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The Ecology of the Caucasian Salamander (*Mertensiella caucasica* Waga) in a Local Population

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Abstract. -The different aspects of ecology of *Mertensiella caucasica* Waga, 1876 were investigated in a local population from Borjomi Canyon (central Georgia) for five years (1985-1990). The aspects of the species' life cycle were more precisely determined. The main fecundity is about 16.9 eggs per female. There are about 2 years in a period from egg deposition (June to first half of July) to the end of metamorphosis in nature. Animals have spent most of the time in shelters after metamorphosis. They appear on the ground surface at night during the breeding period. Commonly the adults don't retreat to a great distance from population localities. Localities are situated in comparatively small plots (100-300m) along the streams. Estimation of adult animal number showed that the population consists of 1189 specimens (1989). Annual adult survival is higher than known values of most amphibians (approaches 0.77). Larval survival is 0.27-0.32 in the second year of life. The characteristics of demography (especially, low renewal rates) and spatial restriction in localities depends mostly on subtle constitution of the species (which is a result of allometric growth specifics). The small recent geographical range of *M. caucasica* is explained as a result of morphological and ecological peculiarities. General morphological constitution limits adaptive possibilities of any particular representative of the European salamander tribe. This is an explanation of quite high ecological similarity of *M. caucasica* and *Chioglossa lusitanica.*

Key Words: Amphibia, Caudata, Salamandridae, *Mertensiella caucasica*, Caucasus Mountains, Georgia, population ecology.

Introduction

Natural populations are the single way of species existence. Autoecological research doesn't allow a complete understanding of the life of a species in nature. That is why there must be information of life cycles, geographical range, population size, number dynamics, etc. On the other hand it is hard to explain ecological aspects of the species existence without any information of their habitat preferences, feeding habits, breeding sites, etc.

By analyzing connections between species population ecology and autecology, as well as morphology and geographical distribution, the most complete notion can be formed. Investigations on some amphibian species biology have allowed scientists to elaborate complex works connected with different aspects of their life history. A wonderful example is Bell's works on the Smooth Newt (Bell and Lawton, 1975; Bell, 1977).

There aren't many data of regular stationary investigations about the ecology of the rare or narrow-ranged species. Long term research of such species enlarges the knowledge of the biology of wide taxonomic groups. Moreover, these investigations may be useful to find out ways of rare species preservation.

A local population of the endemic salamander, *(Mertensiella caucasica)*, from the western Caucasus of Georgia has been investigated for a five year period (1985-1990). This work gives additional information about the life history of this species.

The geographical distribution of the Caucasian Salamander was mainly established in the beginning of this century. Information was summarized by Nikolsky (1913). Later investigations commonly took place in earlier reported localities or in adjacent areas. Some new localities for salamanders were found by Bakradze and Tartarashvili (pers. comm.). The real geographic range of *M. caucasica* was established. The Caucasian Salamander is

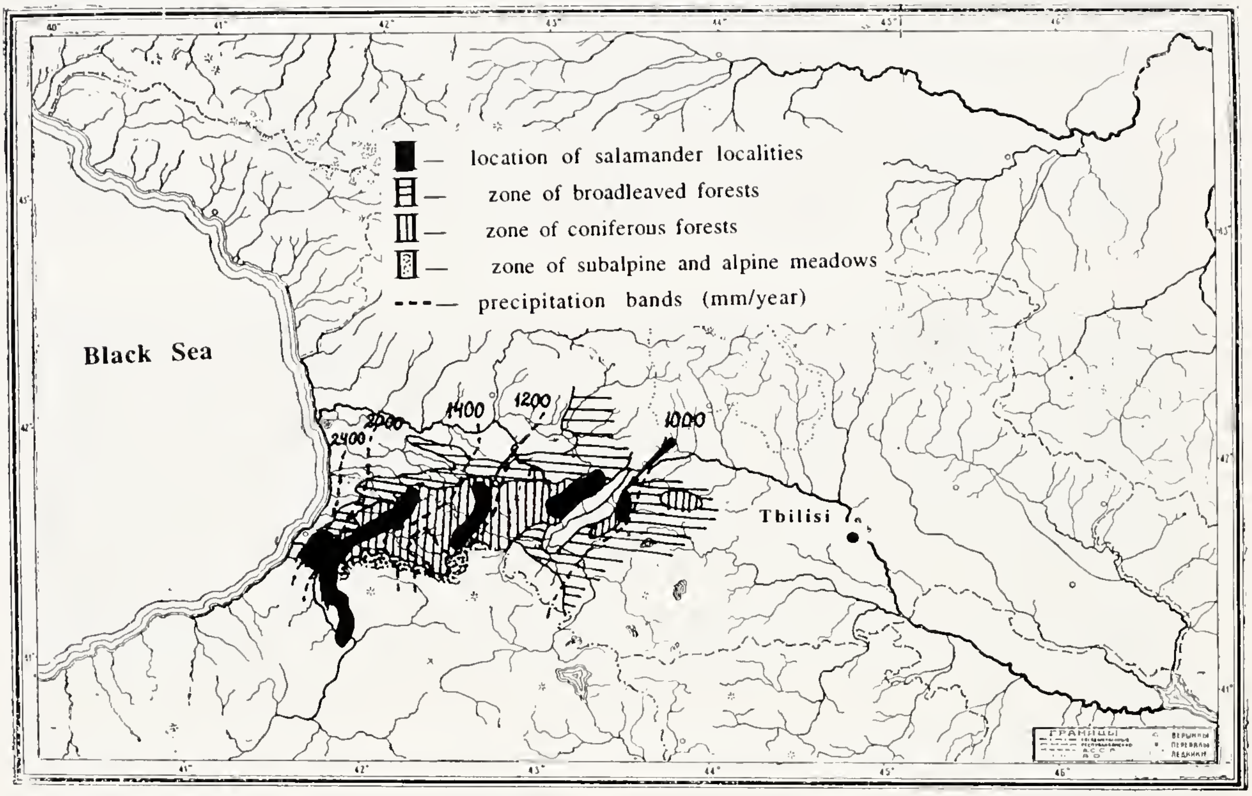

FIG. 1. Distribution of *Mertensiella caucasica.*

distributed in external spurs of the Trialetian Mountain Range. Probably it is the result of historical changes in the Kura River bed (Fig. 1). Populations are mainly distributed in the forest belt, but in some places they can be found close to subalpine meadows. Humidity in the species' locations reaches 1000 mm or more per year (another narrow-ranged representative of the salamander tribe, *Chioglossa lusitanica,* has similar requirements of humidity).

In the most dry part of the range of *M. caucasica*, the eastern one, salamanders live only in coniferous forest. When humidity reaches 1200 mm/year in the middle area, they can also be found in subalpine meadows. Salamanders are distributed in deciduous forest only close to the Black Sea coast, where humidity is very high (2000-2400 mm/year; Fig. 1). The high dependence of the animal on humidity does not itself limit the species distribution, but determines sensitivity of specimens to other environmental factors. It is very interesting that the rheophilous species *Ranodon sibiricus*, more restricted to water habitats than *M. caucasica*, is geographical limited by coniferous forests like *M. caucasica* in eastern localities (Paraskiv, 1953). Local populations, distributed along tributaries of the Chorokh and Kura rivers (in upper flow), are formed by salamanders within its area. Width of streams in salamander plots is not more that 1-1.5 m in spring and because of stepped disposition of streams, they run slowly in some places. There are many slowly draining pools about 20-30 cm in depth with a lot of shelters. The bottoms of streams and pools are covered with stones, and there is a lot of non-decayed organic matter. Stepped disposition of streams is formed by stoned conglomerations and fallen logs. Apparently, mountain ranges between stream canyons don't allow wide salamander migration and local populations are comparatively isolated. There is no evidence that direct migrations of animals occurs during their life cycle. Individuals are found a maximum of 200-300 m distance from streams.

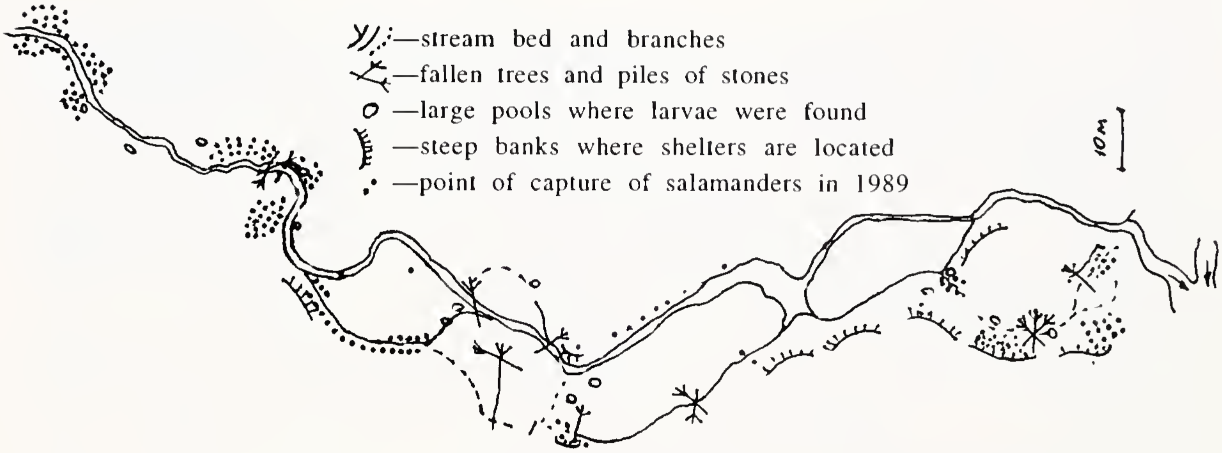

FIG. 2. Schematic diagram of the study site for *Mertensiella caucasica*.

