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Interdependences between Populational, Developmental and Morphological Features of the Caucasian Salamander, *Mertensiella caucasica*

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With 4 Figures

ey words: Caucasian salamander; life mode; intrinsic growth rates; fecundity; mortality; rheophilous abitats; reproductive mode; daintiness.

ummary

Peculiarities of the demography and spatial structure of populations of the Caucasian salamander *lertensiella caucasica* WAGA) make this species highly vulnerable to the variability of environmental onditions. These peculiarities include low intrinsic growth rates of the populations, resulting in low fecundity and late maturation. High dependance upon mountain streams result in a low arrying capacity, small size of local populations, and a high degree of isolation of the separate opulations. These features can be connected with the thin body shape of the salamanders. Body ape variation among European salamander species (Salamandrinae) determines their reproductive ode and peculiarities of their life cycles. Slender body shape prevents evolution of viviparity and multaneously limits fecundity. Perhaps the slim shape of the body evolved as a result of larval laptation to development in running waters. Shortcomings of this adaptation become obvious in etamorphosed salamanders. The life mode of *M. caucasica* allows only narrow habitats with a igh local stability.

ntroduction

From to investigations of the last 10-15 years, we have a comparatively full picture of e general ecology and life cycles of European salamander species. Original works on the opulation ecology of *Salamandra salamandra* (KLEWEN 1986, WARBURG 1986, THIESMEIER 992, etc.) and *Chioglossa lusitanica* (ARNTZEN 1981) have to outlined. These works, gether with data of POLYMENI (1994) on the ecology of *Mertensiella luschani*, allow us analyse the main ecological differences of *Mertensiella caucasica* with their near latives.

Special attention will be directed towards ecological peculiarities of the Caucasian salamander, connected directly with the species' viability and probability of its extinction. Linking morphological characters with the ecological peculiarities was another aim. I want to try to present a survey of the interactions between ecological and morphological features which determine the position of this species in the European salamander tribe.

The population ecology of *M. caucasica* was investigated from 1985 in the Borjomi Canyon, Central Georgia, together with I. Serbinova (Tarkhnishvili & Serbinova 1993, in press). The results of skeletochronological analysis are described by Tarkhnishvili & Gokhelashvili (1994). Only the general characteristics of distribution, metapopulation structure and the life history of *M. caucasica* will be described here as far as its necessary for the comparative analysis.

Distribution habitats and phenology

As early as 1913 Nikolsky summarized the information on *M. caucasica* localities in the present state of Georgia and northeastern Turkey. Further investigations in Georgia added only a few localities to Nikolsky's map, but they didn't change the general picture of the species' distribution obtained earlier. Atatür & Budak (1982) established western limits of the *M. caucasica* distribution (near Giresun). Thus, this species is distributed in forest mountains of the northern Caucasas Minor in areas of annual precipitation of 1000 mm and more, in Lazistanian, the Adjaro-Imeretian mountain ridges and the western part of Trialeti mountain ridge (Fig.1). The species is entirely absent in the Great Caucasus, in spite of its neighbourhood with the areas of distribution and in spite of the presence of appropriate habitats. Where it occurs *M. caucasica* forms small, semi-isolated populations. Salamanders inhabit small streams in their upper sections, divided one from another by small mountain ridges. Some distance away as in the lower parts of the rivers salamanders are absent. Perhaps their absence in middle and lower regions of the rivers is linked with predation by trouts. Such local populations (demes) cover comparatively small plots, 200-500 m along stream-banks, where streams overflow in little creeks and pools and a lot of stony and wood blockages are present, and are used as shelters and breeding sites. Salamander activity is extremely limited both spatially and temporally. Most of the year the animals spent in shelters. The appearance of active adult salamanders on the ground is connected with mating. The first adults (initially males, as in the most of amphibians) appeared at the beginning of May, but most of the animals leave their shelters during June /early July. Some adults could be seen until August. Larvae appeared in open water in May and could be seen until the end of summer. Even during the activity season, the animals are strictly nocturnal. Both, adults and larvae show the highest activity about 3 hours after sunset. In higher altitudes the period of activity shifts towards the indicated later months of the year.

