

How do we share food? Feeding of four amphibian species from an aquatic habitat in south-western Romania

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Abstract

How do we share food? Feeding of four amphibian species from an aquatic habitat in south-western Romania.—The feeding of four amphibian species (*Triturus cristatus*, *Lissotriton vulgaris*, *Bombina variegata* and *Pelophylax ridibundus*) was studied in 2011, in south-western Romania. The diet of the newts was uniform and mostly composed of aquatic preys. The diet of the anurans was more diversified, comprising more prey taxa, mostly terrestrial. The trophic niches of the two newt species overlapped highly but differed from those of the anurans. The trophic niches of the anurans differed from one another. The differences among the four species' diets were determined by the use of different trophic resources, originating from different environments, and by their different sizes. The newts' diet was less diversified because the aquatic habitat was small and poor in trophic availability. The anurans used the aquatic habitat as a base from where they captured terrestrial preys in the surrounding terrestrial environment.

Key words: Amphibian community, Diet, Food composition, Trophic niche, Diversity.

Resumen

¿Cómo compartimos la comida? La alimentación de cuatro especies de anfibios de un hábitat acuático en el sureste de Rumanía.—En 2011 se estudió la alimentación de cuatro especies de anfibios (*Triturus cristatus*, *Lissotriton vulgaris*, *Bombina variegata* y *Pelophylax ridibundus*) en Rumanía. La dieta de los caudados era uniforme y se componía principalmente de presas acuáticas. La dieta de los anuros era más diversificada y comprendía más taxones de presas, en su mayor parte terrestres. Los nichos tróficos de las dos especies de caudado se solapaban en gran medida, pero eran distintos de los de los anuros. Los nichos tróficos de los anuros diferían entre sí. Las diferencias entre las dietas de las cuatro especies se debían a la utilización de recursos tróficos diferentes, procedentes de diversos ambientes, y a sus tallas distintas. La dieta de los caudados era menos diversificada porque el hábitat acuático era reducido y la disponibilidad de alimentos en el mismo, escasa. Los anuros utilizaban los hábitats acuáticos como base desde la que capturaban presas terrestres en el ambiente terrestre circundante.

Palabras clave: Comunidad de anfibios, Dieta, Composición de los alimentos, Nicho trófico, Diversidad.

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Introduction

Small, isolated wetlands are extremely important ecologically but are among the most threatened ecosystems (see Pitt et al., 2012). For amphibians, a declining group due to multiple causes (e.g. Stuart et al., 2004; Collins, 2010), it is important to maintain a high diversity of aquatic habitats at a small spatial scale (e.g. Hartel, 2008; Hartel et al., 2011). However, not all amphibians are equally tied to the same aquatic habitats (Hartel et al., 2011). Thus, it is important to establish to what extent the aquatic habitats of amphibians meet their needs. Feeding can be considered a useful indicator for this purpose (see Kovacs et al., 2007). In recent years, several papers about the feeding of some amphibian species have been published from Romania (e.g. Aszalos et al., 2005; Balint et al., 2010; Cicort-Lucaci et al., 2005, 2007a, 2007b, 2011; Cogalniceanu et al. 2000; Covaci-Marcov et al., 2010a, 2010b, 2010c, 2011, 2012; Dobre et al., 2007; Kovacs et al., 2007; Sas et al., 2009; Iftime & Iftime, 2011), but most have been from the north-western part of the country. The few data available regarding the south west focus only on some species (e.g. Bogdan et al., 2011, 2012a). To date, there are few studies on the feeding of more amphibian species in relation to the habitat and with the way they use its resources (e.g. Fasola & Canova, 1992; Covaci-Marcov et al., 2002, 2010c, 2012; Bisa et al., 2007; Guidali et al., 2000; Cicort-Lucaci et al., 2011; Cogalniceanu et al., 2000; Junca & Eterovick, 2007), and even fewer studies that compare the diet of newts with that of anurans (e.g. Vignoli et al., 2009). To the best of our knowledge, such studies in Romania have only been made separately. This study was performed to determine the food composition of four amphibian species [*Triturus cristatus* (Laurenti, 1768), *Lissotriton vulgaris* (Linnaeus, 1758), *Bombina variegata* (Linnaeus 1758) and *Pelophylax ridibundus*

(Pallas 1771)] in an aquatic habitat in south-western Romania, to establish the differences between them, and to compare the trophic niches and the way the trophic resources are exploited.

