

Feeding Dynamics of One-Summer-Old Brown Frogs during Metamorphosis Termination

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Abstract – Description is given of the peculiarities of trophic relations of one-summer-old brown frogs with the soil mesofauna at urbanized territories in the initial period of their terrestrial life. The biocenotic role of this group is discussed.

The problem of the biocenotic role of amphibians has received reasonably thorough and multiaspected study by many authors. The specific nature of the role of amphibians lies in the fact that they are a connecting link between terrestrial and freshwater trophic chains (Garanin, 1976). A particular place is occupied by amphibians in coastal and aquatic ecosystems where they act, owing to the peculiarities of their development, as consumers of the first order and then pass to predation (Garanin, 1981). The amphibian food range testifies to their significant role in the destruction of insects harmful to agriculture and forestry (Shvarts, 1948; Papanyan, 1949). It is shown that with the increase of the effect of anthropogenic and pyrogenic factors, the utility of certain species increases thanks to the growth of phytophagous consumption (Belova and Kostenko, 1976). Almost total lack of food preference and dependence mainly on the size of the food item (Loman, 1980) is responsible for the consumption by amphibians of insects with a cryptic coloring, as well as of species with an unpleasant taste and smell, which considerably adds to the activity of insectivorous birds (Shvarts, 1948). Amphibian larvae consume a host of organic remains and one-celled algae, thus preventing water from "blossoming" (Gaizhenskene and Uselite, 1977). Feeding on nitrogen-fixing blue-green algae, tadpoles introduce nitrogen into trophic chains (Seal and Bacvar, 1980). The biomass of larvae is so high that their significant role in the transfer of substance and energy in biocenoses is self-evident (Shvarts, 1973).

Formerly (Li and Lin, 1935), anuran larvae were thought to begin feeding on animal food only after complete resorption of their tails. In fact, anuran metamorphosing individuals do not feed only in the period of the breaking through of anterior limbs (Kuz'min, 1987). Digestive enzymes necessary for the digestion of the animal food are already present at the larval stage (Houdry *et al.*, 1979; Sahy and Khare, 1988), whereas towards the end of metamorphosis the larval food range shows an increase in the proportion of animal foods (Belova, 1965; Motkova, 1977). The transition

of tadpoles to feeding on invertebrates takes place prior to the total resorption of the rudimentary tail. This is observed in *Rana clamitans* when the length of the rudiment is 7 mm (Jenssen, 1967) and in brown frogs (according to our data) when the size of the rudiment is in the range from 1 to 13.5 mm. The food range in this period shows the predominance of small invertebrates – springtails, nematodes, aphids, soil-dwelling ticks, etc. (Zhukova, 1981; Leont'eva, 1987; Guyetant, 1967; Wheeler, 1986).

The functional role of the new generation is determined by its number and proportion in a particular community. Amphibians may be far superior in biomass than higher terrestrial vertebrates (Ravkin and Luk'yanova, 1976; Kuranova and Grigor'ev, 1980), i.e., one may assume that the role of amphibians is greater in natural ecosystems than in urban ones. On the other hand, amphibians quite often are among the few vertebrates that inhabit urbanized areas. It is known that in vast areas subject to anthropogenic impact, the course of biogeocenotic processes is governed by several species, ubiquitous. The simplification and change of the biogeocenotic structure and of particular feeding chains leads to the increase of the role of animal organisms in the destruction of the organic matter (Shvarts, 1976).

