

Feeding in anuran communities on islands in the Danube floodplain

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Abstract. Feeding habits and food choice of anurans found on two islands in the lower Danube floodplain were studied for two years. The five most abundant anuran species included in this study were *Bombina bombina*, *Hyla arborea*, *Pelobates fuscus*, *Rana esculenta* and *R. ridibunda*. In *B. bombina* the niche breadths of young and adults were of similar magnitude and the degree of overlap between these size classes was high. In *Rana esculenta* complex young individuals had a much broader trophic niche than adults. A low degree of overlap existed between young and adults, suggesting that the various size classes exploit different segments of the prey resource. Overall, species with a larger size range consumed a higher prey diversity. Prey occurrence was sampled throughout the study on a regular basis. The analysis of selectivity in feeding using Ivlev's index showed that the prey taxa that appeared to be preferred were generally rare in the environment. Detrended Correspondence Analysis revealed that the composition of anuran diets were highly overlapping but differed from the composition of the resource base. The trophic resource was highly partitioned in space and time and thus allowed the coexistence of large populations with similar diets.

Introduction

Amphibians are important components of ecosystems, in part because they direct energy from invertebrates, mainly detritivores, to higher trophic levels (Burton and Likens, 1975). Understanding their position in the trophic network is extremely important and a variety of studies describing the diet of amphibians were done (e.g. Duellman and Trueb, 1986; Larsen, 1992). In Europe, the diet of water frogs of the *Rana esculenta* complex has been well studied (Ratajsky and Vojtkova, 1971; Medvedev, 1974; Sin et al., 1975; Sczerbak and Sczerban, 1980; Gutowski and Krzystofiak, 1988; Török and Csorgo, 1992; Simic et al., 1995; Ghira et al., 1997), but few general conclusions emerge from these studies due to large differences in sample sizes, time of analysis, age class, and lack of information on food availability. A similar situation exists for *Bombina bombina* (Ratajsky and Vojtkova,

1971; Medvedev, 1974; Goncharenko et al., 1978; Sczerbak and Sczerban, 1980; Gutowski and Krzystofiak, 1988).

Most of the above studies were conducted only on adults, and usually at just one moment in time. They give no information on prey availability, thus making impossible any analysis of selectivity or competition for food among species. The only thorough diet study done on an anuran focused on a tropical species, *Dendrobates pumilio* (Donnelly, 1991). Few studies on diet of anurans have been done at the community level (Toft, 1980, 1985; Lieberman, 1986; Kuzmin, 1990, 1995; Beebee, 1996; Caldwell, 1996).

The study of the amphibian communities inhabiting two islands in the lower Danube floodplain started in 1994 as part of an intensive research program on the role and functioning of wetlands associated with large rivers. Geophysical, hydrological, climatic, and biological processes were covered. Amphibians are an important component in these wetlands because they are major contributors to biomass. We gathered data for a detailed analysis of feeding habits of five anuran species. Furthermore, data on availability of litter invertebrates permitted the analysis of selectivity in feeding (Cogălniceanu, 1997b; Cogălniceanu et al., 1998).

We asked the following questions:

1. What are the spatial and temporal feeding patterns?
2. How does body size influence prey choice?
3. How selective is the choice of food?

Methods

Study area. The two islands are situated in the lower Danube floodplain, south of the town of Brăila (Romania). The island of Chiriloaia (45°10'N 27°56'E) has an area of 18 km², while the Small Island of Brăila (44°47'N 27°49'E) is larger, with an area of 76.7 km². The islands are flat, with several large, shallow lakes occupying the interior parts. The vegetation cover is dense, ranging from cattails (*Typha* sp.) and reeds (*Phragmites* sp.) near the lakes and channels, to natural, old willow forests and willow and poplar plantations. Clearcuts and pastures are distributed throughout the forests, contributing to the heterogeneity of the landscape.

Biological and ecological processes on the islands are controlled by the periodic floods of the Danube, described by Bayley (1995) as flood-pulse events. During the spring floods, water level rises more than 4 m, submerging most of the two islands (Cogălniceanu et al., 1997). Most of the animals survive during this interval by aggregating in the higher parts of the islands or seeking refuge on floating debris or old willow trees. During this period, amphibians feed less frequently, with a subsequent decrease in body condition (Cogălniceanu, 1997a). The main predators on the islands are waterfowl, feral pigs and water snakes (*Natrix* sp.).

Sampling methods. Diet must be considered over seasons because both prey availability and amphibian activity show seasonal variation. To achieve this, during 1994 and 1995, 180 one and two-litre pitfall traps were employed to capture litter invertebrates. Twenty sets of traps were used, each consisting of eight traps positioned at equal distance along a 5 m radius circle with the ninth located in the middle. Five transects of 100-150 m length, consisting of four trap sets each, were located along a hydric gradient (two on the island of Chiriloaia and three on the Small Island of Brăila). Sampling started in July 1994, when the water level began to decrease after the spring flood, stopped in January 1995 during the winter frost, and resumed when the water level decreased again in July 1995. Traps were filled with 40% ethylene glycol and were emptied every two weeks.

Aside from invertebrates, several hundred anurans, mainly juveniles and subadults, were captured in the traps. Of the six anuran species inhabiting the islands, enough specimens of the five most common were captured for

diet analysis: *Bombina bombina*, *Pelobates fuscus*, *Hyla arborea*, *Rana esculenta* and *R. ridibunda*. The common toad (*Bufo bufo*) was not included in the study due to its rarity. Since the correct identification of juveniles and subadults of the last two species is very difficult, they were grouped together as *Rana esculenta* complex. Adult ranids were identified to species, but since they were captured at different times and locations in small numbers, they also were grouped. More animals, primarily adults, were also captured during night torch surveys or during the day with nets. Tree frogs (*Hyla arborea*) were captured in traps only in early spring and late autumn, but were easily captured by hand during the day on vegetation. Animals captured in traps died in less than six hours and were well preserved in ethylene glycol. They were stored and preserved in 70% alcohol. Stomach contents were obtained after dissection and stored in 70% alcohol. Animals captured alive were weighed to the nearest 0.01 g with a portable electronic balance, measured with dial callipers to the nearest 0.1 mm, anaesthetised with MS 222 Sandoz, and stomach flushed (Opatrný, 1980; Leclerc and Courtois, 1993). Since frogs are capable of digesting their prey rapidly, the period of time between when a frog is captured and stomach flushed may dramatically affect the results of dietary analyses (Caldwell, 1996). Frogs were stomach flushed as soon as possible after capture, to minimize this source of error.