The Study Area

The studied population inhabits coniferous forest ecosystems along the second range tributary of the Kura River in Borjomi Canyon (eastern part of the species' range) (Fig. 1). The plant association is formed by *Taxus baccate, Picea orientalis* and deciduous spots. The size of the inhabited location is a bit more than 200 m, and it is situated between 1000 and 1300 m altitude, about 2 km from the stream mouth. Slopes are precipitous, built by corrosion of underground tree roots or relatively gradual, partially covered by pteridium, *Matteuccia struthiopteris,* from the adjoining stream banks. There are some stone conglomerations and fallen trees in the study area, shown on the map (Fig. 2). Air temperature is close to stream water temperature (13-15°C in summer) in shelters formed by stones and logs. Dynamics of air temperature in Borjomi Canyon in May to July, 1989 is shown in Fig. 3. Quiet pools and shelters are relative rare, slopes are steeper and stream flow is faster at upper and lower localities. Density of salamanders here falls rapidly as well as away from the stream banks in these places.

Methods

The main quantitative data were obtained during excursions with a lantern after sunset along the study area. The location of each adult animal was mapped, substrate type and distance from stream bank (more or less than 50 cm) was recorded. Adult animals were marked individually by toe-clipping. Combinations from clipped digits in hind-limbs (not more than 2 in 1 foot) responds to individual number of animals from 1 to 99. Zero-1 clipped digit in the front leg mean number of hundred. Marks of salamanders recaptured in the next year were renewed. Data of capture-recapture were statistically counted as in Kaughley (1977). Substrates of animals caught were subdivided in 6 types: shallow water; sand and pebbles above water shore; wet stones; wet ground; moss or lichens; dry ground and stones. These types were ranked according to their humidity. Basic investigations were conducted on 8-10 and 21-23 June, 1986, 24-28 June, and 5-7. August, 1987, 3-5 and 21-24 July, 1988, 16 June-12 July, 1989, 2-9 July, 1990.

We had 337 contacts with males and 202 with females (including specimens found two or more time). Recording of larvae was conducted during night excursions.

We caught females from nature in the reproductive period and obtained eggs using a hormonal stimulation method (Gontcharov et al., 1989) to study some ecological and morphological features of early development. Eggs were incubated in Weiss bowls in dechloronated water at a temperature of 14°C as well as in aquaria at

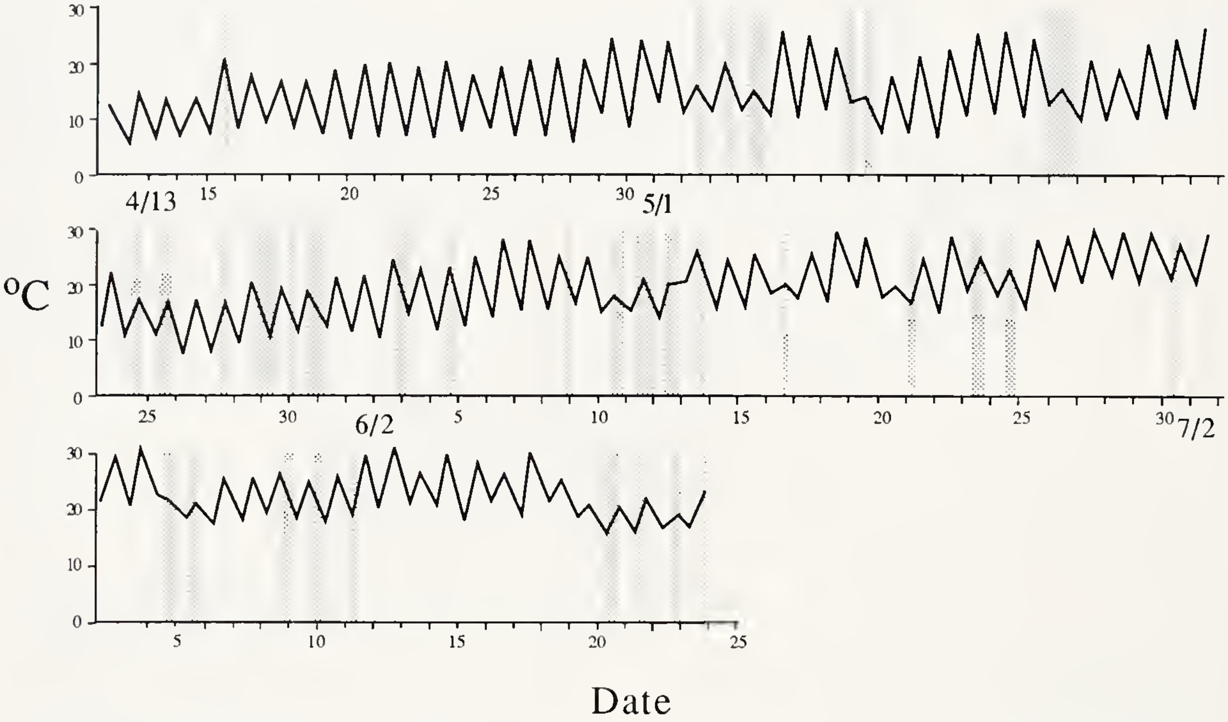

FIG. 3. Air temperature at the *Mertensiella caucasica* study site during the period of reproductive activity. Stippled bars represent periods of rainfall.

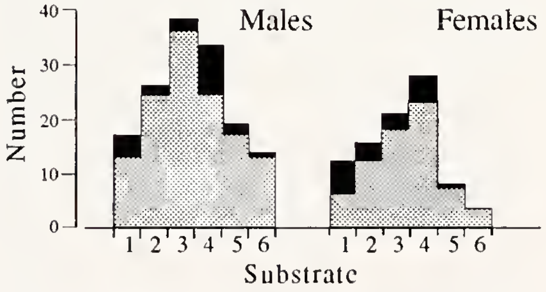

FIG. 4. Location of salamanders by substrate type. 1- shallow water; 2- wet sand and pebbles; 3- wet stones; 4- moist ground; 5- moss or lichens; 6- dry stones. Solid bars represent males. Stippled bars represent females.

a temperature varying from 5-22°C. Before completion of metamorphosis, larvae were kept in 20 liter aquaria, where water was changed every third day. Food consisted of crustaceans (*Daphnia, Cyclops)*, *Tubifex* and Chironomid larvae.

Morphological studies were conducted on larvae, juvenile and adult animals with a binocular magnifies and calipers. Their snout-vent length (L), head length (Lc), and tail length (Lcd) were measured with a precision of 0.1 mm. The coloration patterns of some animals was also recorded.

Results

The niche of larvae and adult specimens.

Salamanders don't have an even distribution within the study site. Preference to every substrate depends on the amount of moisture of each particular substrate. Frequency of captures decreases with distance from water or potential shelters. The number of animals captured out of shelters depends on time and season. Most adult specimens were recorded close to the stream (less than 50 cm from the water shore): 60±4% of males, 62±5% of females. In contrast to data on the ecologically similar species, *Chioglossa lusitanica* (Arntzen, 1981), there is no difference between male and female attachment to water in *M. caucasica*. Animals commonly may be found on wet sand or stones at the water shore, and they avoid dry soil and stones. The distribution of substrate type of captured animals for the

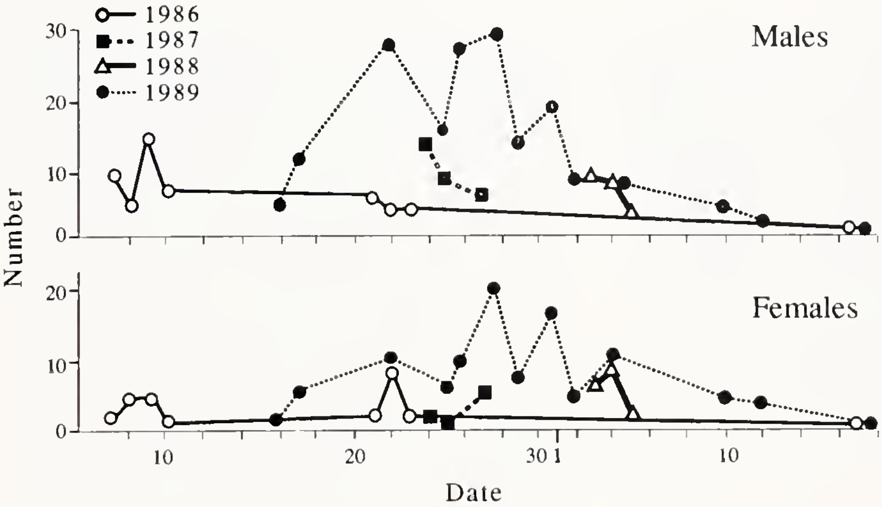

FIG. 5. The seasonal dynamics of salamander occurrence.

period from 1988-1989 is presented in Fig. 4. It is obvious that females avoid open rocky plots, fallen leaves or moss cover. According to our observations, adult salamanders spend only a small part of their life on the surface of the ground. Even during the active period, only a small part of the population leaves their shelters at night. Apparently, salamanders spent the rest of the time in shelters, where they live and feed. Seasonal dynamics and diurnal activity are reported on a number of captures during excursions in a 4 year period (Fig. 5). The number of animals found above ground decreased in July. The decrease in capture was especially sharp in the 5-15 July period. Even after rains, individuals could hardly be found in the second half of July (Fig. 5). Earlier seasonal activity of males is noted for other flowing-water (Arntzen, 1981) and standing-water (Golubev, 1981; Beneski et al., 1986) tailed amphibians. According to phenological data the large number of salamanders found in June is connected with their reproductive activity.