From 1984–1988 in the territory of the city of Ekaterinburg and its suburb, study was made of the population dynamics of one-summer-old brown frogs (*Rana arvalis* Nilss. and *R. temporaria* L.) and of the content of the gastrointestinal tract at the 53rd and 54th stages (Dabagyan and Sleptsova, 1975). Simultaneously, a census of soil-dwelling invertebrates was carried out. During each census six soil core samples, 0.045 m² in size and 0.05 m thick, were taken. The samples were turned over and placed in glass funnels under electric lamps, and invertebrates were forced into vessels containing a 70% ethanol solution. Altogether, 89 total samples (534 core samples) were treated. The census of one-summer-old frogs was performed using mass marking by cutting off toes. Since changes in the food

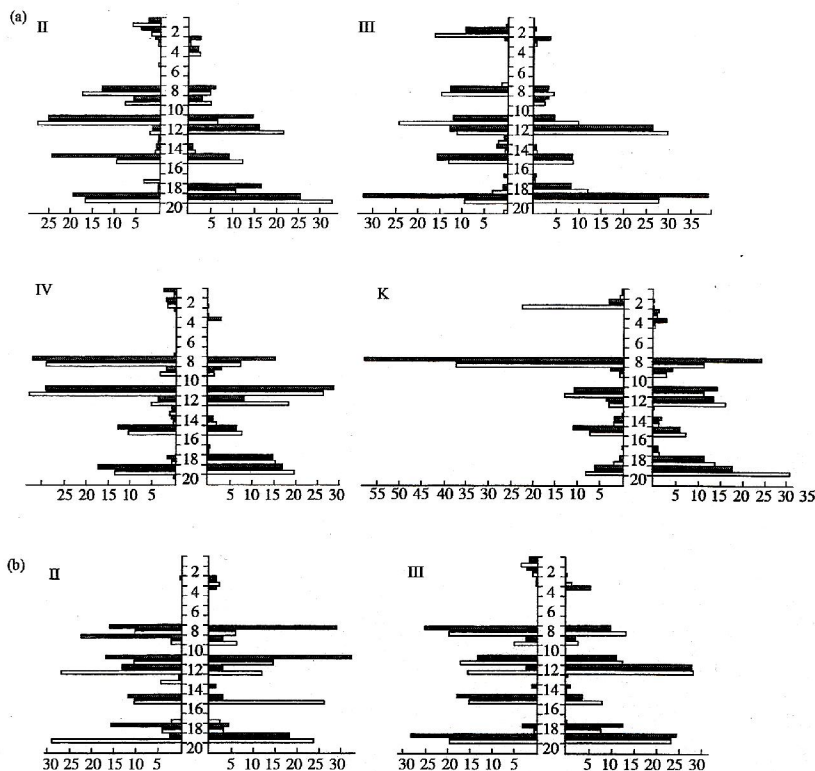


Fig. 1. The range of invertebrate groups occurring in soil samples and in the stomach content of one-summer-old (a) *Rana arvalis* and (b) *R. temporaria* (in % from the total number of invertebrates; overall data for 1985 - 1988).

Plotted on the axis of ordinates - systematic groups; on the abscissa - percentage; on the left - soil mesofauna; on the right - stomach content; 1 - Oligochaeta; 2 - Nematoda; 3 - Mollusca; 4 - Crustacea; 5 - Isopoda; 6 - Diplopoda; 7 - Myriapoda; 8 - Acari; 9 - Aranei; 10 - Pseudoscorpiones; 11 - Collembola; 12 - Homoptera; 13 - Thysanoptera; 14 - Hemiptera; 15 - Coleoptera; 16 - Neuroptera; 17 - Lepidoptera; 18 - Hymenoptera; 19 - Diptera; 20 - Psocoptera; crosshatched columns - the 53rd stage; uncrossed columns - the 54th stage.

range and in the availability of invertebrates in nature each year were comparatively alike, Figs. 1 and 2 show integrated data. During the investigation period, 1267 stomachs of *R. arvalis* and 471 stomachs of *R. temporaria* were examined. The division into zones with different levels of anthropogenic impact was performed in accordance to our previous studies: II - mul-

tile-storied building; III - low building; IV - forest park; K - suburban plot.

