NORTH-WESTERN JOURNAL OF ZOOLOGY 10 (2): 236-244
Article No.: 141501
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Predation on heteropterans within an assemblage of anurans at Kis-Balaton, Hungary

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Received: 02. December 2012 / Accepted: 08. December 2013 / Available online: 30. January 2014 / Printed: December 2014

Abstract. Taxonomic and functional groups of heteropterans consumed by six anuran species (*Bombina bombina, Pelobates fuscus, Bufo bufo, Hyla arborea, Rana arvalis, Pelophylax esculentus* complex) from four localities of Kis-Balaton wetland area in western Hungary were compared. Altogether 821 heteropteran specimens belonging to 76 species were found in the diet of anurans during a 5-year study. Consumed heteropteran species diversity was highest in anurans foraging in the driest microhabitats. Functional heteropteran groups were established by ecological parameters: humidity preference and vertical distribution on vegetation. Cluster analysis indicated that heteropteran diet of anurans is habitat dependent and intraspecific similarity was low between habitats. Vertical distribution of heteropterans was more strongly correlated with similarity between anuran species. Anuran species with similar foraging strategies formed separate groups in each habitat. Results support the theory that anurans having opportunistic and non-specific feeding habits are more accustomed to unpredictable environments.

Key words: anuran diet, foraging strategies, heteropterans, Kis-Balaton.

Introduction

It is an observed phenomenon that under certain conditions, species of a particular animal taxon can coexist, which is attracting much scientific interest (eg. Werner et al. 2009). Research in this field covers a broad range of biotopes and species but studies of amphibians in Hungary are rare (Vági et al. 2013). Many of the studies focusing on resource partitioning and animal community structure of amphibians have been carried out in the tropics and North America (Santos et al. 2004), Vitt & Caldwell 1994), due primarily to the high species diversity in these regions. Recently, however, more research is being conducted in the Eurasian moderate climate zones, from Spain to Russia (Kuzmin 1990, Cogălniceanu et al. 2000, Burghelea 2010, Covaciu-Marcov et al. 2010, Mollov & Stojanova 2010, Crnobrnja-Isailović 2012). Concurrently, interest is still growing in the field of trophic relationships of amphibian communities, particularly in understanding factors responsible for patterns of coexistence.

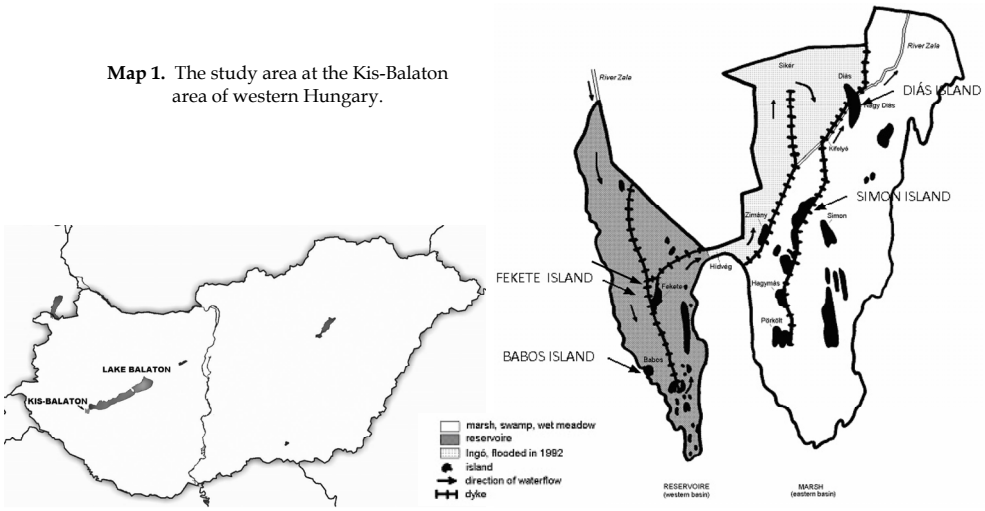
Amphibians are considered carnivorous, generalist and opportunistic predators although some specialist species also exist (Pough et al. 2004). Their diet composition usually reflects the distribution of potential prey that is available in the environment as well as seasonal or long term change (Kovács & Török 1995).