Material and methods

The study area was located near Maru village, in the Tarcu Mountains, in south-western Romania ($45^{\circ} 27' 26.21''$ N, $22^{\circ} 26' 42.13''$ E). The habitat was a pond of approximately 8 m long and 4 m wide, situated at an altitude of 430 m a.s.l. In this habitat we found large newt populations (see Bogdan et al., 2012b, also see a detailed habitat description). The study took place between March and July, in 2011. We analyzed 599 amphibian stomach contents (407 newts and 192 anurans) during a total of six field trips (table 1). Field trips were made once every three weeks for the newts and one a month for the anurans, after the newts had left the habitat. The study was stopped in July because of drought. The amphibians were captured with nets. Stomach contents were sampled using the stomach flushing method (Solé et al., 2005), after which the amphibians were set free. The composition of the food was analyzed by percentage abundance (%A) and frequency of occurrence (%f), while also establishing the origin for each prey (aquatic or terrestrial). Food diversity was estimated using the Shannon-Wiever Index (H) (Shannon & Wiever, 1949). The trophic niche overlap, using the percentage abundance of the food items, was calculated using the Pianka Index (Q) (Pianka, 1973). The obtained pairwise values were used to create a correlation matrix to perform the tree clustering analysis (Statistica 6.0). The samples from different periods at the same species and between different species from the same period were compared by the values of the frequency of occurrence of the food items using the Mann-Whitney test (Zar, 1999).

Table 1. The number of studied amphibians, the frequency of occurrence of empty stomachs, the stomachs with animal content, plant fragments, shed-skin, amphibian eggs, and inorganic elements: Tc. *Triturus cristatus*; Lv. *Lissotriton vulgaris*; Pr. *Pelophylax ridibundus*; Bv. *Bombina variegata*.

| | 25 III 2011 | | 14 IV 2011 | | 5 V 2011 | |
|---------------------------|-------------|-------|------------|-------|----------|--------|
| | Tc | Lv | Tc | Lv | Tc | Lv |
| No. of studied amphibians | 50 | 51 | 41 | 50 | 50 | 50 |
| % of empty stomachs | 6.00 | 1.96 | — | 2.00 | — | — |
| % with animal content | 74.00 | 96.08 | 90.24 | 96.00 | 90.00 | 100.00 |
| % with non-animal content | 92.00 | 82.35 | 95.12 | 94.00 | 100.00 | 78.00 |
| % with plant fragments | 50.00 | 62.75 | 65.85 | 78.00 | 88.00 | 58.00 |
| % with shed-skin | 42.00 | 29.41 | 53.66 | 30.00 | 36.00 | 40.00 |
| % with amphibian eggs | 64.00 | 5.88 | 58.54 | 16.00 | 26.00 | 6.00 |
| % with inorganic elements | 6.00 | 7.84 | 2.44 | 20.00 | — | — |

Results

Feeding differed for each species of amphibian and for each period. Unfed animals were more numerous in spring (table 1). We identified two types of stomach content: animal and non-animal. The first category consisted of 4,574 prey belonging to 62 prey taxa. Only quantitatively important taxa are shown in tables 2 and 3. Taxa found in low amounts or consumed only occasionally are included in the category 'Others' (Turbelaria–Planariidae, Nematomorpha, Hirudinea, Gastropoda, Arachnida–Acarina, Crustacea–Amphipoda, Crustacea–Ostracoda, Crustacea–Isopoda, Chilopoda, Plecoptera, Coleoptera–larve, Lepidoptera, Homoptera–Aphididae, Orthoptera, Dermaptera, Mecoptera, Trichoptera, Urodela–Larve, Urodela–*L. vulgaris*, Diptera–Brahiocera–Tabanidae, Diptera–Nematocera–Tipulidae, Hymenoptera–undetermined and eight Coleopteran groups (Cantaridae, Carabidae, Coccinellidae, Curculionidae, Chrysomelidae, Elateridae, Scarabeidae, Staphylinidae).

The most important prey taxa for the newts were aquatic Nematocera larvae, Crustacea Cladocera and Copepoda. *L. vulgaris* consumed microcrustaceans more frequently, while *T. cristatus* fed more frequently on larger preys (earthworms or mayfly larvae). For the anurans, the most important prey were coleopterans and dipterans (tables 2, 3). *L. vulgaris* had the highest value for average number of preys/individual (12.42). The maximum number of preys/individual (37) was the same in the case of the two newts. Newts consumed the lowest number of preys at the beginning of spring (tables 2, 3). Most prey consumed by newts were aquatic, while most prey consumed by anurans were terrestrial (table 4). The non-animal stomach contents consisted of plant remains, shed skin fragments, amphibian spawn, and inorganic elements. The plant fragments and shed skin were consumed by all species, throughout all

the periods, while the inorganic elements were also consumed by all the species but not in each period. Spawn was consumed only by newts, varying in frequency during the seasons (table 1). Generally, the non-animal stomach contents appeared together with animal prey, but a few individuals from all species consumed them exclusively.

