Age structure of six Georgian anuran populations and its dynamics during two consecutive years
(Anura)

Der Altersaufbau von sechs georgischen Anurenpopulationen und seine Veränderung in zwei aufeinanderfolgenden Jahren
(Anura)

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ABSTRACT

During two consecutive years, the age distribution of the reproductive portion of coexisting populations of *Pelodytes caucasicus, Hyla arborea, Bufo verrucosissimus, B. viridis, Rana macrocnemis* and *R. ridibunda* was studied using skeletochronological methods. Significant interspecific differences were found for the mean age of adults and population turnover rates, while the minimum age of maturation was two years for most species. The youngest mean age was found in *P. caucasicus* and *R. ridibunda*, the oldest in female *Bufo* spp. Turnover rates were higher in early maturing species.

KURZFASSUNG

Während zweier aufeinanderfolgender Jahre wurde der Altersaufbau des fortpflanzungsfähigen Anteils sympatrischer Amphibienpopulationen von *Pelodytes caucasicus, Hyla arborea, Bufo verrucosissimus, B. viridis, Rana macrocnemis* und *R. ridibunda* mit skeletochronologischen Methoden untersucht. Signifikante interspezifische Unterschiede ergaben sich hinsichtlich des Durchschnittsalters der Adulten und der Turnover-Raten der Populationen, während die Geschlechtsreife bei den meisten Arten relativ einheitlich frühestens mit zwei Jahren erreicht wurde. Das geringste Durchschnittsalter fand sich bei *P. caucasicus* und *R. ridibunda*, das höchste bei weiblichen *Bufo* spp. Turnover-Raten waren bei Arten mit früh einsetzender Geschlechtsreife höher.

KEYWORDS

Amphibians, *Bufo verrucosissimus, Bufo viridis, Hyla arborea, Pelodytes caucasicus, Rana macrocnemis, Rana ridibunda*; skeletochronology, population ecology, longevity, sexual maturity, mortality, life cycle, turnover rates; Georgia (Caucasus).

INTRODUCTION

A large amount of information about age structure of amphibian populations was obtained using skeletochronological methods (for reviews see ISHCHENKO 1989; CASTANET & SMIRINA 1990). Nevertheless, only in a few studies age structure of two or more populations inhabiting the same locality was described (e. g. GIBBONS & MacCARTHY 1983; LEDENTSOV & MELKUMYAN 1986; FRANCILLON-VIELLOT & al. 1990).

The age structure of a population varies depending on the actual conditions of life provided by the locality and, as a consequence, on the year of study (e. g. ISHCHENKO & LEDENTSOV 1987). On the other hand, species overlap considerably in terms of age of maturation, longevity and other characteristics connected with age structure. Hence, the analysis of samples concurrently collected in the same locality was used as a very promising approach for correct interspecific comparison of age structure.

The present paper describes the age structure and its dynamics in coexisting populations of six anuran species in Central Georgia during two consecutive years.

MATERIAL AND METHODS

In 1992 and 1993, samples (table 1) of tubular bones (hip bone, os ilium = h; phalanges = p) of sympatric *Pelodytes caucasicus* (p), *Hyla arborea* (h), *Bufo viridis* (p), *Bufo verrucosissimus* (p), *Rana ridibunda* (h), and *Rana macrocnemis* (h, p) were obtained from individuals found near their breeding sites during the peaks of their reproductive activity (April-June). These individuals were considered sexually mature.

The amphibians were collected in pools and creeks in the forested canyon of a tributary of the river Kura (Borjomi Canyon, Georgia, 900 - 1200 m asl). A description of the study area is given by TARKHNISHVILI (1993).

The second phalange of the fourth toe of the right foot of live animals and hip bones of preserved specimens were used for skeletochronological analysis. Standard skeletochronological techniques (KLEINENBERG & SMIRINA 1969; SMIRINA 1989; CASTANET & SMIRINA 1990) were applied. Only the narrowest parts of the bones were analysed. Sections (25 μm) were prepared in a cabinet-kryostat and stained in BOEMER haematoxylin.

