

A long-term study on the population ecology of the moor frog (*Rana arvalis*) in Moscow province, Russia

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Eine Langzeitstudie zur Populationsökologie des Moorfrosches (*Rana arvalis*) in der Provinz Moskau, Russland

In der Langzeitstudie (1987–2007) einer *Rana arvalis*-Population in der Provinz Moskau standen die Körpergröße der Männchen und Weibchen und deren altersabhängige Fortpflanzung im Mittelpunkt. Die zwischen dem Eidurchmesser und den Körpergrößen abhängigen Fortpflanzungserfolgen bestehenden Korrelationen schwächten sich mit zunehmendem Alter der Weibchen ab. Hingegen bestand eine positive Allometrie zwischen der Körperlänge und der Fekundität (Eizahl). Gerichtete interannuelle Änderungen der Körperlänge und der Fortpflanzungsparameter gingen einher mit einer Abnahme der reproduzierenden Individuen der Population. Die Überlebensrate geschlechtsreifer Tiere hing von dem prämetamorphen (larvalen) Überleben ab und war in den früheren Untersuchungsjahren mit besseren aquatischen Lebensbedingungen größer. Deshalb wurde sowohl bei hoher als auch bei niedriger Ausgangsgröße der Jungtier-Kohorten eine abnehmende Nettofortpflanzungsrate (R_0) ermittelt. Der Anstieg des Nachwuchses übte einen starken Einfluss auf R_0 aus, und zwar über den Rückgang der prämetamorphen Überlebensrate und in geringerem Umfang über die Abnahme der Körperlänge und Fekundität der drei- und vierjährigen Weibchen. Die Änderungen der jährlichen Anzahl reproduzierender Weibchen waren ziemlich abrupt. Im Zeitraum von 1992 bis 1998 wurde eine generelle Tendenz der Abnahme der Weibchenzahl gefunden, und ihre Anzahl blieb bis zuletzt niedrig. Hauptursache hierfür war eine beträchtliche Verschlechterung der prämetamorphen Lebensbedingungen in den Gewässern. Es wurden ein Sexualdimorphismus der Körperlänge sowie der Wachstums- und Überlebensraten ermittelt. Diese geschlechtsbezogenen Unterschiede blieben auch erhalten bei einem allmählichen Anstieg der Größe der geschlechtsreifen Frösche und einer Abnahme ihrer Überlebensrate, entsprechend der Abnahme der Populationsgröße.

Schlüsselbegriffe: Amphibia, Anura, Ranidae, *Rana arvalis*, Populationsdynamik, Körpergröße, Sexualdimorphismus, Reproduktionsparameter, Überleben, Nettofortpflanzungsrate.

Abstract

A long-term study (1987–2007) on a *Rana arvalis* population in Moscow province focused on body length of males and females, and age-dependent reproductive characteristics. Correlations between egg diameter and reproductive effort with female body length weakened with age, whereas the relationship between body length and fecundity was characterized by positive allometry. Significant directional interannual changes in body length and reproductive characteristics paralleled with a relative decrease of the mature part of the population. The survival of mature females and

males depended on premetamorphic survival, and was higher in earlier study years characterized by more favorable conditions in the aquatic phase. A decrease in net reproduction rate (R_0) and, therefore, a limitation of population growth, was revealed both at relatively high and low levels of initial cohort size. The increase in the estimated recruitment exerts a strong influence on R_0 via the decrease in the premetamorphic survival and, to a lesser extent, via a decrease in body length and fecundity of three- and four-year-old females. Changes in the annual number of breeding females were rather abrupt; however, a general long-term tendency for a decrease in female numbers was observed from 1992 to 1998, and the numbers remained low until present. The main reason for this decrease was a considerable deterioration of premetamorphic conditions, i.e. a decrease in carrying capacity of the aquatic environment. Sexual dimorphism in body length and growth rates (males were larger as a group and in an each given age, so they grew faster), maturation rates (2- or 3-year-old males became mature more often) and survival (males had lower survival relative to the initial cohort size) were revealed. These sexual differences remained present despite a gradual increase in the size of mature frogs, and a decrease of their survival, corresponding to the decrease in population size.

Key words: Amphibia, Anura, Ranidae, *Rana arvalis*, population dynamics, body size, sexual dimorphism, reproductive characteristics, survival, net reproduction rate.

