

Feeding Ecology of the Caucasian Salamander (*Mertensiella caucasica*), with Comments on Life History

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Abstract. -The feeding and developmental ecology of the Caucasian Salamander (*Mertensiella caucasica*) were studied in western Georgia. Age changes of larval feeding rate are weak. The main food of larvae consists of gammarids and insects. Larval prey size spectrum widens and displaces to more large objects during ontogenesis. However age, diurnal, seasonal and habitat differences in diet are weak. The majority of preys are consumed with negative electivity. During metamorphosis feeding does not cease. A review of literature on adult Caucasian Salamander feeding is presented. A comparison of larval development data with skeletochronology suggests that metamorphosis takes place after the second wintering. Three to five annual rings were counted in tubular bone diaphyses of mature specimens.

Key words: Amphibia, Caudata, Salamandridae *Mertensiella caucasica*; Caucasus Mountains, Georgia, feeding, larvae, electivity.



FIG. 1. Stream habitat of *Mertensiella caucasica* in Akhaldaba Region, Georgia.

Introduction

The Caucasian Salamander, *Mertensiella*

caucasica (Waga, 1876) is a stenobiont species which lives near rocky streams in mountain forests of western Georgia and adjacent areas of Turkey (Figs. 1, 2, and Plate 1). Members of this relict genus were widely distributed in Europe in the Pliocene (Borja and Mlynarski, 1979). Data on Caucasian Salamander ecology are very poor, especially on feeding ecology. The latter are limited to food composition and feeding behaviour in captivity (Knoblauch, 1905; Lantz, 1911; Mertens, 1942; Obst and Rotter, 1962; Rotter, 1958; Wolterstorff, 1942), speculations on diet based on invertebrate fauna in the environment (Cyren, 1911; Hemmerling and Obst, 1968; Lantz, 1911; Mertens, 1942), and observations and dissections of single specimens (Basoglu and Özeti, 1973; Ekvimishvili, 1940; Knoblauch, 1905; Nikolsky, 1913; Sikmashvili, 1970; Wolterstorff et al., 1936). Quantitative data on adult diet are presented only in papers by Bozhansky and D.V.Semenov (1982) and Ekvimishvili (1948).

Methods

From June to August, 1985 the ecology of the Caucasian Salamander was studied in the Akhaldaba environs, Borzhomi (41° 51' N 43° 23' E) region, Georgia. In the same



FIG. 2. Mountain forest habitat of *Mertensiella caucasica* in Akhaldaba Region, Georgia.

months of 1986 additional material on newly metamorphosed salamanders was collected. Adults were measured (snout-vent length- L., tail length- L. cd.), marked by toe-clipping and released. Besides that, we have captured larvae and newly metamorphosed specimens. Animals of these two age groups as well as adult clipped toes were fixed immediately in 5% neutral formaldehyde solution.

Before treatment, fixed larvae were immersed in water for several hours. I measured them by ocular-micrometer under a stereoscopic microscope or (larger specimens) by vernier calliper with a precision of 0.1 mm. Then I dried them with filter paper and weighed them with a precision of 1 mg. To determine the salamander age, numbers of annual rings in femoral (larvae) or finger (adults) bone sections were counted (according to

Smirina and Sofianidu, 1985). For the sake of species' conservation I didn't make dissections of mature salamanders. I have obtained information on their feeding from the literature cited above.

To study larval and newly metamorphosed salamander feeding, entire digestive tracts were obtained. Their contents were studied under a microscope. The bulk of food was dried with filter paper and weighed with a precision of 0.1 mg. Food objects were identified and measured under the microscope. From their linear dimensions, reconstructed weights were determined (for details see Kuzmin, 1984 a, 1984b).

I have determined percentages of each prey category by its weight and number. Because of uncertainty of prey length and mass as measures of its size availability for

Caudata, ratio $d_{\max}/L_t$ or. (see Kuzmin, 1985) was used, where $d_{\max}$ =maximum prey diameter (width or height), L_t or.=width of amphibian mouth (between hind angles of lip folds). It must be noted that some later identical parameter was successfully used in *Onychodactylus japonicus* feeding behaviour investigations (Kusano and Hayashi, 1985).