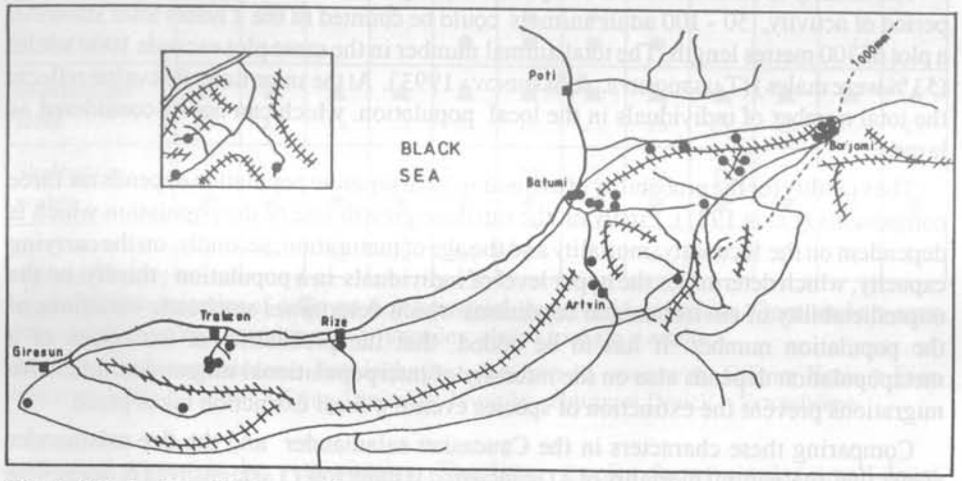

Fig. 1. Distribution of *Mertensiella caucasica* according to the literature. Broken line = 1000 mm (level of annual precipitation). ≻≻≻ = mountain ridges. Upper left corner: Distribution of the local populations in Borjomi Canyon.

Verbreitung von *Mertensiella caucasica* nach Angaben aus der Literatur. Unterbrochene Linie = 1000 mm (Höhe der jährlichen Niederschläge). ≻≻≻ = Gebirgszüge. Obere linke Ecke: Verteilung der lokalen Populationen im Borjomi Canyon.

Reproduction and ontogenesis

The female deposit their eggs two or three days after mating. Each female deposits 11 to 24 ($\bar{x}$ = 16.9) eggs of 4.4 to 6.0 mm in diameter. During this period the water temperature exceeds 15-16 °C (for most of year the water is much more colder). The period from egg deposition to hatching takes 50 days when the temperature is 20 °C (Tarkhnishvili & Serbinoa in press). In nature hatching occurs perhaps in autumn. The total length of hatchlings varies between 17 and 20 mm, snout vent length between 10.5 and 11.5 mm. The forelimbs are fully developed, and buds of the hindlimbs have just appeared. The larvae are very secretive. They are seen in open water only in the summer of the next year, and reach the size which is sufficient for metamorphosis after the next hibernation. Growth rates are comparatively lower than in the fire salamander. Probably some larvae metamorphose after 3 or 4 hibernations (Tarkhnishvili & Gokhelashvili 1994) at a snout -vent length that ranges from 32.9 to 42.4 mm. Metamorphosis commonly takes place in July-August. The juveniles move to the shelters and seldomly appear on the surface before maturation. It is likely that maturation occurs earliest 10 years after metamorphosis (Tarkhnishvili & Gokhelashvili 1994). The habitat dynamics of *M. caucasica* during the year are presented in Figure 2.

Population dynamics

The density of salamanders is comparatively high in their main habitats. During the period of activity, 50 - 100 adult animals could be counted in the 2 hours after sunset in a plot of 300 metres length. The total animal number in the same plot exceeds 1000 adults (53 %were males) (TARKHNISHVILI & SERBINOVA 1993). At the same time, this value reflects the total number of individuals in the local population, which can not be considered as large.

The viability (or the probability of extinction) of a separate population depends on three components (LEIGH 1981). Firstly on the intrinsic growth rate of the population which is dependent on the fecundity, mortality and the age of maturation; secondly, on the carrying capacity, which determines the upper level of individuals in a population; thirdly, on the unpredictability of environmental conditions which determines stochastic variations of the population number. It has to be added, that the probability of extinction of a metapopulation depends also on the intensity of interpopulational migrations. Intensive migrations prevent the extinction of species even if a local extinction takes place.