Lines of arrested growth (LAGs, annual circles, year rings) in cross sections of amphibian tubular bones correspond with periods of starvation and, therefore, also with hibernations. The first (innermost) LAG usually disappears before maturation as a result of growth of the endostal cavity. Sometimes the second LAG is also resorbed totally or partly (ALEXANDROVSKAYA & KOTOVA 1986; READING 1988; SMIRINA 1989). We estimated the age of the animals bearing in mind that inner LAGs were probably resorbed (see RESULTS).

In 10 specimens of both *R. macrocnemis* and *P. caucasicus*, and in 3 specimens of the other species except *Hyla*, both hip bone and toe phalange sections were examined.

SMIRINA & al. (1986) showed that formation of additional and duplicated LAGs was to be induced e. g. by two weeks of starvation. These lines are usually less clear than regular LAGs and never cover the whole perimeter of the section. In some cases we observed such indistinct or interrupted lines. They were not counted when an animal's age was estimated.

Calculations

The following characteristics of age structure were used for interspecific comparisons.

1. Minimum age of maturation (min AM).

2. Maximum age of maturation (max AM).

In most samples (except *R. ridibunda* males) the youngest age class was not the most voluminous one. An increasing number of specimens in consecutive age classes may be due to unequal maturation of the members of a cohort. BELL (1977) supposed that the modal age can be considered the age at which all or almost all specimens of a population begin to breed. This seems to be true for populations with stable age structure where modal age does not vary from year to year, and the number of individuals clearly declines in age classes above the modal class. On the other hand, the modal age could reflect the cohort whose initial number was particularly high, independently of the age of maturation (e. g. LEDENTSOV 1990). However, if the number of individuals in any age class exceeds the number in any preceding class, this could be the result of graduated maturation (especially in cases where numbers increase gradually). We consider the modal age as an index of the potentially oldest age of maturation.

3. Mean age of adult animals (MA).

The arithmetic mean of the age of the individuals of a sample.

4. "Longevity".

The maximum age of adult animals in the samples was used as a rough index which, unfortunately, does not fully reflect longevity. The age of the oldest specimens in the sample depends on sample size, age of maturation and annual mortality rates.

5. Indices of mean annual mortality (IAM) and renewal (=turnover) rate (RR).

Composition of age classes in populations depends on age-specific mortality rates as well as on the initial number of simultaneously present cohorts and their mortality rates (ISHCHENKO & LEDENTSOV 1987; LEDENTSOV 1990). Nevertheless, we used the age distribution of pooled samples (two years of study; 1992+1993) for calculation of IAM.

The mean annual mortality index (IAM) was calculated by dividing the number of specimens in the modal age class by the sample size (N) minus the number of specimens younger than modal age.

$$\text{For } N = n_1 + \ldots n_{mo} + \ldots n_k,$$
$$IAM = n_{mo} \cdot (n_{mo} + \ldots n_k)^{-1}.$$

The renewal rates of the populations (RR) were calculated in the following manner. The age of

a specimen, which was (i) in 1992, became (i + 1) in 1993. Age distribution (% specimens in age classes) in the samples collected in 1992 was compared with the age distribution in the samples collected in 1993, by shifting the values of 1993 one class unit to the left.

RR was estimated according to PESENKO (1982):

$$RR = 1 - J_{j,k}, \text{ where}$$

$$J_{j,k} = \Sigma \min p_{ij}, p_{(i+1),k} \cdot (\Sigma \max p_{ij}, p_{(i+1),k})^{-1}.$$

p_{ij} is the percentage of age class (i) in the 1992 sample, $p_{(i+1),k}$ is the percentage of age class (i + 1) in the 1993 sample. It must be noted that the index RR cannot reflect the real turnover rate in the population as it does not consider annual variation of the population size. But most amphibian populations of the study area are very stable; e. g., the numbers of individuals of female *R. macrocnemis*, *B. verrucosissimus* and *P. caucasicus* did not differ by more than 100% each from 1989 to 1993 (TARKHNISHVILI in prep.).