Prey items were classified by taxon, to family or ordinal level, and life stage, using a binocular microscope. Their body length and width was measured to the nearest 0.1 mm using either dial callipers or a micrometer, according to size.

The spatial distribution and activity patterns of amphibians were investigated on a monthly basis, during the day and by night during torch surveys, along the same transects used to sample invertebrates by pitfall traps (Cogălniceanu, 1997b). Only the animals active along a 3 m wide strip were counted.

Data analysis. The abundance of the various preys was estimated from stomach contents. Frequency of occurrence was determined by dividing the number of stomachs that contained a particular prey by the total number of stomachs with prey. Consideration of both abundance and frequency for the same sample can give an indication of the homogeneity of feeding. For instance, high values for both indicate that the entire population is using the same food source, whereas high numerical abundance and low frequency for a food category indicate that only certain individuals within the population utilise this food source. The latter might indicate an aggregated distribution of the respective prey item and/or a tendency for active foraging by that predator (Hyslop, 1980).

The rate of feeding activity was estimated as the percentage of stomachs containing food with respect to the total number of stomachs examined (Sala and Ballesteros, 1997).

Diet diversity was estimated with Shannon-Wiener diversity index (H) for each species and within a species for different size classes, by pooling the prey types for a species or size class (Magurran, 1988):

$$H = - \sum (n_i/N) \ln(n_i/N)$$

where n_i is the number of prey category i and N is the total number of prey.

Rarefaction analysis was done for the diet diversity of each anuran species based on subsets of m samples (where m varies between 1 and N frogs) using EstimateS 5.0 (Colwell, 1997). One hundred subsets were randomly chosen and an average measure was computed. The diversity accumulation curves obtained were used to compute the minimum sample sizes, i.e. the sample size which gives at least 95% of the diet diversity calculated for the total sample size for each species. A hyperbolic function was used according to Kovacs and Török (1997):

$$H = H_{\text{lim}} - a/N$$

where a is the slope, H_{lim} is the maximal diet diversity, and N is the number of specimens investigated.

Since the probability of being caught in pitfall traps and the chance of being eaten by amphibians seem to be similarly affected by activity and abundance in most invertebrate groups, changes in both stomach contents and pitfall traps were considered as directly comparable parameters (Zimka, 1974). Therefore selectivity in feeding was estimated using Ivlev's E_i index (Ivlev, 1961):

$$E_i = (n_i - r_i)/(n_i + r_i),$$

where n_i represents the relative abundance of prey taxa i in stomach contents and r_i represents the abundance in the environment. E_i can vary between -1 and 1 . A 0.5 threshold was used according to Cogălniceanu et al. (1998); prey taxa with $E_i > 0.5$ are considered preferred and those with $E_i < -0.5$ are considered avoided.

Niche overlap was estimated using Pianka's index (Pianka, 1973):

$$Q = \frac{\sum p_{ij} p_{ik}}{\sqrt{\sum p_{ij}^2 p_{ik}^2}}$$

where p_{ij} and p_{ik} represent the abundance of prey category i in the food of predators j and k . The value of Q varies between 0 (no common resource) and 1 (perfect overlap).

For the analysis of selectivity in feeding the different prey taxa encountered in food and environment were grouped in 24 categories, usually at a higher taxonomic rank. Infrequent prey taxa encountered only in the environment or only in food, together with rare categories of prey less than 1% in abundance, present in only one of the anuran species studied, were grouped in the "Other" category. *Hyla arborea* was not included in selectivity analysis since it feeds aboveground and prey availability was only estimated at groundlevel.

We employed ordination techniques to assess whether prey composition is a function of the year of study, month of study, island, or species of anuran. First, we performed a Detrended Correspondence Analysis (DCA; Hill and Gauch, 1980) to determine whether there were any gradients in prey composition, and to evaluate how any such gradients relate to prey taxa or pitfall trap "resource" samples. In this and subsequent analyses, we grouped the data by month, year, island and anuran species in order to reduce within-sample noise (many stomachs had few prey items, so the ordination of individual stomachs would not have been reliable). Second, we performed a series of partial Canonical Correspondence Analyses (pCCAs; ter Braak, 1988) on the diet data alone to test whether prey taxa composition is a function of month, year, island, and anuran species. Although it is typical in CCA for the majority of explanatory variables to be quantitative (ter Braak, 1986), all of our variables (individual months, years, islands, and species) are qualitative and are hence represented by dummy variables. The covariables we employed were all the variables except the ones being tested; e.g. the pCCA testing the effects of anuran species included year, months, and islands as covariables. Statistical significance in CCA was assessed using randomization tests of the trace statistic using 300 iterations; permutation blocks were defined by the covariables (Legendre and Legendre, 1998; ter Braak and Šmilauer, 1998). Since we treat this study as exploratory, P -values were interpreted provisionally, and we made no attempt to correct for multiple comparisons (Legendre and Legendre, 1998). All ordinations were performed using Canoco 4.0 for Windows (ter Braak and Šmilauer, 1998) with log-transformed species abundance and downweighting of rare species.

Results

Diet analysis

The analysis of stomach contents was done on 641 amphibians. In all, 3,147 prey items belonging to 74 prey categories were identified. A total of 55,364 invertebrates from 53 taxa were captured with pitfall traps and identified during the study. All prey items consist only of terrestrial invertebrates in three of the anuran species studied. In *R. esculenta* complex, several aquatic organisms were also identified: Crustacea (Amphipoda and Decapoda), Lamellibranchiata, Heteroptera and fish. Insects were consumed most, ranging from 58.8% in *P. fuscus* and 61.2% in *B. bombina*, to 81.3% in *Rana esculenta* complex and 91.9% in *Hyla arborea*. Coleopterans are the most abundant prey item consumed, representing more than 10% of the food, ranging between 12.8% in *Pelobates fuscus* to 24.4% in *Rana esculenta* complex. Diptera are the second most abundant prey, ranging between 4.9% in *Pelobates fuscus* to 13.1% in *Rana esculenta* complex. Snails (Gastropoda, Pulmonata) are an important prey for *B. bombina* and *Pelobates fuscus*, while ants (Hymenoptera, family Formicidae) represent an important item in the food

of all of the species studied, except *B. bombina*. Snails appear to be commonly used by both *B. bombina* and *Pelobates fuscus*. The same is true for collembolans by *B. bombina*, for Homoptera (Cicadidae) by *Hyla arborea* and for ants by *Pelobates fuscus* and *Rana esculenta* complex. Spiders are consumed by all species. Cannibalism appears to be quite common in *Rana esculenta* complex; 23% of the adults studied contained at least one juvenile in their stomachs (table 1).