Two weeks after metamorphosis the food range of *R. arvalis* showed qualitative and quantitative changes (Fig. 1) most markedly displayed in assemblages subjected to a significant anthropogenic impact (zone II). In assemblages of one-summer-old individuals inhabit-

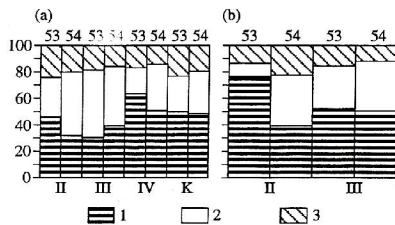


Fig. 2. The relationship between trophic groups in the food range of one-summer-old brown frogs (overall data for 1984 - 1988) of (a) *Rana arvalis* and (b) *R. temporaria*. 1 - Saprophagans; 2 - phytophagans; 3 - predators; 53 and 54 - developmental stages.

ing zones II and III, the proportion of phytophagous increased with the age of the animals from 30.8% at the 53rd stage to 51.2% at the 54th stage, whereas the proportion of carnivores and saprophages either decreased or did not change at all. In the forest park and in the control area there were no significant changes in the ratio of trophic groups (Fig. 2).

The evaluation of the similarity of the food range of metamorphosed and growing one-summer-old *R. arvalis* and *R. temporaria* demonstrated their extensive overlap and closeness independent of the level of the anthropogenic load (see Table 2). Food range overlap was determined according to a modified index of Morisita (Hurlbert, 1978). The most significant changes were in the stomach content of one-summer-old frogs of out-of-city populations, as well as in the availability of invertebrates in nature. The degree of the overlap of the content of the gastrointestinal tract with the availability of invertebrates in nature for metamorphosed larvae in zone II was inferior to that of growing one-summer-old frogs. This was in direct contradiction to the results obtained in other zones and in the control zone. The data on *R. temporaria* tadpoles were similar:

Table 1. Consumption of invertebrates by one-summer-old frogs at the 54th stage, % from the number of food items consumed at the 53rd stage

Year	Zone					
	II	III	IV	K	II	III
	<i>Rana arvalis</i>				<i>R. temporaria</i>	
1984	187	5.6	170.9	-	148.8	29.4
1985	207.5	243.8	157.3	45.4	34.7	180.3
1986	46.3	72.3	30.6	62.1	-	160.3
1987	102.5	32.4	35.7	28.9	-	112.4
1988	34	60.2	28	12.7	82.6	60.1

the degree of the overlap of the content of the gastrointestinal tract with the availability of invertebrates in nature increased with age (see Table 2). We found that the average number of food items per one stomach towards the 54th stage, as compared to the 53rd, considerably increased (from 0.6 - 11.9 to 2.9 - 19.5). The pressure of the generation of one-summer-old frogs on invertebrates within a city, despite a decrease in numbers, mostly remained at a reliably higher level ($p \leq 0.001 - 0.005$) than in natural communities (Table 1). Likewise, similar data were obtained for the brown frog, although the survival rate of the one-summer-old individuals of this species within a city was lower than that of the moor frog (see Table 4).

The census of soil micro- and mesofauna in the habitats of one-summer-old frogs revealed that from the moment of leaving the water for land until achievement of the 54th stage, in 62.5% of cases the populations showed an increase in the total number of individuals per unit area (Table 3). In habitats within a city such an increase was observed only in 25% of cases. This was possibly accounted for by the fact that the efficiency of the withdrawal of invertebrates in urban isolates, on the average, was 2.1 times greater. In zone II for two weeks there was an increase in the number of ticks, spiders, springtails, thrips, Hymenoptera, and Lepidoptera and a decrease in the number of nematodes, Coleoptera and dipterans. Homoptera were represented only by phytophagous (Aphidina, Cicadinea, Aphrophoridae); among Hymenoptera phytophagous (Cynipoidea) were also noted. In the control during this period there was an increase in the proportion of nematodes and a decrease in tick number. In all other zones significant changes were recorded only in groups 1 and 2 (see Fig. 1).

