

Trophic niche overlap in syntopic postmetamorphic amphibians of the Carpathian Mountains (Ukraine: Soviet Union)

Zur Überschneidung der trophischen Nischen bei syntopen, verwandelten Amphibien aus den Karpaten (Ukraine: Sovietunion)

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KURZFASSUNG: An zwei Orten in den Karpaten wurden zwischen- bzw. innerartliche Überschneidungsvarianten der trophischen Nischen innerhalb acht gemischter Amphibiengesellschaften untersucht, die in unterschiedlicher Weise aus metamorphosierten *Salamandra salamandra*, *Triturus alpestris*, *Triturus montandoni*, *Bombina variegata*, *Bufo bufo* und *Rana temporaria* zusammengesetzt sind. Die intraspezifische Aufteilung der Ressourcen kann stärker ausgeprägt sein als die interspezifische. Die Überschneidungsmuster in den untersuchten Gesellschaften werden eher auf morphophysiologische Besonderheiten der Amphibienarten, als auf Konkurrenz zwischen ihnen zurückgeführt.

ABSTRACT: Eight variants of trophic niche overlap in different assemblages of postmetamorphic *Salamandra salamandra*, *Triturus alpestris*, *Triturus montandoni*, *Bombina variegata*, *Bufo bufo* and *Rana temporaria* were analyzed in two districts of the Carpathian Mountains. Intraspecific resource partitioning can be more pronounced than interspecific. In the assemblages studied, niche overlap patterns are explicable by morpho-physiological peculiarities rather than by competition of the amphibians.

KEYWORDS: Amphibians, *Salamandra salamandra*, *Triturus alpestris*, *Triturus montandoni*, *Bombina variegata*, *Bufo bufo*, *Rana temporaria*, *Lacerta vivipara*, trophic niche overlap, assemblages, feeding, diet, prey, Ukraine, Soviet Union

INTRODUCTION

The relative importance of the factors which cause resource partitioning in amphibian assemblages differs among taxa and varies among communities at different geographic locations (TOFT 1985). The batrachofauna of the Carpathian Mountains is one of the richest in Europe and therefore gives a good opportunity for the analysis of food resource partitioning in amphibian assemblages. However, the feeding of Carpathian species was studied mainly aut-ecologically (for review see SZCZERBAK & SZCZERBAN 1980). A few syntrophological data are reported by KMINIAK (1978). The structure and

overlap of trophic niches have recently been studied in larvae of newts and salamanders by KUZMIN (in press). In the present paper feeding niche interrelations are discussed for amphibians of postmetamorphic stages.

MATERIAL AND METHODS

In June and July 1988 feeding was studied in 187 newly metamorphosed, one-year old and adult specimens of the Spotted Salamander, *Salamandra salamandra*, the Carpathian Newt, *Triturus montandoni*, and the Alpine Newt, *T. alpestris*, the Yellow-bellied Toad, *Bombina variegata*, the Common Toad, *Bufo bufo*, and the Grass Frog, *Rana temporaria*, in the environs of two villages in the Ukrainian Carpathian Mountains: Lugy, Rakhov district (757 m above sea level) and Malaya Ugolka, Tyachev district (c.410 m above sea level). Additionally, data on 16 salamander larvae, 15 newt larvae and 7 specimens of the Viviparous Lizard, *Lacerta vivipara*, were subject to niche overlap analysis. A sample of 12 adult Carpathian Newts collected on land (Mount Petros, Rakhov district, June 9th, 1961, Zoological Museum of Moscow State University no. 1174) was included as well.

Amphibians used for food investigations are frequently collected from large areas and/or during long periods. Of course, this provides large sample sizes. But in such cases the degree of trophic niche overlap is greatly affected by habitat, microhabitat, and temporal differences. To avoid these influences niche overlap was estimated only from simultaneously collected samples of one microhabitat. In this way 8 series were sampled:

1. Malaya Ugolka, beech forest, a plot of about 900 m², June 30th; an assemblage of *T. montandoni*, *S. salamandra* and *R. temporaria*.
2. Malaya Ugolka, rocky stream bank along the edge of a beech forest, June 29th, July 14th; an assemblage of *S. salamandra* and *B. variegata*.
3. Lugy, marshland meadow of about 400 m², June 22nd; an assemblage of *T. montandoni*, *B. variegata* and *R. temporaria*.
4. Lugy, same as 3., July 22nd; an assemblage of *B. bufo* and *R. temporaria*.
5. Lugy, marshy pondside, about 6 m², near the edge of a mixed forest, July 11th; an assemblage of *B. variegata* and *B. bufo*.
6. Lugy, overgrown pond with weak water flux, about 10 m x 3 m x 0.2 m, near a mixed forest, June 19th; an assemblage of *T. alpestris* and *T. mon-*

tandoni.