Three native frogs (tree frog, *Hyla arborea*; moor frog, *Rana arvalis*; edible frog complex, *Pelophylax esculentus* complex) and three toads (fire-bellied toad, *Bombina bombina*; spadefoot toad, *Pelobates fuscus*; common toad, *Bufo bufo*) coexist in a wetland of western Hungary (Kovács & Török 1997), occurring on the same islands having relatively small areas (1.5-6.0 ha). These species differ in foraging time and microhabitat use (Gasc et al. 1997).

Heteropterans are common in the diet of anuran species although usually comprising a relatively small proportion (Sas et al. 2009, Burghelea, 2010). Heteropterans occupy different microhabitat types (Jonsson 1985, Rédei et al. 2004). Vertical distribution and humidity preference are two ecological features used by Soós (1963), Wagner (1966) and Benedek (1969) to characterise their preference in species occurring in Central Europe.

In this study we established heteropteran functional prey groups to identify food resource partitioning of anuran species. Resource partitioning was tested with six anuran species in a single plot, Diás Island, within the Kis-Balaton wetland complex. In addition we studied whether intra-habitat or intraspecific difference is a significant factor in resource utilization with *P. esculentus* complex and *R. arvalis*, occurring in four and two study plots, respectively.

Map 1. The study area at the Kis-Balaton area of western Hungary.



Materials and methods

Study area

Anurans were collected from four islands of the Kis-Balaton area of western Hungary (see Map 1). Diás and Simon Island are situated in a marsh adjacent to reed beds and bogs. Diás Island is small (2.5 ha) and flat, emerging only 2 m above the water level. Its vegetation is patchy, with a half-submerged alder forest at the edge, a meadow in the middle and sparse *Carex* and *Typha* tussocks. Simon Island is slightly larger (6 ha) and drier than Diás, being a 4-5 m high hummock. General vegetation structure is similar but the tree composition in the forest covering the majority of the island shows considerable variability, being an old, abandoned plantation of maple, locust, oak and lime.

The two other islands (3-4 ha) are located in an artificial reservoir. Planted poplar forests and regularly mowed meadows characterise their vegetation. Both islands have small inner waterbodies; an inlet with a very narrow neck in Fekete Island and a pond in Babos Island.

Data collection and statistics

Anuran specimens were collected three times a year (first weeks of May, July, September) from 1992-1996. The number of collected individuals was similar during each sampling period. The flushing method was used to obtain the stomach contents of the animals (Leclerc & Courtois 1993). Prey items were preserved in 70% methanol and identified to order level; heteropterans to species level. Heteropteran species were grouped by two ecological characters: vertical distribution and humidity preference (Table 1). By vertical distribution heteropterans were grouped as follows: species foraging on ground or water surface only (*s*), on both ground surface and herbs (*g*), on herbs only (*h*) and on canopy (*c*). Based on humidity preference heteropterans were classified into three groups as aquatic (*a*), wet terrestrial (*w*) and dry terrestrial (*d*) species (Soós 1963, Wagner 1966, Benedek 1969).

Data from consecutive years were pooled by the anuran species living in a given habitat. Heteropteran species diversity in the anuran diet was estimated using the Shannon-Weaver Index (Shannon & Weaver 1949, Kovács & Török 1997):

$$H=-[\Sigma\, p_i \ln p_i\,]$$

where p_i is the relative abundance of the i prey taxon.

Calculations were accomplished by Dolph Schluter`s NICHE software. Similarities between anuran species consuming heteropteran species were calculated by cluster analysis (Euclidean distance, single linkage) with STATISTICA software.

Results

We collected heteropterans from 472 anuran specimens during the five year period. All six species occurred at Diás Island, *Pelophylax esculentus* c. and *R. arvalis* on Simon Island and *Pelophylax esculentus* c. only on Fekete and Babos Islands. In Hungary, such high anuran species richness within an anuran assemblage in such small areas is not uncommon (Anthony 2002). However, according to our observations, the number and density of anurans were extraordinarily high.