P. ridibundus showed the highest food diversity ($H = 3.161$ in May). This species showed more diverse feeding than *B. variegata* during every sampling period (table 4). Newts had the lowest food diversity (table 4). During most sampling periods, *L. vulgaris* had a less diversified diet than *T. cristatus*, but the latter still had the smallest diversity value throughout the entire study ($H = 0.645$ in May). The trophic niches that overlapped most were those of the newts (fig. 1), both during the same period and in different time frames (between *T. cristatus* from May and July, $Q = 0.99$). The two anuran species used different trophic niches than newts (fig. 1). We also found differences in the trophic niches between *B. variegata* and *P. ridibundus*. Differences between the newts' feeding were never significant, but those between the newts and *P. ridibundus*, were always significant. The greatest differences were found between *P. ridibundus* and *L. vulgaris* on the 18th of June (Mann–Whitney test $Z = -4.022$, $df = 1$, $P = 0.000010$). Significant differences were also recorded between the feeding of the newts and *B. variegata*. Significant differences occurred between *B. variegata* and *P. ridibundus* only one time (Mann–Whitney test $Z = 2.247$, $df = 1$, $P = 0.0225$).

Discussion

The food composition of the four amphibian species resembled the diet of other populations of the same species previously studied, both in Romania (e.g. Do-

Tabla 1. Número de anfibios estudiados, frecuencia de la presencia de estómagos vacíos, estómagos con contenido animal, fragmentos de plantas, mudas de piel, huevos de anfibios y elementos inorgánicos: Tc. *Triturus cristatus*; Lv. *Lissotriton vulgaris*; Pr. *Pelophylax ridibundus*; Bv. *Bombina variegata*.

| 28 V 2011 | | | | 18 VI 2011 | | | | 19 VII 2011 | |
|-----------|-------|-------|-------|------------|-------|-------|-------|-------------|-------|
| Tc | Lv | Pr | Bv | Tc | Lv | Pr | Bv | Pr | Bv |
| 45 | 49 | 59 | 22 | 51 | 50 | 30 | 30 | 21 | 30 |
| — | — | 1.69 | — | — | — | — | 3.33 | — | — |
| 95.56 | 97.96 | 88.14 | 90.91 | 98.04 | 96.00 | 96.67 | 93.33 | 95.24 | 90.00 |
| 95.56 | 87.76 | 71.19 | 95.45 | 96.08 | 90.00 | 70.00 | 76.67 | 76.19 | 86.67 |
| 51.11 | 65.31 | 54.24 | 95.45 | 74.51 | 62.00 | 53.33 | 63.33 | 61.90 | 76.67 |
| 37.78 | 10.20 | 16.95 | 36.36 | 13.73 | 26.00 | 16.67 | 13.33 | 23.81 | 23.33 |
| 60.00 | 40.82 | — | — | 62.75 | 20.00 | — | — | — | — |
| 15.56 | 14.29 | 10.17 | — | 17.65 | 8.00 | 10.00 | 3.33 | — | — |

Table 2. Abundance of animal prey in percentages: I. Larvae; aq. Aquatic; ter. Terrestrial; * Mean values under 3%. (For abbreviations of species see table 1.)