In *R. arvalis* the similarity of the content of the gastrointestinal tract with the range of the soil microfauna changed from the 53rd to the 54th stage. Thus, in assemblages of zones III and IV and in the control zone, the overlap with the available food items in nature slightly decreased (from 43 - 94 to 27 - 81%), whereas in assemblages of zone II it increased (from 45 - 70 to 38 - 79%; Table 2). In *R. temporaria*, resemblance to the available food items in nature increased in zones III and II.

The load of the population on the invertebrate fauna is characterized in greater detail by the selectivity index, which is defined as the ratio of occurrence of any group of food items in stomachs to the occurrence of this group in nature (if the index is equal to 1, then eating up is determined by occurrence; if it is greater than 1, one may speak about the preference of a certain group and vice versa). In Fig. 1 the interpretation of graphical data enables us to make a visual assessment of the selectivity index. In zone II one-summer-old frogs mainly ate away molluscs, Homoptera, Hemiptera, Coleoptera, Lepidoptera, Hymenoptera, and dipterans, while in the control one they fed on spiders, springtails, Homoptera, Lepidoptera, Hymenoptera, and dipterans.

Table 2. Similarity of the food range of one-summer-old brown frogs at the 53rd and 54th stages with invertebrates available in nature, %

Year	Zone															
	II				III				IV				K			
	1	2	3	4	1	2	3	4	1	2	3	4	1	2	3	4
<i>Rana arvalis</i>																
1985	83	70 <i>n</i> = 13	38 <i>n</i> = 14	68	83	68 <i>n</i> = 15	36 <i>n</i> = 15	67	88	83 <i>n</i> = 16	75 <i>n</i> = 55	76	65 <i>n</i> = 30	45 <i>n</i> = 19	27	24
1986	76	63 <i>n</i> = 16	54 <i>n</i> = 11	—	75	67 <i>n</i> = 9	63 <i>n</i> = 25	63	80	64 <i>n</i> = 30	32 <i>n</i> = 19	75	91 <i>n</i> = 30	43 <i>n</i> = 30	37	56
1987	85	45 <i>n</i> = 32	79 <i>n</i> = 32	70	91	93 <i>n</i> = 15	81 <i>n</i> = 13	81	94	93 <i>n</i> = 61	77 <i>n</i> = 44	97	91 <i>n</i> = 27	67 <i>n</i> = 30	59	99
1988	93	58 <i>n</i> = 39	65 <i>n</i> = 43	82	89	46 <i>n</i> = 30	63 <i>n</i> = 22	85	91	94 <i>n</i> = 69	68 <i>n</i> = 67	91	39 <i>n</i> = 30	81 <i>n</i> = 27	67	88
<i>R. temporaria</i>																
1985	73	61 <i>n</i> = 16	71 <i>n</i> = 12	43	61	21 <i>n</i> = 28	94 <i>n</i> = 21	11	—	—	—	—	—	—	—	—
1986	—	—	—	—	31	55 <i>n</i> = 23	61 <i>n</i> = 21	49	—	—	—	—	—	—	—	—
1987	—	—	—	—	85	73 <i>n</i> = 30	80 <i>n</i> = 30	97	—	—	—	—	—	—	—	—
1988	53	26 <i>n</i> = 15	74 <i>n</i> = 6	43	71	49 <i>n</i> = 28	46 <i>n</i> = 24	36	—	—	—	—	—	—	—	—

Note: *n* is the number of examined stomachs; 1 is the 53rd stage with the 54th one; 2 – the 53rd stage with invertebrates available in nature; 3 – the 54th stage with invertebrates available in nature; 4 – overlap of food items in nature.

Table 3. Invertebrate density, individuals/m² by the time of the onset of the 53rd and 54th stages

Year	Stage	Zone II	N*	Zone III	N	Zone IV	N	Suburban plot	N
1985	53	1567.5	2	1667.5	2	1022.7	4	667.0	1
	54	6670	2	2134.4	2	3779.7	4	11405.7	1
1986	53	—	—	3893.8	2	1567.5	2	1827.3	2
	54	2267.8	1	1853.9	2	2040.6	2	1387.0	2
1987	53	2201.1	2	2890.3	3	2081.0	4	2701.4	2
	54	1900.9	2	2423.4	4	1600.9	4	5902.9	2
1988	53	2684.7	5	1984.3	4	1445.2	5	3134.9	2
	54	2067.7	4	1450.7	4	1760.9	5	3068.2	2

Note: N – number of total samples.