Species foraged in distinguishably different microhabitats. According to our observations on Diás Island, *P. esculentus* c. were found mostly on the bank or in the water and occasionally on the central meadow. *B. bombina* was almost always observed in the water and very rarely on land. *R. arvalis* was predominantly terrestrial and preferred the edge between the alder forest and meadow. *H. arborea* were collected chiefly from the

Table 1. Heteropteran species found in the diet of anurans and their ecological characters (A=aquatic, W=wet terrestrial, D=dry terrestrial, s=ground or water surface, g=ground surface or herbs, h=herbs only, c=canopy)

Species	Humidity preference	Vertical distribution
Acanthosoma haemorrhoidale Linnaeus, 1758	D	c
Aelia acuminata Say, 1832	D	h
Agnocoris reclairei Wagner, 1949	D	c
Arma custos Wagner, 1949	D	c
Arocatus roeseli Herrich-Schäffer, 1835	D	c
Ceraleptus gracilicornis Herrich-Schäffer, 1835	D	g
Coreus marginatus Linnaeus, 1758	D	h
Corythucha ciliata Say, 1832	D	c
Cymatia coleoptrata Fabricius, 1776	A	s
Derephysia foliacea Fallén, 1807	D	h
Drymus brunneus Sahlberg, 1848	W	s
Drymus ryei Saunders, 1892	W	s
Drymus sylvaticus Fabricius, 1775	D	s
Elasmucha grisea Linnaeus, 1758	D	c
Empicoris culiciformis De Geer, 1773	D	c
Eurydema oleraceum Linnaeus, 1758	D	h
Eusarcoris aeneus Scopoli, 1763	D	h
Eusarcoris ventralis Westwood, 1837	D	h
Gerris argentatus Schummel, 1832	A	s
Gerris asper Fieber, 1861	A	s
Gerris lacustris Linnaeus, 1758	A	s
Gerris odontogaster Zetterstedt, 1828	A	s
Gerris paludum Fabricius, 1794	A	s
Gerris thoracicus Schummel, 1832	A	s
Graphosoma lineatum Linnaeus, 1758	D	h
Halticus apterus Linnaeus, 1761	D	h
Hebrus pusillus Fallén, 1807	W	s
Himacerus apterus Fabricius, 1798	D	c
Holcostethus vernalis Wolff, 1804	D	h
Hydrometra gracilentum Horváth, 1899	A	s
Ilyocoris cimicoides Linnaeus, 1758	A	s
Ischnodemus sabuleti Fallén, 1829	D	h
Kleidocerys resedae Panzer, 1797	D	c
Legnotus limbosus Geoffroy, 1785	D	g
Lygus rugulipennis Poppius, 1911	D	h
Megalonotus chiragra Fabricius, 1787	D	s
Mesovelia furcata Mulsant et Rey, 1852	A	s
Microvelia buenoi Drake, 1920	A	s
Microvelia reticulata Burmeister, 1835	A	s
Nabis brevis Scholtz, 1847	D	h
Nabis ferus Linnaeus, 1758	D	h
Nabis pseudoferus Remane, 1949	D	h
Nabis punctatus Costa, 1847	D	h
Nabis rugosus Linnaeus, 1758	D	h
Nepa cinerea Linnaeus, 1758	A	s
Notonecta glauca Linnaeus, 1758	A	s
Notonecta lutea Müller, 1776	A	s
Orthonotus rufifrons Fallén, 1807	D	h
Oxycarenus lavaterae Fabricius, 1787	D	c
Pachybrachius fracticollis Schilling, 1829	W	g
Palomena prasina Linnaeus, 1761	D	c
Peritrechus nubilus Fallén, 1807	W	s
Phytocoris tiliae Fabricius, 1776	D	c
Picromerus bidens Linnaeus, 1758	D	c

Table 1. (continued)