Comparing these characters in the Caucasian salamander and the fire salamander shows that the natural mortality of *M. caucasica* is quite low (TARKHNISHVILI & SERBINOVA 1993). At the same time, fecundity is low and the period from egg to maturation takes a long time. Fecundity of the fire salamander in Middle-Europe is two times higher (THIESMEIER 1992) and the number of newborns per female is even higher than that, because the female gives birth to developed larvae and the period before metamorphosis lasts only a few months. Annual survival of adult *M. caucasica* (mixed data for both sexes) reaches about 70 %. Average survival rates of *S. salamandra terrestris*, calculated from the data of KLEWEN (1986), reach 66%, i.e. a similar value. Unfortunately, the age of maturation of this species in Europe is unknown. WARBURG (1994) established that in Israel fire salamanders become mature a few years after metamorphosis. Thus, the intrinsic rates of *M. caucasica* population growth are lower than in the fire salamander. In spite of similar mortality rates, the fecundity of the Caucasian salamander is two times lower and the period before maturation is longer. The total equilibrium number of *S. salamandra* populations is also higher, e.g. KLEWEN (1986) counted 4507 adults in one local population. In fire salamanders the size of populations varies in a larger range. This species does not depend as much on the banks of streams. Larvae were born also in streams where the current is slow or in stagnant waters. Thus, larger parts of streams are suitable for reproduction. The fire salamander can move freely in forests and an exchange of animals between different populations is bound to be higher than in *M. caucasica*. Unfortunately, comparable data of *Salamandra atra* and *M. luschani* are rare. The fecundity of both species is extremely low (two young per female: see ÖZETI 1979, KLEWEN 1988). However, taking into account embryonal and larval mortality, the real fecundity of *M. caucasica* may be similar. Data on mortality of *S. atra* and *M. luschani* are not available.

Judging from FACHBACH's (1988) data, the ages of mature *S. atra* are comparable with that of *M. caucasica*. As populations of *M. luschani* have a larger territory and density appears high enough (POLYMENI 1994), this species has some advantages in carrying capacity and migration possibilities. Demography of *M. caucasia* and *Chioglossa*

Ground surface					▲	▲	▲	▲				
Open water					●	▲ ●	▲ ●	●				
Shelters on land	▲ △	▲ △	▲ △	▲ △	▲ △	▲ △	▲ △	▲ △	▲ △	▲ △	▲ △	▲ △
Shelters in water	●	●	●	●	●	○ ●	○ ●	○ ●	○ ●	●	●	●
	J	F	M	A	M	J	J	A	S	O	N	D

Fig. 2. Habitat dynamics of different developmental stages of *M. caucasica*. Open circle = eggs; closed circle = larvae; open triangle = juveniles; closed triangle = adults.

Habitatdynamik verschiedener Entwicklungsstadien von *M. caucasica*. Offener Kreis = Eier; schwarzer Kreis = Larven; offenes Dreieck = Juvenile; schwarzes Dreick = Erwachsene.

lusitanica appear to be very similar. The latter species forms similar small local populations which consist of up to 1000 individuals. Furthermore it is confined to upper parts of streams with fast flowing water. The number of deposited eggs is small (ARNTZEN 1981).

In both species low growth rates of populations, low carrying capacity and high isolation of local populations are obviously compensated by habitats with very stable environmental conditions. Therefore they are more vulnerable than other Salamandrinae if changes in the environmental occur.

Morphology and adaptations to the microhabitat

The morphological characters of European salamanders and the morphological peculiarities of *M. caucasica* may explain some adaptations to the habitat. Common features of European salamanders, distinguishing them from other species of Salamandridae, are 1) smooth skin (most Salamandridae, have rough, grainy skins). Probably the high sensivity of salamanders to decreasing humidity is reflected on their skin. Although they are terrestrial animals they need humid environments. As a rule salamanders are confined to forests, frequently to mountain forests; 2) presence of large oocytes (independent of the breeding mode), the largest are present in the Salamandridae family. THIESMEIER (1994) stated that stream-breeding Salamandridae have larger oocytes than pond-breeding ones. It is difficult to state which character developed erlier: either increasing of egg size as an adaptation to breeding in streams with a low density of food, or large eggs - because of low surface/volume ratio - require high oxygen and low water temperature, thus limiting breeding sites to streams with cold running water. In any case, large oocytes are a plesiomorphous character which is likely to be typical for the common ancestors of recent European salamanders. It may be considered as a preadaptation to viviparity in some species but originally it was not connected with viviparity; 3) peculiarities of colouration pattern: most European salamanders (except some variations of *M. luschani)* do not have a light-coloured belly which is typical also for most of the Salamandridae. Such a colouration is closer to that of representatives of other Caudata and correlates with a humidophilous mode of life. These common characters don't exclude differences among different species in body size and shape. ÖZETI (1967) has shown that *Salamandra-* and *Mertensiella* - species can be arranged in a row of increasing daintiness of their body shape from thick and strong *S. salamandra* to thin, slender and elongated *M. caucasica.* Many osteological peculiarities are connected with general body proportions. This row could be prolonged by adding *C. lusitanica* which is similar to *M. caucasica* in constitution and morphology (BORJA & MLYNARSKI 1979). Taking into account the degree of daintiness, three morpho-ecological groups can be outlined among European salamanders. Group 1 includes *C. lusitanica* and *M. caucasica*; group 2 *M. luschani* and *S. atra*; and group 3 *S. salamandra* including all the variations of this species. Body size of species increases in the same direction.