Introduction

Mechanisms of population regulation are traditionally divided into those dependent and independent of population density (for a review see BEGON et al. 1986, HIXON et al. 2002). In amphibians with complex life cycles, the relationship between density-dependent and density-independent factors at different phases of their life cycle has to be taken into account. As a rule, attention is focused on density-dependent factors responsible for negative feedback between mortality rates in the aquatic and the following terrestrial phase (HELLRIEGEL 2000, VONESH & DE LA CRUZ 2002), and the predictions obtained with such models correspond to the observed delayed effects on the following cohort (reducing the total number of eggs laid). In *Rana temporaria*, there is negative feedback between the survival of individuals in the aquatic phase and the net reproduction rate, due to changes in reproductive characteristics and mortality of females (LYAPKOV et al. 2002a, 2002b).

On the other hand, it was suggested 25 years ago that the dynamics of mortality in the aquatic and terrestrial phases of amphibian life cycle depend on the relationship between the carrying capacities of corresponding ecological niches (WILBUR 1980). In a population of *R. japonica* with stable spawning ponds, the main mortality factor at the larval stage was predation by crayfish (MARUNOUCHI et al. 2002). In *R. macrocnemis*, the most important cause of regulation was density-dependent dispersal of metamorphs (TARKHNISHVILI & GOKHELASHVILI 1999). Evidently, the question of relationships between density-dependent and density-independent factors of population regulation in complex life cycle of amphibians needs further research (for review, see HIXON et al. 2002, ALTWEGG 2003).

Brown frog species of the temperate zone are a convenient model object for this type of research. The number of breeding adults in a population may reach thousands of

individuals (MANTEIFEL & BASTAKOV 1989, ISHCENKO 1999, LYAPKOV 2005a), but they usually breed in relatively small, often temporary ponds. Therefore such populations may be characterized by a high initial density, and large numbers of metamorphs emerged from spawning ponds. Therefore, density-dependent number regulation may operate in both aquatic and terrestrial phases of the life cycle. Moreover, brown frogs demonstrate high intra-population variation in the number of breeders and their reproductive characteristics between cohorts (ISHCHENKO 1999, 2003, LYAPKOV et al. 2001a, 2001b, 2002a, 2002b, LYAPKOV 2005a). Long-term studies of a *R. temporaria* population at the Zvenigorod Biological Station (ZBS) of Moscow State University (55 km westward of Moscow) enabled to reveal a limiting effect of the initial population size on premetamorphic survival (LYAPKOV & SEVERTSOV 1994), as well as on reproductive and demographic characteristics of females (LYAPKOV et al. 2002a, 2002b). It was shown that an increase in the number of breeders causes a decrease in net reproduction rate of a cohort to values below 1.

From 1987 to 1991, I studied reproductive characteristics and the size and age distribution of *R. arvalis* females collected in spawning ponds of the ZBS. In 1989–1991, the metamorphs emerging from the pond were collected and labeled by group marks (using toe clipping, LYAPKOV et al. 2000). During several spring seasons (1992–1996), adult frogs were captured near the same spawning pond, and individuals that had been marked earlier were recorded among them. In this period, the abundance of adult individuals was considerably lower than in previous years. The results of recaptures of females (LYAPKOV et al. 2001a, 2001b) and males (LYAPKOV et al. 2007), as well as the results of comparative studies of 1987–1991 vs 1992–1996 (LYAPKOV et al. 2006) are already published. The same methodology than in 1987–1992 was again used for 1998–2007 in this population. As a result, this long-term study allows us to monitor the dynamics of 15 consecutive cohorts (individuals born between 1982 and 2000), and to evaluate the relationships of demographic and reproductive characteristics with the estimated recruitment, as well as the dynamics of the reproductive part of the population. Generalizing from previous results, I set the following tasks for this paper:

(1) To estimate the scale of variation and long-term trends in body length, age, and reproductive characteristics of frogs from one population; (2) to analyze the dependence of reproductive characteristics on female size, age, and number; (3) to reveal sex differences in body size, age distribution and age-specific survival, as well as long-term trends in the degree of expression of these differences; (4) to determine the pattern of dependence of the net reproduction rate on the initial cohort size, female survival, size and fecundity; and (5) to reveal the significance of density-dependent and density-independent factors of population regulation at pre- and postmetamorphic stages of the life cycle.