| | 25 III 2011 | | 14 IV 2011 | | 5 V 2011 | |
|----------------------------------|-------------|-------|------------|-------|----------|-------|
| | Tc | Lv | Tc | Lv | Tc | Lv |
| Oligocheta – Lumbricidae | 3.28 | * | 9.91 | – | – | – |
| Gasteropoda [snails] [aq.] | – | – | * | – | 4.20 | – |
| Gasteropoda [snails] [ter.] | – | – | – | – | – | – |
| Bivalvia | – | – | – | * | 8.40 | – |
| Arachnida – Araneae | – | * | – | – | – | – |
| Crustacea – Cladocera | 9.02 | * | * | 9.50 | * | 8.62 |
| Crustacea – Copepoda | 25.41 | 71.60 | – | 32.85 | * | 17.73 |
| Crustacea – Ostracoda | – | * | – | – | – | * |
| Collembola | – | – | – | – | * | * |
| Ephemeroptera [I.] | 7.38 | 3.50 | 9.05 | * | 15.13 | 11.82 |
| Ephemeroptera | – | – | – | – | * | – |
| Plecoptera [I.] | – | – | 5.60 | 4.67 | – | * |
| Odonata [I.] | * | – | – | * | 5.04 | – |
| Odonata | – | – | – | – | – | – |
| Homoptera – Cicadellidea | – | – | * | – | – | – |
| Heteroptera [aq.] | – | – | * | – | – | * |
| Heteroptera [ter.] | – | – | – | * | – | * |
| Coleoptera – Dytiscidae | * | – | – | * | – | – |
| Coleoptera – undet. [ter.] | – | – | * | * | * | – |
| Coleoptera – Carabidae | – | – | – | – | * | – |
| Trichoptera [I.] | 6.56 | * | 3.45 | * | 3.78 | * |
| Lepidoptera [I.] | – | – | – | * | – | * |
| Diptera – Nematocera [I.] | 45.08 | 16.87 | 61.21 | 46.38 | 44.12 | 56.16 |
| Diptera – Nematocera – Culicidae | – | – | * | – | – | * |
| Diptera – Brahicera [I.] | – | – | – | – | 10.08 | – |
| Diptera – Brahicera [I.] | – | – | – | * | * | – |
| Diptera – Brahicera – Muscidae | – | * | – | * | – | * |
| Hymenoptera – Formicidae | – | – | – | – | – | – |
| Hymenoptera – Apidae | – | – | – | – | – | – |
| Anura [I.] | – | – | 3.02 | * | * | * |
| Others | 3.27 | 8.03 | 7.76 | 6.6 | 9.25 | 5.67 |

bre et al., 2007; Covaciuc-Marcov et al., 2010a, 2011; Ferentí et al., 2010; Cicort-Lucaci et al., 2011; Bogdan et al., 2012a) and in other regions (e.g. Çiçek & Mermec, 2006; Paunović et al., 2010; Mollov, 2008; Mollov et al., 2010; Kuzmin, 1990). This is more obvious for newts, which more frequently consume micro-crustaceans and Nematocera larvae (e.g. Dobre et al., 2007; David et al., 2009; Covaciuc-Marcov et al., 2010a). However,

the differences in feeding in different habitats seems to be greater for anurans than for newts (e.g. Tóth et al., 2007; Ferentí et al., 2010; Çiçek, 2011).

Although we found differences between the food composition for all four species, those between newts and anurans were almost always significant. The newts' diet was more uniform and focused on the aquatic habitat's trophic resources. The fact that

*Tabla 2. Abundancia de presas animales en porcentajes: I. Larvas; aq. Acuático; ter. Terrestre; * Valores medios inferiores al 3 %. (Para las abreviaturas de las especies ver tabla 1.)*

| 28 V 2011 | | | | 18 VI 2011 | | | | 19 VII 2011 | |
|-----------|-------|-------|-------|------------|-------|-------|-------|-------------|-------|
| Tc | Lv | Pr | Bv | Tc | Lv | Pr | Bv | Pr | Bv |
| * | — | 6.12 | — | — | — | 3.10 | * | * | — |
| — | — | — | — | * | — | — | — | — | — |
| — | — | * | * | — | — | * | 8.96 | 3.33 | * |
| — | * | — | — | * | — | — | — | — | — |
| — | — | 4.42 | * | * | — | 6.19 | 6.72 | 4.44 | 6.19 |
| — | 18.21 | — | — | * | 37.37 | — | — | — | — |
| — | 6.87 | — | — | — | * | — | — | — | — |
| — | — | — | — | 3.33 | — | — | — | — | — |
| — | — | * | 28.97 | — | — | — | * | — | 2.06 |
| 4.11 | * | * | — | * | * | — | — | — | — |
| * | — | * | 10.28 | * | — | * | * | * | * |
| — | — | — | — | — | * | * | — | — | — |
| * | * | — | — | * | * | * | — | * | — |
| — | — | 4.42 | * | — | — | * | — | * | * |
| — | — | * | 3.74 | — | — | 4.42 | * | 3.33 | — |
| * | * | * | * | — | * | * | — | — | 4.12 |
| — | * | 3.40 | * | — | — | * | * | 6.11 | 4.12 |
| * | — | * | 7.48 | — | — | 3.98 | * | * | — |
| * | * | 12.93 | 5.61 | * | * | 11.50 | 8.96 | 10.56 | 18.56 |
| — | — | 9.86 | 3.74 | — | — | 11.06 | * | 4.44 | — |
| — | — | — | — | — | * | * | — | * | * |
| — | — | * | * | * | * | * | 4.48 | * | * |
| 87.40 | 68.06 | * | — | 73.78 | 53.38 | * | — | * | 15.46 |
| — | — | 5.10 | 10.28 | 8.67 | — | 3.54 | 22.39 | * | 10.31 |
| — | — | — | * | — | — | — | * | — | — |
| — | — | 7.48 | * | 3.56 | — | — | — | * | * |
| — | * | 9.52 | * | — | * | 15.49 | 8.96 | 33.89 | 15.46 |
| * | — | 4.42 | 6.54 | * | — | 7.08 | 5.97 | 5.00 | 11.34 |
| — | — | * | — | — | — | * | — | 5.00 | — |
| * | — | * | — | * | — | * | — | — | — |
| 8.49 | 6.86 | 32.33 | 23.36 | 10.66 | 9.25 | 33.64 | 33.56 | 23.9 | 12.38 |