The beginning of the reproductive period is determined by air and water temperature. The active season begins when minimal night temperature is about 15°C (Fig. 3). After mating and egg deposition, activity decreases. Apparently, the decreasing number of specimens found in July does not depend on regular migrations. Observations of adjacent parts of the stream did not have any result in late July and August. The decrease in animal numbers either depends on the dispersion of individuals in the forest (or along stream banks, as proposed by Arntzen, 1981, for *C. lusitanica*), or more probably, they are in shelters most of the time because of greater abundance of their food, such as Gammaridae and Lumbricidae, there.

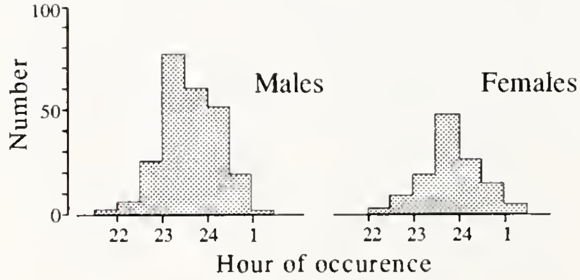

FIG. 6. Number of salamanders observed by hour of day.

The main nocturnal period of activity of *M. caucasica* is between 2200 and 0100. No active salamander has been found before 2130, and active animals have been rather rare before 2230. The number of active animals decreased after 0130-0200. The peak of activity was observed at about 2300 (Fig. 6).

Other nocturnal tailed amphibians also have a short active period and the time of activity is species specific (Semlitch and Peachmann, 1985). In the summer,

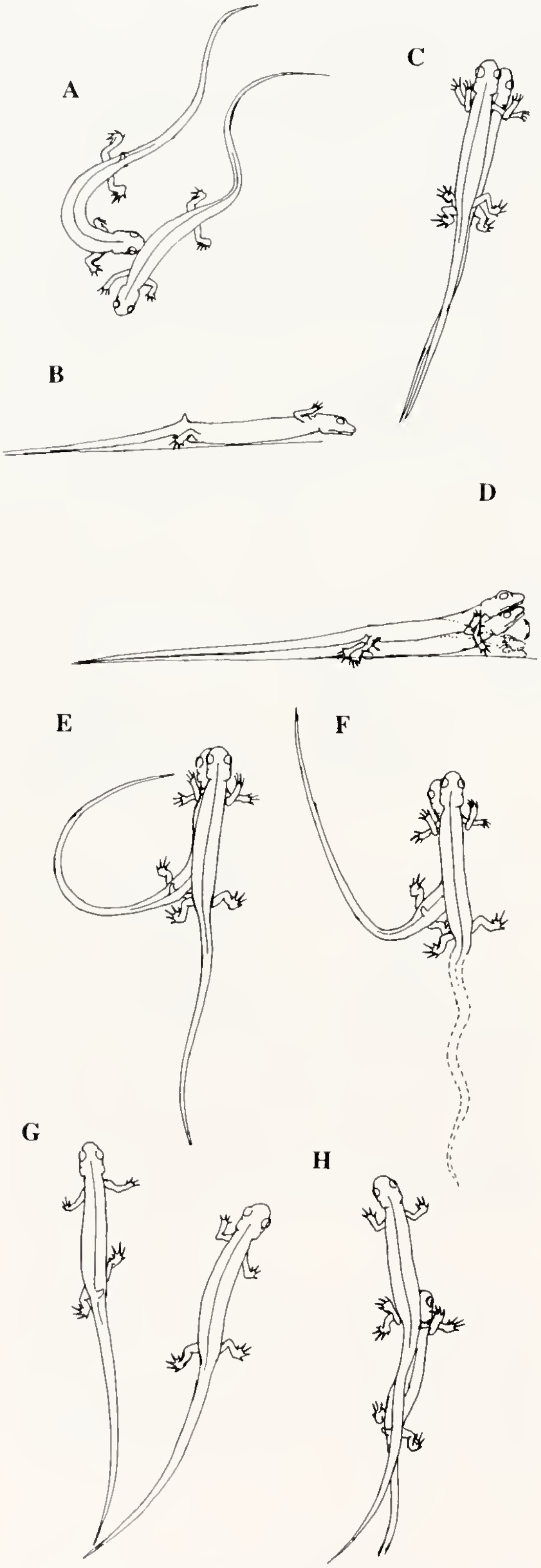

FIG. 7. Consecutive stages of courtship and amplexux in *Mertensiella caucasica.*

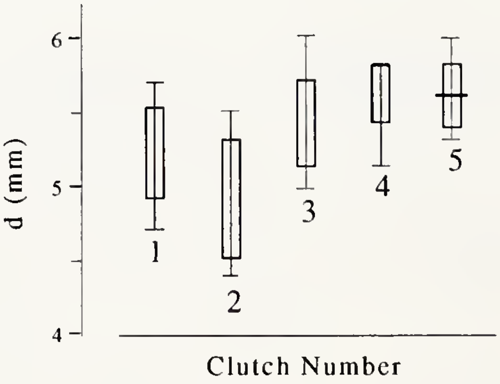

FIG. 8. Inter and intra-clutch variability in fertilized eggs of *Mertensiella caucasica.*

salamander larvae can be found in some parts of the stream bed in small pools with slowly drying water. Outside of the shelters, they are mainly in shallow water with a depth of less than 5 cm. Generally, the number of larvae doesn't exceed 10 individuals (maximum 14) in a pool. Comparatively large premetamorphosed larvae can be found in the stream. They move actively along the stream. Like adults, larvae spend most of the time in shelters. The first individuals can be seen in open water in late May. Larvae leave their shelters at twilight, when absolute sunlight is about 10 Lk. There are no nitrates in the water composition in salamander breeding and developing sites. The pH reaches 7.8-8.3 and the hardness of the water is 0.6-2.8 mg/equivalent l. Juveniles rarely leave their shelters during the period from the end of metamorphosis until first breeding.

The diet of larvae, juveniles, and adults reflects their biotopical preferences and does not show specialization in any invertebrate group (Kuzmin, 1992). Both terrestrial and aquatic organisms are found in the diet of adult salamanders (Ekvtimishvili, 1948; Kuzmin, 1992). Only terrestrial organisms are found in the diet of juveniles (Kuzmin, 1992).

Space used by salamanders.

The requirements of salamanders to environmental characters limit the space they use even within a local habitat. Thus, salamander distribution isn't homogeneous in a given locality. Obviously, animals prefer places with plenty of shelters. The mean number of salamanders captured during night excursions per 10 m along the stream bank in 1986, 1987, and 1989 was 9.2 ±1.86 males and 5.26±1.13 females. According to the "mean crowding" index of Lloyd (1967) ($m=\bar{m}+\frac{\sigma^2}{m}-1$) the mean value is respectively 21.84 and 12.78. The highest density was observed in places where there were logs and wooden blocks, combined with stone conglomerations, and a lot of small pools and shelters under tree roots. The total number of adults recorded for the 1986-1990 period, including recaptures was 455. The place where each specimen was found in 1989 is noted in Fig. 2. This data could give a notion of real space distribution of animals. Note that larvae can be found outside of the local population habitat significantly more often than adults. This is connected with the fact that some of the larvae leave the shelters and continue development in the lower parts of the stream (see below). Apparently, this process does not disturb normal metamorphosis and juvenile animals return to the population locality.

Life Cycle.

The salamander breeding period in investigated habitats occurs from the second half of June until early July. Most of the females found in July are ready for egg deposition. The large oocytes can be observed through the transparent ventral skin. There are well distinguished mating corns at the adult male shoulders. Amplexing animals were found on the ground close to shelters. Cyren (1911) and Obst and Rotter (1962) described normal sexual behavior of salamanders in water in natural and laboratory conditions. We observed normal sexual behavior twice: on 28 June, 1988 and 4 July, 1990. In the first case it took place about 2 m from the stream bank in a conglomeration of tree roots. In the second case it happened close to water, at the entrance of a rock chink. We don't exclude the possibility of normal copulation in water. For example, mating of *C. lusitanica* may take place both in streams and on the shore. The consequent states of courtship and amplexus are shown in Fig. 7, b-f. According to our observations, sexual behavior of *M. caucasica* is similar to that of *Salamandra salamandra* (Joly, 1966). The corn on the dorsal side of male tails has no special role in courtship and amplexus. We have also observed an attempt of copulation (Fig. 7h) on 28 June, 1989 and 2 males in an amplexus pose on 8 June, 1986. Apparently, we have observed, in the latter case, rival combats, described for *S. salamandra* by Kästle (1986), but in this work the behavioral display is not the same.