The intensity of feeding was estimated by the number of prey individuals/stomach (fig. 1). The lowest number of prey items/stomach was observed in *Hyla arborea*, with an average of 2.2 prey items/stomach. *Pelobates fuscus* had a higher value of 5.5 prey/stomach but also the highest percentage of empty stomachs (38%). *Rana esculenta* complex has a higher average value of 6.4 prey items/stomach and *B. bombina* has the highest average value of 7.9 prey/stomach. The highest number of prey items/stomach was found in a juvenile *B. bombina* (snout-vent length 29.5 mm) which had consumed 66 invertebrates, of which 55 were collembolans.

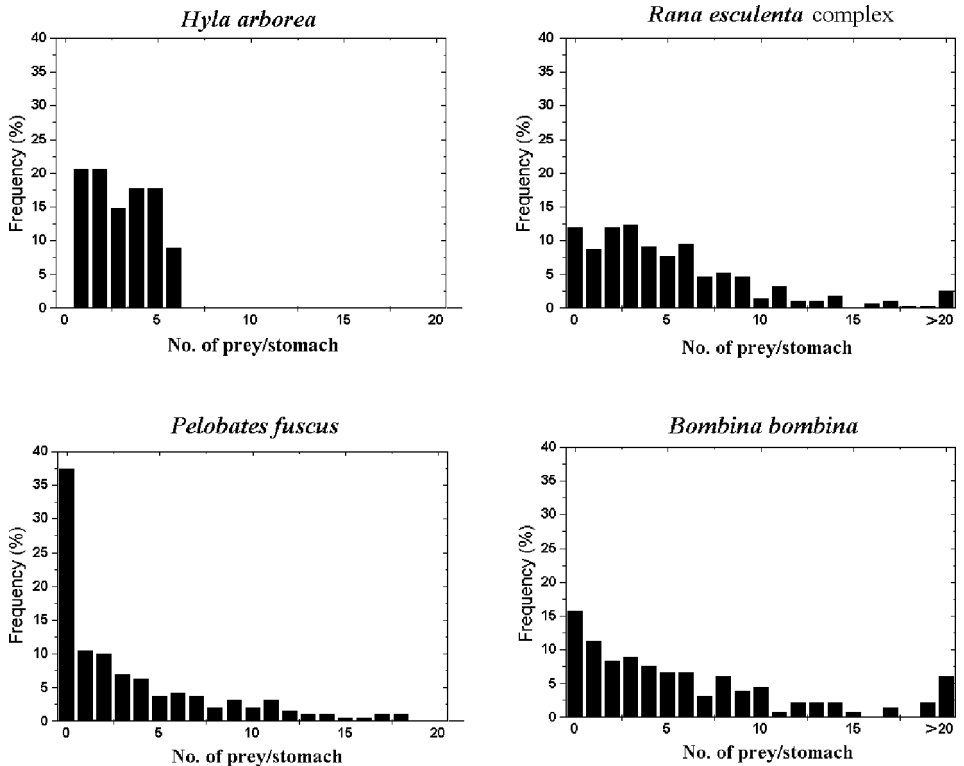


Figure 1. The frequency of occurrence of the number of prey individuals per stomach in anuran species.

Table 1. Main prey taxa encountered in amphibian stomachs. *n*: number of individuals per taxon, *A*(%): percent of the total number of prey accounted for by the particular prey type, and *F*(%): frequency of occurrence, expressed as the percentage of stomachs containing a particular prey/total number of stomachs analysed.

TAXA	<i>Bombina bombina</i>			<i>Hyla arborea</i>			<i>Pelobates fuscus</i>			<i>Rana esculenta</i> complex		
	<i>n</i>	<i>A</i> (%)	<i>F</i> (%)	<i>n</i>	<i>A</i> (%)	<i>F</i> (%)	<i>n</i>	<i>A</i> (%)	<i>F</i> (%)	<i>n</i>	<i>A</i> (%)	<i>F</i> (%)
Amelida, Oligochaeta	5	0.54	3.31	0	0	0.00	5	0.75	4.20	5	0.34	2.07
Crustacea, Isopoda, Oniscoidea	61	6.59	24.79	0	0	0.00	53	7.98	24.37	38	2.57	9.13
Gastropoda, Pulmonata	144	15.5	42.98	1	1.35	3.70	127	19.2	52.10	46	3.11	13.69
Diplopoda, Julida	1	0.11	0.83	0	0	0.00	36	5.42	23.53	2	0.14	0.83
Chilopoda, Lithobiomorpha	61	6.59	14.05	0	0	0.00	8	1.2	4.20	1	0.07	0.41
Arachnida, Acarina	40	4.32	14.88	0	0	0.00	12	1.81	8.40	20	1.35	3.73
Arachnida, Araneae	48	5.18	23.97	5	6.76	14.81	28	4.22	18.49	106	7.18	25.73
Insecta, adults	9	0.97	5.79	3	4.05	11.11	11	1.65	8.40	32	2.16	10.79
Insecta, larvae	3	0.32	2.48	0	0	0.00	14	2.11	10.92	24	1.62	10.37
Collembola	214	23.1	35.54	0	0	0.00	47	7.08	21.01	48	3.25	10.37
Heteroptera	7	0.76	4.96	2	2.7	7.41	3	0.45	2.52	60	4.06	15.35
Lepidoptera	16	1.73	12.40	3	4.05	7.41	22	3.31	14.29	50	3.38	17.01
Orthoptera	1	0.11	0.83	1	1.35	3.70	3	0.45	2.52	39	2.64	11.20
Homoptera, undetermined	0	0	0.00	0	0	0.00	4	0.6	3.36	5	0.34	1.24
Homoptera, Aphididae	47	5.08	12.40	0	0	0.00	17	2.56	7.56	85	5.75	7.47
Homoptera, Cicadidae	7	0.76	2.48	34	45.9	51.85	12	1.81	9.24	84	5.69	21.16
Hymenoptera, undetermined	13	1.4	9.92	2	2.7	7.41	14	2.11	8.40	51	3.18	16.18
Hymenoptera, Formicidae	10	1.08	7.44	8	10.8	18.52	124	18.7	42.02	159	11.07	28.22
Hymenoptera, Vespidae	5	0.54	4.13	0	0	0.00	0	0	0.00	11	0.74	4.15
Hymenoptera, Ichneumonidae	5	0.54	4.13	0	0	0.00	2	0.3	1.68	20	1.35	4.98
Diptera, adults, undetermined	3	0.32	2.48	1	1.35	3.70	9	1.36	5.04	28	1.9	8.30
Diptera, larvae, undetermined	29	3.13	5.79	0	0	0.00	6	0.9	3.36	29	1.96	7.05
Diptera, Muscidae, adults	43	4.64	14.05	2	2.7	7.41	4	0.6	3.36	78	5.28	17.84
Diptera, Muscidae, larvae	0	0	0.00	0	0	0.00	7	1.05	1.68	35	2.37	0.83
Diptera, Culicidae	0	0	0.00	0	0	0.00	7	1.05	4.20	2	0.14	0.83
Diptera, Chironomidae	10	1.08	7.44	1	1.35	3.70	0	0	0.00	22	1.49	4.98
Coleoptera, undetermined	15	1.62	12.40	4	5.41	14.81	29	4.37	18.49	76	5.15	14.94
Coleoptera, Carabidae, adults	10	1.08	8.26	1	1.35	3.70	26	3.92	15.13	98	6.64	22.41
Coleoptera, Carabidae, larvae	14	1.51	10.74	0	0	0.00	6	0.9	4.20	22	1.49	6.22
Coleoptera, Chrysomelidae	16	1.73	12.40	5	6.76	14.81	6	0.9	4.20	18	1.22	7.47
Coleoptera, Curculionidae	19	2.05	13.22	0	0	0.00	6	0.9	5.04	43	2.91	11.62