Materials and methods

Mature *R. arvalis* (most of them amplexant pairs) were collected in several forest ponds in the vicinity of ZBS during the breeding seasons of 1987–1991 and 1998–2007. In particular, frogs were collected from an overgrowing peat bog (the main spawning

pond of the study population, which provides regular recruitment of metamorphs), and from relatively small permanent and temporary pools. Egg clutches from females were obtained under laboratory conditions (each amplexant pair laid a clutch in a separate aquarium). The body length of both sexes and the fecundity of females were determined. The egg diameter was measured to an accuracy of 0.05 mm using a binocular microscope with an ocular micrometer. Fecundity was estimated from the total volume (or mass) of an egg clutch and the volume (or mass) of its fragment containing a certain number of eggs. Reproductive effort (E) was calculated as $E = F \cdot D^3 / SVL^3$, where F is fecundity, D is egg diameter, and SVL is snout-vent length (CHERDANTSEV et al. 1997). This index shows the volume of the clutch relative to the female body volume. It may be used for evaluating the contribution of a female to reproduction, as its relation to female body length is similar to the relationship of relative clutch mass with female body length. This similarity is confirmed by the fact that correlations between E and relative clutch mass are fairly strong: 0.601 in *R. arvalis* from ZBS (collected between 1998 and 2002), and 0.528 in *R. temporaria* from ZBS (LYAPKOV et al. 2002a). In a *R. arvalis* population from Talitskii region of Sverdlovsk province, the correlation between the two indices was weaker, but still statistically significant ($r = 0.378$, $p < 0.001$, ISHCENKO 2003).

The age of most individuals was determined with skeletochronology, using cross sections of the median part of the third phalanx of the fourth digit on the hind limb stained with Ehrlich haematoxylin. On the basis of its estimated age, a frog was attributed to a certain cohort. Data on the number of annually breeding females (i. e. clutches, see below) and their age distribution enabled to estimate the number of females of each age in each year, and, therefore, female survival relative to the initial number of females in each cohort. The same calculations were performed for males; the sex ratio was taken as 1 : 1. The initial cohort size was calculated as the average fecundity in a given year, multiplied by the number of recorded egg clutches, and the estimated recruitment of females was determined by dividing the resulting value by two.

In 1982, 1983 and 1984, data on number and size of metamorphs emerging from the main breeding pond were obtained. To collect the metamorphs, the pond was encircled with polyethylene drift-fences covering 35 % of the shoreline. Therefore, for the estimation of the number of metamorphs, a correction factor was taken into account. 81 540 metamorphs emerged in 1982, 156 160 in 1983, and 290 270 in 1984. Using these data, I calculated premetamorphic survival in each of the three cohorts, and the survival on each age class of mature frogs relative to metamorph number.

From 1989 to 1991 metamorphs emerging from the main breeding pond were also group-marked to provide information about their birth year. A total of 12 113 juveniles were marked in 1989, followed by 4 311 in 1990, and 476 in 1991 (for details see LYAPKOV et al. 2000, 2001a, 2001b). Between 1992 and 1996, frogs entering the breeding pond were captured to identify marked individuals among them. Egg clutches from recaptured marked females were obtained in the laboratory. Taking into account that all marked females in 1992 were represented only by three-year-olds, the fecundity in that year was additionally determined by analyzing a sample of clutches from natural spawning ponds. Some females began to breed at the age of two years, although even

three-year-old females were not necessarily involved in breeding (LYAPKOV et al., 2001a, 2001b). Therefore, to estimate the average fecundity of three-year-old females in the cohorts of 1989–1991 more correctly, their average fecundity was multiplied by a correction factor calculated as the ratio between the total number of females that reached the age of three years in a given cohort, and the number of three-year-old females that arrived for breeding (for details see LYAPKOV et al. 2001a, 2001b).

Based on these data, it was only possible to trace the fate of each cohort from determining the number of eggs to the last breeding of mature females, but not of each individual frog. Therefore, I estimated the following population-ecological parameters based on life-tables of each cohort. I calculated the survivorship up to a given age, and the net reproduction rate R_0 (the number of progeny produced throughout the life span of a given cohort recalculated per female) as

$$R_0 = \sum l_x m_x,$$

where m_x is an average fecundity of the age class x (recalculated per female), and l_x is the proportion of individuals that reached the age x relative to the estimated recruitment of females in the cohort (BEGON et al. 1986).