Copulated females have a slightly opened cloaca. There are more than three days between copulation and egg deposition. Each female deposits from 11 to 24 eggs (N=9, M=16.9, σ=3.9). Inter- and intra-clutch variability of fertilized eggs sizes is shown in Fig. 8. Darevsky and Polozhikhina (1966) found that the sizes of 90 eggs found in nature ranged from 5.0-5.6 mm. Females deposit separate eggs, sticking them to the substrate in shaded places. Activity of animals gradually decreases after the completion of the reproductive period.

Egg development takes 45 days until hatching in aquaria, where the average temperature is 14.8°C. When the temperature changes from 6° to 26° (M=16.5, σ=4.7) development is extended to about 48-51 days. We can expect similar developmental rates in nature, when the temperature of the water is about 14-15° in July to August. The hatching of most part of the generation takes place not earlier than late August. Larvae found in June can be divided into 3 groups on the basis of snout-vent length: the I group- L=14.6-19.5 mm (M=106-180 mg); the II group- L=23.7-27.5 mm (M=330-664 mg); the III group- L=29.0-35.4 mm (M=632-1400 mg). By virtue of larval size distribution, Freytag (1954) as well as Koroljov (1986) concluded a 3 year period of larval development in the Caucasian Salamander. Kuzmin (1992) established no annual ring in the I and II larvae group hip bones and only one annual ring in the III group larvae

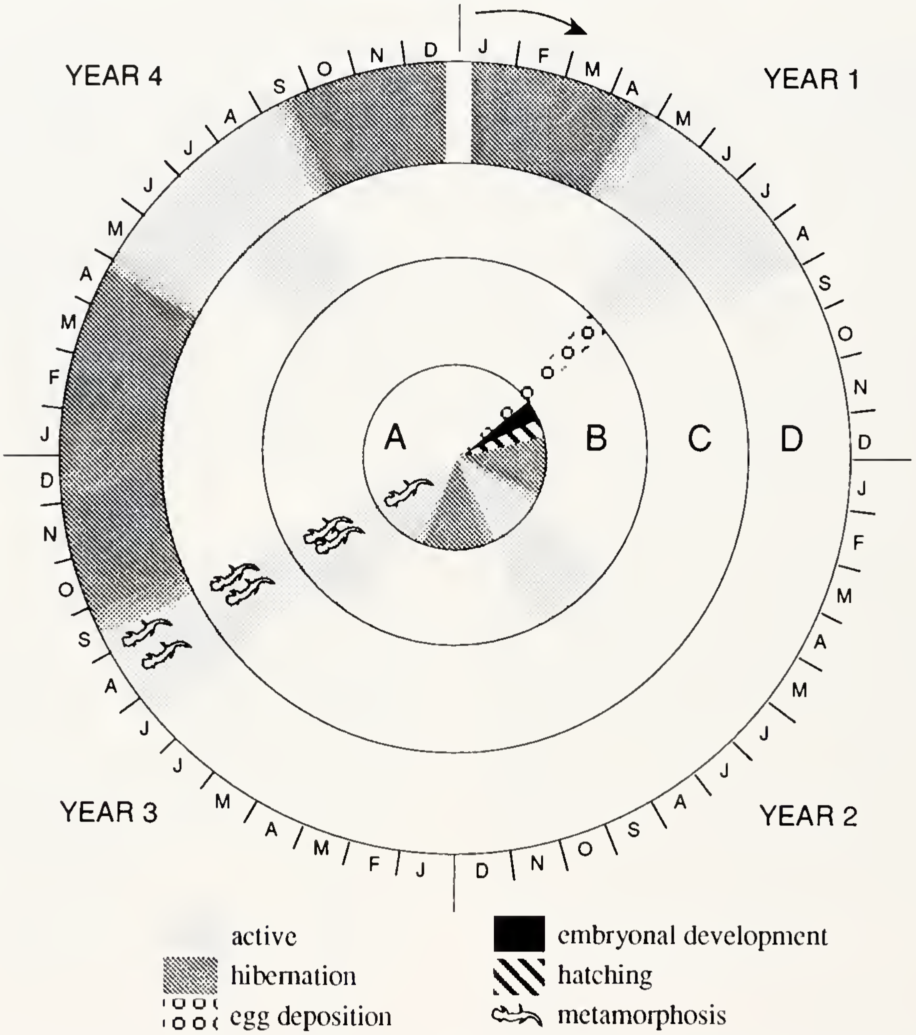

FIG. 9. The reproductive cycle of *Mertensiella caucasica*. A- underground parts of the stream bed; B- open water; C- surface and temporary shelters on the ground; D- constant shelters on the ground.

hip bones. On the basis of this information Kuzmin (1992) supposed that larvae of I and II size groups had most probably hatched in the given year. Nevertheless, analysis of time of reproduction and embryonic development during the year opposes Kuzmin's opinion.

Apparently, salamander larvae remain in shelters after hatching and go out when water temperature increases al least to 13°C (at the beginning of the next summer). Lack of annual ring on hip bones can be explained by incomplete development of hind legs just after the hatch. Larvae growth is delayed by autumn temperature decreasing. Thus, animals of the I and II size groups have a previous year hatch and represent a single generation.

Size differences within a generation are formed by prolonged breeding time (not only between breeding locations [Mertens, 1968], but within populations, too) and/or by variation of individual growth rates. Larvae have developed during the warm period of the second year. After hibernation, they have a metamorphosis in July-August of the 3rd year. Their development from fertilized egg to completed metamorphosis takes about two years in nature.

Salamanders have a concealed life during the period after metamorphosis and before maturity. According to Kuzmin (1992), 3-

5 annual rings can be observed in hip bones of adults. Therefore, salamanders can first breed in the 3rd year after metamorphosis. The total life cycle of the Caucasian Salamander from egg to egg is about 4 years (Fig. 9).

Growth and Development

Embryogenesis of *M. caucasica* is similar to other large-size egg amphibian development (Fig. 10 a-c). Analyzing experimental observations, hatching takes place when total length is 17-20 mm (L=10.5-11.5 mm). When hatching starts, a larvae has well developed external gills and a tail fin. Sometimes the rudiments of 3 toes can be distinguished on the hind legs. Pigmentation is formed by a couple of faded pigmented stripes. There are rare individual melanophores on the surface of the stripes. A line of small circular non-pigmented patches lays along each stripe (Fig. 10 d). The gut is filled with yolk. The total length of the smallest larva caught in nature was at least 25 mm (commonly, L=15 mm, minimum=14.6 mm). Larvae found in nature already have no yolk in the gut. Their external gills are smaller than those of animals that have not yet hatched. There are 4-5 toes on the hind legs and more pigment cells (Fig. 10 e).

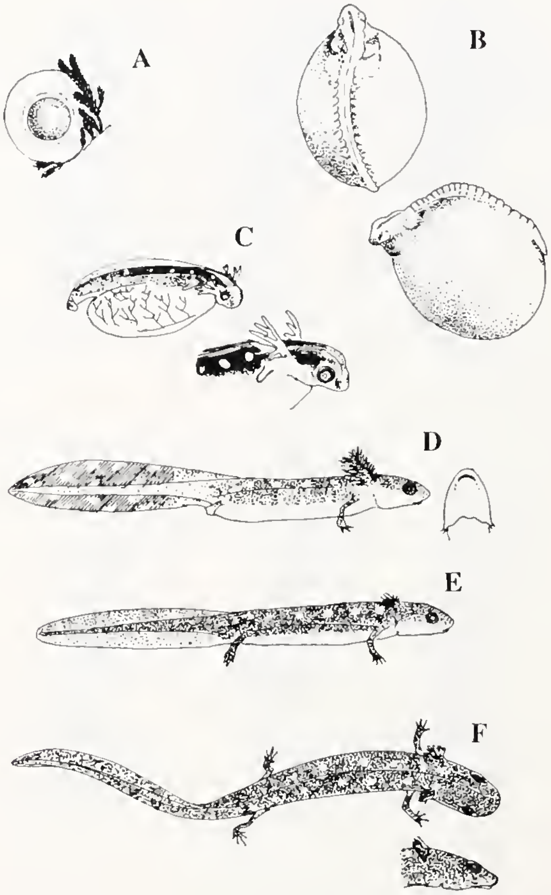

FIG. 10. Embryo and larval development of *Mertensiella caucasica.*

In laboratory conditions, when temperature is 14.8°C, yolk disappears from the frontal part of the gut 16 days after hatching at a length of 13.8114 mm. The first larvae with a snout-vent length of 15-16 mm can be found in streams in early June, but most of them appear in July. The small larvae, which have over wintered, appear in stream pools in small, probably sibling groups. The largest group (8 larvae) was found on July 5, 1988. Individual sizes in that group provides some information about intra-clutch larval size variation: when L=17.35±0.48, min=16.0, max=19.2, coefficient of variation approaches 7.8, L total=29.25±0.60, min=27, max=31.3, CV=5.8%. Summer growth of first hibernated animals (in 1985) is shown in the histograms of June and August larval size distribution (Fig. 11). Mean total length increases 6.27 mm for 70 days and the specific growth approaches 0.24%/day. At the same time homogeneity of generation increases: CV=23% in June and becomes 9.9% in August. This process is probably caused by more rapid growth and/or comparatively high mortality of the small larvae.