Feeding rate in different groups of salamanders was compared by digestive tract-fill indices:

$$Y = \frac{m \cdot 1000\%}{M - m}$$

where m =food mass, M =total consumer mass. Caloric content of different preys was determined using the methods of Cummins and Wuysheck (1971). After this, the mean caloric content of food was counted.

Trophic niche overlap was determined using Morishita similarity index in the form:

$$I_{\lambda} = \frac{\sum_i p_{ij} p_{ik}}{\sum_i (p_{ij}^2 + p_{ik}^2)}$$

where p_{ij} =percent of i -th component in the diet of j -th predator, p_{ik} =percent if i -th component in the diet of k -th predator, and $0 \leq I_{\lambda} \leq 1$.

To estimate feeding electivity the contents of larval digestive tracts were compared with the invertebrate fauna of the stream. Invertebrates were counted after their total sampling from stream pools where salamanders were collected. The feeding electivity is estimated using Ivlev's formula:

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

Where r_i =percent of i -th component in the diet, p_i =its percent in environmental complex, and $-1 \leq E \leq +1$. Observations on the feeding behavior in captivity were also conducted (for methods see Kuzmin,

1986).

Results

Body Size and Skeletochronology

All larvae sampled are clearly divided into 3 groups by their L_t : 15.4-19.5 mm (106-108 mg), 23.7-27.5 mm (330-644 mg) and 29.0-35.4 mm (632-1400 mg). These three groups morphologically differ from each other (Fig. 3). Size groups 1 and 2 contained mainly specimens that were born in the given year. Annual rings in their femoral bone sections are as a rule absent (Fig. 4). Larger larvae (size group 3) had one annual ring, commonly only vaguely expressed. On the femoral bone sections of two newly metamorphosed animals (captured in June and August 1985) one annual ring is also recognized. From 10 marked adults captured 13 June, 1985 ($L_t = 66.7 \pm 1.6$ mm; $L_{cd} = 171.5 \pm 4.3$ mm) annual rings were successfully counted in 7. Each specimen had on the average 3.57 ± 0.30 (3-5) rings.

Diet and Feeding Behaviour

Quantity of food consumed.—In laboratory conditions Caucasian Salamanders lived some time on endogenous yolk and transfer to active feeding takes place at larval size group 1 (I. A. Serbinova, pers. comm.). It must be noted that all the smallest larvae found in nature belong to group 1. The latter already feed upon exogenous prey with high intensity. Yolk is not recognized in their digestive tracts. Furthermore, digestive tract-fill index (J) changes slightly with age. Its values are similar in different months and in different size groups (July: group 1- $40.1 \pm 5.4\%$; 2- $34.1 \pm 4.2\%$; 3- $41.5 \pm 15.2\%$. August: group 2- $41.8 \pm 7.2\%$; 3- $34.8 \pm 3.0\%$). Just after metamorphosis J remains almost on the same level ($34.8 \pm 5.5\%$). There are little differences in J values between the larvae from medium and lower stream currents ($39.5 \pm 4.3\%$ and $35.4 \pm 7.0\%$ respectively). Salamander larvae are more active at night than in the daytime. The values of J are influenced by this ($L_t = 16$ -