Table 1. (Continued).

TAXA	<i>Bombina bombina</i>			<i>Hyla arborea</i>			<i>Pelobates fuscus</i>			<i>Rana esculentia</i> complex		
	n	A(%)	F(%)	n	A(%)	F(%)	n	A(%)	F(%)	n	A(%)	F(%)
Coleoptera, Coccinellidae	0	0	0.00	0	0	0.00	2	0.3	1.68	26	1.76	8.30
Coleoptera, Cryptophagidae	6	0.65	4.13	0	0	0.00	0	0	0.00	9	0.61	2.90
Coleoptera, Elateridae	6	0.65	4.96	1	1.35	3.70	3	0.45	1.68	8	0.54	3.32
Coleoptera, Staphylinidae	44	4.75	17.36	0	0	0.00	6	0.9	5.04	46	3.11	16.18
Coleoptera, Scarabeidae	2	0.22	1.65	0	0	0.00	1	0.15	0.84	8	0.54	2.07
Trichoptera	7	0.76	5.79	0	0	0.00	0	0	0.00	10	0.68	3.73
Amphibia	0	0	0.00	0	0	0.00	0	0	0.00	22	1.49	7.88
Other	5	0.54	1.65	0	0	0.00	4	0.6	3.36	13	0.88	4.15

Table 2. Slope (a), asymptote of hyperbolic curves fitted to data of rarefaction analysis representing diet diversity (H_{lim}), the minimum number of anurans required to estimate diet diversity (n), and the minimum number (n^*) according to Kovacs and Török (1997).

Anuran species	a	H_{lim}	n	n^*
<i>Rana esculenta</i> complex juveniles	2.89	3.34	71	–
<i>Rana esculenta</i> complex adults	3.08	3.18	45	22-28
<i>Pelobates fuscus</i>	2.72	3.18	60	16-24
<i>Bombina bombina</i>	2.75	3.07	64	13
<i>Hyla arborea</i>	1.94	2.10	21	32

The percentage of stomachs with food was lowest in *Pelobates fuscus* (62%), and higher in *B. bombina* (85%) and *Rana esculenta* complex (88%). In *Hyla arborea* all individuals analysed had at least one prey item in their stomach.

The trophic niche breadth (fig. 2) showed that *Hyla arborea* has the lowest prey diversity while *Rana esculenta* complex has the highest one. Young (juveniles and subadults) *Rana esculenta* complex have a much broader trophic niche than adults. A low degree of overlap exists between the diet of young and adults in *Rana esculenta* complex, suggesting that the various size classes exploit different segments of the trophic resource. In *B. bombina*, the difference between the niche breadths of young and adults was minimal and the degree of overlap was high. Overall, the degree of overlap among species is moderate, but indicates that the species have the potential to compete.

The Shannon-Wiener rarefaction curves indicate that species differ in both their feeding strategies and in their diet (fig. 3). The minimum sample size for encompassing 95% of diet diversity computed for each species is much smaller than the actual sample size, and, except for *Hyla arborea*, differ from the ones estimated by Kovacs and Török (1997) (table 2). Minimum diet sample size must be calibrated for each particular study depending on the diversity of prey types and on the taxonomic precision used in describing prey categories. Kovacs and Török (1997) used only 38 prey categories while we used 74 in the present study (fig. 3).

The trophic resource is exploited differently by the distinct size classes (fig. 4). *Rana esculenta* complex has the largest body length range, up to 120 mm; no other species exceeded 50 mm. The individuals sampled represented all body lengths. About 70% of the individuals studied were juveniles and subadults.

Prey size classes are similar among the anuran species. The large range of body sizes in *Rana esculenta* complex is correlated with a large range of prey sizes. Prey with body length larger than 10 mm belong to Lumbricidae, larvae of Lepidoptera, and Miriapoda. Nevertheless, an even greater range of prey sizes can be observed in *Pelobates fuscus*, which has a narrow range of body size.

The comparison of prey body length measured for each anuran species reveals that, except for *Hyla arborea*, there are significant differences among species (table 3). Prey size did not differ significantly between adults and juveniles in *B. bombina* ($t = 0.60$,