Morphological changes, connected with metamorphosis (i.e. yellow coloration of unpigmented spots, decreasing of gill size, reduction of tail fin- Fig. 10 f) began in animals with at least 30 mm snout-vent length. They approach that size in the 3rd year of larval development. Comparing sizes of the 2nd and 3rd year larvae, the specific body growth rate is 0.12%/day in the period between August and June of the next year. Commonly, metamorphosis takes place at a snout-vent length of 30-35

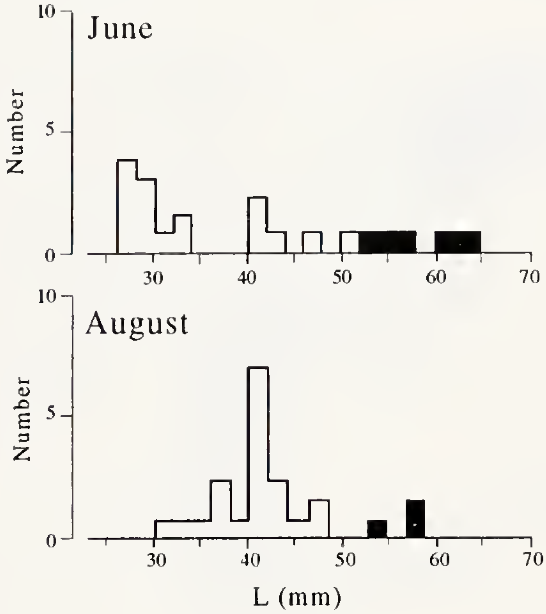

FIG. 11. Size distribution of *Mertensiella caucasica* larvae at the study site in 1985.

mm. Maximal larval size approaches 35.4 mm (L total=70.3 mm) in the population studied. Snout-vent length of metamorphosed animals varies within the limits of 32.9-42.4 mm (body mass, M=694-1592 mg, N=11). At the same time 2 larvae, with L=43.8 and 44.6 mm, are in a collection from the surroundings of Batumi (Kuzmin, pers. comm.). Animals of all three size groups can be found in streams even in May (Korolyov, 1986).

Peculiarities of natural growth of *M. caucasica* are similar to *C. lusitanica.* Although this species passes metamorphosis at smaller sizes (i.e. L=24-25 mm) their linear growth for two summer months approaches 0.29%/day and 0.10%/day for the rest of the year (Arntzen, 1981) and it is very similar to the analogous index of *M. caucasica*. The slow growth of salamander larvae is mainly the result of low water temperature in streams. The specific total length growth rate of a single animal (from 27.9 to 56.7 mm) was 0.54%/day, and total length increased from 37.0 to 59.2 mm was 0.42%/day under laboratory conditions, at 23-25°.

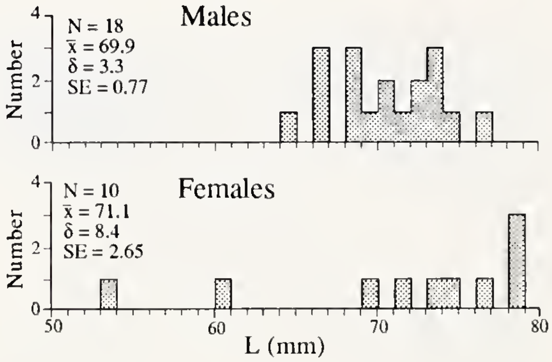

FIG. 12. Size distribution of adult *Mertensiella caucasica* in the study area. L- snout-vent length.

The snout-vent length of adults varies insignificantly. Data on animals measured in the studied population are shown in Fig. 12. There aren't considerable intersexual differences in sizes and general body proportions, but apparently females can begin breeding at a smaller body size. Other authors (Cyren, 1911; Knoblauch, 1905; Nesterov, 1911) reported that mean L in males approached 68.9 mm (N=7) and females, 63.5 mm (N=11). The animal body length of an outlying population (Goderdzi Mountain Pass) varies between 68-77 mm in males and 56-73 mm in females. However, our population does not show any specifics in adult animal size distribution.

We will briefly discuss morphological changes in the period from the beginning of active feeding to the end of metamorphosis. When larvae begin to feed, melanophores gradually disperse from the lateral sides, filling the ventral surface of the larval body. Even the size II larval group have only a narrow non-pigmented stripe remaining on the ventral side. All lower surface is filled by pigmented cells and non-pigmented patches remain only on the lateral sides of the size III larval group. These patches are used as a substrate of xanthophores and iridiophors, forming yellow spots later on (Tarkhnishvili and Tartarashvili, 1987). The intensity of basic coloration is correlated with the size of the animal that has already started metamorphosis. The animals with a large size at the beginning of metamorphosis have a dark-brown (not as dark as in spotted salamander) coloration with bright and comparatively large yellow spots. Smaller size larvae do not have such an intense basic coloration and spot pattern is more or less reduced (spots are smaller and/or poorly expressed). The intensity of salamander pigmentation, like other tailed amphibians, may vary depending on the light intensity at the larval location (Fernandez and Collins, 1988).

Ground coloration of adults varies from reddish-brown (similar to *Chioglossa lusitanica* or some *M. luschani* subspecies (Winter et al., 1987) to dark brown. The spotted pattern may be expressed in a different degree to full reduction (especially in light colored specimens) (Fig. 13). Poorly pigmented animals with comparatively reduced spots (described by Tartarashvili and Bakradze (1989) as the subspecies *M. c. djanashvilii*- Fig. 13 a) predominate in some populations from the surroundings of Batumi, at the Black Sea coast. Nevertheless, dark colored animals, with well developed spots (Fig. 13 e, f) predominate in the population from the subalpic zone (Mountain Pass Goderdzi, in Bakradze's collection). Salamanders with an intermediate intensity of coloration are more abundant in our studied population, but there are some specimens with less or more reduced spot pattern. There is also a female, colored as the form described by Tartarashvili and Bakradze. Probable, the specific coloration of adults is connected with the character of larval development, which depends on the special climatic conditions of each habitat. That is why many light-colored animals occur in the warm sea cost habitat and dark colored ones are found at high altitudes. Populations from Borjomi Canyon are in an intermediate place. Or course, we don't exclude the possibility of inheritable fixing of one or another coloration type in different populations.

The Caucasian salamander is included with the Luschan Salamander, *M. luschani*, in the same genus because of the tail corn, the secondary sexual character of males (Özeti, 1967). This character appears in males with a length of at least 130 mm and it seems to be of no functional importance as some investigators have proposed, for example Cyren, (1911).

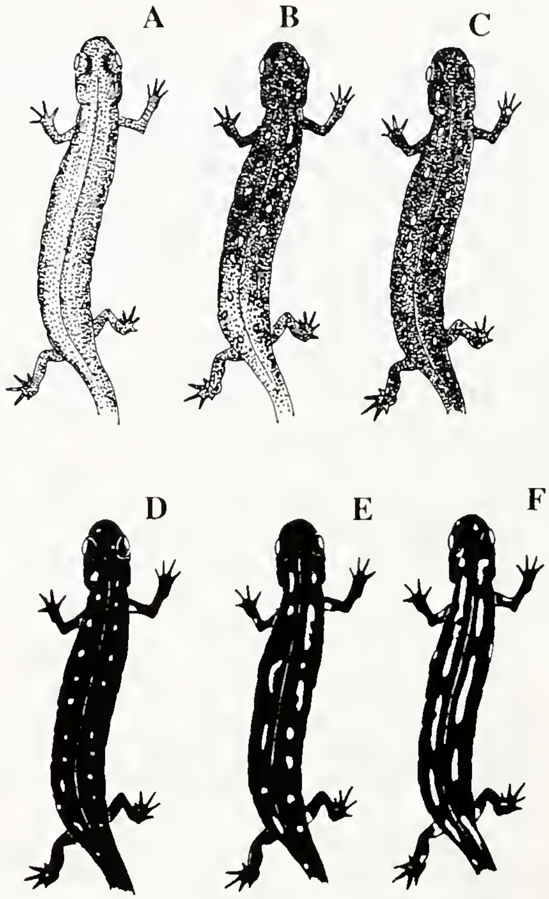

FIG. 13. Color variation in *Mertensiella caucasica*.