newts hunt in the aquatic habitat has been recorded previously (e.g. Denoël & Andreone, 2003; Kutrup et al., 2005; Vignoli et al., 2009; Covaciuc-Marcov et al., 2010a, 2010b), and few exceptions have been documented (Cicort-Lucaciuc et al., 2007a). The reduced food diversity of the newts is a consequence of the consumption of aquatic preys, which are probably less diversified in a small habitat. Quantitatively,

however, newts consume a greater number of prey than anurans, mainly due to the consumption of microcrustaceans. Microcrustaceans are the basis of the diet of *L. vulgaris*, a smaller species (Fuhn, 1960) that feeds on the smallest prey. Anuran feeding focuses on terrestrial preys. This brings them into contact with numerous insects, a group with a high number of species, mostly terrestrial (see Radu &

Table 3. The frequency of occurrence of animal prey (are included the same taxa as for percentage abundance): I. Larvae; aq. Aquatic; ter. Terrestrial. (For abbreviations of species see table 1.)

| | 25 III 2011 | | 14 IV 2011 | | 5 V 2011 | |
|----------------------------------|-------------|-------|------------|-------|----------|-------|
| | Tc | Lv | Tc | Lv | Tc | Lv |
| Oligocheta – Lumbricidae | 8.00 | 1.96 | 31.71 | – | – | – |
| Gasteropoda [snails] [aq.] | – | – | 7.32 | – | 8.00 | – |
| Gasteropoda [snails] [ter.] | – | – | – | – | – | – |
| Bivalvia | – | – | – | 12.00 | 2.00 | – |
| Arachnida – Araneae | – | 1.96 | – | – | – | – |
| Crustacea – Cladocera | 8.00 | 7.84 | 2.44 | 26.00 | 4.00 | 14.00 |
| Crustacea – Copepoda | 18.00 | 74.51 | – | 50.00 | 2.00 | 28.00 |
| Crustacea – Ostracoda | – | 1.96 | – | – | – | 2.00 |
| Collembola | – | – | – | – | 2.00 | 2.00 |
| Ephemeroptera [I.] | 18.00 | 23.53 | 26.83 | 22.00 | 50.00 | 56.00 |
| Ephemeroptera | – | – | – | – | 2.00 | – |
| Plecoptera [I.] | – | – | 9.76 | 16.00 | – | 8.00 |
| Odonata [I.] | 4.00 | – | – | 8.00 | 22.00 | – |
| Odonata | – | – | – | – | – | – |
| Homoptera – Cicadellidea | – | – | 2.44 | – | – | – |
| Heteroptera [aq.] | – | – | 2.44 | – | – | 2.00 |
| Heteroptera [ter.] | – | – | – | 2.00 | – | 2.00 |
| Coleoptera – Dytiscidae | 2.00 | – | – | 4.00 | – | – |
| Coleoptera – undet. | – | – | 2.44 | 2.00 | 8.00 | – |
| Coleoptera – Carabidae | – | – | – | – | 2.00 | – |
| Trichoptera [I.] | 14.00 | 13.73 | 17.07 | 4.00 | 18.00 | 4.00 |
| Lepidoptera [I.] | – | – | – | 2.00 | – | 2.00 |
| Diptera – Nematocera [I.] | 44.00 | 66.67 | 65.85 | 92.00 | 60.00 | 80.00 |
| Diptera – Nematocera – Culicidae | – | – | 7.32 | – | – | 6.00 |
| Diptera – Brahicera [I.] | – | – | – | – | 16.00 | – |
| Diptera – Brahicera [I.] | – | – | – | 2.00 | 2.00 | – |
| Diptera – Brahicera – Muscidae | – | 1.96 | – | 4.00 | – | 2.00 |
| Hymenoptera – Formicidae | – | – | – | – | – | – |
| Hymenoptera – Apidae | – | – | – | – | – | – |
| Anura [I.] | – | – | 12.20 | 2.00 | 2.00 | 2.00 |

Radu, 1967), so amphibians that feed from the terrestrial environment have a more diversified diet. Of the two anurans, *P. ridibundus* consumed a higher amount of terrestrial preys a fact also observed for other populations (e.g. Çiçek & Mermer, 2006; Mollov et al., 2010). Unlike *P. ridibundus*, *B. variegata* more often used the trophic resources from the aquatic habitat, a finding also noted previously (e.g. Ferentj et al., 2010; Covaciuc–Marcov et al., 2011).