The number of mature females in the *R. arvalis* population was estimated using annual (1982–2007) censuses of egg clutches in all sites used for spawning, which can be divided into three types: (1) one large permanent pond (surface area 5450 sq.m), that contained 40 % to 70 % of all clutches, (2) about ten less stable and smaller ponds (with approximately the same total surface) and (3) numerous shallow desiccating pools (with the total surface of an order lower than of all permanent ponds). Most of these sites are in forests near the frog terrestrial hibernation habitats (for details, see LYAPKOV et al., 2006).

The data were processed using Excel spreadsheets and the STATISTICA 6.0 program package.

Results and discussion

Long-term number dynamics in breeding females

According to long-term censuses of egg clutches between 1982 and 1997 (fig. 1), the number of mature female *R. arvalis* had three peaks with subsequent declines, with the last decline resulting in lower numbers than in all previous years. From 1998 to 2007, the population size fluctuated at a lower level. This considerable decrease of numbers is probably explained by an increasing anthropogenic impact, decreasing surface area of the main breeding pond, and an introduction of the fishes *Carassius* sp. and *Percottus glenii* (for details, see LYAPKOV 2005a).

According to these long-term trends, I distinguished three periods of population changes: first – from 1982 to 1991, second – from 1992 to 1997, and third – from 1998 to 2007. Sets of samples from these three periods are compared below.

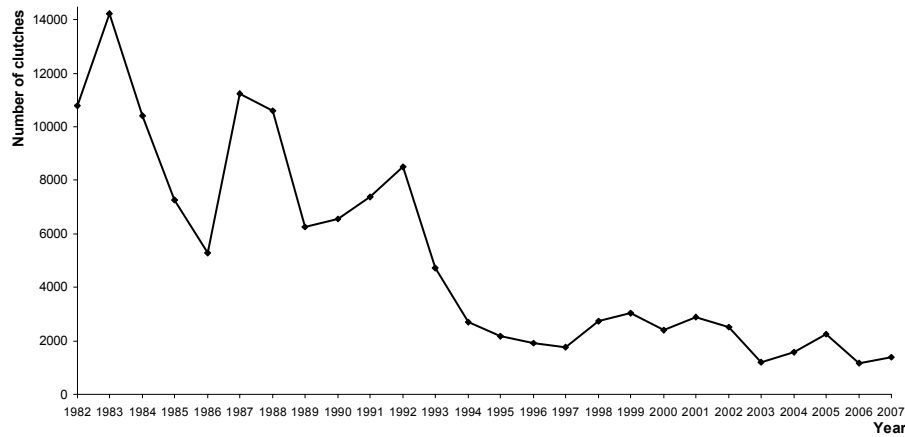


Fig. 1: Long-term dynamics of the annual numbers of breeding females in a *Rana arvalis* population from the Zvenigorod Biological Station.
Langzeitdynamik der jährlichen Anzahl reproduzierender Weibchen in der *Rana arvalis*-Population an der Biologischen Station Zvenigorod.

Sex differences in size and age

Body length. Mature individuals varied markedly in size; their body length ranged from 40 to 64 mm in females, and from 44 to 65 mm in males. In both sexes, the annual average values were low in the first years of observation, and increased in later years; this was the case despite females being only represented by three-year-olds in 1992, and only three- and four-year-olds in 1993, while in period 1 their age ranged from three to nine years. Correspondingly, the frequencies of larger individuals increased from period 1 to period 3 (fig. 2 a, b), and female body length differed significantly between the three periods (tab. 1). In males, the average body length for period 1 was significantly lower than in periods 2 and 3 (two-way ANOVA with post-hoc multiple comparisons, tab. 2).

The frequency of relatively large individuals was higher in males than in females (fig. 2a, b), and male average body length was significantly higher in each period as well as in the whole sample. Moreover, males within each period were larger than females in each age, which can only be explained by a higher male annual increment in body length.

Age composition. In general, the age distribution was positively skewed, differing from normal distribution. The minimal age in females (fig. 2c) was two years (only two individuals with the minimal body length of 45 mm). The maximal age identified was ten years (with a body length of 61 mm). In period 1, the majority of females bred for the first time after the fourth hibernation, and three-year-old females were less frequent than five-year-old females. During periods 2 and 3, 4-year-old individuals were the modal age class; however, the proportion of 3-year-old frogs considerably increased and exceeded the proportion of 5-year-olds. The average age for period 1 was significantly higher than averages for periods 2 and 3 (4.45, 4.04 and 3.94 respectively).