7. Malaya Ugolka, marsh, about 100 m², near the edge of a beech forest, June 30th; an assemblage of *B. variegata*.
8. Luga, marshy stream near the edge of a mixed forest, June 22nd; an assemblage of *S. salamandra* larvae and *T. montandoni*.

The ingested food from adult *B. variegata* and *R. temporaria* was obtained by squeezing their stomach (according to BULAKHOV 1976). Afterwards the animals were released. The other specimens collected were preserved in 5% neutral formaldehyde solution. Each amphibian prey was measured and determined on family level by means of a microscope. The proportional quota of each family in the total prey number was calculated. From these data (in table 1 clustered to orders or higher systematic units) MORISITA similarity index values, used as measure of niche overlap, were determined:

$$I_{x'} = \frac{2 * \sum_i (P_{ij} * P_{ik})}{\sum_i (P_{ij}^2 + P_{ik}^2)},$$

where P_{ij} = percentage of the i -th component in the j -th predator's diet, and P_{ik} = percentage of the i -th component in the k -th predator's diet. $0 \leq I_{x'} \leq 1$.

To estimate the relationships between predators and their resources, I have compared amphibian stomach contents (in assemblage no. 1) with the invertebrate fauna of the environment. The mesofauna was counted by picking it out manually from 3 biocenometer samples (15 cm x 15 cm x 2 cm each), the soil microfauna by subsequent separation in BERLESE funnels. As a measure of feeding selectivity IVLEV's (1961) index was used:

$$E = \frac{r_i - p_i}{r_i + p_i},$$

where r_i = percentage of i -th component in the diet, and p_i = percentage of i -th component in the environment. $-1 \leq E \leq +1$. Values of E were determined only for preys of available size for the amphibians in question.

RESULTS

I n t r a s p e c i f i c o v e r l a p

In each species food composition of newly metamorphosed specimens is different from that of adults mainly by the quota of small objects - Acarina, Collembola, Aphidinea, etc. (tables 1A, 2). This is due to the amphibian's body size. Size differences between newly metamorphosed and adult *T. montandoni*, for example, are more pronounced (assemblage no. 1: SVL = 19.7 ± 0.4 mm and 39.7 ± 1.6 mm respectively) than between newly metamorphosed and one-year old *R. temporaria* (assemblage no. 3: SVL = 12.5 ± 0.44 mm and 19.5 ± 0.73 mm). This causes a wider trophic niche overlap between the two constituents of the latter group compared to those of the former (table 3). Due to pronounced size differences between newly metamorphosed and adult *R. temporaria* niches are overlapping in a less degree (table 3, assemblage no. 1). The niches of one-year old and adult *B. variegata* (which are both nearly equal in size) almost coincide (table 3, assemblage no. 7).

The degree of male-female trophic niche overlap shows a great intraspecific variability depending on the sample (*T. alpestris*, aquatic: 0.66; *T. montandoni*, aquatic: 0.95; *T. montandoni*, terrestrial: 0.44; *S. salamandra*: 0.55; *B. variegata*: 0.21). Apparently these differences are not connected with constant sex-specific feeding rates: male-female differences are insignificant at $p \leq 0.05$ for an average number and relative mass of prey (per body mass unit) in one stomach.

I n t e r s p e c i f i c o v e r l a p

Feeding niches of newly metamorphosed *S. salamandra* and adult *B. variegata* are almost completely distinct (table 3, assemblage no. 2) because of great differences in the taxonomic composition and size of the prey (tables 1A, 2). Hydrobionts - Gammaridae (Crustacea) - and fast-flying insects - Ephemeroptera, Cicadoidea (Homoptera), Diptera, Hymenoptera - forming an important component of the diet of *B. variegata* (16.7% and 18.7% respectively) are not used by *S. salamandra*.