RESULTS

Peculiarities of the samples

In most cases the relative size of the endostal cavity was bigger in the phalange than in the corresponding hip bone, but there were marked interspecific and individual differences. Sections of relatively narrow cavities (diameter equal or less than diameter of tubular bones of conspecific animals after first post-metamorphic hibernation) usually showed fragmented LAGs with markedly smaller diameters than the regular lines. In such cases we considered the innermost LAG, whether partly resorbed or complete, as the first annual circle, and estimated the age at least equal to the number of LAGs (n). In the case of relatively wide endostal cavity we estimated the age as (n + 1).

R. macrocnemis. LAGs clearly visible, diameter of endostal cavity variable, LAG of first hibernation partly visible or totally resorbed in both hip bone and phalange sections. According to our field observations, the size of all first-hibernated individuals was close to that of adults in late July. Hence, we are absolutely sure that the second LAG is never resorbed in this population. According to the distances between the LAGs, growth was most intensive between first and second hibernation, and sometimes even in the third year of life (fig. 1, Rm). The ring representing the last hibernation was not expressed, since the animals were collected just after leaving their winter shelters. Age was calculated as (n + 2) or (rarely) (n + 1), depending on the size of the endostal cavity.

R. Ridibunda. LAGs clearly visible, endostal cavity wide, also in hip bones, first LAG always resorbed (judging from diameters of bones of first-hibernated individuals). Frogs reached adult size at the end of the second year of life. Hence, the innermost LAG visible was always the LAG of the second hibernation. LAG of last hibernation always clear (fig. 1, Rr). Age was calculated as (n + 1).

H. arborea. Only males were studied. LAGs very clear, endostal cavity of hip bones narrow, LAG of first hibernation usually visible. According to the distances between the LAGs, growth is regular (fig. 1, Ha). Age was calculated as (n), rarely as (n + 1).

B. verrucosissimus. Some vague additional lines were present in several individuals [E. g. LAGs 2, 3, 4 (fig. 1, Bve) are repeatedly interrupted parallel lines, restricted to one half of the section. Lines 5 and 6 are also close to one another but distinctly separated along all of their perimeter, and, hence, were considered as separate LAGs.]. Diameter of endostal cavity intermediate in phalanges, intermediate to narrow in hip bones. According to our field observations, growth of the toad is relatively slow in the second year of life. Hence, partial resorption of

the second LAG cannot be excluded in some specimens. On the basis of the endostal cavity diameter it was difficult to say in which toads the second line was resorbed. Growth rates of first-hibernated toads display considerable individual variation (snout-vent length at the end of summer varies from 3 to 6 cm), and diameter of the second LAG is also highly variable. We considered the age of mature toads at least as (n + 1).

B. viridis. Additional lines are frequently present. Judging from the distances between the LAGs, growth is very discontinuous. This corresponds to our field observations (snout-vent length at the end of the toads' second summer varied from 30 to 50 mm). [LAG no. 2 (fig. 1, Bvi) resembles a line of resorption (HEMELAAR 1981). However, the inner line which intersects the LAGs is considered as true resorption line. The lines outside this line do not intersect, and, thus, can be considered true LAGs]. Diameter of endostal cavity narrow in both phalange and hip bone. Inner LAGs usually partly resorbed (fig. 1, Bvi). Age was estimated at least as (n + 1) or (n), depending on diameter of endostal cavity.

P. caucasicus. LAGs were always clearly visible (fig. 1, Pc), endostal cavity wide in phalanges, narrow in hip bones. LAG of first hibernation always visible (partly or totally) in hip bones, never in phalange sections. In the phalanges of some individuals the second LAG was also partly resorbed. Age was estimated (by phalange section) as (n + 1).

Minimum age of maturation

Minimum age of maturation (minAM) was two years for most species except for female *Bufo* spp. and male *H. arborea* among which no specimen was younger than three years.

Maximum age of maturation

Determination of the maximum age of maturation (maxAM) was rather delicate, because in some samples two or even three age classes could be considered as modal ones.