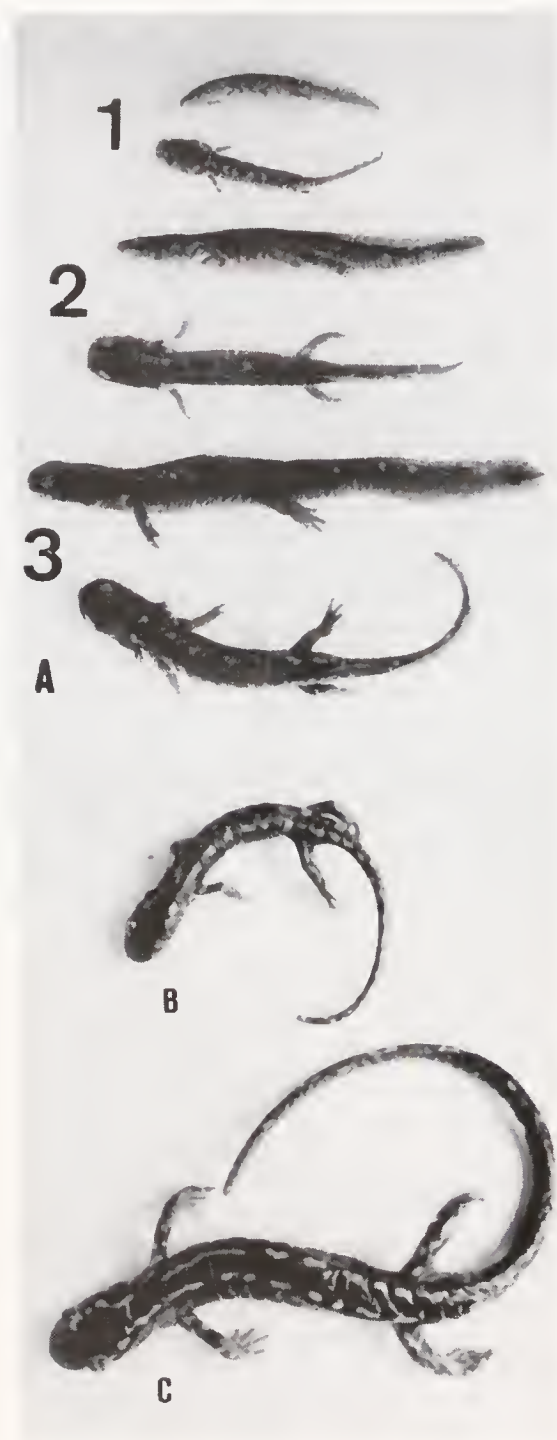


FIG. 3. Caucasian Salamanders of different ages. A- larvae of three size groups (1-3); B- newly metamorphosed specimen; C- adult specimen.

17 mm: 01 h - 53%; 12-13 h - 40%).

Mean caloric content of food of different

groups has a weak monthly variation (1.01-1.24 cal/mg).

Average number of preys per digestive tract increases with larval size from 3.00 ± 0.43 (group 1) to 4.88 ± 1.43 (group 3).

Food spectrum of larvae widens in ontogenesis. Along with widening, there is a marked displacement of prey size spectrum to larger and larger objects (Table 1, A, B). Maximum values of $d_{\max}/L_{t.or}$ reached 62.6%.

The main food of salamander larvae are gammarids and larval insects (Table 2). The smallest invertebrates, *Ostracoda* and *Hydracarina*, occur in the diet of smallest salamanders. Generally, age changes of diet are weak (see Table 2). Food similarity (I_k') by prey numbers are: for groups 1 and 2 - 0.73; 1 and 3 - 0.82; 2 and 3 - 0.61. For weight proportions they are 0.80, 0.73, and 0.52, respectively. Likewise in summer (group 2 - June and August: $I_k' = 0.97$ by prey number and 0.50 by weight) and day (group 1: 12-13h and 01 h: $I_k' = 0.82$ and 0.75) larval diets changed very slowly. Larval food differences are slightly more apparent in medium and lower stream currents ($I_k' = 0.59$ and 0.42).

Metamorphosed salamander food composition changes sharply due to habitat change (see Table 2). Terrestrial insects become dominant. Food becomes more and more diverse with age. Crustaceans, arachnids and insects are the main adult salamander's prey (see Table 2). At the same time interpopulational differences in their feeding are insufficient: for Akhaldaba (Bozhansky and Semenov, 1982) and Baniskhevi (Ekvtimishvili, 1948) samples $I_k' = 0.87$ by numeric percents. Sexual differences in diets are absent (Bozhansky and Semenov, 1982).

Apart from food items, plant remains, parasitic nematods (in newly metamorphosed salamanders) soil and sand were found in the digestive tracts of

different stages.