The newts showed a uniform diet, as other populations from western Romania (e.g. Cicort–Lucaciuc et al., 2005, 2007a, 2007b; Covaciuc–Marcov et al., 2010a), probably because the habitats they used had approximately the same trophic offer. However, in other areas, the newts' diet may present differences, sometimes focusing on leeches (Griffiths & Mylott, 1987). The overlap of the newts' trophic niches was also a consequence of the almost exclusive use of the

Tabla 3. Frecuencia de la presencia de presas animales (se incluyen los mismos taxones que para el porcentaje de abundancia): I. Larvas; aq. Acuático; ter. Terrestre. (Para las abreviaturas de las especies ver tabla 1.)

| 28 V 2011 | | | | 18 VI 2011 | | | | 19 VII 2011 | |
|-----------|-------|-------|-------|------------|-------|-------|-------|-------------|-------|
| Tc | Lv | Pr | Bv | Ic | Lv | Pr | Bv | Pr | Bv |
| 4.44 | — | 13.56 | — | — | — | 16.67 | 3.33 | 4.76 | — |
| — | — | — | — | 1.96 | — | — | — | — | — |
| — | — | 6.78 | 9.09 | — | — | 3.33 | 23.33 | 9.52 | 3.33 |
| — | 2.04 | — | — | 1.96 | — | — | — | — | — |
| — | — | 20.34 | 9.09 | 7.84 | — | 36.67 | 23.33 | 33.33 | 20.00 |
| — | 30.61 | — | — | 1.96 | 54.00 | — | — | — | — |
| — | 12.24 | — | — | — | 4.00 | — | — | — | — |
| — | — | — | — | 1.96 | — | — | — | — | — |
| — | — | 1.69 | 9.09 | — | — | — | 3.33 | — | 3.33 |
| 26.67 | 4.08 | 1.69 | — | 9.80 | 10.00 | — | — | — | — |
| 20.00 | — | 10.17 | 18.18 | 11.76 | — | 16.67 | 10.00 | 9.52 | 3.33 |
| — | — | — | — | — | 2.00 | 3.33 | — | — | — |
| 8.89 | 4.08 | — | — | 1.96 | 6.00 | 10.00 | — | 14.29 | — |
| — | — | 18.64 | 9.09 | — | — | 10.00 | — | 9.52 | 3.33 |
| — | — | 3.39 | 13.64 | — | — | 30.00 | 3.33 | 23.81 | — |
| 4.44 | 2.04 | 3.39 | 4.55 | — | 2.00 | 10.00 | — | — | 10.00 |
| — | 2.04 | 15.25 | 9.09 | — | — | 16.67 | 10.00 | 47.62 | 10.00 |
| 4.44 | — | 6.78 | 31.82 | — | — | 20.00 | 6.67 | 9.52 | — |
| 4.44 | 4.08 | 32.20 | 18.18 | 7.84 | 2.00 | 63.33 | 30.00 | 47.62 | 43.33 |
| — | — | 28.81 | 13.64 | — | — | 43.33 | 6.67 | 28.57 | — |
| — | — | — | — | — | 2.00 | 3.33 | — | 4.76 | 6.67 |
| — | — | 5.08 | 4.55 | 5.88 | 2.00 | 6.67 | 20.00 | 14.29 | 6.67 |
| 93.33 | 91.84 | 1.69 | — | 76.47 | 80.00 | 3.33 | — | 9.52 | 30.00 |
| — | — | 20.34 | 22.73 | 17.65 | — | 23.33 | 56.67 | 9.52 | 16.67 |
| — | — | — | 9.09 | — | — | — | 10.00 | — | — |
| — | — | 1.69 | 9.09 | 17.65 | — | — | — | 9.52 | 3.33 |
| — | 4.08 | 32.20 | 13.64 | — | 2.00 | 50.00 | 26.67 | 71.43 | 36.67 |
| 4.44 | — | 18.64 | 22.73 | 1.96 | — | 33.33 | 16.67 | 33.33 | 30.00 |
| — | — | 1.69 | — | — | — | 6.67 | — | 23.81 | — |
| 2.22 | — | 1.69 | — | 1.96 | — | 3.33 | — | — | — |

trophic resources in the aquatic habitat. Using this habitat, the newts showed a similar food composition. The anurans, however, using the terrestrial environment, did not overlap their trophic niches, a finding also observed previously (e.g. Cogalniceanu et al., 2000). Thus, in both the newts and the anurans diet is as diversified as the habitat from where they hunt.