Species	Humidity preference	Vertical distribution
Piesma maculatum Laporte, 1832	D	g
Plea minutissima Leach, 1817	A	s
Podops curvidens Costa, 1847	D	s
Podops inuncta Fabricius, 1775	D	s
Prostemma guttula Fabricius, 1787	D	s
Pyrrhocoris apterus Linnaeus, 1758	D	s
Raglius vulgaris Schilling, 1829	D	s
Saldula opacula Zetterstedt, 1839	W	s
Saldula saltatoria Linnaeus, 1758	W	s
Sciocoris distinctus Fieber, 1851	D	s
Sciocoris homalonotus Fieber, 1851	D	s
Scolopostethus affinis Schilling, 1829	D	g
Scolopostethus decoratus Hahn, 1831	D	g
Scolopostethus thomsoni Reuter, 1874	D	g
Sigara striata Linnaeus, 1775	A	s
Stenodema calcaratum Fallén, 1807	D	h
Stygnocoris fuligineus Geoffroy, 1785	D	s
Stygnocoris sabulosus Schilling, 1829	D	s
Syromastes rhombeus Linnaeus, 1767	D	h
Trapezonotus dispar Stal, 1872	D	s
Tritomegas bicolor Linnaeus, 1758	D	g
Tritomegas sexmaculatus Rambur, 1842	D	g

sunward side of reeds, bushes and trees although in early spring and late autumn (after and before hibernation) individuals were found moving on the ground. *P. fuscus* and *B. bufo* were primarily mobile at night. Both could be found far from water although some animals were also collected at the shoreline.

Differences in microhabitat use were also evident on Simon Island. While *R. arvalis* found their prey in the forest, *P. esculentus* c. foraged close to the edge or in the swamp surrounding the island and rarely in the middle. At the other two islands (Fekete and Babos) *P. esculentus* c. occurred only in the water.

Diet diversity varied between 1.29-2.81, with heteropterans constituting between 0.65-14.60% of the diet composition of the six anuran species (Table 2). The lowest diversity of heteropterans was found in *B. bombina* and the highest in *R. arvalis*. There were no significant correlations between diversity and number of sampled anuran specimens, number of heteropteran specimens, average number of heteropterans/stomach and average proportion of heteropterans in the diet (Pearson correlation, all $r<0.3$ and $p>0.1$, $n=10$).

Seventy-six heteropteran species were consumed of which six were common, by frequency, in the diet (Table 3). Diversity of the heteropterans consumed by the terrestrial anuran species living on the drier islands was the highest. The two pond skaters *Gerris* forage mainly on the surface of standing waters. The saucer bug *Ilyocoris cimicoides* is larger (11-13 mm) and a typical aquatic predator. Phytophagous *Kleidocerys resedae* is common on poplar and alder trees, while *Ischnodemus sabuleti* and *Pachybrachius fracticollis* are typical swamp bugs feeding on *Glyceria* and other *Graminae* (Soós 1963, Wagner 1966, Benedek 1969).

Table 2. Diet diversity of six anuran species (H), proportion of heteropterans in the diet (ph), number of anurans (na) and heteropterans (nh) at the four study sites of Kis-Balaton wetland area, Hungary

Island	Species	H	ph	na	nh
Babos	*Pelophylax esculentus* c.	1.86	2.75	31	71
Diás	*Bombina bombina*	1.29	0.82	26	40
Diás	*Bufo bufo*	2.48	5.30	17	25
Diás	*Hyla arborea*	1.35	0.65	36	76
Diás	*Pelobates fuscus*	2.37	8.90	32	40
Diás	*Rana arvalis*	2.55	14.60	87	126
Diás	*Pelophylax esculentus* c.	2.01	7.56	88	163
Fekete	*Pelophylax esculentus* c.	2.06	3.33	92	192
Simon	*Rana arvalis*	2.81	8.64	32	39
Simon	*Pelophylax esculentus* c.	1.75	4.82	30	48

Relatively few aquatic heteropterans (0.8-7.1%) were eaten by the predominantly terrestrial anurans (*H. arborea, P. fuscus* and *R. arvalis*) on both islands where they occurred (Fig. 1). The only exception was *B. bufo* which consumed 2.8-25.0%

Table 3. Proportion of the six most common heteropteran species in the combined diet of six anuran species at the four study sites of Kis-Balaton wetland area, Hungary.