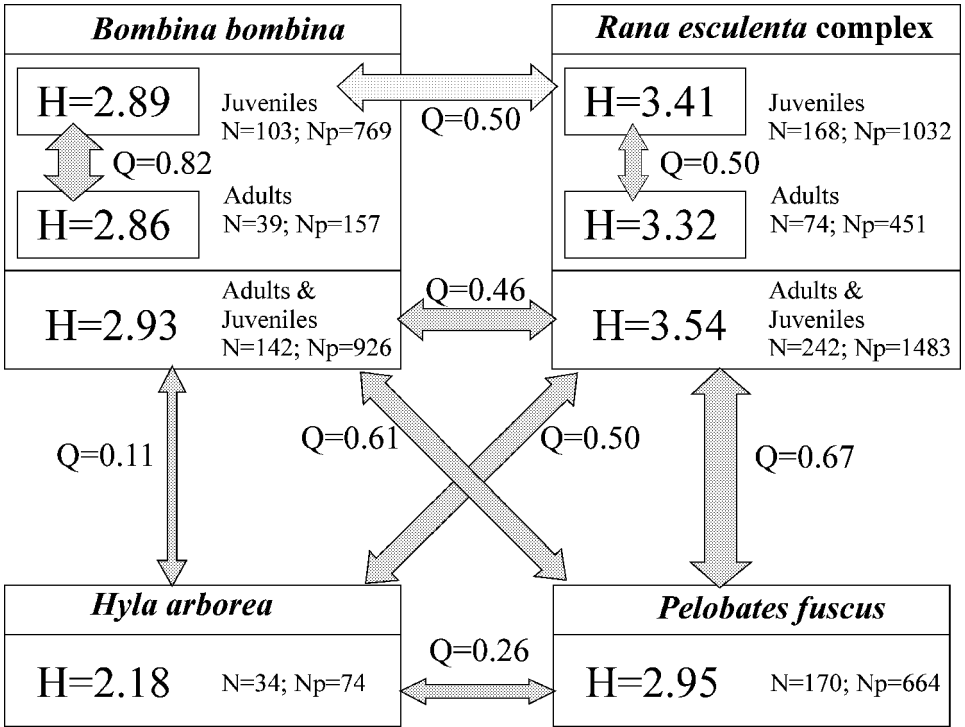


Figure 2. The trophic niche breadths, estimated using the Shannon-Wiener diversity index (H) and niche overlap, estimated with Pianka's index (Q). Where N represents anuran sample size and N_p the number of prey individuals.

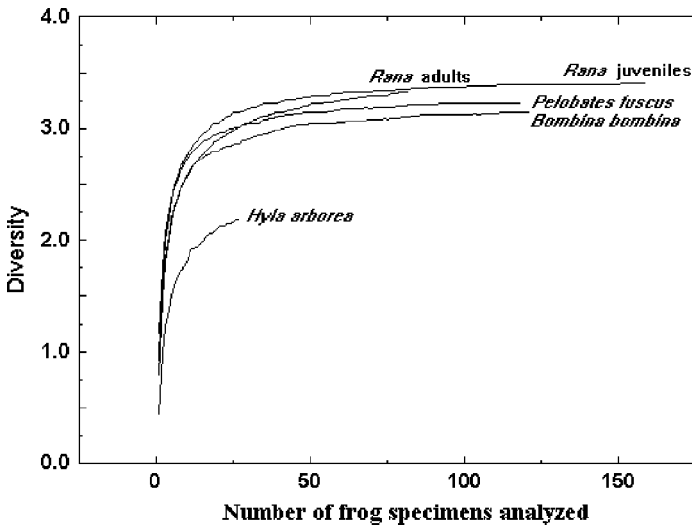


Figure 3. Shannon-Wiener diversity index accumulation curves.

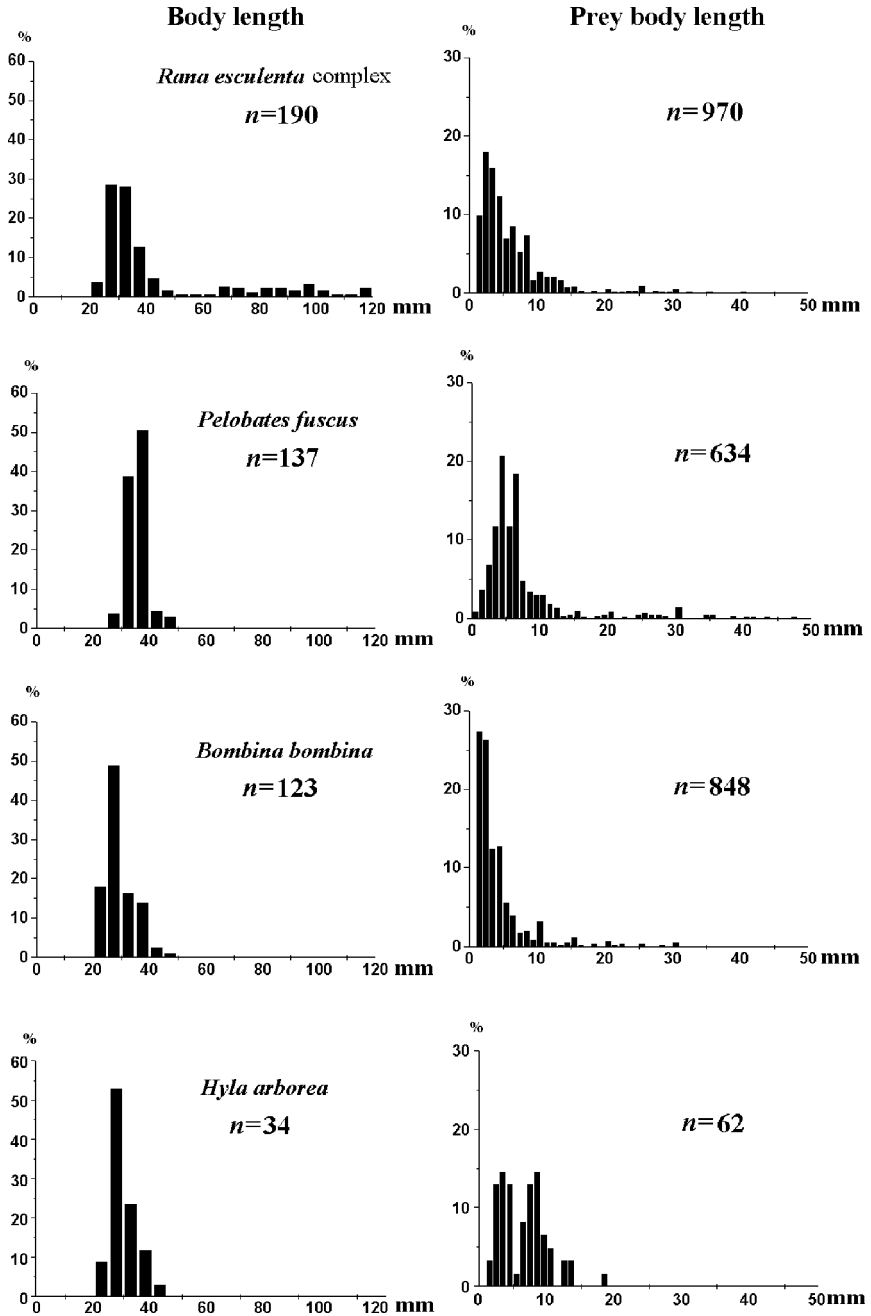


Figure 4. The frequency of size classes for both anurans (left) and their prey (right). Where n represents the sample size.

Table 3. Comparative analysis of prey body lengths between four anuran species (t -test, $\alpha = 0.05$). Where *** $P < 0.001$; NS not significant.