The niches of adult *S. salamandra* and newly metamorphosed *T. montandoni* also overlap to a small degree only (assemblage no. 1). This is caused by differences in the predators' sizes: the body length of the salamander (SVL = 93.7 ± 1.8 mm) is 4.5 times that of the young newt. Correspondingly, the latter

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Table 1A: Food composition (% prey number) of juvenile (juv.), adult (ad.), and subadult (sad.) terrestrial and semiaquatic amphibians. A - assemblage number; B - amphibian species; C - sample size; l. - larvae; i. - imagines.

Tab. 1A: Nahrungszusammensetzung bei juvenilen (juv.), adulten (ad.) und subadulten (sad.) terrestrischen und semiaquatischen Amphibien (in % der Beutetier-Gesamtzahl). A - Vergesellschaftung Nr.; B - Amphibienart; C - Stichprobengröße; l. - Larven; i. - Imagines.

Prey taxa	A	1					2		3				4		5		-
	B	<i>T.m.</i> juv.	<i>T.m.</i> ad.	<i>S.s.</i> ad.	<i>R.t.</i> juv.	<i>R.t.</i> ad.	<i>S.s.</i> juv.	<i>B.v.</i> ad.	<i>T.m.</i> ad.	<i>B.v.</i> ad.	<i>R.t.</i> juv.	<i>R.t.</i> sad.	<i>B.b.</i> juv.	<i>R.t.</i> juv.	<i>B.v.</i> juv.	<i>B.v.</i> ad.	<i>T.a.</i> ad.
	C	8	6	12	12	4	12	9	7	11	16	13	11	10	12	14	10
Oligochaeta	-	4.9	6.9	1.2	15.4	11.8	-	35.5	67.2	-	9.1	-	-	-	-	-	-
Gastropoda	15.6	3.2	17.5	1.2	15.4	29.5	-	3.2	-	2.9	4.6	9.1	4.8	1.6	4.6	33.4	
Myriapoda	3.2	9.8	26.7	2.4	7.7	5.9	4.2	-	-	-	-	-	-	-	-	1.5	13.4
Aranei	1.6	8.2	6.9	11.0	15.4	5.9	10.4	-	1.6	5.8	2.3	-	4.8	-	-	-	
Acarina	42.2	18.0	-	4.9	-	5.9	-	-	-	-	-	27.3	-	65.1	30.8	-	
Isopoda	3.1	-	3.5	1.2	-	5.9	-	-	-	-	2.3	-	-	-	-	-	
Collembola	28.2	19.6	-	24.4	-	17.7	8.3	9.7	-	23.2	4.6	30.7	26.2	20.6	23.1	6.7	
Aphidinea	-	-	-	-	-	-	-	-	4.9	11.6	-	-	7.1	4.8	-	-	
Lepidoptera, l.	-	6.6	15.5	-	7.7	5.9	6.3	3.2	8.2	1.5	2.3	-	2.4	-	1.5	13.3	
Coleoptera, l.	-	-	5.2	6.1	15.4	-	-	-	1.6	-	-	1.1	-	-	1.5	20.0	
Coleoptera, i.	-	-	6.9	15.9	7.7	11.8	12.5	-	4.9	1.5	2.3	9.1	2.4	-	7.7	-	
Hymenoptera, i.	-	-	-	3.7	-	-	2.1	6.5	-	3.0	4.6	3.4	2.4	-	4.6	-	
Diptera, l.	1.6	26.2	5.2	3.7	7.7	-	20.8	35.4	3.3	5.8	20.5	5.7	4.8	3.2	4.6	6.7	
Diptera, i.	-	1.6	3.4	13.4	7.7	-	12.5	6.5	6.6	36.2	45.5	4.6	31.0	4.8	15.4	6.7	
others	4.7	1.6	1.7	12.2	-	-	22.9	-	-	8.8	2.3	9.1	16.7	-	3.1	-	

use smaller prey (tables 1A, 2). The diets of newly metamorphosed newts as well as of adults are more similar to those of other small amphibians, e. g. *R. temporaria* froglets. The diets of the large amphibians, adult *S. salamandra* and adult *R. temporaria*, are similar and differ from those of the other species of the assemblage (table 2). So their trophic niche overlap in terms of prey taxa is more pronounced (table 3).