	Diás Island		Fekete Island		Simon Island		Babos Island	
	n	%	n	%	N	%	n	%
Gerris argentatus	15	3.1	64	31.2	1	1.0	20	31.7
Gerris odontogaster	2	0.4	24	11.7	5	5.1	6	9.5
Ilyocoris cimicoides	7	1.4	35	17.1	-	-	23	36.5
Ischnodemus sabuleti	1	0.2	-	-	25	25.5	-	-
Kleidocerys resedae	227	46.8	-	-	3	3.1	-	-
Pachybrachius fracticollis	22	4.5	2	1.0	9	9.2	-	-
Total	274	58.3	125	65.1	43	49.4	49	69.0

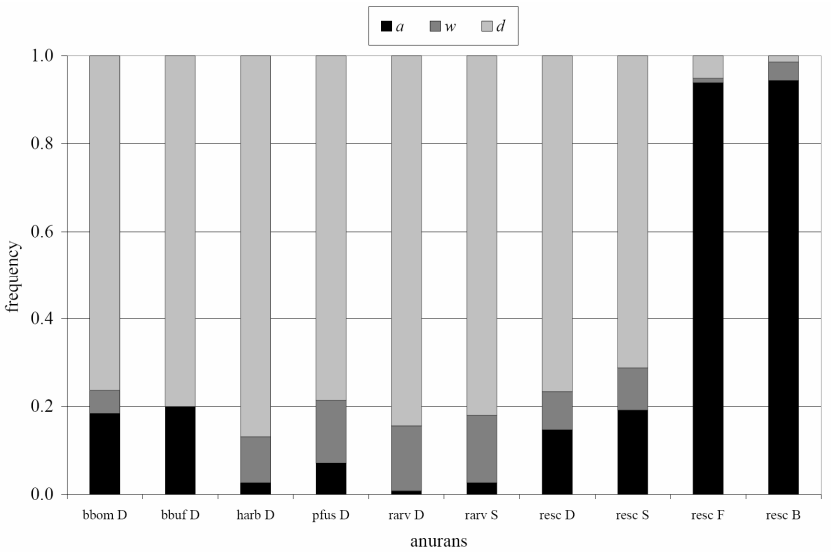


Figure 1. Distribution of three functional groups by humidity preference of heteropterans in the diet of anuran species at four study sites in Kis-Balaton area (*a*=aquatic, *w*=wet terrestrial, *d*=dry terrestrial heteropteran species, bbom=*Bombina bombina*, bbuf=*Bufo bufo*, harb=*Hyla arborea*, pfus=*Pelobates fuscus*, rarv=*Rana arvalis*, resc=*P. esculentus* c. (referring to earlier genus '*Rana*' name), B=Babos, D=Diás, F=Fekete, S=Simon Islands).

more aquatic heteropterans than other anurans. Heteropterans caught in the water dominated the diet of *P. esculentus* c. living on both Fekete and Babos Islands.

Typical terrestrial foragers, *B. bufo, P. fuscus* and *R. arvalis*, searched for prey on the ground or in the herb layer (Fig. 2). As expected *H. arborea* ate a considerable number of heteropterans living in tree canopies. Heteropterans in the diet of *P. esculentus* c. on Diás and Simon Islands showed wide vertical distribution. The majority found in the diet of anurans on Fekete and Babos Islands were aquatic surface predators. The above pattern remained unchanged when the bugs were classified by humidity preference. Surprisingly, the strongly aquatic *B. bombina* consumed many heteropterans living in the canopy, mostly *Kleidocerys resedae*, comprising nearly 70% of their heteropteran diet.