Perhaps almost all male *R. ridibunda* matured after two hibernations. In most species, all or almost all specimens matured after three hibernations. Some female

R. macrocnemis, B. viridis and male *H. arborea* probably did not mature before four hibernations, and some female *B. verrucosissimus* matured even later (up to seven years). MaxAM varied from year to year in most species.

Mean age

Judging from data pooled from both study years, the lowest mean age (MA) (2.7 - 3.0 years) was established for *P. caucasicus, R. ridibunda* and male *R. macrocnemis*. Intermediate values (3.6 - 4.4 years) were found in female *R. macrocnemis*, male *Bufo* spp. and *H. arborea*. A high mean age was typical for female *Bufo* spp., especially *B. verrucosissimus*. Standard deviation of the mean age was lowest in *P. caucasicus, R. ridibunda* and male *R. macrocnemis*, and highest in *Bufo* spp., male *H. arborea* and female *R. macrocnemis*.

Annual mortality and renewal rates (table 2)

The highest index of annual mortality (IAM) for pooled samples was found in *P. caucasicus* (0.78 - 0.83) followed by *R. macrocnemis* (about 0.67). The indices of annual mortality of *R. ridibunda* and *Bufo* spp. varied from 0.4 to 0.5. The lowest value was observed in *H. arborea* (0.34).

The index of renewal rate (RR) varied between 0.67 and 0.78 for most species. Comparatively low renewal rates were found in *R. macrocnemis* (0.37 - 0.46) and, especially, in male *B. verrucosissimus* (0.24).

"Longevity"

The oldest specimens (9-12 years) were found among *H. arborea, B. verrucosissimus* and female *B. viridis*. The oldest *Rana* spp., *P. caucasicus* and male *B. viridis* specimens had hibernated 6-7 times.

DISCUSSION

In most anuran species of the temperate climate some specimens mature already after two hibernations (BARBAULT & al. 1980; SMIRINA 1983; GIBBONS & MacCARTHY 1983; HEMELAAR 1981; ALEKSANDROVSKAYA & KOTOVA 1986; LEDENTSOV & MELKUMYAN 1986; LYKENS & FORESTER 1987; ISHCHENKO & LEDENTSOV 1987; LECLAIR & CASTANET 1987). In general, our data confirm this rule. Nevertheless, minimum age of adult females of *Bufo* spp. as well as of male *H. arborea* was three years. Minimum age of maturation therefore seems to depend rather on species-specific growth rates than on the maximum body size of the adult.

Interspecific differences in maximum age of maturation and mean age of adults were obvious. In general, these parameters are correlated. "Young" specimens predominated in the reproductive portion of the populations of *P. caucasicus, R. ridibunda* and male *R. macrocnemis*, "old" specimens in *Bufo* spp. and *H. arborea*.

In their microbiotope preferences, *R. macrocnemis* and *P. caucasicus* were more similar to *B. verrucosissimus* than to *R. ridibunda*; inversely, *B. viridis* inhabited localities more similar to those occupied by *R. ridibunda* than by *B. verrucosissimus* (TARKHNISHVILI 1993). One could conclude, that, within one climatic zone, the mean age of maturation might

Fig. 1 (opposite page): Sections of tubular bones of Georgian anurans studied. Rm - *Rana macrocnemis*; Rr - *Rana ridibunda*; Bve - *Bufo verrucosissimus*; Bvi - *Bufo viridis*; Pc - *Pelodytes caucasicus*; Ha - *Hyla arborea*. 1, 2, 3 ... - lines of arrested growth (LAGs), parallelling hibernations. hb - hip bone; tp - toe phalange. Sex and assumed age of animal are indicated.