Feeding electivity.—This has been studied in June larvae. *Limoniidae* are positively elected by the larvae of group 3 ($E=+0.52$), whereas in the diet of younger ones, these insects are not found. Electivity to a close family, Chironomidae, decreases during ontogenesis (group 1: $E=-0.13$; 2: -0.42 ; 3: -1). The larvae of group 3 ignored the smallest object - *Ostracoda* ($E=-1$). This prey is consumed almost unselectively by smaller larvae (group 1: $E=+0.03$; 2: -0.05). Gammaridae are utilized with weak electivity (1: $+0.06$; 2: -0.32 ; 3: $+0.23$). Salamanders of all three groups negatively selected *Trichoptera* (1: -0.73 ; 2: -0.42 ; 3: -0.43).

Feeding behaviour. In captivity, larvae ($L.=30-35$ mm) noticed the large prey (Gammaridae 3-10 mm long, *Planaria* about 10 mm) from distances of 10-16 mm, approached up to 2-3 mm and attacked. *Planaria* orientation in the mouth takes 10-20 seconds; larger gammarids, about 40 seconds. In natural conditions salamander larvae exhibit diurnal foraging more frequently than adults. Among the latter this is observed mainly in wet and dark places. During the winter salamander feeding ceases. In the summer they forage in shallow water more frequently than in early spring and autumn (Ekvtimishvili, 1948). Under the water adults waited for moving invertebrates (Knoblauch, 1905). This may be an adaptation to foraging in a lotic environment. According to Knoblauch (1905), salamander feeding requirements do not decrease even at 9°C . My observations reveal the upper thermal limit of adult foraging activity as $23-25^{\circ}\text{C}$ range. At these temperatures animals respond to approaching invertebrates, but don't make attempts to catch them.

Discussion

From spring to autumn larvae of different size groups are found in streams (Berg, 1910; Cyren, 1911; 1968; Hemmerling and Obst, 1968; Koroljov, 1986; Mertens, 1942; my data). Evidently

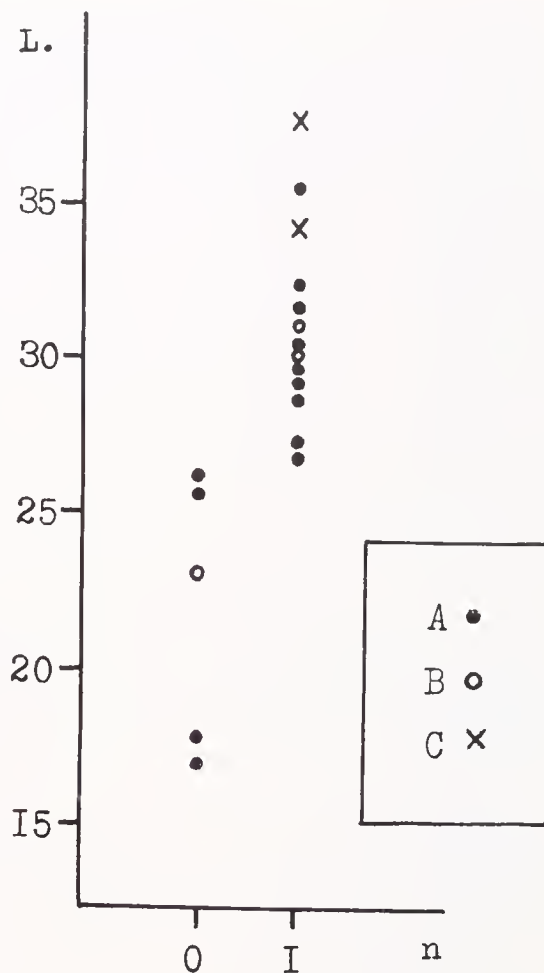


FIG. 4. The number of annual rings (n) in the sections of femoral bone diaphyses of young Caucasian Salamanders of different body length (L.). A- larvae, June; B- Larvae, August; C- newly metamorphosed specimens.

group 1 consists of recently hatched larvae that have begun their active feeding. Group 3 is metamorphic. Their share in larval samples markedly decreased to August due to entering land by metamorphs. Thus, the lack of annual rings in the bones of most of the specimens from groups 1 and 2 indicates their birth was mainly in the given year. Animals larger than 27 mm and newly metamorphosed specimens had one annual ring, so they had survived one wintering. The largest specimens of a given birth year only slightly differ from the smallest that had wintered. This could be explained by a prolonged salamander breeding period.