	<i>Rana esculenta</i> complex	<i>Pelobates</i> <i>fuscus</i>	<i>Bombina</i> <i>bombina</i>
<i>Pelobates fuscus</i>	$t = 4.6^{***}$	–	–
<i>Bombina bombina</i>	$t = 8.6^{***}$	$t = 11.5^{***}$	–
<i>Hyla arborea</i>	$t = 0.5^{NS}$	$t = 1.1^{NS}$	$t = 4.4^{***}$

$P = 0.5$), but did so between adults and juveniles in *Rana esculenta* complex ($t = 8.34$, $P < 0.001$).

Significant positive correlations were reported between *Pelobates fuscus* body length and average, maximum and minimum prey size (Cogălniceanu et al., 1998). In *B. bombina* predator and prey length are uncorrelated except for adults (maximum prey size $r = 0.47$, $P < 0.01$, $n = 41$; average prey size $r = 0.49$, $P < 0.001$; minimum prey size $r = 0.24$, not significant). In *Rana esculenta* complex, the correlation coefficient is higher than 0.50 in all three cases ($n = 228$, $P < 0.001$). Analysed separately for adults and juveniles, there is no correlation in juveniles and a very low positive one in adults.

Selectivity analysis

The values of Ivlev's selectivity index (E_i) were computed separately for each anuran species on each island (table 4). There are striking differences between species and sites, but some trends can be observed. For example, some of the most abundant prey taxa in the pitfall traps (Crustacea, Myriapoda, Acaria, Collembola, Formicidae and Carabidae) are underrepresented in stomachs and are therefore considered avoided. The taxa that appear to be preferred according to Ivlev's index are quite rare in the environment (i.e. their relative abundance is less than 1%). No prey taxon appears to be avoided at one site but preferred at another or avoided by one species but preferred by another. Most of the prey taxa preferred by one species were also preferred by at least one more, while most prey taxa avoided by one species were also avoided by at least another one.

Detrended Correspondence Analysis (DCA) reveals that the composition of anuran diets is different from the composition of the resource base (fig. 5). Sample scores for resource are generally to the upper right of those of the anuran diets, and are more tightly clustered. Consistent with this, species scores for prey taxa considered 'avoided' according to Ivlev's index (table 4) are to the upper right of the prey taxa that are considered 'preferred'.

Although they are distinguishable from the resource base, the diets of the anuran species are hardly distinguishable from each other. This result is consistent with the high dietary overlap between species (fig. 3). Month of capture, year of the study, and study site had even less distinguishable effects than that of anuran species in the DCA. Neither did the third and fourth DCA axes reveal any interpretable patterns with respect to these factors. Spatial, temporal, and interspecific differences are therefore unrelated to the most important gradients in prey composition. However, it is possible that there is a relationship

Table 4. Ivlev's selectivity index (E_i) for the anuran species studied. Prey abundance in the environment over the two year period in percentage, as measured from pit-fall trap captures. * Preferred prey taxa ($E_i > 0.5$); ** Avoided prey taxa ($E_i < -0.5$). 1 — Island of Chiriloaia; 2 — Small Island of Brăila

	Prey abundance		<i>Rana esculenta</i> complex		<i>Bombina bombina</i>		<i>Pelobates fuscus</i>	
	1	2	1	2	1	2	1	2
	Crustacea, Isopoda, Oniscoidea	11.82	6.11	-0.66**	-	-0.37	-0.51**	-0.10
Miriapoda	4.21	6.78	-0.88**	-0.88**	0.26	-0.54**	0.15	0.09
Arachnida, Acarina	8.78	11.26	-0.62**	-0.93**	-0.32	-0.70**	-0.72**	-0.75**
Arachnida, Aranea	6.68	7.52	0.17	-0.33	-0.14	0.03	-0.16	-0.07
Arachnida, Opiliones	0.56	0.33	-0.35	-	-	-	-0.33	0.67*
Insecta, Collembola	19.10	19.70	-0.73**	-0.54**	0.11	0.06	-0.40	-0.85**
Heteroptera	0.66	0.37	0.73*	0.80*	0.10	-	-0.08	-
Lepidoptera	0.26	0.03	0.87*	0.99*	0.74*	0.97*	0.88*	0.99*
Orthoptera	0.21	1.30	0.83*	-0.01	-0.28	-	0.16	-
Homoptera, Aphididae	0.93	0.96	0.80*	0.45	0.68*	0.82*	0.29	0.67*
Homoptera, Cicadidae	0.56	0.75	0.87*	0.81*	0.19	-	0.51*	0.37
Hymenoptera (all except ants)	1.81	1.70	0.59*	0.53*	0.04	0.56*	0.11	-0.02
Hymenoptera, Formicidae	20.27	5.63	-0.44	-0.54**	-0.89**	-	-0.24	0.45
Diptera	2.98	6.25	0.46	0.52*	0.47	0.59*	0.18	-0.12
Coleoptera adults	1.13	4.50	0.64*	0.38	0.14	-0.39	0.64*	0.19
Coleoptera larvae	3.70	2.72	-0.23	0.30	-0.39	-	-0.53**	-0.25
Coleoptera, Carabidae	11.38	18.53	-0.23	-0.31	-0.83**	-	-0.54**	-0.24
Coleoptera, Chrysomelidae	0.14	0.21	0.80*	0.60*	0.85*	0.90*	0.72*	-
Coleoptera, Curculionidae	0.09	0.52	0.93*	0.41	0.86*	-	0.72*	0.52*
Coleoptera, Chryptophagidae	0.20	0.35	0.65*	0.42	0.48	0.70*	-	-
Coleoptera, Anthicidae	0.07	0.09	0.71*	-	0.26	-	-	-
Coleoptera, Elateridae	0.04	0.26	0.90*	0.24	0.89*	-	0.91*	-
Coleoptera, Staphylinidae	0.71	3.55	0.69*	-0.25	0.72*	0.48	-0.11	-
Other	3.70	0.57	0.39	0.91*	0.71*	0.75*	0.78*	0.95*