Cluster analysis based on the ecological functional groups of heteropterans demonstrated that vertical distribution of heteropterans segregated the anurans and their habitats more than humidity preference (Fig. 3). According to humidity preference (Fig. 3A), it is evident that wetter habitats (Fekete Island, Babos Island) are distant from the drier ones (Diás Island, Simon Island), however, interspecific similarities were high within the dry and wet habitat clusters. Based on the vertical functional groups (Fig. 3B), the dry and wet habitat clusters were grouped similarly, although interspecific similarities were reduced. Including all seven functional groups in the analysis, results

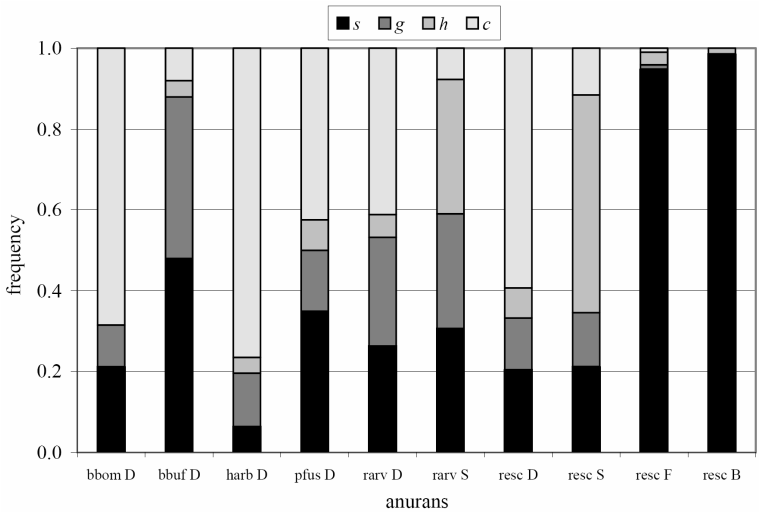


Figure 2. Distribution of four functional groups by vertical distribution of heteropterans in the diet of anuran species at four study sites in Kis-Balaton area (heteropteran species; *s*: foraging on ground or water surface only, *g*: on both ground surface and herbs, *h*: on the herbs only, *c*: on the canopy). For other abbreviations see Fig. 1.

were comparable to those when only vertical functional groups were involved (Fig. 3C). The highest similarities (shortest distances) were found between the two populations of *P. esculentus* c. living on Fekete and Babos Island. All species (except *B. bufo*) occurring on Diás Island formed one group. Within this cluster there was closer relationship between *P. fuscus*-*R. arvalis* and *P. esculentus* c.-*B. bombina.* Another cluster consisted of *R. arvalis* and *P. esculentus* c. on Simon Island and *B. bufo* on Diás Island.

Discussion

The role of heteropterans in the diet of anurans

Heteropteran species formed 0.65-14.60% of the diet of anuran species in the Kis-Balaton area, complementing other studies that show heteropterans occupy relatively lesser portions of anuran diets (Cogălniceanu et. al. 2000, Mollov & Stojanova 2010). The proportion of other prey groups including coleopterans, dipterans, and arachnids were higher, however heteropterans occupy a wide range of microhabitat types from aquatic to terrestrial and their vertical distribution is non-restrictive. Only six species were dominant forming 35-78% of the heteropteran diet. A similar pattern was found by Holzinger et al. (1996) in gastropods eaten by anurans in the Kis-Balaton area, where 5 of 35 snail species dominated the anuran diet. Heteropteran size ranged between 3-15 mm, with each size category being consumed by all anuran species, suggesting that it is unlikely that heteropteran size effects niche separation of anuran species or microhabitat partitioning. Lőw & Török (1998) found similar size preference in sympatric populations of *P. esculentus* c. and *R. arvalis* in western Hungary. However, McAlpine & Dilworth (1989) described the role of prey-size in the niche separation between three *Rana* species in a Canadian habitat. They demonstrated no significant difference in choice of prey size between species which occupied microhabitats that slightly overlapped. However, those species consumed prey of a wide size range, and selected microhabitats that more greatly overlapped. Toft (1980), and Vitt & Caldwell (1994) clearly showed the relationship between prey types and microhabitat use in tropical rainforest anuran assemblages. Besides the taxonomic analysis of prey, functional classification have also been applied in other studies (Dolmen & Koksvik 1983, Kuzmin 1990, 1991, Joly & Giacoma 1992), similar to that worked out by Wiens & Rotenberry (1979) on birds. These former studies deal with newts in their aquatic phase, therefore the established types involved planktonic, nectonic, and benthic forms. They found prey types as very important factors, which at least partly determine niche segregation. Shlia-