Abb. 1 (gegenüberliegende Seite): Schnitte von Röhrenknochen der untersuchten Georgischen Anuren. Rm - *Rana macrocnemis*; Rr - *Rana ridibunda*; Bve - *Bufo verrucosissimus*; Bvi - *Bufo viridis*; Pc - *Pelodytes caucasicus*; Ha - *Hyla arborea*. 1, 2, 3 ... - Linien verminderten Wachstums (LAGs), die Überwinterungen widerspiegeln. hb - Hüftbein; tp - Zehenknochen. Geschlecht und vermutetes Alter des Tieres sind in der jeweiligen Abbildung angegeben.
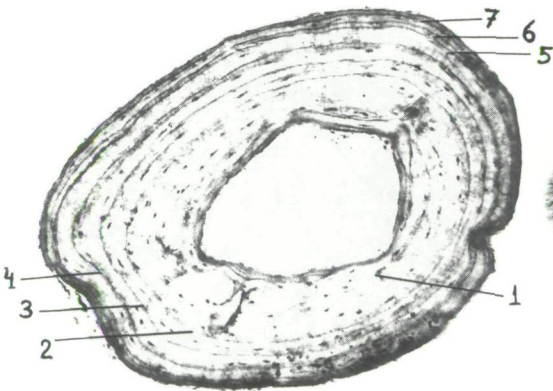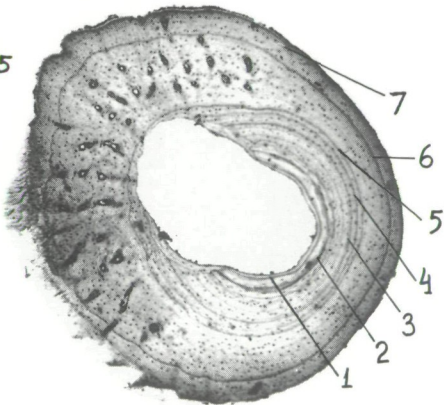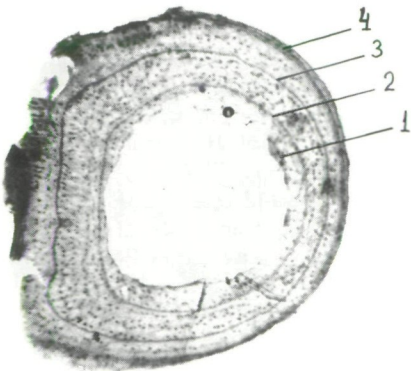
Rm, female, tp, 5 a
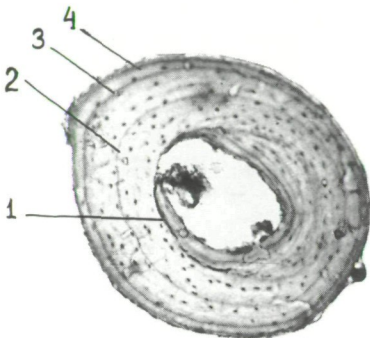
Rr, female, hb, 4 a
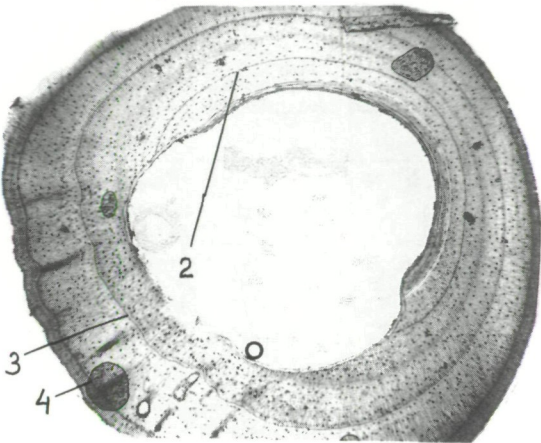
Bve, female, tp, 8 a