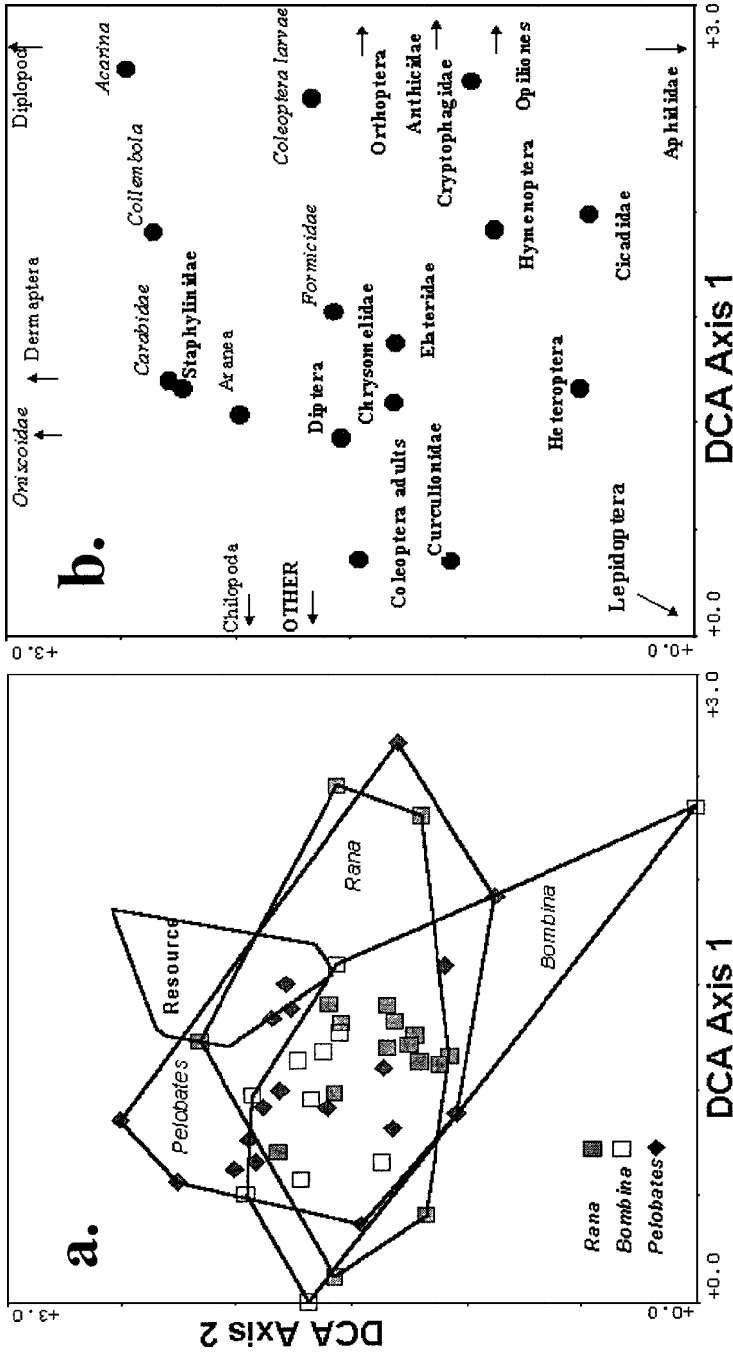


Figure 5. Detrended Correspondence Axes 1 and 2, with eigenvalues of 0.126 and 0.067 respectively. (a) Sample scores. Polygons surround samples belonging to the same anuran species; resource (i.e. estimated from captures using pitfall trap) samples are too numerous to plot and are therefore not shown individually. (b) Species scores for prey taxa. Arrows point out to taxa beyond the range of the sample scores. Bold face: prey taxa with Ivlev selectivities > 0.5 for at least one island or anuran species. Italics: prey taxa with Ivlev selectivities < -0.5 for at least one island or anuran species. Normal face: insufficient data, or selectivities not as above.

between prey composition and these factors that DCA could not detect; such relationships are best revealed by direct gradient analysis techniques such as CCA (ter Braak and Prentice, 1988; Palmer, 1993).

Not surprisingly, CCA revealed that resource availability is highly significantly different from diets ($P < 0.003$). All subsequent CCAs are based only on dietary data. CCA including species identity, month, year, and island as the explanatory variables revealed that these factors taken together are significantly ($P < 0.003$) related to prey composition. However, the ordination diagrams were difficult to interpret with such a varied set of variables, so we performed a series of partial ordinations. Partial CCA (pCCA) using island identity (i.e. Small Island of Brăila vs. Chiriloaia) as an explanatory variable, and factoring out (i.e. using as covariables) species identity, month, and year is not significant. Neither was pCCA using year (1994 vs. 1995) as a variable and everything else as covariables. Therefore, the years and islands can be viewed as replicates as far as anuran diets are concerned.

Using the months of the study as environmental variables and predator identity, year, and island as covariables pCCA is significant ($P = 0.007$). The resulting ordination diagram displays a seasonal progression of frog diet that mirrors prey availability, but as this is not a surprising result it is not displayed here.

Finally, we performed pCCA with anuran diets as the environmental variables and everything else as covariables. The trace statistic is significant ($P < 0.003$), indicating that the three species differ in their diets. The triangular arrangement of the anurans on the ordination diagram (fig. 6) indicates that all three have distinctive diets; if one predator had an intermediate diet it would appear between the other two. *Pelobates fuscus* prefers prey on the right of fig. 6, such as Opiliones and Diplopoda, *B. bombina* those on the top left, such as Chilopoda and Acarina. *Rana esculenta* complex prefers prey on the bottom left, such as Orthoptera and Heteroptera. Taxa located between two anuran species indicate that they are shared in the diet. For example, Staphylinidae, Cryptophagidae, and Diptera are shared by all species.

The results of the pCCA are generally consistent with those of Ivlev's index (table 4). That is, prey taxa on the ordination diagram are generally close to the predator(s) that prefer(s) them, and taxa preferred by all predators are in the middle. On the other hand, avoided taxa occur away from the predators that avoid them. For example, Carabidae are avoided (according to Ivlev's index) by *Pelobates* and *Bombina*, and therefore occur close to *Rana*. This points out that 'preference' is a relative concept in diet studies: a prey item can be preferred by one predator in contrast to another predator, but still be avoided in relationship to its availability.