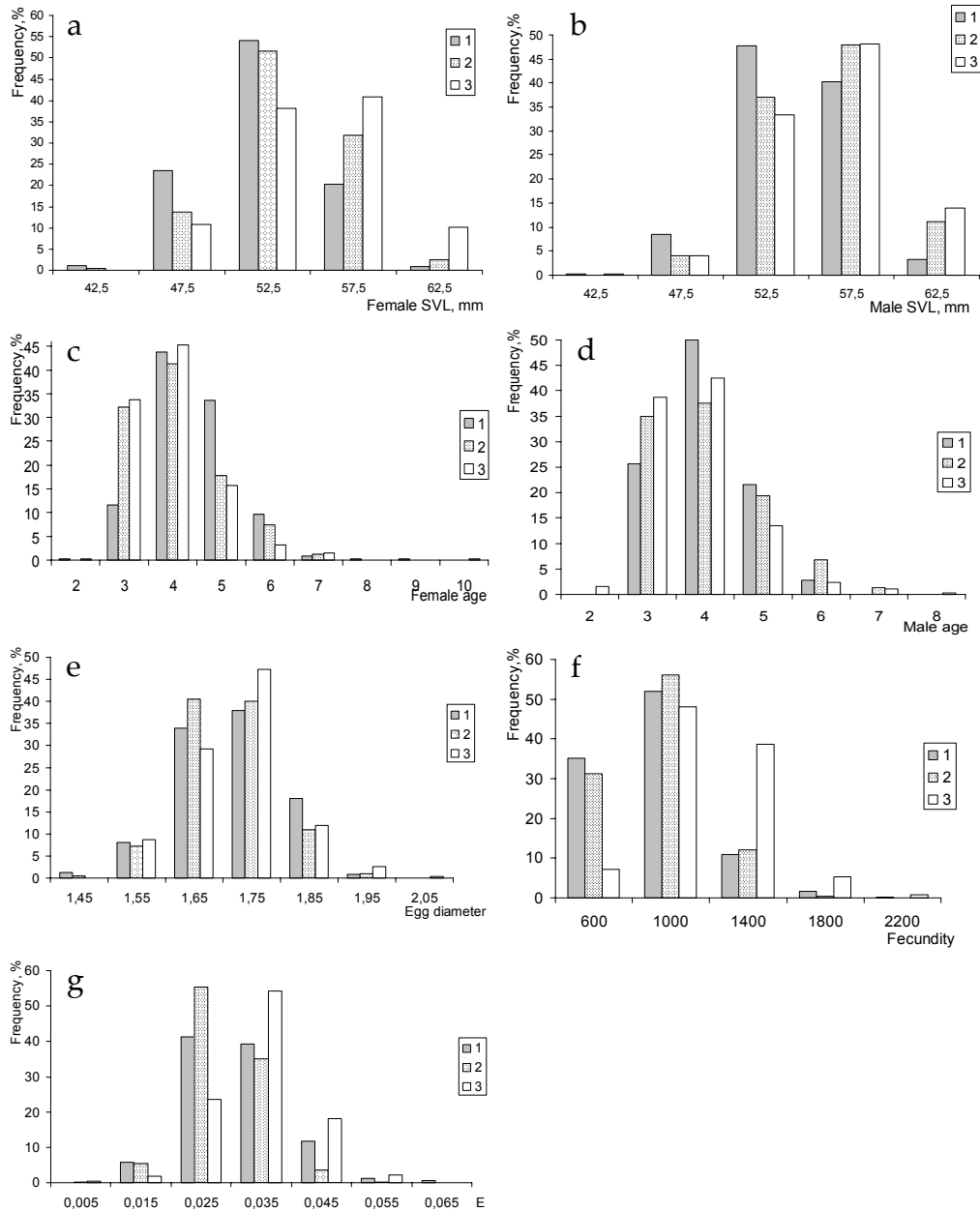


Fig. 2: Frequency distributions of various characteristics of breeding *Rana arvalis*: (a) female body length, (b) male body length, (c) female age, (d) male age, (e) egg diameter, (f) fecundity, and (g) reproductive effort. Grey columns = period 1, stippled columns = period 2, white columns = period 3. Häufigkeitsverteilungen unterschiedlicher Parameter reproduzierender Moorfrösche: (a) Körperlänge der Weibchen, (b) Körperlänge der Männchen, (c) Alter der Weibchen, (d) Alter der Männchen, (e) Eidurchmesser, (f) Fekundität und (g) Reproduktionserfolg. Graue Säulen = 1. Periode, punktierte Säulen = 2. Periode, weiße Säulen = 3. Periode.