Bvi, female, hb, 7 a
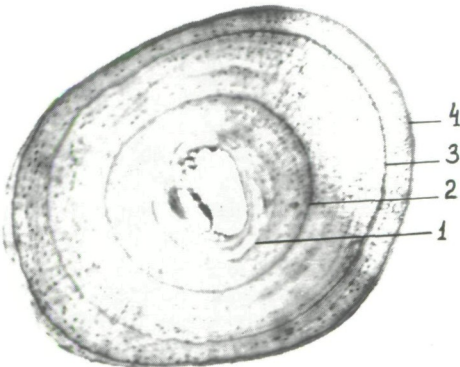
Pc, male, tp, 4 a

Ha, male, hb, 4 a

Table 1: Age distribution in the studied Georgian anuran populations. Percentage of specimens in age classes '1 year' through '12 years', and mean age of adults.
Spec. - species; m - males; f - females; N - sample size; MA and SD - mean age (years) and standard deviation of MA; in bold face with asterisk - modal age classes. Ha - *Hyla arborea*; Pc - *Pelodytes caucasicus*; Bvi - *Bufo viridis*; Bve - *B. verrucosissimus*; Rr - *Rana ridibunda*; Rm - *R. macrocnemis*.

Tab. 1: Altersverteilung in den untersuchten georgischen Anurenpopulationen. Prozentuelle Verteilung der Individuen auf die Altersklassen "1 Jahr" bis "12 Jahre" sowie Durchschnittsalter der Adulten.
Spec. - Art; m - Männchen; f - Weibchen; N - Stichprobenumfang; MA und SD - Durchschnittsalter (in Jahren) und Standardabweichung von MA; fett gedruckt mit Asterisk - modale Altersklassen; Ha - *Hyla arborea*; Pc - *Pelodytes caucasicus*; Bvi - *Bufo viridis*; Bve - *B. verrucosissimus*; Rr - *Rana ridibunda*; Rm - *R. macrocnemis*.

Spec.	sex	year	N	2	3	4	5	6	7	8	9	10	11	12	MA	SD
Ha	m	1992	15		13	33*	13	13	7	7	7			7	5.60	2.52
	m	1993	18		50*	17	33								3.83	0.93
	Σ		33		33*	24	24	6	3	3	3			3	4.41	1.49
Pc	m	1992	81	30	49*	17	3	1							2.96	0.72
	m	1993	47	32	62*	6									2.74	0.55
	Σ		128	30	54*	13	2	1							2.88	0.75
	f	1992	27	33	59*	8									2.74	0.42
	f	1993	21	19	62*	19									3.00	0.50
	Σ		48	27	60*	13									2.85	0.62
Bvi	m	1992	20	5	40*	20	25	10							3.95	0.98
	m	1993	5		60*	40									3.40	
	Σ		25	4	44*	24	20	8							3.69	1.06
	f	1992	7		14	29*	29*		14		14				5.43	
	f	1993	4		25	50*	25								4.00	
	Σ		11		18	36*	27		10		10				4.91	2.00
Bve	m	1992	21	14	38*	29	10	4			4				3.76	1.56
	m	1993	28		21	29*	29*	14	7						4.57	1.01
	Σ		49	6	29*	29*	20	10	4		2				4.04	1.45
	f	1992	31		7	10	10	13	30*	22	4	4			6.52	1.73
	f	1993	25		4	16	40*	28	12						5.25	0.85
	Σ		56		5	13	23*	20	23*	13	1	1			5.96	1.48
Rr	m	1992	5	40*	20	40*									3.00	
	m	1993	14	50*	29	21									2.71	0.86
	Σ		19	48*	26	26									2.79	0.86
	f	1992	5	80*	20										2.20	
	f	1993	8	25	38*	12	25								3.38	1.05
	Σ		13	46*	31	8	15								2.92	1.12
Rm	m	1992	50	42*	42*	10	6								2.78	0.85
	m	1993	42	26	48*	14	10	2							3.13	0.91
	Σ		92	36	45*	11	8	1							2.95	0.94
	f	1992	18	22	39*	28	11								3.39	0.98
	f	1993	12	8	25	42*	8	8	8						4.03	1.10
	Σ		30	17	33*	33*	10	3	3						3.60	1.19

be connected rather with the taxonomic position of the species than with its ecological niche.

R. ridibunda was the only species characterized by a constant age of maturation in all specimens studied: they always matured after two hibernations.

Inversely, some large females of *B. verrucosissimus* matured at the age of three to seven years. In most species, the difference between early-maturing and late-maturing specimens did not exceed one year.