Systematics prefer apomorphous characters which are independent of functional significance, e. g. the protuberance on the dorsal side of *Mertensiella* males (the function of which is unclear) is the only reason to place them into a separate genus. Perhaps it is correct from a phylogenetical point of view. Morpho-ecological groups considered here cannot reflect genealogical relationships of species, but body shape clearly correlates with ecological peculiarities and the reproductive mode.

C. lusitanica and *M.caucasica* are oviparous species: they deposit undeveloped eggs and breeding is strictly limited (especially in *C. lusitanica)* to mountain streams. *M. luschani, S. atra* and *S. lanzai* give birth to two fully metamorphosed young. *S. salamandra* bears larvae or metamorphosed specimens (THIESMEIER & HAKER 1990), but its fecundity is the highest (in Middle-Europe often 60 larvae, THIESMEIER 1992). Species of the second and the third groups are not as strictly limited to mountain streams as species of the first group and have a different spatial structure of populations. Species of the first and the second group have a narrow and recent regional distribution, whereas *S. salamandra* is widely distributed in Europe and Middle East.

Adaptive possibilities increase in this line from *C. lusitanica* and *M. caucasica* to *S. salamandra* at the expense of 1) increasing homoeostatic possibilities and decreasing of attachement to specific breeding sites and 2) increasing of real fecundity (taking into account embryonal and larval mortality).

LUBISHCHEV (1969) noted that a good taxon does not only include common features of form. To a taxon belongs also the direction of character variability at the range of species. The value of the European salamander tribe is in the presence of its species spectra, varying in body shapes and additionally in oocyte size and skin structure (in a community variability will also be visible in many other characters but the characters picked out here appear the most significant from the population-ecological point of view). Different species can therefore reach the same position on the slim body shape line independently.

What determines the slender gracile body shape of *M. caucasica* and corresponding ecological features ? Perhaps salamander ancestors had large oocytes. The development of viviparity was one of the ways for further evolution. Evolution of viviparity depends

on the breeding site. Generally this mode of reproduction permits easy migration and may induce the formation of large continuous metapopulations. A strong body is necessary for the evolution of viviparity. Slim forms can not care for embryos a long time and maintain high viability. Even the necessary energy for the development of large oocytes can significantly increase the mortality of females: annual mortality of *M. caucasica* adult females is higher than the mortality of adult males (TARKHNISHVILI & SERBINOVA in press). Finally, viviparity widens the ecological niche and makes species more independent of rheophilous environments. Another line of evolution of the stream-breeding salamanders with large eggs presupposes the retention of oviparity. As a result, animals remain strongly dependent upon small mountain streams. Larval development in such streams needs complex adaptations. First, newly hatched larvae must to be comparatively large and well-developed. Larvae of *M. caucasica* hatch on the stage comparable to GLAESNER stage 43 of newt larvae (TARKHNISHVILI & SERBINOVA in press). Newts *(Triturus)* hatch in the stages 36-37. Hatching of large, well developed larvae prevents their drift and needs large eggs. The necessity of large eggs prevents higher fecundity. Moreover, large eggs require water with a high oxygen content. These requirements prevent breeding in slowly running and stagnant waters.

A further adaptation is the slender body shape of larvae; elongated bodies and negative rheotaxis of larvae prevent drift. Moreover, slim larvae can successfully hide even in very narrow shelters (THIESMEIER 1994). Perhaps a non-adaptive modification is the permanent presence in running water.