TABLE 1. Prey size composition of Caucasian Salamander larvae (June, 1985).

A. Proportions $d_{\max}/L_t$ or., %			
$d_{\max}$, mm	Larval size groups		
	1 (n=13)	2 (n=9)	3 (n=9)
0.1-0.5 (0.3)	8.2	5.5	4.5
0.6-1.0 (0.8)	21.8	14.7	11.9
1.1-1.5 (1.3)	35.3	23.9	19.4
1.6-2.0 (1.8)	49.0	33.1	26.9
2.1-2.5 (2.3)	62.6	42.3	34.3
2.6-3.0 (2.8)	-	51.5	41.8

B. Proportions by numbers of prey with different $d_{\max}$, %			
$d_{\max}$, mm	Larval size groups		
	1	2	3
0.1-0.5 (0.3)	41.0	12.9	10.7
0.6-1.0 (0.8)	41.0	41.9	14.3
1.1-1.5 (1.3)	10.3	16.1	10.7
1.6-2.0 (1.8)	5.1	12.9	39.3
2.1-2.5 (2.3)	2.6	12.9	17.9
2.6-3.0 (2.8)	-	3.2	7.1

Thus, Caucasian Salamander larvae completed their metamorphosis during the next year after hatching. So the opinions of a 3 year (Koroljov, 1986) or less than 1 year (Zhordaniya, 1975) larval period of the Caucasian Salamander are not confirmed.[†]

According to some authors (Bozhanski

and Semenov, 1982), Caucasian Salamanders reach their maturity after the second wintering. The secondary sex character, male dorsal spine on the tail base, appears when the total length ($L + L_{cd}$) reaches about 130 mm (Hemmerling and Obst, 1968; Obst and Rotter, 1962). My skeletochronological data do not allow me to make a perfect determination of adult salamanders age, because of the lack of data on the inner annual ring resorption rate. Therefore, we must consider their age to be not less than the number of annual rings (after Smirina and Sofianidu, 1985), i.e. 3-5 years.

[†] If the first wintering occurs in larvae just before the start of their hind limb skeleton ossification, the annual ring of this wintering will be absent. If so, the first annual ring must reflect the second wintering. If this is confirmed, Tarkhnishvili and Servinove's (in Press) proposal of a two-year larval period for *M. caucasica* is true.

The main changes of salamander trophic niche during ontogenesis take place under

TABLE 2. Prey taxonomic spectrum of *Mertensiella caucasica* in ontogenesis. 1-3 - larval size groups; juv. - newly metamorphosed specimens; by horizontal: 1-% by prey number; 2-% by prey weight. For adults from Baniskhevi (n=67) data of Ekvimlishvili (1948); from Akhaldaba (n=21) data of Bozhansky and Semenov (1982).