Both mean age and maximum age of maturation changed from year to year, especially in the late-maturing species *B. verrucosissimus*, *H. arborea*, and female *R. macrocnemis*. This could be connected with morpho-physiological characteristics of the various generations (sensu cohorts), depending on environmental conditions in the year of their formation (ISHCHENKO & LEDENTSOV 1987).

Maximum age within samples correlated with the age of maturation. Individuals of late-maturing species reached high

Table 2: Indices of mean annual mortality (IAM.100%) and renewal (turnover) rates (RR. 100%) 1992/1993 in the studied Georgian anuran populations.
m - males; f - females; Spec. - species; Ha - *Hyla arborea*; Pc - *Pelodytes caucasicus*; Bvi - *Bufo viridis*; Bve - *B. verrucosissimus*; Rr - *Rana ridibunda*; Rm - *R. macrocnemis*.

Tab. 2: Mittlere jährliche Mortalitätsraten (IAM.100%) und Turnover-Raten (RR.100%) 1992/1993 der untersuchten georgischen Anurenpopulationen.
m - Männchen; f - Weibchen; Spec. - Art; Ha - *Hyla arborea*; Pc - *Pelodytes caucasicus*; Bvi - *Bufo viridis*; Bve - *B. verrucosissimus*; Rr - *Rana ridibunda*; Rm - *R. macrocnemis*.

Spec.	m		f	
	IAM	RR	IAM	RR
Ha	34.3	70	-	-
Pc	77.5	78	82.9	65
Bvi	45.8	71	44.4	76
Bve	42.4	24	33.3	76
Rr	47.4	68	46.2	67
Rm	67.8	46	66.7	37

maximum age like *H. arborea* and female *Bufo* spp. (up to eight or nine reproductive seasons). *P. caucasicus* as well as *Rana* spp. (except female *R. macrocnemis*) usually had up to six reproductive seasons in their life.

The indices of mean annual mortality (IAM) and population turnover rate (RR) did not correspond well with one another. IAM depended obviously on the age class selected as modal class and on the initial number of simultaneously present generations (sensu cohorts). In some cases the modal class was not clearly expressed (e. g. female *B. verrucosissimus* and *R. macrocnemis*) or changed from year to year.

However, in different ways IAM and RR depended on the peculiarities of the survival curve. Both indices increased when annual mortality rates were high. None the less, IAM decreased when mortality increased in the oldest age classes, whereas RR increased. Inversely, IAM increased and RR decreased when mortality was uniformly distributed among classes.

In *P. caucasicus*, an early-maturing species with a high renewal rate, both IAM

and RR displayed the highest values. None the less, *R. ridibunda*, another early-maturing species, showed a comparatively low value of IAM, because mortality rates increased sharply after 4 - 5 years of life, while mortality was low in two to three years old frogs. Conspicuously low values of IAM were found for the late-matured female *B. verrucosissimus* and male *H. arborea* populations, the individuals of which were characterized by increasing mortality rates after 5-8 years of life. Other species were characterized by intermediate IAM values (0.42 - 0.46 in *Bufo* spp. to 0.67 in *R. macrocnemis*).

RR was high for most species except *R. macrocnemis* and, especially, male *B. verrucosissimus*. In these two species, intermediate or low mortality rates correlated with a uniform distribution of mortality throughout different age classes. The shape of the age distribution curves of female *R. macrocnemis* and male *B. verrucosissimus* were almost congruent in both years of observation, though the curves of 1993 were shifted one class unit to the right.

Summarizing our data, the following conclusions can be drawn:
1. The minimum age of maturation is two years for most Anura but can be higher in species with low growth rates after metamorphosis. In most species, the difference between the youngest and the oldest age of maturation does not exceed one year.
2. For a given climatic zone, maximum age of maturation and mean age of adults are species-specific values, related rather with the taxonomic position of the species than with its ecological peculiarities. Longevity is higher in late-maturing species.
3. Population turnover rates are usually higher in early-maturing than in late-maturing species. Nevertheless, the shape of the survival curve is not correlated with the age of maturation. Intraspecific annual variation of age structure and composition of age cohorts can be higher than interspecific differences.

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