At the moment of hatching the body shape of *M. caucasica*-larvae is virtually identical to new-born larvae of the fire salamander. Perhaps this period is the most vulnerable in the both species. During the subsequent development, allometric growth of the head and tail is different in the Caucasian and the fire salamander. The Caucasian salamander develops in a more rheophilous environment and is characterized by a faster growth of the tail and a slower growth of the head (MERTENS 1942, TARKHNISHVILI & SERBINOVA in press). In *M. caucasica* - larvae the allometric coefficient of tail growth reaches 1.71; the coefficient of head growth, 0.52. As a result, the body of *M. caucasica* - larvae acquirs its typical slender shape shortly after hatching. Allometric growth of salamander larvae takes place during the entire development until maturation is reached and results in the typical morphology of adult animals with slender body and very long tail (Fig. 3). Epigenetical correlations are thought to play a majors role.

A slimmer larval body during the early developmental stages increases the viability of larvae, but simultaneously limits adaptive possibilities of adult salamanders. Evolution of viviparity becomes impossible. A thin body prevents moving from regions with high humidity, because of the high surface/volume ratio of the animal's body and increases the danger of desiccation. It limits populational ranges and carrying capacity as well as migration possibilities. Also, it limits the activity of the salamanders which spend most of the time in humid shelters . At it is impossible to raise fecundity one encounters an additional reason which prevents animal dispersion.

The close links between morphological and ecological features (Fig.4) prevents *M. caucasica* to leave the narrow borders of its niche in which the species lives for historical reasons. Semi-isolated local populations are vulnerable and this vulnerability has to be

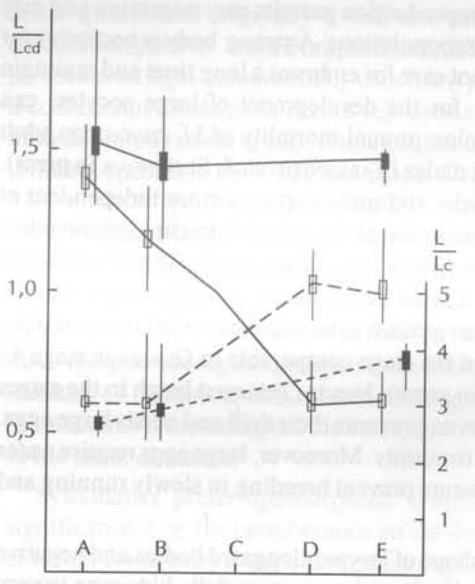

Fig. 3. Developmental changes of general body proportions of *M. caucasica* (open square) and *S. salamandra* (closed square). L = snout-vent length; L_{cd} = tail length; L_c = head length; continuous line = L/L_{cd}; dotted line = L/L_c.

Änderung der Körperproportionen von *M. caucasica* (helles Viereck) und *S. salamandra* (schwarzes Viereck). L = Länge Schnauze-Kloakenöffnung; L_{cd} = Schwanzlänge; L_c = Kopflänge; durchgezogene Linie = L/L_{cd}; gepunktete Linie = L/L_c.

compensated, e.g. by stability of environmental conditions. This kind of stability can only be reached in very narrow and a greater number of habitats.

The presented arguments can explain the limiting of this species' range during its history. According to Borja & Mlynarski (1979), *M. caucasica* was widely distributed in Europe in the Pliocene. This is indicated also by the absence of *M. caucasica* in the Great Caucasus (although this species had at least a chance for colonising these mountains after the last ice age). It should be emphasized that *M. caucasica* is an endangered species with weak adaptive possibilities . This species is particulary dependent upon the stability of the environmental conditions in its habitat. and requires the special attention of environmentalists.

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Abhängigkeiten zwischen populationsbiologischen, entwicklungsgeschichtlichen und morphologischen Merkmalen des Kaukasussalamanders *Mertensiella caucasica*

Demographische Besonderheiten und die räumliche Struktur der Populationen des Kaukasussalamanders (*Mertensiella caucasica* Waga) machen diese Art extrem anfällig für variable Umweltbedingungen. Zu diesen Besonderheiten gehört eine niedrige Wachstumsrate der Population, die zu einer niedrigen Fruchtbarkeit und späten Geschlechtsreife führt. Eine enge Bindung an Bergbäche führt zudem zu einer niedrigen Ausbreitungskapazität und geringen Größe lokaler Populationen sowie einem hohen Grad von Isolation zwischen den getrennten Populationen. Dies alles ist verknüpft mit einer schlanken Körpergestalt. Die Variation der Körpergestalt

