, *R. dalmatina* is known to spend very little time at the oviposition site (Pavignano *et al.* 1990, Vignoli *et al.* 2007a) and to be anorexic during the aquatic reproductive phase as it feeds exclusively upon terrestrial prey caught in woodland habitats (e.g., see Török & Csörgő 1992, Aszalós *et al.* 2005). Thus, this frog could not interact for food with the other species during the aquatic reproductive phase. Concerning *H. intermedia*, although many individuals are anorexic during the aquatic reproductive phase (Vignoli *et al.* 2007a), almost a third of the reproductive population continued to feed, as shown by the plateau phase reached in the diet diversity curve (this study). These individuals might interact with other syntopic species at the study pond, and thus need to be considered for this study (see below).

In terms of use of trophic resources, TER species (i.e., *B. bufo*, *H. intermedia*, *R. dalmatina*, and the green frogs) foraged exclusively on terrestrial animals apart from the green frogs that also fed on aquatic prey (i.e. Coleoptera and Odonata larvae), showing an unusual behaviour in comparison to all other European anurans (except for *Bombina* and *Discoglossus*; Salvidio *et al.* 1999). Conversely, AQU species (*T. carnifex* and *T. vulgaris*) fed primarily on aquatic animals and rarely on terrestrial arthropods falling on the water surface (i.e. Homoptera and Orthoptera). However, excluding the species whose diet spectrum was not assessed properly due to small sample sizes (*B. bufo* and *R. dalmatina*), the two groups are consistent in that the species with the more generalist dietary habits (wider diet spectrum) were also those with the larger body size (i.e., respectively green frogs for TER, and *T. carnifex* for AQU). The green frogs and *H. intermedia* showed the lower overlap degree in terms of volume of prey, the green frogs feeding on prey substantially larger than *H. intermedia* (i.e., juveniles of *Natrix natrix*, adults of *H. intermedia*, large ground beetles, and butterflies). *Triturus carnifex* and *T. vulgaris* showed an overall high overlap in trophic resource use in terms of both number and volume of prey. As reported in previous studies (Griffiths & Mylotte 1987, Joly & Giacoma 1992, Fasola 1993, Eniang *et al.* 2003), a larger size enables a wider range of prey size to be consumed, because both large and small amphibian species feed on the same small prey type (i.e.: collembola and aquatic crustaceans for respectively TER and AQU guilds).

In terms of assembly structure, our null model analyses revealed that TER species were arranged along the trophic niche dimension in a non-random way, evidencing that the various species are organized along the generalist-specialist nature of the assemblage, where quantitative features (and not the quality) of the various food resources are responsible for the community structure (see the arguments on the RA2 algorithm discussed by Luiselli 2008b). On the contrary, the AQU species were randomly assembled along the trophic niche dimension. There are several explanations for these differences among guilds. For TER, the observed non-random structure in terms of diet spectrum, could be due to (i) different prey/predator-size relationships (green frogs being significantly larger than *H. intermedia* and preying upon organisms on average larger in size than those selected by *H. intermedia*), (ii) to a discrepancy in micro-habitat use (evidenced by Vignoli *et al.* 2007b), (iii) to a different phenology (as observed by Vignoli *et al.* 2007a, b) influencing foraging activity and seasonal prey availability, and/or (iv) to a limited resource availability. Conversely, the observed random structure of the assemblage in AQU group may likely depend on a non-limiting resource availability. In our study pond, the green frogs and *H. intermedia*, although showing a large overlap in the selection of oviposition sites restricted to breeding period, segregated along the spatial (macro- and micro-habitat use) and temporal niche dimensions (Vignoli *et al*. 2007a, b). A further segregation along the trophic axis of the ecological niche could be explained at least in part as a consequence of both the former resource partitioning patterns (responsible for differences in prey type) and in part due to the interspecific discrepancy in body size that is known to affect food size selection (Pilorge 1982). The limited food resource availability is the less likely among the three proposed explanations for the observed assembly structure, because Mediterranean habitats surrounding wetlands are known to host a rather rich and diversified fauna of terrestrial arthropods (Blasi *et al*. 2007). Both these patterns are confirmed by previous studies. In particular, for terrestrial amphibians (most studies being conducted on anurans) micro-habitat resource partitioning and body size discrepancy among species are demonstrated as factors influencing dietary patterns and facilitating species coexistence (e.g., Barbault 1974, Toft 1980, Salvidio *et al*. 1999, Hirai & Matsui 2001, Eniang *et al*. 2003, Macale *et al*. 2008). For aquatic amphibians, i.e., newts and salamanders, the investigations on the trophic dimension of the ecological niche highlighted that the feeding spectra largely overlap among species at least at the adult stage. This pattern is mainly due to both generalist feeding habits of most adult urodelans and the superabundance of food resources commonly occurring in eutrophic ponds that constitute the elective habitats for newts and salamanders and the most common site where researchers have conducted these kind of studies (e.g., Avery 1968, Griffiths 1986, Griffiths & Mylotte 1987, Fasola & Canova 1992, Joly & Giacoma 1992, Fasola 1993). Moreover, the observed interspecific, typically slight discrepancies in feeding habits within urodelans assemblages are mainly due to differences in prey size (determined by divergence in species body size) being responsible of the main amount of trophic spectrum interspecific diversity (e.g., Griffiths & Mylotte 1987, Fasola & Canova 1992, Joly & Giacoma 1992).

In general, in amphibian community studies there has been some confusion in the interpretation of sympatric *vs*. syntopic condition of the studied species assemblages. Species breeding and/or foraging at the same pond or stream can be defined as syntopic, whereas sympatric species inhabit an area whose boundaries are arbitrary defined, often at a scale higher than that of species perceptual range: i.e., a forest (Salvidio *et al*. 1999), a mountain system (Lizana *et al*. 1990), a protected area (Reques & Tejedo 1991), that comprise different aquatic habitats. Sympatric species, as potentially exploiting distinct aquatic habitats for reproduction and/or feeding, could not interact at all, making trivial any attempt to analyse interspecific relationships. Studies on anuran species assemblage are likely affected by this bias more than those on urodelans, because, except for the reproductive period, adult anurans are usually active in terrestrial habitats and disperse over large areas, whereas urodelans have a prolonged aquatic phase accomplishing reproduction and feeding in water. As a consequence of this ambiguity, we feel that several studies generically focusing on sympatric species of amphibians (particularly frogs and toads) referring to community or assemblage of species may not be comparable, and may lack a genuine biological sense. Therefore, we recommend that future studies should focus on comparisons among syntopic species.

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