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Table 1B: Food composition (% prey number) of aquatic adults of *T. montandoni* and *T. alpestris* of assemblage no. 6.Tab. 1B: Nahrungszusammensetzung (in % der Beutetier-Gesamtzahl) von wasserlebenden adulten *T. montandoni* und *T. alpestris* in Vergesellschaftung Nr. 6.

Prey taxa	<i>T. alpestris</i> (n=10)	<i>T. montandoni</i> (n=10)
Lumbricidae (Oligochaeta)	7.0	1.6
Daphnidae (Crustacea)	-	75.4
Diaptomidae (Crustacea)	-	9.5
Asellidae (Crustacea)	2.3	-
Ephemeroptera, larvae	-	2.4
Plecoptera, larvae	-	0.79
Trichoptera, larvae	18.6	2.4
Lepidoptera, larvae	4.7	-
Hydrophilidae, larvae (Col.)	4.7	-
Dytiscidae, larvae (Col.)	2.3	-
Chrysomelidae, larvae (Col.)	37.2	1.6
Chironomidae, larvae (Dipt.)	4.7	1.6
Tipulidae, larvae (Dipt.)	9.3	-
<i>Triturus</i> sp., ova	2.3	1.6
Ranidae, larvae	7.0	2.4

Specific niche overlap in prey taxa is not always in accordance with overlap in prey size. For example, in spite of maximum similarity in average prey size (table 2), the taxonomic spectra of prey of *T. montandoni* and *B. variegata* are less similar than in other members of the assemblage no. 3 (table 3). A greater overlap of the taxonomic spectra of prey is achieved even between adult *T. montandoni* and the newly metamorphosed *R. temporaria*, which are separated by prey size (table 2). Grass Frogs of both age groups preyed much more upon fast-flying insects (36.2% and 52.4% respectively) than other members of assemblage no. 3 (6.5% and 6.6%). This is typical for *R. temporaria* and is also seen in other assemblages (no. 1 and no. 4: 7.7% - 18.3% and 31.0% respectively). It is evidently due to the well developed jumping capability of this species compared to the others.

When *R. temporaria* froglets (SVL = 13.8 ± 0.41 mm) and *B. bufo* of similar size (12.9 ± 0.24 mm) are syntopic, their trophic niches differ mainly by the dimensions of prey velocity and spatial distribution. Contrary to the frogs, the

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Table 2: Average prey number per specimen (N), and prey length (X) of syntopic Carpathian amphibians.

Tab. 2: Mittlere Anzahl der Beutetiere pro Exemplar (N) und Länge (X) der Beutetiere bei syntopen Amphibien aus den Karpaten.

assemblage no.	species	N \pm s _n	length of prey (mm)	
			X \pm s _x	min - max
1	<i>T.m.</i> juv.	8.0 \pm 0.73	1.6 \pm 0.17	0.3 - 5.0
	<i>T.m.</i> ad.	10.3 \pm 3.3	3.6 \pm 0.34	0.3 - 12.0
	<i>S.s.</i> ad.	4.0 \pm 0.50	12.5 \pm 1.2	3.0 - 30.0
	<i>R.t.</i> juv.	7.7 \pm 0.93	4.5 \pm 0.51	0.5 - 30.0
	<i>R.t.</i> ad.	3.3 \pm 1.0	21.7 \pm 7.8	3.0 - 110.0
2	<i>S.s.</i> juv.	2.1 \pm 0.23	4.1 \pm 0.91	0.5 - 17.0
	<i>B.v.</i> ad.	5.3 \pm 1.0	7.4 \pm 1.1	2.0 - 30.0
3	<i>T.m.</i> ad.	5.0 \pm 1.4	11.0 \pm 2.2	2.0 - 32.0
	<i>B.v.</i> ad.	5.6 \pm 0.37	14.2 \pm 1.6	1.0 - 30.0
	<i>R.t.</i> juv.	4.1 \pm 0.60	1.7 \pm 0.12	0.5 - 7.3
	<i>R.t.</i> ad.	3.5 \pm 0.61	4.3 \pm 0.58	1.5 - 17.0
4	<i>B.b.</i> juv.	8.7 \pm 1.9	1.9 \pm 0.12	0.3 - 4.0
	<i>R.t.</i> juv.	4.2 \pm 0.70	2.0 \pm 0.15	0.8 - 3.5
5	<i>B.b.</i> juv.	5.7 \pm 1.6	0.82 \pm 0.15	0.3 - 1.5
	<i>B.v.</i> ad.	4.6 \pm 1.4	4.9 \pm 0.83	0.5 - 30.0
6	<i>T.a.</i> ad.	4.3 \pm 0.54	11.5 \pm 2.9	1.5 - 82.0
	<i>T.m.</i> ad.	13.4 \pm 9.5	1.8 \pm 0.26	0.7 - 16.0