Tab. 1: Average values (\bar{x}) and variation coefficients (CV, %) of body length (SVL), and reproductive characteristics of *Rana arvalis* in three different periods of the study (1982 to 1991, 1992 to 1997, and 1998 to 2007).

Durchschnittswerte (\bar{x}) und Variationskoeffizienten (CV, %) der Körperlänge (SVL) und Reproduktionsparameter von Moorfröschen in den drei Untersuchungsperioden (1982–1991, 1992–1997, 1998–2007).

Period	Age	Female SVL			Male SVL			Fecundity		Egg diameter		Reproductive effort	
		n	\bar{x}	CV	n	\bar{x}	CV	x	CV	x	CV	x	CV
1 1982–1991	3	53	50.64	6.64	114	53.21	5.32	824	29.06	1.66	4.99	0.028	22.71
	4	201	52.07	5.81	221	54.89	5.44	935	29.99	1.69	5.06	0.031	26.20
	5	154	53.71	5.54	96	56.87	3.76	915	25.93	1.75	4.34	0.031	24.20
	6	44	54.89	4.45	12	58.42	2.87	919	31.05	1.77	3.78	0.031	30.87
	all	485	52.73	6.22	480	54.87	5.83	916	28.89	1.71	5.22	0.031	25.78
2 1992–1997	3	130	52.07	5.76	103	54.00	4.84	895	25.99	1.67	4.79	0.030	22.39
	4	167	53.89	4.98	111	55.96	5.07	908	24.19	1.69	3.67	0.028	21.34
	5	72	56.03	4.31	57	58.07	4.66	970	23.88	1.73	3.48	0.028	21.98
	6	30	57.07	4.22	20	58.80	3.92	943	20.72	1.78	3.39	0.029	19.13
	all	449	53.98	6.36	589	56.29	5.83	923	25.37	1.70	4.61	0.029	21.46
3 1998–2007	3	129	52.30	5.57	149	54.35	5.05	1057	22.30	1.65	4.57	0.033	21.93
	4	173	56.04	4.89	164	57.91	5.09	1193	22.30	1.72	4.47	0.035	20.69
	5	60	59.28	4.59	52	59.34	4.70	1267	19.92	1.78	3.73	0.035	18.25
	6	12	60.10	4.06	9	59.35	5.42	1332	25.50	1.80	3.92	0.036	27.40
	all	382	55.49	6.98	435	56.56	6.30	1176	23.25	1.72	5.21	0.034	21.13

Six 2-year-old males with a minimal body length of 49.5 mm were collected with a maximal age of eight years. The modal age class, as in females, was represented by 4-year-old individuals; in all three periods, the proportion of 3-year-olds was higher than 5-year-olds (fig. 2d).

In each period, the frequency of 3-year-olds was higher in males than in females, meaning that males reproduce earlier, whereas the frequencies of individuals older than 4 years were lower. Consequently, in periods 1 and 3 the mean age in males (tab. 1) was lower than in females (in period 2 the difference was not significant), despite their higher average body length. Average male age of in periods 1 and 2 was significantly higher than in period 3 (4.01, 4.02 and 3.81 respectively). This means that males, as well as females, are involved in reproduction at earlier ages in response to the decrease in population size.

Reproductive characteristics, their among-age variation and long-term trends

Egg diameter (fig. 2e, tab. 1). This character varied from 1.4 to 2.0 mm. Its variation (see CV in tab. 1) was close to that of body length and lower than variation in age, fecundity, and reproductive effort. The variation between the three periods was less distinct than the variation in body length, and only the difference between periods 2 and 3 was significant.

Fecundity (fig. 2f, tab. 1). The minimum and maximum recorded values of fecundity were 350 and 2138 eggs. On the whole, the positively skewed distribution of this characteristic differed significantly from a normal distribution (Kolmogorov-Smirnov

test for normality: $d = 0.058$, $p < 0.01$). Compared to other characteristics, fecundity showed the highest variation (see CV tab. 1). The difference between periods 1 and 2 was not significant, but both average values were significantly lower than in period 3.