The decrease in the pressure of one-summer-old frogs upon invertebrates in natural groups of amphibians should be accounted for by the death of a significant proportion of one-summer-old individuals in each particular micropopulation due to a greater number of trophic relationships and levels, i.e., the number of predators is high. In such cases, significant death rates

are not fatal for the population as a whole (Shvarts, 1980) since the number of micropopulations is great. The situation in urban areas is different. Here most populations (not divided into several micropopulations) are spatially separated and maintain no contact with each other. In this case the number of such assemblages and their population are small. Therefore, a failure in the

Table 4. Survival rate of one-summer-old frogs towards the 54th stage, % from the 53rd

Year	<i>Rana arvalis</i>				<i>R. temporaria</i>	
	Zone					
	II	III	IV	K	II	III
1984	68.1 <i>n</i> = 720	8.0 <i>n</i> = 1870	44.7 <i>n</i> = 1572	—	45.2 <i>n</i> = 126	10.9 <i>n</i> = 3840
1985	49.7 <i>n</i> = 169	80.6 <i>n</i> = 992	51.1 <i>n</i> = 1414	14.2 <i>n</i> = 367	10.1 <i>n</i> = 525	8.1 <i>n</i> = 3952
1986	20.1 <i>n</i> = 1830	66.7 <i>n</i> = 180	24.2 <i>n</i> = 227	38.6 <i>n</i> = 685	—	63.9 <i>n</i> = 833
1987	51.6 <i>n</i> = 2382	11.6 <i>n</i> = 3105	22.6 <i>n</i> = 2222	20.6 <i>n</i> = 1035	—	46.5 <i>n</i> = 5113
1988	17.6 <i>n</i> = 2901	42.2 <i>n</i> = 313	19.7 <i>n</i> = 3053	7.5 <i>n</i> = 1455	17.5 <i>n</i> = 400	28.8 <i>n</i> = 2649

Note: *n* is the number at the 53rd stage.

Table 5. The average body length of one-summer-old *R. arvalis*, mm

Years	1984	1985	1986	1987	1988
Zone II	15.4 ± 0.35 <i>n</i> = 64	18.5 ± 0.37 <i>n</i> = 27	18.6 ± 0.3 <i>n</i> = 64	14.9 ± 0.22 <i>n</i> = 64	17.3 ± 0.23 <i>n</i> = 104
Suburban population	12.9 ± 0.26 <i>n</i> = 35	16.8 ± 0.24 <i>n</i> = 49	15.7 ± 0.18 <i>n</i> = 60	13.9 ± 0.2 <i>n</i> = 60	15.0 ± 0.14 <i>n</i> = 57

reproduction of each particular assemblage has more severe effects upon it (up to its complete disappearance) due to the absence of the migrant inflow.

Populations of the moor frog in zone II occupy small plots but the animal density here is higher than in zone III and in the forest-park (Vershinin and Krinitsyn, 1985). In view of this, the impact of urban assemblages upon invertebrates appears to be more intensive. In natural biogeocenoses the death of one-summer-old brown and moor frogs leaving water bodies takes place during the 1 - 3rd week of their terrestrial life (Ishchenko, Ledentsov, 1985; Smirina, 1980). There are grounds for believing that the death of one-summer-old frogs at the start of their terrestrial life depends on their density (Severtsov, 1986). Predators may be one of the density-dependent factors of mortality (Lyapkov, 1987). According to our data, mortality in the first two weeks after metamorphosis was considerably higher ($p \leq 0.05 - 0.01$ for zone II) out-of-city than in urbanized territories (Table 4), and mortality of the brown frog within a city was higher than that of the moor frog. One of the reasons for the high survival of *R. arvalis* in urban populations during the period from the 53rd to the 54th stage lies obviously in the almost complete lack of natural enemies, except for man (Zhukova, 1978), as well as in the fact that large one-summer-old frogs are less vulnerable to such predators as shrewmice, which are capable

of exterminating up to 65.1% of the entire population in one and one-half months (Lyapkov, 1987). We found that during the total period of observations the body length of one-summer-old *R. arvalis* in zone II was reliably ($p \leq 0.01$) greater than that in the control zone (Table 5).