toads feed on small numbers of fast-flying forms (4.6%), whereas slow-moving soil mites play an important role in their diet (table 1A: no. 4). Prey size is similar in both species (table 2).

Where adult *B. variegata* (SVL = 38.7 \pm 0.49 mm) are syntopic with newly metamorphosed *B. bufo* (SVL = 10.1 \pm 0.20 mm) the latter preyed upon fewer fast-flying forms (4.8% vs. 18.5%, assemblage no. 5). This is evidently due to different jumping capabilities in these amphibians. Their niches also differ by prey length (table 2), according to the differences in the predators' body size.

The sample of syntopic adults of *T. alpestris* and *T. montandoni* exhibits a surprisingly low degree of trophic overlap (table 3). The diets of the two species are clearly different both in taxa (table 1B) and in size (table 2). These

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Table 3: Trophic niche overlap [I_x] of syntopic Carpathian amphibians of the assemblages no. 1 - 7. Sample size in parentheses.

Tab. 3: Die Überschneidung der trophischen Nischen [I_x] von syntopen Amphibien der Vergesellschaftungen Nr. 1 - 7. Stichprobenumfänge in runden Klammern.

1. <i>T.m.</i> juv. (8) / <i>T.m.</i> ad. (6): [0,59]	3. <i>T.m.</i> ad. (7) / <i>B.v.</i> ad. (11): [0,16]
<i>T.m.</i> juv. (8) / <i>S.s.</i> ad. (14): [0,10]	<i>T.m.</i> ad. (7) / <i>R.t.</i> juv. (16): [0,29]
<i>T.m.</i> ad. (6) / <i>S.s.</i> ad. (14): [0,23]	<i>T.m.</i> ad. (7) / <i>R.t.</i> sad. (13): [0,49]
<i>T.m.</i> juv. (8) / <i>R.t.</i> juv. (12): [0,40]	<i>B.v.</i> ad. (11) / <i>R.t.</i> juv. (16): [0,10]
<i>T.m.</i> juv. (8) / <i>R.t.</i> ad. (4): [0,16]	<i>B.v.</i> ad. (11) / <i>R.t.</i> sad. (13): [0,26]
<i>T.m.</i> ad. (6) / <i>R.t.</i> juv. (12): [0,50]	<i>R.t.</i> juv. (16) / <i>R.t.</i> sad. (13): [0,80]
<i>T.m.</i> ad. (6) / <i>R.t.</i> ad. (4): [0,22]	
<i>S.s.</i> ad. (14) / <i>R.t.</i> juv. (12): [0,21]	4. <i>B.b.</i> juv. (12) / <i>R.t.</i> juv. (10): [0,59]
<i>S.s.</i> ad. (14) / <i>R.t.</i> ad. (4): [0,55]	
<i>R.t.</i> juv. (12) / <i>R.t.</i> ad. (4): [0,32]	5. <i>B.b.</i> juv. (12) / <i>B.v.</i> ad. (14): [0,79]
2. <i>S.s.</i> juv. (7) / <i>B.v.</i> ad. (9): [0,10]	6. <i>T.a.</i> ad. (10) / <i>T.m.</i> ad. (10): [0,04]
	7. <i>B.v.</i> sad. (11) / <i>B.v.</i> ad. (12): [0,88]

differences are also shown in the spatial distribution of the prey: in the diet of *T. montandoni* terrestrial objects account for 3.2%, in *T. alpestris* for 51.2%. Since the newt's body length is subequal (*T. montandoni*: SVL = 44.5 ± 1.6 mm, *T. alpestris*: SVL = 51.5 ± 1.0 mm), the food differences recorded seem to be explicable only by a terrestrial stay of *T. alpestris* before they were sampled. I have repeatedly observed their movements between water bodies during moist weather. Differences in the average number of prey per digestive tract which reflect different patterns of foraging activity (*T. alpestris*: 4.3 ± 0.54; *T. montandoni*: 13.4 ± 9.5) provide an indirect confirmation of this.