For all four species, the differences between the feeding were due to the differences in size. *L. vulgaris*

and *B. variegata* are smaller than *T. cristatus* and *P. ridibundus*, respectively (see Fuñ, 1960), their diet being therefore less diversified and their number of prey taxa more limited. Trophic partitioning due to size of the predator has been indicated previously (e.g. Kuzmin, 1990; Cogalniceanu et al., 2000; Bisa et al., 2007; Ferentj & Covaci-Marcov, 2011). Aside from the fact that *T. cristatus* consumed larger prey, it also consumed spawn more frequently than *L.*

Table 4. The number of animal prey, the maximum and average number of animal prey/individual, the percentage abundance of aquatic and terrestrial prey and the Shannon–Weaver diversity index. (For abbreviations of species see table 1.)

| | 25 III 2011 | | 14 IV 2011 | | 5 V 2011 | |
|--|-------------|-------|------------|-------|----------|-------|
| | Tc | Lv | Tc | Lv | Tc | Lv |
| No. of animal preys | 122 | 486 | 232 | 621 | 238 | 406 |
| % of aquatic preys | 96.72 | 99.18 | 87.07 | 98.87 | 96.22 | 98.28 |
| % of terrestrial preys | 3.28 | 0.82 | 12.93 | 1.13 | 3.78 | 1.72 |
| Maximum no. of preys/individual | 17 | 25 | 37 | 37 | 26 | 31 |
| Average no. of preys/individual | 2.44 | 9.53 | 5.66 | 12.42 | 4.76 | 8.12 |
| Feeding diversity (Shannon–Wiever index) | 1.55 | 0.98 | 1.47 | 1.39 | 1.91 | 1.37 |

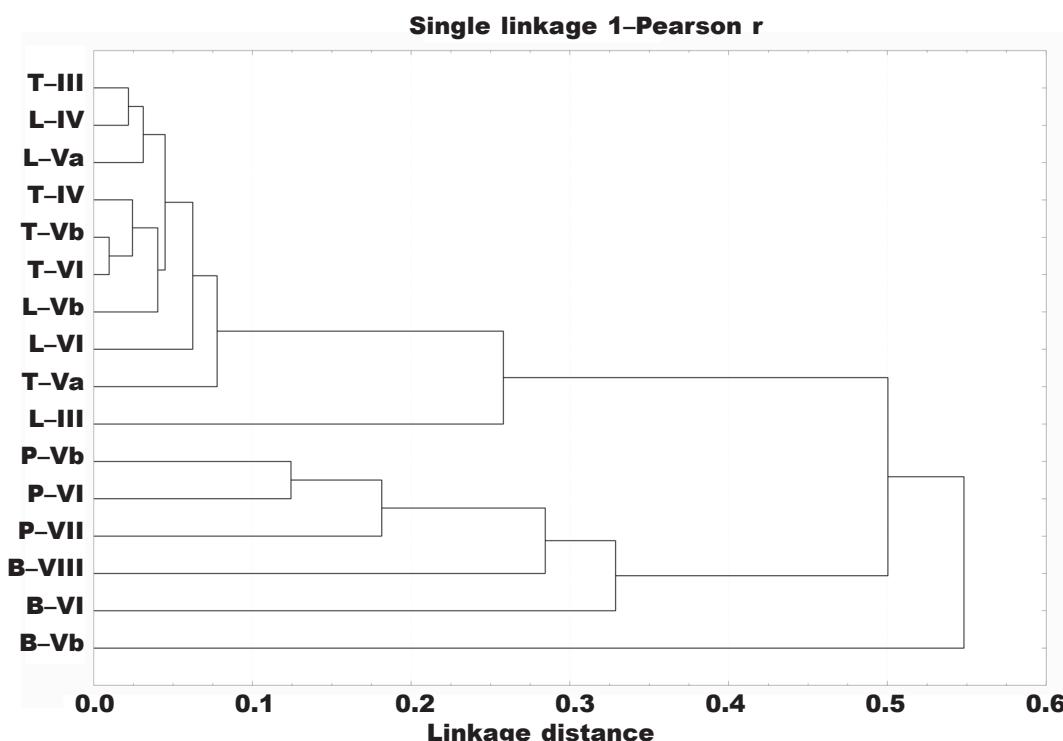


Fig. 1. Tree clustering based on Pianka's pairwise values, representing the trophic niche overlap of the studied species over the study period: III. March; IV. April; Va. Start of May ; Vb. End of May; VI. June; VII. July; T. *Triturus cristatus*; L. *Lissotriton vulgaris*; P. *Pelophylax ridibundus*; B. *Bombina variegata*.