The large body size of one-summer-old frogs appears to be linked to one further peculiarity of their feeding behavior. We revealed that prior to the entire tail resorption some of the one-summer-old individuals coming to land began feeding. We discovered a reliable ($p \leq 0.05$) difference between zone II and the control zone in the proportion of those frogs possessing a rudimentary tail who feed (Table 6). In different assemblages, this proportion greatly varied (from 13.2 to 51.7%). In *R. temporaria* it was high in zone II and slightly less in zone III; there was no considerable difference in the average body length of one-summer-old individuals from different zones [16.0 ± 0.22 mm (*n* = 44) and 15.1 ± 0.55 (*n* = 39), respectively]. The average body length was greater in one-summer-old *R. arvalis* from zone II (see Table 5).

Evidently, the low occurrence in zone II of one-summer-old frogs feeding prior to the completion of metamorphosis derives from the fact that large one-summer-old individuals have certain energy reserves

Table 6. The proportion of one-summer-old frogs starting to feed with a rudimentary tail, % (overall data for 1977, 1980 - 1988)

Zone	<i>Rana arvalis</i>		<i>R. temporaria</i>	
	Total number	%	Total number	%
II	112	30.4	55	49.1
III	68	45.6	145	36.6
IV	379	37.5	—	—
K	157	43.9	—	—

not possessed by small ones (Crump, 1981) and perish unless they start feeding immediately (Shvarts, 1981). For the same reason, even at the start of their terrestrial life, one-summer-old frogs in zone II have a greater radius of individual activity, and their food range is less similar to that of soil invertebrates than in other zones. The difference may be caused by the fact that at the 53rd stage their food already includes flying species and other invertebrates that are lacking in the complex of the soil mesofauna. This is also evident by a decrease in the proportion of saprophages and an increase in the occurrence of phytophagous in food composition. After nearly two weeks, the resemblance of the content of the gastrointestinal tract of the one-summer-old frogs in zone II to the range of soil invertebrates increases. This is possibly explained, on the one hand, by a lesser increase of the invertebrate population in habitats of zone II and, on the other hand, by a spatial limitation of its terrestrial portion and, consequently, by a high density of one-summer-old frogs. Under such circumstances, amphibians consume the most widespread groups of invertebrates, this being confirmed by the increased occurrence of phytophagous in the food range of the larvae of urban populations. The fact that two weeks after metamorphosis the invertebrate population increases more slowly in urban habitats is possibly the result of a higher extinction of invertebrates in urban assemblages (since the mortality rate of tadpoles is low, while their size is larger), as well as the consequence of a lower diversity of food items. Greater differences in the range of soil invertebrates in the given period indirectly testifies to this (see Fig. 1). From general approaches to the study of population energetics, it is known that when there is a reduction in reserves and diversity of resources ensuring the compensation of the organism's expenditures at the population level, a greater number of population functions is realized. In this case the individual efficiency of the energy utilization decreases, whereas the population efficiency increases (Mezhzhherin, 1988). As a result of the evolution of the biosphere under conditions of anthropogenic impact, new less restricted biogeocenoses work more to the benefit of the biosphere as a whole (Shvarts, 1976).

Thus, the specifics of population dynamics and the peculiarities of the spatial organization of the communities under consideration are responsible for the growth

of the ecological efficiency of a new generation of brown frogs by the start of their terrestrial life in urban isolates with a high level of anthropogenic impact.

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