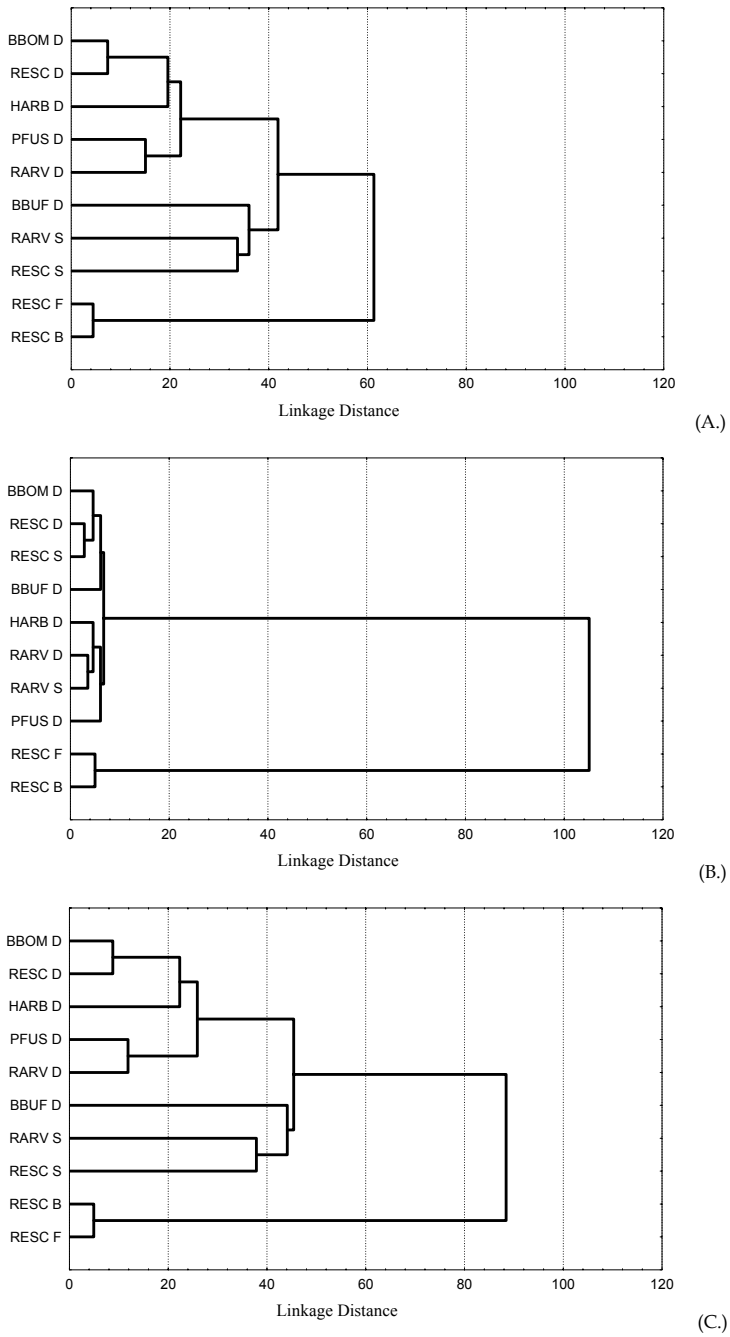


Figure 3. Tree diagram by functional groups of heteropterans found in the diet of six anuran species at four study sites in Kis-Balaton area. For abbreviations see Fig. 1. **(A.)** Linkage distance by the humidity preference of heteropterans; **(B.)** Linkage distance by the vertical distribution of heteropterans; **(C.)** Linkage distance involving both the humidity preference and vertical distribution of heteropterans.

chtin (1985) formed three groups (aquatic, terrestrial, flying) of the prey of *P. fuscus, B. viridis, R. arvalis, P. ridibundus. B. bombina* in an eastern Russian habitat. Similar to our results, *P. fuscus, R. arvalis* and *B. viridis*, which are sibling species of *B. bufo*, consumed almost only terrestrial prey, while the diet composition of *B. bombina* was typically aquatic containing a high proportion of collembolans.