Fig. 1. Tres agrupamientos basados en los valores de superposición de Pianka que representan la superposición de los nichos tróficos de las especies estudiadas a lo largo del período del estudio: III. Marzo; IV. Abril; Va. Inicio de mayo; Vb. Final de mayo; VI. Junio; VII. Julio; T. Triturus cristatus; L. Lissotriton vulgaris; P. Pelophylax ridibundus; B. Bombina variegata.

Tabla 4. Número de presas animales, número máximo y promedio de presas animales por individuo, porcentaje de la abundancia de presas acuáticas y terrestres e índice de diversidad de Shannon–Weaver. (Para las abreviaturas de las especies ver tabla 1.)

| 28 V 2011 | | | | 18 VI 2011 | | | | 19 VII 2011 | |
|-----------|-------|-------|-------|------------|-------|-------|-------|-------------|-------|
| Tc | Lv | Pr | Bv | Tc | Lv | Pr | Bv | Pr | Bv |
| 365 | 335 | 294 | 107 | 450 | 281 | 226 | 134 | 180 | 97 |
| 95.07 | 97.91 | 5.78 | 10.28 | 82.00 | 98.58 | 9.29 | 3.73 | 5.56 | 21.65 |
| 4.93 | 2.09 | 94.22 | 89.72 | 18.00 | 1.42 | 90.71 | 96.27 | 94.44 | 78.35 |
| 27 | 23 | 29 | 27 | 21 | 16 | 17 | 12 | 17 | 12 |
| 8.11 | 6.84 | 4.98 | 4.86 | 8.82 | 5.62 | 7.53 | 4.47 | 8.57 | 3.23 |
| 0.64 | 1.06 | 3.16 | 2.52 | 1.17 | 1.12 | 3.05 | 2.85 | 2.60 | 2.42 |

vulgaris. In contrast, *L. vulgaris* consumed smaller preys from the water body, such as microcrustaceans. These results again show how these two species use the aquatic habitat (e.g. Dolmen & Koksvik, 1983; Covaci–Marcov et al., 2010a).

The feeding of the four species showed marked seasonal variations. The average number of consumed preys/individual (feeding intensity) increased in the warm season for the newts, whereas for the anurans, and especially for *B. variegata*, feeding intensity decreased in summer, probably due to the drought. In other cases the intensity of amphibian feeding was lower in summer, due to the higher temperature (e.g. Yu et al., 2009). Seasonal variation in the feeding of amphibians determined by environmental conditions has been frequently documented (see Fasola & Canova, 1992; Kovács et al., 2007; Sas et al., 2009; Bogdan et al., 2012a).

Despite the fact that they occupied the same habitat, and that their trophic niches overlapped considerably, the two newt species coexisted, benefiting as in other cases by the generalist feeding and the high trophic offer (see Vignoli et al., 2009). Contact between the two species was low, as in other cases *T. cristatus* fed occasionally on common newts (e.g. Cicort–Lucaci et al., 2005), while at Maru this was only recorded once. In the case of the anurans, competition is avoided by using different trophic niches in relation to their size, *P. ridibundus* hunting larger preys. Using different hunting grounds modifies the feeding of anurans even in habitats with an abundant yet uniform trophic offer (Covaci–Marcov et al., 2010c).

The habitat in Maru seemed to satisfy the amphibians' trophic needs, as they consumed abundant and diversified food. Anurans and urodelas overlapped in the habitat only for a short period. However, even when they overlapped in space and time, they did not explore the same trophic resources and thus did not compete with each other. The newts consumed a lot of small aquatic preys, while anurans consumed many and diverse terrestrial preys, exploiting the aquatic habitat differently both in space

and time. For the newts, the aquatic habitat is crucial for feeding, and ultimately for survival of the population. As this is tied to the aquatic habitat, the newts are more vulnerable to its changes. This is of concern, as newts are very attached to the same aquatic habitat, returning to it for mating year after year (e.g. Joly & Miaud, 1989; Sinsch et al., 2006). For anurans, individuals migrate between habitats, as described for *B. variegata* (e.g. Hartel, 2008). The anurans probably used the habitat from Maru only for laying eggs, before moving to some of the streams in the area. Thus, the results from Maru confirm that for diverse amphibian communities comprising both newts and anurans, conservation strategies should look after both the aquatic habitat and the neighboring terrestrial areas (see Dodd & Cade, 1998; Semlitsch & Bodie, 2003; Denoël & Lehman, 2006).

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