The comparative scarcity of *T. alpestris* in the area studied did not allow me to obtain a terrestrial sample of this species simultaneously with *T. montandoni*. The food of *T. alpestris* specimens collected in the mixed forest of Lügy during one month (table 1A) clearly differs from that of *T. montandoni* from the assemblage of the edge of this forest (assemblage no. 3).

Postmetamorphic amphibians share their habitats with other vertebrates. Due to frequent foraging upon gammarids, the trophic niche of *B. variegata* (assemblage no. 2) markedly overlapped with that of *S. salamandra* larvae (n=8) of stage II (according to JUSZCZYK & ZAKRZEWSKI 1981) which inhabited the stream: $I_x = 0.35$. At the same time *B. variegata* living along pondsides

preyed on terrestrial invertebrates only. Therefore the trophic niche of this species is completely separated from those of *T. montandoni* and *T. alpestris* larvae which also inhabited these ponds: $I_x = 0$.

However, adult *T. montandoni* sometimes occurred in marshy streams together with *S. salamandra* larvae of stages I-II (assemblage no. 8) for which niche overlap is clearly expressed by $I_x = 0.63$ ($n = 8$ for each sample). This is mainly due to secondary prey: Bithyniidae (Mollusca, Gastropoda): 3.7% and 1.8% respectively; Molannidae (Insecta, Trichoptera): 7.4% and 3.6%; Dryopidae (Insecta, Coleoptera): 14.8% and 1.8%; Chironomidae (Insecta, Diptera): 29.6% and 38.2%. Amphibians may share their microhabitat with *Lacerta vivipara* (assemblage no. 3). The latter ($n = 7$) as an active forager eats many fast-flying insects (Cicadoidea (Homoptera) and Diptera form 40% of its diet) and a few earthworms (10%). Therefore the degree of trophic niche overlap with *R. temporaria* is higher (one-year old: $I_x = 0.52$; newly metamorphosed: $I_x = 0.50$) than with adult *B. variegata* ($I_x = 0.28$). Overlap with adult *T. montandoni* is lowest ($I_x = 0.08$).

Food selectivity

Food selectivity in assemblage no. 1 is in agreement with the food composition in percents (table 1A). The smallest prey (0.5 mm - 2 mm long) is consumed with highly positive selectivity only by newly metamorphosed *T. montandoni* and *R. temporaria* (Acarina: $E = +0.43$ and $+0.53$ respectively; Pseudoscorpiones (Arachnoidea): $+0.46$ and $+0.75$; Entomobryidae (Insecta, Apterygota): $+0.56$ and $+0.65$). Larger adult newts exhibited a lower selectivity concerning the prey categories above ($+0.04$; -0.02 and $+0.57$ respectively). The largest amphibians, adult *S. salamandra* and *R. temporaria*, did not consume this kind of prey ($E = -1$). Some small objects (1 mm - 3 mm) are more positively selected by newly metamorphosed *T. montandoni* than by adult newts and *R. temporaria* froglets (Gastropoda: $+0.75$; $+0.15$ and -0.38 respectively; Symphyla (Myriapoda): $+0.72$; -1 and -1 ; Oniscomorpha (Myriapoda): $+0.23$; -1 and -1 ; Oniscidae (Crustacea, Isopoda): $+0.23$; -1 and -0.44). Selectivity for larger larvae of Lycoriidae (Insecta, Diptera) (5-7 mm) shows a reverse tendency (-0.22 ; $+0.83$ and $+0.22$ respectively). Lumbricidae (Oligochaeta) and Lithobiomorpha (Myriapoda) of 5 mm - 30 mm, not taken by newly metamorphosed *T. montandoni* ($E = -1$), are consumed with different selectivity by adult newts ($+0.60$ and $+0.02$) and *R. temporaria* froglets ($+0.79$ and -0.12). Juliformia

(Myriapoda) and larval Pieridae (Insecta, Lepidoptera) of close size eaten by adult *T. montandoni* (+0.48 and +0.93) are not taken by newly metamorphosed of both newt and frog ($E = -1$).