Prey taxa	June						August		June		June-Sept.	Sum-
	1 (n=13)		2 (n=9)		3 (n=9)		2 (n=11)		juveniles n=7		adult n=67	adult n=23
	1	2	1	2	1	2	1	2	1	2	1	1
OLIGOCHAETA	-	-	3.6	0.59	-	-	-	-	-	-	2.3	1.7
GASTROPODA	-	-	-	-	-	-	6.4	13.2	-	-	7.6	6.7
Crustacea												
Ostracoda	13.9	0.10	14.2	0.74	-	-	17.0	0.62	-	-	-	-
Gammaridae	38.9	36.3	17.9	25.1	55.2	77.2	29.8	48.5	-	-	2.0	5.9
Asellidae	2.8	2.7	-	-	3.7	7.8	-	-	20.0	28.9	-	-
Oniscidae	-	-	-	-	-	-	-	-	-	-	23.9	16.9
MYRIAPODA	-	-	-	-	-	-	-	-				
Diplopoda et Chilopoda									4.0	4.3	5.1	4.2
ARACHNIDA												
Acarina	2.8	0.14	-	-	-	-	-	-	12.0	0.97	1.5	0.80
Aranei	-	-	-	-	-	-	-	-	4.0	0.32	2.5	0.80
Opiliones	-	-	-	-	-	-	-	-	-	-	2.5	0.80
Pseudo- scorpiones	-	-	-	-	-	-	-	4.0	0.32	0.32	2.5	0.80
INSECTA												
Collembola	-	-	-	-	-	-	-	-	40.0	11.4	4.6	-
Blattoidea	-	-	-	-	-	-	-	-	-	-	-	0.80
Ephemeroptera l.	13.9	18.0	39.3	45.7	20.7	8.5	36.2	12.6	-	-	0.50	-
Plecoptera l.	-	-	-	-	-	-	-	-	-	-	4.6	-
Lepidoptera l.	-	-	-	-	-	-	-	-	4.0	21.5	-	-
Lepidoptera i.	-	-	-	-	-	-	-	-	-	-	-	0.80
Coleoptera i.	8.3	16.8	10.7	9.7	-	-	4.3	8.8	-	-	14.5	3.3
Tricoptera l.	2.8	13.7	7.1	16.8	6.9	4.7	-	-	-	-	1.3	17.8
Orthoptera	-	-	-	-	-	-	-	-	-	-	1.3	17.8
Dermaptera	-	-	-	-	-	-	-	-	-	-	-	0.80
Hemiptera	-	-	-	-	-	-	-	-	-	-	1.3	-
Hymenoptera	-	-	-	-	-	-	-	-	-	-	1.3	-
Chironomidae l.	16.7	12.2	7.1	1.4	-	-	2.1	0.11	4.0	4.3	-	-
Limoniidae l.	-	-	-	-	13.8	1.9	2.1	0.77	-	-	-	-
Tipulidae l.	-	-	-	-	-	-	2.1	15.4	-	-	-	-

l.-larvae; i.-imago

the transfer from endogenous to exogenous feeding and, to a smaller degree, at metamorphosis. The rest of the time food changes are insignificant. This weak feeding variability is in accordance with the results of single specimen dissections from different parts of the species range (Basoglu and Ozeti, 1973; Knoblauch, 1905; Nikolsky, 1913; Wolterstorff et al., 1936).

Some authors (Hemmerling and Obst, 1968; Mertens, 1942) considered larval size variability to be a result of their different food provisions. But the data on larval age presented above together with weak age and spatial variability of digestive tract-fill index and diet confirms the opposite. A shortage of small invertebrates in streams, however, could be a factor influencing the comparatively large sizes Caucasian

Salamander larvae feed on, as compared with larvae of limnophilous tailed amphibians (Cyren, 1911). Narrow trophic spectrum consisting of relatively large invertebrates as far as low occurrence of small forms in stream samples served as its indirect confirmation.

Positive electivity in larval feeding is weakly expressed. Evidently, their diet reflects mainly the available invertebrate composition in the environment. A low percentage of larval *Trichoptera* in salamander diets may be connected with their low electivity. Probably the latter is due to the difficulty of swallowing this energetically unprofitable prey (sand case mass could be of 5-6 times heavier than the food object).

The environmental conditions of the Caucasian Salamander are very uniform and almost unchanged since Pleistocene (Wolterstorff et al., 1936). Indirect confirmation of an endemic ecological pattern is the parasitological data. The Caucasian Salamander is the host of four parasitic nematod species. Three of them are specific for this amphibian (Lomakin, 1982; Sharpilo, 1976, 1978; Timofeeva and Sharpilo, 1979). Thus, the high Caucasian Salamander trophic niche stability at each step of its life history reflects the stenobiont state of this species in the western Transcaucasian relict ecosystems.

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