Reproductive effort (fig. 2g, table 1). This index was characterized by a positively skewed distribution away from the normal distribution (Kolmogorov-Smirnov test for normality: $d=0.042$, $p<0.05$), and a high variation. As in the case of fecundity, the average value of period 3 was significantly higher than average values of periods 1 and 2.

The above-mentioned increase in body length from period 1 to period 3 in both sexes occurred within each age, and similar increases were also revealed for reproductive characteristics (except for egg diameter, tab. 1). To estimate the significance of age groups and study periods on body length and reproductive characteristics, I used two-way ANOVA (factors »age« and »period«). The factor »period« had three levels, and the factor »age« had four levels (three, four, five and six years). Besides the effects of age and period, the long-term changes in body length (see above) may have considerable influence on reproductive characteristics. Thus, analysis of covariance (ANCOVA) was used with body length as a covariate.

Period and age had significant effects on body length, fecundity, and egg diameter (tab. 2); age had a non-significant effect only on reproductive effort. After adding body length as a covariate in the ANCOVA (tab. 3), the effect of period on egg diameter became non-significant; its effect on reproductive effort became weaker and remained non-significant. At the same time, ANOVA revealed a significant effect of the interaction of these two factors (tab. 2), providing evidence for an increase in reproductive characteristics with aging in different periods. In the ANCOVA, the interaction effect on fecundity became non-significant, also indicating that these characteristics are influenced by body length rather than age.

Tab. 2: The influence of factors »age« and »period« on body length and reproductive characteristics (two-way ANOVA, cross-classified design).

Der Einfluss der Faktoren »Alter« und »Periode« auf die Körperlänge und Reproduktionsparameter (zweiseitige ANOVA, »cross-classified«-Ansatz).

Character	Factor	d.f.	MS	F	p
Female SVL	Age	3	1149.7	141.6	<0.000
	period	2	841.5	103.6	<0.000
	Age*period	6	67.0	8.3	<0.000
Male SVL	Age	3	930.2	120.8	<0.000
	period	2	114.6	14.9	<0.000
	Age*period	6	27.3	3.5	0.002
Fecundity	Age	3	736896	11.9	<0.000
	period	2	4841584	78.4	<0.000
	Age*period	6	179152	2.9	0.008
Egg diameter	Age	3	0.4625	82.8	<0.000
	period	2	0.0265	4.7	0.009
	Age*period	6	0.0233	4.2	<0.000
E	Age	3	0.0001	1.7	0.159
	period	2	0.0015	29.6	<0.000
	Age*period	6	0.0001	2.2	0.038

Tab. 3: The influence of factors »age« and »period« on reproductive characteristics in the moor frog *R. arvalis* (ANCOVA with SVL as a covariate).

Der Einfluss der Faktoren »Alter« und »Periode« auf die Reproduktionsparameter bei den Moorfröschen (ANCOVA mit Kopf-Rumpf-Länge als Kovariate).

Character	Factor	d.f.	MS	F	p
Fecundity	SVL	1	17358739	376.3	<0.000
	Age	3	329974	7.2	<0.000
	period	2	1561575	33.9	<0.000
	Age*period	6	72751	1.6	0.150
Egg diameter	SVL	1	0.64585	129.0	<0.000
	Age	3	0.12571	25.1	<0.000
	period	2	0.00758	1.5	0.220
	Age*period	6	0.01572	3.1	0.005
E	SVL	1	0.00016	3.0	0.082
	Age	3	0.00004	0.8	0.475
	period	2	0.00136	26.2	<0.000
	Age*period	6	0.00011	2.2	0.041

Strong differences in age compared to the effects of sex- and locality-related differences were also observed in a study on the relationship between geographic and intrapopulation variation in body length (ISHCHENKO 1999). In another long-term study, VERSHININ (2002) revealed considerable differences in the annual average fecundity between some urban and suburban *R. arvalis* populations in the city of Yekaterinburg, and showed that population fluctuations occurred synchronously. This result indicates the significance of environmental effects on fecundity development rather than possible effects of migration between spatially separated populations.