The largest members of the assemblage, adult *S. salamandra* and adult *R. temporaria*, positively selected larger prey (5 mm - 110 mm) like earthworms (+0.05 and +0.79 respectively), snails (+0.06 and +0.42) and caterpillars (+0.89 and +0.79). Besides that, beetles and their larvae of intermediate size are positively selected by *S. salamandra* (5 mm - 9 mm prey size: larvae of Carabidae: +0.13; imagines of Carabidae: +0.59; larvae of Chrysomelidae and imagines of Curculionidae: +0.32 each) and adult *R. temporaria* (8 mm - 28 mm prey size: larvae of Carabidae: +0.62; imagines of Staphylinidae: +0.62). Among millipedes *S. salamandra* consumed the larger ones (17 mm - 30 mm) with higher selectivity than the small ones (3 mm - 12 mm): Juliformia (+0.38) and Polydesmida (+0.29) versus Symphyla (-1) and Oniscomorpha (-0.09). Fast-flying imagines of Diptera were consumed by tailed amphibians with low selectivity (newly metamorphosed *T. montandoni*: -1; adult *T. montandoni*: +0.02; adult *S. salamandra*: -0.28), in contrary to *R. temporaria* where the index value was high (froglets: +0.70; adults: +0.18).

DISCUSSION

The main criterion of trophic resource partitioning in the amphibians studied is prey size which is usually connected with predator size. The larger amphibians are, the larger and more diverse is their prey. However, along with the extension of the food spectrum a certain displacement to larger prey takes place: adult *S. salamandra* and *R. temporaria* did not use preys of a length of 0.3 mm - 0.5 mm (mites, pseudoscorpions, collembolans) which were readily eaten by newly metamorphosed specimens of each species. This is possibly connected with the relative diminution of prey available during the amphibian growth: with the eye size increasing, the vision would become less accurate due to reduction of the number of retinal receptory elements per square unit (MARGOLIS & MANTEIFEL 1978). The increase of selectivity for large prey and the decrease of small prey with increasing amphibian size could be considered an indirect confirmation of this hypothesis.

In their terrestrial phase the amphibian species studied feed mainly upon strato- and herpetobiont invertebrates. The percentage of the fast-flying forms (Dip-

tera, Hymenoptera, Cicadoidea (Homoptera)) in the diet increases with the development of the amphibian jumping capability. It is highest in *R. temporaria* and lowest in all Caudata. A similar pattern of resource partitioning was described for amphibian assemblages in Mongolia (KUZMIN 1987, 1988). Not only terrestrial forms, but also semiaquatic species like *B. variegata* forage exclusively on land. According to my observations stream bank gammarids (Crustacea, Amphipoda) are eaten by *B. variegata* outside the water. In general prevalence of terrestrial prey distinguishes *B. variegata* from *B. bombina* (SZCZERBAK & SZCZERBAN 1980), but KMINIAK (1978) noted underwater feeding in the former species as well.

Interspecific differences in activity and habitat use might influence the degree of niche overlap. Evidently, this is exactly the case in aquatic coexistence of *T. alpestris* and *T. montandoni*, where great differences in their diets are registered.

Factors of food resource allocation mentioned above seem to be fixed phylogenetically, but not species-specific as a whole. So variability of the postmetamorphic amphibian trophic niche can be more pronounced intraspecifically than interspecifically. Compared to the qualitative food similarity formerly noted for some of these species by KMINIAK (1978), even male-female diet overlap is not always high.

At present the species' position within the community is widely understood as being determined by competition (e. g. PIANKA 1983). In batrachology it is often suggested that the degree of diet similarity reflects competition which, in return, is considered to determine the trophic niche overlap value (e. g. SHLYAKHTIN 1986; SHLYAKHTIN & NOSOVA 1989). But because of the ignorance of the amount of resources in the environment and their interactions with the consumers (HURLBERT 1978), the niche overlap value is not a measure of competition. So "competitive" explanations of niche interrelations are improper in such cases. In the amphibian assemblages analyzed above trophic niche interrelations are satisfactory explained by morpho-physiological peculiarities of the species, and speculations on competition become unnecessary.

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