The main changes of general body proportion occur during ontogenetic development. First, relative tail length increases after hatch. Mertens (1968) reported this for larvae with a total length of more than 45 mm. Based on our data, comparatively rapid tail growth begins at the earliest stages of development and extends to the adult stage. On the other hand, comparative length of head decreases (Fig. 14). The changes of general proportions have different intensity in different developmental stages. Allometrical dependence of head and body length on the total length of the I and II size group larvae is described by equations:

$Lcd=0.35L^{1.26}$

$Lv=1.71L^{0.26}$

The coefficients of allometric equations for the III size group larvae is different:

$Lcd=0.08L^{1.71}$

$Lc=1.5L^{0.52}$

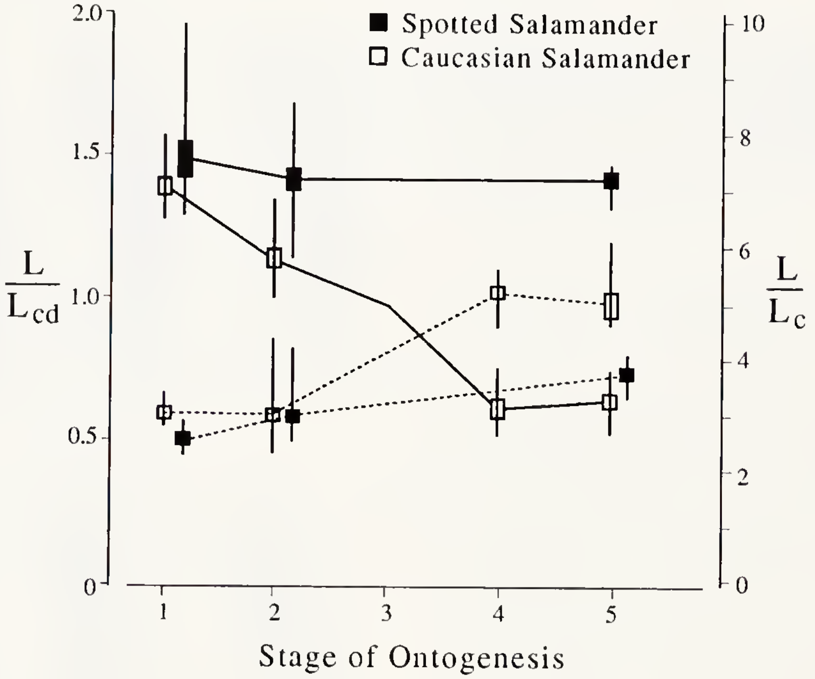

Fig. 14. Changes in body length proportions in *Mertensiella caucasica* (open square) and *Salamandra salamandra* (solid square) during ontogenesis. 1- larvae with total length less than 35 mm; 2- larvae with total length greater than 35 mm; 3- yearlings; 4- juveniles; 5- adults. solid line- L/L_{cd}; broken line- l/L_c.

The coefficients of static allometrical equations for recently metamorphosed animals are:

$$Lcd=0.23L^{1.42}$$
$$Lc=1.04L^{0.62}$$

Hence, the most rapid comparative increasing of tail length is during late larval development. The comparative decreasing of head is the most rapid in the I and II size groups, but later this process isn't so clear. Nevertheless, it takes part in metamorphosis.

Plenty of eco-morphological features separate *M. caucasica* from the other representatives of European salamander tribe, depended on subtilization (Özeti, 1967). The latter is a base determined ecological similarity between *M. caucasica* and *C. lusitanica* (Borja-Sanchiz and Mlinarsky, 1979). Perhaps this is a reason of similar breeding ways of these species differing from other European salamanders. The changes of general proportion of *M. caucasica* and *S. salamandra,* which are shown in Fig. 14, allow a comparison of these species. The general trends of body proportion changes are common in the two species (as in most Tetrapoda): the comparative length of head (L/Lc) decreases and that of tail (L/Lcd) increases. But in these tendencies, both are quite rapid in *M. caucasica.* In *S. salamandra* the changes are gradual and moreover, tail length growth is poorly distinguished (Fig. 14).

Population Number Dynamics and Regulation.

The analysis of our 1986-1990 capture-recapture data allow us to study population number, number dynamics and demographic peculiarities. We obtained quite full information in 1989. In that year the captured animal number, in relation to real population number, was comparatively high. The general picture of results is shown in Table 1. We had 532 contacts with animals. We met an animal twice in the same night only on 7 occasions. They were on the surface, essentially not moving. In all cases animals were captured again in the same plot, not more than an hour later. The 50 animals of 68 recaptured

TABLE 1. Mark-recapture results for *Mertensiella caucasica* in 1989.

Date	i	n_i	R_i	Males										
6-16	1	5	5	1										
6-17	2	11	11	0	II									
6-22	3	27	26	0	1	III								
6-25	4	15	7	0	1	1	IV							
6-26	5	26	29	0	2	5	0	V			x_{ij}			
6-28	6	28	28	2	2	1	2	2	VI					
6-29	7	13	13	1	0	1	0	0	0	VII				
7-1	8	18	18	0	1	2	0	1	1	0	VIII			
7-2	9	8	8	0	0	2	0	1	1	0	0	IX		
7-4	10	7	7	1	1	1	0	0	0	0	0	1	X	
7-10	11	4	4	0	0	0	0	1	0	0	0	0	1	XI
7-12	12	2	2	0	0	1	0	1	0	0	0	0	0	0
r_i				4	8	14	2	6	2	0	0	1	1	0
N_i						579	619	349	681			104	44	
SE_i						151	376	135	474			97	25	
$P_{i,i+1}$						1	1	1	0.22 ($P_{6,9}$)			0.45		
$A_{i,i+1}$						70 ($A_{3,5}$)								

Date	i	n_i	R_i	Females										
6-16	1			I										
6-17	2			0	II									
6-22	3			0	0	III								
6-25	4			0	1	0	IV							
6-26	5			0	0	0	0	V			x_{ij}			
6-28	6			1	1	0	1	0	VI					
6-29	7			0	0	0	0	1	0	VII				
7-1	8			0	1	0	0	2	0	0	VIII			
7-2	9			0	0	0	0	0	1	0	0	IX		
7-4	10			1	0	0	0	1	2	0	0	0	X	
7-10	11			0	0	0	0	0	0	1	0	0	0	XI
7-12	12			0	0	0	0	2	0	0	0	0	0	0
r_i				2	3	0	1	6	3	1	0	0	0	0
N_i							78		340	497				
SE_i							66		200	476		97	25	
$P_{i,i+1}$							1		1					
$A_{i,i+1}$						70 ($A_{3,5}$)	265 ($A_{4,6}$)		157					

Note: i, j- the number of census; n_i- the number of specimens examined in i-th census; R_i- the number of recaptured and escaped specimens; $x_{4,\ III}$- the number of animals recaptured in the 4-th census that had been marked during the 3-rd census; r_i- the total number of recaptured specimens that had been marked in the i-th census; N_i- the estimate of population size in the moment i, using the Jolly-Seber method; SE_i- standard error (Jolly-Seber); $P_{i,\ j}$- the probability of the individual remaining in the active part of the population between the i-th and j-th census; $A_{i,\ j}$- the number of specimens supplemented the active part of the population between the i-th and j-th census.

in a year of marking were caught in the same or adjacent plot (the place of 28 captured animals was not recorded). On the basis of these data, we conclude that these salamanders have a low moving ability and a short period of nocturnal activity. Only an approximate representation of activity dynamics can be given by captured animal number, though in some cases, data of captured animals are used as an index of number (Bozhanski and Semenov, 1982). We used the Jolly-Seber method (see Caughley, 1977) to estimate the real number of the local population and its dynamics during the breeding period in 1989. The total number of breeding animals was 1187 and the percentage of males was 58±0.001. The greatest number of active animals was in the end of June. Females appeared a bit later than males.

Unfortunately, the data of 1986-1988 don't allow us to correctly estimate the number of salamanders in those years. It varied from 10-20 to 460 individuals, when the errors exceeded mean values, i.e. significantly lower than real quantity. The highest value (460) was recorded when the Schumacher method was used on 1990 data. The values recorded for the 1986-1988 data didn't exceed 200. Thus, the annual number value significantly increases when the research period is prolonged and captured specimen number increases. That is because only a small part of the population left their shelters, even in the highest activity period in late June to early July.

The estimate of the *C. lusitanica* population (Arntzen, 1981) is different because of the permanent migration of part of the population. The number of two local populations of this species is 1236 and 1324 respectively. This is similar to our information about *M. caucasica*, moreover, the study sites have a size similar to ours. Usually, the number of animals in the widely distributed in Europe *S. salamandra* populations can exceed some thousand specimens (Klewen, 1986). Their populations are spread over several hectares, and animals can be found far from the breeding sites.

The capture of salamanders marked in previous years gives some information about mortality rates of adults. Ninety eight males and 45 females were marked in June, 1989. There were 38.5% (OM=7.8%) recaptured males of the total of 39 found in July 1989, and 28.9% (OM=7.3%) recaptured females of the 38 total found. The 31.8% (OM=5.7%) of males and 17% (OM=5.9%) of females captured in July 1990 were marked in June 1989. Hence, survival rates of the period from July, 1989 to July, 1990 is Pm=31.8/38.5=0.83 for males and Pm=17/28.9=0.59 for females. The part of all marked adults was 33.8±9.3% in July, 1989 and 26.2±4.2% in July, 1990. Hence, the annual survival approached 0.77. It should be noted that only 8 individuals (9.0±2.0%) of all 89 marked in 1986-1988 were found again in 1989. This is quite a high number because 89 individuals aren't more that 10% of the adult population.