It is difficult to demonstrate the presence of competition between anuran species in their adult age. Although competition for food in certain amphibian assemblages has been demonstrated (Hecnar & M'Closkey 1997, Denton & Beebee 1994), it is unlikely that competition for heteropteran prey causes segregation between anurans in our study. The highest overlap of consumed heteropteran species in two coexisting anurans was less than 75% in Diás Island where the mean overlap was 43% between all species.

Surprisingly we found a uniquely high proportion of tree bugs in the diet of *B. bombina* of Diás Island, contrary to Lác (1958) who identified almost only aquatic heteropterans in this toad. A possible cause of this phenomenon is that the microhabitat where this toad occurs is shadowed by poplar trees from which the heteropterans drop in the water and become easy prey for aquatic predators. The presence of aquatic heteropterans in the terrestrial *B. bufo*'s diet was also unexpected. According to our field observations this toad preferred colonial prey, such as ants. This probably also holds true for the aquatic amphipod, an unusual prey type for a terrestrial anuran, which was eaten in considerable amounts.

Diet diversity

The diet diversity showed an unexpected pattern. Based on Schoener's (1974) finding, i.e. more patched habitat can be more greatly partitioned by predators, we assumed that heteropteran diversity in the diet of *P. esculentus* c. on Diás Island and Simon Island, the most heterogeneous habitats, was higher than at the other two sites. However, we found the highest diversity in this species on Fekete Island, probably due in part by the larger sample size than at Babos and Simon Islands (Kovács & Török 1997). Where sample sizes were approximately the same, there was a slightly higher diversity at the wet (Fekete and Diás) than dry islands (Babos and Simon). On the other hand, ranking the anurans by heteropteran diversity, we found that anuran species which foraged in drier habitats consumed the most diverse heteropteran diet.

Clusters in the anuran community

The cluster analysis clearly showed that interhabitat differences more strongly segregated anuran assemblages than interspecific differences, i.e. coexisting species consumed a more analogous diet than individuals of a certain species living in another habitat. *P. esculentus* c. on the two wet study plots (Fekete and Babos Islands) consumed similar compositions of heteropterans. At Diás Island, where all the studied species occurred, those anurans were included in the same sub-clusters whose microhabitat use was similar.

The pattern demonstrated by the cluster analyses reflects the general ecology of the examined species. Characteristic habitat (e.g. wet or dry) or vegetation layers (e.g. surface or shrub) occupied by European amphibian species is now widely known even from internet portals (www.amphibiaweb.org/search/index.html, www.khvsz.mme.hu) and field guides (Kwet 2009). In our study, the functional groups of the consumed heteropterans on Diás island pooled *B. bombina* and *P. esculentus* c. in the same cluster showing their preference for aquatic or wet habitat types. *H. arborea* is proximate to this cluster because, although it occupies the shrub layer when foraging, host vegetation grows primarily on lakeshores or riverbanks. A second cluster was formed by those species which find their hunting area in drier habitat patches: *P. fuscus*, *R. arvalis* and *B. bufo* were collected in the middle of Diás island on the central meadow or in the surrounding forest and rarely at the water's edge. Finally, the heteropteran diet of *B. bufo* in Diás island was clustered closer to *R. arvalis* and *P. esculentus* collected on the drier Simon island, where the proportion of forest cover to island area is higher.

Our study on the heteropteran diet of anurans indicates that, in unpredictable and heterogeneous environments, the opportunistic and non-specific feeding of this taxon is an evolutionary adaptive strategy. A selected prey group (ie. heteropterans) that can be classified by distinct ecological features as functional groups also enables us to make predictions of the microhabitat use of a specific amphibian species or the habitat partitioning in amphibian assemblages.

Acknowledgements. We are indebted to S. Fiar, Cs. Gergely and M. Németh for help in the field, to Balaton-felvidék National Park Directorate for permission to work in the protected study area and for an anonymous referee who significantly improved the paper. We also thank Richard A. Griffiths for his comments and suggestions on an earlier version of the manuscript. This study was supported by National Science Fund (#2231) and by Eötvös University and Ministry of Education (#0146).

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