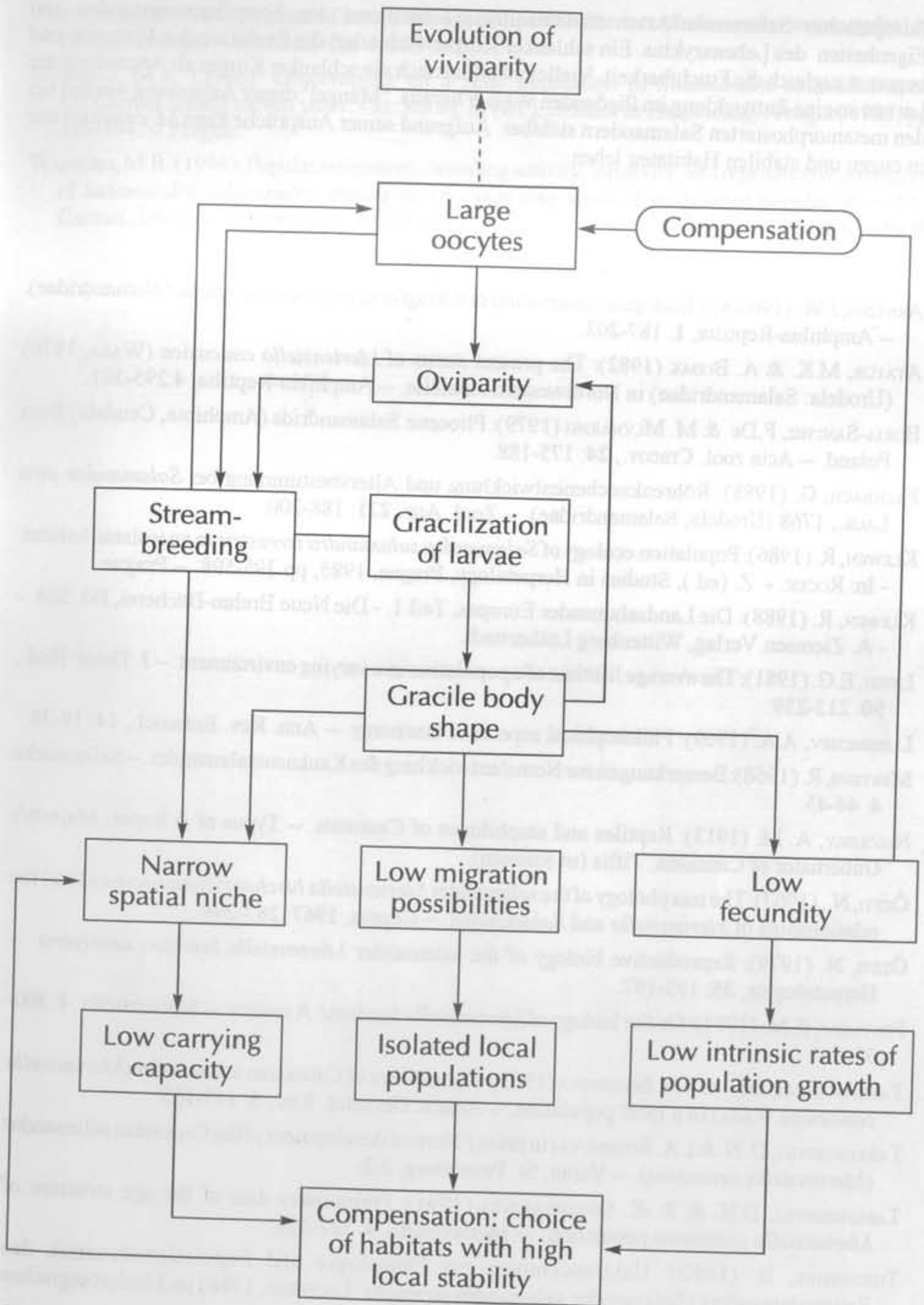

Fig. 4. Relations between morphological and ecological featurs of *M. caucasica*.
Beziehungen zwischen morphologischen und ökologischen Merkmalen von *M. caucasica*.

Europäischer Salamander-Arten (Salamandrinae) bestimmt den Fortpflanzungsmodus und Eigenheiten des Lebenszyklus. Ein schlanker Körper verhindert die Evolution der Viviparie und begrenzt zugleich die Fruchtbarkeit. Vielleicht bildetesich ein schlanker Körper als Anpassung der Larven an eine Entwicklung im fließenden Wasser heraus. "Mängel" dieser Anpassung werden bei den metamorphosierten Salamandern sichtbar. Aufgrund seiner Ansprüche kann *M. caucasia* nur in engen und stabilen Habitaten leben.

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