Unfortunately, there is a lack of information about renewal rates of tailed amphibian populations. Ignoring age structure, the annual mean survival of *Ambystoma maculatum* approaches 0.72 for males and 0.60 for females (the mean male number is 641 and capturing of males is a bit more often (Husting, 1965). These data are quite similar to ours. On the other hand, annual survival of the Smooth Newt is only 0.45 for males and 0.55 for females in England (Bell, 1977). There are considerable low survival rates of *Notophtalmus viridescens* and some Anura when higher mortality of males is observed (Ischenko, 1989). Klewen's (1986) quantitative data for *S. salamandra* show that annual survival varies between 0.55-0.81 (mean 0.66 in four years of investigation. A higher female survival was recorded for the genus *Desmognathus* (Husting, 1965).

The Caucasian Salamander has a comparatively low population renewal rate, when mortality is low. Perhaps, this kind of population dynamics is typical for populations with low total number and high male survival. Organ (see Husting, 1965) mentioned that a higher male survival was a result of significant energy expenses of females during breeding.

We can only indirectly estimate salamander mortality before mating. On the basis of adult female number and mean fecundity, we estimate that there were 8000-9000 eggs deposited in the study site.

TABLE 2. Data on mark-recapture of *Mertensiella caucasica* from 1986 to 1988.

		1986								1987				1988					
Sex	Data	6-7	6-8	6-9	6-10	6-21	6-22	6-23		6-24	6-25	6-27		7-3	7-4	7-5	7-22		
	n_i	9	5	14	7	6	4	4	49	13	8	6	27	6	7	2	1	16	95
f	R_i	9	2	8	7	5	2	3	36	10	8	4	23	5	4	1	1	11	70
	m_i	0	1	2	0	0	1	1	5	0	0	0	0	0	1	0	0	1	6
	n_i	2	5	5	2	2	8	2	28	2	0	5	7	6	8	1	0	15	48
m	R_i	2	4	4	1	1	4	2	18	0	0	0	0	0	1	1	1	3	20
	m_i	0	1	0	0	0	1	0	3	0	0	0	0	0	0	0	0	0	3

Note: n_i- number of individuals examined in the i-th census; R_i- number of recaptured and escaped individuals; m_i- total number of individuals captured in the i-th census that were marked in the same year (but on another day).

Nevertheless, significantly few larvae could be found in the stream when salamander density was the highest.

Korolyov (1986) found only 90 larvae in 1984 in the whole area of the stream described here. Bozhansky and Semenov (1982) counted 1-33 larvae in every 700 m of flow in August. We found 116 larvae in the study site in June, 1985, of which 91 had already gone through hibernation. In the beginning of July, 1990, 74 larvae of the I and II size groups (hibernated once) were counted in the same plot. The number of second year larvae is quite constant in different years. Although it was considerably lower that the total number of eggs deposited, it did not have an influence on the real larval mortality rates in the first year. More probably, larvae were carried by flow along the stream and were distributed more uniformly than adults and eggs.

On the base of the 2nd and 3rd year larvae proportion at the site, we were able to judge larval mortality from egg deposition to the second year. The twice hibernated were 27.8% (1985) to 31.9% (1990) of the total number of once hibernated specimens. Apparently these values express the real survival rates of a year (within twelve months).

The stable larval density and ratio of the second and third year animals at the locality is a result of the stability of the adult salamander population number, and moreover, conversely to stagnant water amphibians, quite constant developmental conditions. The later is a reason of Caucasian Salamander number dynamics peculiarities. The basic reasons of natural salamander mortality are not completely clear. Perhaps, egg and larval mortality caused by ponds drying up is not as important for *M. caucasica* as it is for many amphibians (for example, *Ambystoma maculatum*, Albers et al., 1987). There are practically no predatory insect larvae dangerous to salamander larvae in the stream. Young trout *(Salmotrutta labrax)*, which are possible predators, are also very rare. Perhaps the main reasons of larval mortality are over wintering and larval diversion into the stream flow. Grass Snakes (*Natrix natrix)* could of course cause great damage during metamorphosis. There were from one to five just metamorphosed specimens in the stomachs of the five Grass Snakes captured in the salamander locality. We did not find any adult salamanders in snake stomachs. It is unlikely the low vulnerability of adults is connected with autotomy ability or coloration. The juvenile animals do not have the same coloration as adults and they are able to autotomise also (Golubev, 1981). The reason is rather adult animal size and antipredator behavior of this species described by Brodie et al. (1984).

Discussion

According to the view of adaptionists, the peculiarities of the morphology of the Caucasian Salamander mainly are a result of general body constitution. The vulnerability of this species results in the high requirements to environmental condition, especially temperature and humidity. The comparative large body surface reduces homeostatic ability. Another main feature of *M. caucasica* as well as of *C. lusitanica* delimiting these species from all other European salamanders is breeding by egg deposition, when fecundity is comparatively low.

The biogeographical and ecological characteristics of *M. caucasica* can be explained by consequences of its morphological type. On the basis of paleontological date, *Mertensiella* aff. *caucasica* was distributed sympatrically with the Spotted Salamander in an area extending to central Europe in the Pliocene. The reduction of the range of *Mertensiella* was the result of the last glacial periods (Borja-Sanchiz and Mlinarsky, 1979). Nevertheless, the present range of *S. salamandra* is quite wide (Thorn, 1968), while the range of *M. caucasica*, like other representatives of the tribe, *M. luschani* and *C. lusitanica*, is comparatively narrow and in areas with mild climate. It is unlikely that the Spotted Salamander can affect the geographic range of these species. Although members of the genus *Mertensiella* are allopatric to *S. salamandra*, *C. lusitanica* has a wide sympatric zone with this species (Bas Lopez, 1984). The absence of *S. salamandra* in the Caucasus, including the Great Caucasus, obviously depends on historical reasons. The geographic range of subtle species is limited most of all by climatic factors. Wolterstorff et al. (1936) mentioned that the range of *M. caucasica* has not changed considerably since the Eocene. Perhaps the low homeostatic ability of adults limits their migratory possibilities.

As we already noted, the captures of animals far from their population locality were very rare. The salamanders don't penetrate the comparatively distant mountain systems like the Great Caucasus. They also don't occur in comparatively dry localities along the Trialeti Mountain Range in the East (Fig. 1) where there is no relief limit. This is one of the reasons for the restricted salamander distribution. On the basis of different research (Obst and Rotter, 1962; Tartarashvili, pers. comm.) we conclude that the area of salamander localities of high altitude and on the Black Sea coast isn't larger than ours. *Chioglossa lusitanica* localities have a similar distribution (Arntzen, 1981). On the other hand, a small population area might depend on attachment to the breeding sites (stream plots suitable for egg deposition and larval development). Spotted salamander populations are always distributed in significantly wider areas (Klewen, 1985).

As a result of the small area of the localities and the lack of breeding sites, the population number is limited at a comparatively low level, about 1000 individuals, when the sex ratio is close to equal. This amount is enough to maintain the populations demographically and genetically (Lande and Barrowclough, 1989). The potential population growth rate is also limited by comparatively low fecundity. Nevertheless, the breeding sites are used rather efficiently. Temporary ponds vulnerable to periodic natural disturbances aren't used for egg deposition. Thus, the population renewal possibilities of *M. caucasica* are different from stagnant-water amphibians. A significant part of the latter species are not able to breed efficiently because many of the breeding ponds within localities are destroyed during egg and larval development. Apparently the egg deposition of *M. caucasica* is done only in places suitable for further development. This type of reproduction is correlated with the high stability of population number though the resilience to habitat transformation is low.

This described model of population dynamics practically excludes the number of outbursts caused by climatic perturbations which could stimulate considerable migrations. Since, settling of investigated species is determined by the low tolerance of adults, the small area of population localities and breeding sites, and the low fecundity. Hence the main reason for the narrow geographical range of *M. caucasica* are its morphological features and the stable type of population cycle.

In analyzing morphological reasons of Caucasian Salamander ecological specifics in comparison to related species, we can not accept as a main character only body proportions. Ecological particularities of all the European salamander tribe mainly depend on comparatively large egg formation (and probably skin structure). These characters limit European salamanders to breed only in flowing water in comparatively wet places.

Although the European salamander adaptive type allows comparatively wide interspecies variability in some features, for example coloration patterns and degree of subtilisation, the general morphological constitution restricts adaptive ability of particular representatives of the group. In a sense *M. caucasica* is a morpho-ecological equivalent of *C. lusitanica.* These species have similar life cycle, population spatial structure and number dynamics, climatic and biotopic preferences, etc. The central adaptive possibility and the feature determined place in the group can be distinguished among a lot of morphological characteristics. There are some other features which separate these species and reveal the independent origin of both of them. This is, for example, tail corn in males. Nevertheless, this structure does not take place among main ecological features of species and reflects only the complexity of the phylogenetical ways.

Color patterns have rarely been used in phylogenetical speculations, but this characteristic is a favorable object of adaptationists. The presence of light-colored specimens in some *M. caucasica* populations, their predominance in other populations of this species and in *M. luschani* and, finally, fully reduced of spotted specimens in *C. lusitanica* are not connected with variability of the plant cover in localities and do not affect their ecological preferences. We can't speculate about the adaptive meaning of coloration in this case. Coloration is closely related to the climate type of localities. Apparently, we could consider this characteristic as a fixed non-adaptive reaction to temperature and humidity changes.