Discussion

Six species of anurans coexist in high numbers on the two islands that we studied apparently due to abundant food and to lax competition for food. All anuran species studied,

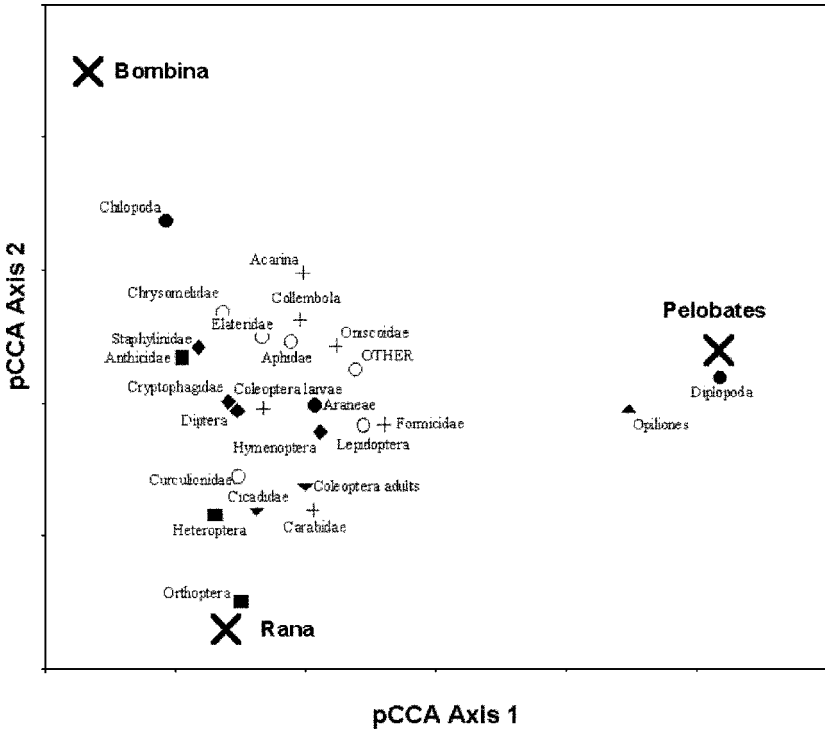


Figure 6. pCCA biplot of species scores of prey taxa (squares preferred by *Rana esculenta* complex only in at least one island; triangles preferred by *Pelobates fuscus* only, open circles preferred by all species, diamonds preferred by both *Rana* and *Bombina*, downward triangles preferred by both *Rana* and *Pelobates*, crosses avoided by at least one species, filled circles either not preferred nor avoided or insufficient data) and centroids of anuran species (large X's). Eigenvalues of the first two axes were 0.026 and 0.069, respectively.

except *Hyla arborea*, have high diet diversity, being generalist feeders. Nevertheless, there are differences in both prey types and sizes exploited by the species. Since frogs swallow their prey alive, predator-prey interactions are strongly dependent on prey size relative to predator size. There are significant differences between the size of the prey consumed by the anuran species studied, suggesting that size is important in the partitioning of the food resource.

If competition with other species is not severe, intraspecific competition will force individuals to exploit those parts of the potential resource range where competition with conspecifics is reduced (Putman, 1994; Hansson, 1995). In this way, juveniles tend to exploit small prey more intensively, limiting competition with adults and extending the domain of the trophic resource exploited by the full population. Thus, species with a large size range are expected to consume a higher prey diversity.

Species differ in resource use in three primary ways: in the food they eat, the space they occupy, and the time in which they are active (Schoener, 1974). The differential use

Table 5. The different use of the trophic resource in time and space (modified from Cogălniceanu, 1997b).

	<i>Rana esculenta</i> complex	<i>Bombina</i> <i>bombina</i>	<i>Hyla</i> <i>arborea</i>	<i>Pelobates</i> <i>fuscus</i>
Activity pattern	continuous	continuous	mainly diurnal	strictly nocturnal
Spatial niche	wide range of habitats	banks and shallow water	above-ground vegetation	terrestrial habitats

of resources along the temporal and spatial dimensions of the niche in the anuran species studied is summarized in table 5. The spatial niche is partitioned either vertically, with *Hyla arborea* occupying the upper parts of the vegetation, or horizontally between burrowers (*Pelobates fuscus*) and bank dwellers (*B. bombina* and *Rana esculenta* complex). There is also a temporal dimension that further partitions the resource.

The trophic niche overlap is low between juveniles and adults of water frogs due to the large differences in size and to the differential use of the habitat. Adults are concentrated on the banks and in deeper water, whereas juveniles inhabit shallow water. Cannibalism is quite frequent and might be one of the causes for habitat partitioning. The larger trophic niche of water frog juveniles is consistent with Christian's (1982) study on *Pseudacris triseriata*. He suggested that juveniles have the largest growth potential and also the largest appetite, and a large appetite makes an animal less discriminatory.

When individuals experience resource depletion it matters little whether the resource is shared with members of the same or of other species. During periods of stress the trophic resource may be more finely partitioned (Grant, 1968). Food limitation on the islands studied appears only during relatively short periods of time with extreme environmental conditions. This is caused either by floods, when water sometimes covers the islands entirely, limiting the feeding grounds and affecting the abundance of invertebrates (Cogălniceanu et al., 1997; Bosman et al., 1997), or by droughts, when amphibians are less active and restricted to the remaining moist habitats. Food availability was not estimated at high water levels, so only speculations can be made about whether resources are more finely partitioned during periods of food limitation.

Prey availability estimated with pitfall traps is dependent on both abundance and activity of prey (Thiele, 1977), and is unavoidably biased. Pitfall traps may be regarded as analogous to sit-and-wait predators (Cornish et al., 1995). There are factors other than abundance in the environment that influence food composition, like capture success, predator activity patterns, gape size, and microdistribution of prey, period of activity and speed of prey movement.

Differential resource selection has been proposed as one of the principal mechanisms by which species coexist (Putman, 1994). Since the availability of various resources is not uniform, in both time and space, use may change as availability changes. There is a great variety of methods that attempt to quantify selectivity in the use of resources. One of them is the use of indices of selectivity. From the large variety of indices of

selectivity proposed (see Chesson, 1978; Manly et al., 1995) we used only Ivlev's, due to its simplicity and biological significance. The multivariate methods employed in this study were useful in disentangling the effects of differences between predator species from the effects of year, month, and study site. Ordination techniques are ideal in cases with high dietary overlap, because they allow for gradation in the composition of food. DCA revealed that prey composition was slightly different from (and much more variable than) resource availability, but that predator species did not vary much in diet one from another. We suggest that pCCA is useful for the analysis of diet since it can focus on only one set of variable at a time, while factoring out the effects of other sets of variables. Therefore it can be tailored to very specific questions. Univariate preference statistics were a useful complement to ordination methods, because the former helped to distinguish whether similarities in diet were caused by mutual preference or mutual avoidance of a food item.

We suggest that in the anuran communities we studied the spatial and temporal dimensions are the main factors contributing to the partitioning of the trophic resource. The partial segregation in time and space of the different species and size classes reduces competition and thereby allows the coexistence of large populations with similar diet preferences.

Acknowledgements. Part of the study was financed by the European Community (ERMAS I project). Maureen Donnelly, Pim Arntzen, Stanley Fox, Günter Gollmann, and two anonymous reviewers provided helpful comments on previous versions of the manuscript. Cristina Cotoceanu helped with the management of the data.

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Received: April 6, 2000. Accepted: August 18, 2000.