In conclusion, we would like to give an opinion on an interesting detail connected with the distribution of *M. caucasica.* Three anuran species, the Colchic Toad (*Bufo verrucosissimus*), the Caucasian Parsley frog (*Pelodytes caucasicus*), and the Asia Minor Frog (*Rana macrocnemis*) live sympatrically with the Caucasian Salamander. *Rana macrocnemis* is distributed all over the Caucasus. *Bufo verrucosissimus* and *Pelodytes caucasicus* like *M. caucasica* do not penetrate the eastern part of the Trialeti Mountains because of lack of humidity. However, they are distributed in some locations in the Great Caucasus. The northern parts of the Trialetian and Adjaro-Imeretian mountains are more that 50 km from the southern parts of the Great Caucasus in Central Georgia. There are no suitable localities for forest amphibians between these mountain systems. The comparatively small transitional zone could have been crossed many times by *B. verrucosissimus* and *P. caucasicus* after the Great Caucasus system was formed. If we take into consideration the comparatively high fecundity (about 500 eggs per year for *P. caucasicus* and 10,000 eggs per year for *B. verrucosissimus)* and the temporal variability of the breeding sites, a few climatically favorable seasons could cause a great increase in population number and as a final result, a massive migration. According to the peculiarities of *M. caucasica* population dynamics, we can not expect any similar process. Hence, the lack of *M. caucasica* in the Great Caucasus has historical rather than autecological reasons.

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Literature Cited

ALBERS, P. H. AND R. M. PROUTY 1987. Survival of spotted salamanders eggs in temporary woodland ponds of coastal Maryland. Environmental Pollution 46(1):45-61.

ARNTZEN, J. W. 1981. Ecological observation on *Chioglossa lusitanica* (Caucata, Salamandridae). Amphia Reptilia 3/4:187-203.

BAS LOPEZ, S. 1984. Biogeographia de los amfibies y reptiles de Galicia, un ensago de sintesis. Amphibia Reptilia 5:289-310.

BELL, G. A. C. 1977. The life of the smooth newt *(Triturus vulgaris)* after metamorphosis. Ecological Monographs 47(3):279-299.

BELL, G. A. C. AND J. H. LAWTON. 1975. The ecology of the eggs and larvae of the smooth newt, *Triturus vulgaris* (Linn.). Journal of Animal Ecology 44(2):393-424.

BENESKI, J. T., E. J. ZABISKO, AND J. H. LARSEN. 1986. Demography and migratory patterns of the eastern long-toed salamander, *Ambystoma macrodactylum columbianum*. Copeia 1986(2):398-408.

BOZHANSKI, A. T. AND D. V. SEMONOV. 1982. [The data on the biology of the caucasian salamander *(Mertensiella caucasica)]*. Zoologichesky Zhurnal 61(8):1118-1129. (In Russian).

BORJA-SANCHIZ, F. DE AND M. MLYNARSKI. 1979. Pliocene salamandids (Amphibia, Caudata) from Poland. Acta Zoologica Cracov 24(4):175-188.

BRODIE, E. D., R. A. NUSSBAUM, AND M. DI GIOVANI. 1984. Antipredator adaptations of Asian salamanders (Salamandridae). Herpetologica 40(1):56-68.

CYREN, O. 1911. Beiträge zur Kenntnis der Kaukasichen Feuer-salamanders, *Salamandra caucasica* (Waga), seiner Lebensweis und Fortpflanzung. Bericht der Senckenbergischen Naturforschended Gesellschaft, Frankfurt a/M 42:175-189.

DAREVSKY, I. S. AND V. F. POLOZHIKHINA. 1966. [On the reproductive biology of the caucasian salamander- *Mertensiella caucasica* (Waga)]. Zoologichesky Zhurnal 45(3):465-466. (In Russian).

EKVTIMISHVILI, Z. 1948. [Feeding of the caucasian salamander]. Trudy Zoologitcheskogo Instituta AN GSSR 8:239-245. (In Georgian).

FERNANDEZ, P. J. AND J. P. COLLINS. 1988. Effect of environment and ontogeny on color pattern variation in Arizona tiger salamanders *(Ambystoma tigrinum nebulosum* Hallowell). Copeia 1988(4):928-938.

FREYTAG, G. E. 1954. Der Kaukasus-Salamander, ein seltener Terrarien pflegling. Die Aquarien und Terrarien Jahrbuch:115-119.

GOLUBEV, N. S. 1981. [The peculiarities of the tail autotomy and regeneration of the caucasian salamander]. Voprosy gerpetologii. Nauka, Leningrad 5:40. (In Russian).

GONTCHAROV, B. F., O. I. SHUBRAVY, I. A. SERBINOVA, AND V. K. UTESHEV. 1989. The USSR program for breeding amphibians, including rare and endangered species. International Zoo Yearbook 28:10-21.

HUSTING, E. L. 1965. Survival and breeding structure in a population of *Ambystoma maculatum*. Copeia 1965(3):352-362.

ISCHENKO, V. G. 1989. [The reproductive tactics and demography of amphibian population]. Itogi nauki i tekhniki. Zoologiya pozvonochnykh. V. 17. Problemy populyatsionnoy ekologii zemnovodnykh i presmykayushchikhsya. Moscow, VINITI:5-51. (In Russian).

JOLY, J. 1966. Sur l'ethologie sexuelle de *Salamandra salamandra* (L.). Z. Tierpsychol. 23(1):8-27.

KÄSTLE, W. 1986. Rival combats in *Salamandra salamandra*. Pp. 525-528 *In* Z. Rocek (ed.), Studies in Herpetology. Prague.

KAUGHLEY, G. 1977. Analysis of vertebrate populations. A. Wiley- Interscience Publications., London, New York, Sydney, Toronto. 361 pp.

KLEWEN, R. 1986. Population ecology of *Salamandra salamandra terrestris* in an isolated habitat. Pp. 395-398 *In* Z. Rocek (ed.), Studies in Herpetology. Prague.

KOROLJOV, A. V. 1986. Some data on the larvae of *Mertensiella caucasica*. Pp. 281-283 *In* Z. Rocek (ed.), Studies in Herpetology. Prague.

KUZMIN, S. L. 1992. Feeding ecology of the Caucasian Salamander (*Mertensiella caucasica)* with comments on life history. Asiatic

Herpetological Research 4:123-131.

LANDE, R. AND G. F. BARROWCLOUGH. 1989. The effective numbeity of population and genetic variability and their application in the population monitoring. Pp. 117-157 *In* M. E. Soulé (ed.) Viable populations for conservation. Mir, Moscow. (Russian translation).

KNOBLAUCH, A. 1905. Der Kaukasische Feuersalamander, *Salamandra caucasica* (Waga). Berichte der Senckenbergischen Naturforschenden Gesellschaft in Frankfurt am Main 36:89-110.

LLOYD, M. 1967. Mean crowding. Journal of Animal Ecology 36(1):1-30.

MERTENS, R. 1968. Bemerkungen zur "Normalentwicklung" des Kjaukasus-Salamanders. Salamandra 4:44-45.

NESTEROV, P. V. 1911. *Salamandra caucasica* Waga. Izvestiya Kavkazskogo Muzuya 5:319-327. (In Russian).

NIKOLSKY, A. M. 1913. Herpetologia Caucasica. Kantselariya Namestnika E. I. V. na Kavkaze, Tiflis. 272 pp. (In Russian).

OBST, F. J. AND J. ROTTER. 1962. Notizen zu *Mertensiella caucasica* (Waga) 1876. Aquarien und Terrarien Zeitschrift 15(2):50-52; (3):84-86.

ÖZETI, N. 1967. The morphology of the salamander *Mertensiella luschani* (Steindachner) and the relationships of *Mertensiella* and *Salamandra*. Copeia 1967(2):287-298.

PARASKIV, K. P. 1953. [Siberian salamander *(Ranodon sibiricus)*]. Izvestiya AN KazSSR, Biologicheskaya seriya 1:47-56. (In Russian).

SEMLITCH, R. D. AND H. K. PEACHMANN. 1985. Diel pattern of migratory activity for several species of pond-breeding salamanders. Copeia 1985(1):86-91.

TARKHNISHVILI, D. N. AND R. V. TARTARASHVILI. 1987. [On the development of spotted pigmentation in some Salamandridae]. Zoologichesky Zhurnal 66(9):1328-1338. (In Russian).

TARTARASHVILI, R. V. AND M. L. BAKRADZE. 1989. [The new subspecies of the Caucasian Salamander]. Soobshcheniya AN GSSR 133(1):177-179. (In Russian).

THORN, R. 1968. Les salamandres d'Europe, d'Asie et d'Afrique du Nord. Editions Paul Lechevarier, Paris. 376 pp.

WOLTERSTORFF, W., L. A. LANTZ, AND W. HERRE. 1936. Ein Import des kaukasischen Salamanders *(Mertenjsiella caucasica)*. Zoologischer Anzeiger 116(1/2):1-13.