Relationships between reproductive characteristics, body length and age

To present a general relationship between reproductive characteristics and female body length and age, all study years were pooled. A highly significant positive correlation with body length was revealed for fecundity and egg diameter, but not for reproductive effort (tab. 4). The dependence of reproductive characteristics on female body size was positive in the case of fecundity, and negative in the cases of egg diameter and reproductive effort (tab. 4). However, only the dependence of fecundity on female body length is really allometric. The curve of fecundity as a function of SVL continues to rise ($b > 1$), i.e. the larger the absolute female body size, the greater the proportion of resources that the individual allocates for reproduction. Remarkably, this pattern becomes stronger in later years, and reaches its maximum in period 3 (see tab. 4), connected with the relatively large size of females.

Body length and egg diameter showed a positive correlation with age (tab. 4, see also tab. 1). The correlation of fecundity with age was non-significant in period 1, but, like the correlation of fecundity with body length, became significant in periods 2 and 3. The correlation of reproductive effort with age was non-significant, and did not change among periods (tab. 4).

Along with calculating regressions and pairwise correlations between certain characters, we used principal component analysis (PCA) in order to obtain a more general

Tab. 4: Reproductive characteristics, body length (SVL) and age in *Rana arvalis* females (pooled data over each of three study periods). The regression equation is defined as reproductive characteristic = body length^b.

Reproduktionseigenschaften, Körperlänge (SVL) und Alter bei Moorfrosch-Weibchen (zusammengefasste Daten über jede der drei Untersuchungsperioden). Die Regressionsgleichung ist definiert als Reproduktionseigenschaft = Körpergröße^b.

Related characters	Period	Correlation		Regression
		r	n	b
Fecundity with SVL	1	0.468	483	1.720
	2	0.527	447	1.712
	3	0.560	277	1.758
Egg diameter with SVL	1	0.488	484	0.136
	2	0.474	447	0.134
	3	0.515	277	0.135
E with SVL	1	0.104	483	-0.876
	2	0.037	447	-0.891
	3	0.027	277	-0.839
Fecundity with age	1	0.035	459	
	2	0.111	402	
	3	0.311	277	
Egg diameter with age	1	0.419	459	
	2	0.383	402	
	3	0.495	277	
E with age	1	0.026	459	
	2	-0.056	402	
	3	0.074	277	

picture of relationships between female body length, age, and reproductive characteristics, applying variance-maximizing rotation of the normalized factor loadings («varimax normalized»). Factor loadings between traits (joint contributions to each of the four PCs) proved to be similar in females of different ages, allowing us to pool frogs of all ages, as well as to add age to the set of analysed characters. The analysis of different periods produced similar results (tab. 5). Fecundity strongly correlated with reproductive effort, contributing mainly to the first PC. Other characters usually made the largest contribution to the second, third or fourth PC. Age did not demonstrate strong correlations with any other parameter. The lack of strong correlation between body length and fecundity can be explained by the relatively small size in adults (relative to some other brown frog species, see LYAPKOV 2008). The relationship between fecundity and egg diameter has two components (tab. 5): factor loadings to the first PC show a weak positive correlation, whereas for the third PC, with a small contribution of body length but the maximum contribution of egg diameter, this correlation is negative. This is confirmed by differences between two correlation coefficients for fecundity and egg diameter: the parametric correlation coefficient equals zero (0.094), while the partial correlation coefficient, with the effect of body length being controlled for (corresponding to a component independent of general body size), is weakly but significantly negative (-0.228).

At the same time, the relationships between the characteristics varied slightly because of differences between the three periods. The relation between both fecundity and age

Tab. 5: Principal components analysis (factor loadings, maximum values are underlined) on the relationships between different characteristics of *Rana arvalis* females. Prp. total – the proportion of the variation, explained by a given principal component.

Hauptkomponentenanalyse (Gewichtung der Faktoren, Maximalwerte sind unterstrichen) der Beziehung zwischen verschiedenen Eigenschaften von Moorfroschweibchen. Prp. total = Variationsanteil, erklärt durch eine gegebene Komponente.

Period	Character	PC1	PC2	PC3	PC4
1	SVL	0.130	<u>0.939</u>	0.248	0.198
	Age	-0.008	0.169	0.189	<u>0.967</u>
	Fecundity	<u>0.903</u>	0.398	-0.131	0.000
	Egg diameter	0.096	0.226	<u>0.947</u>	0.209
	E	<u>0.960</u>	-0.087	0.256	0.000
	Prp. total	0.353	0.226	0.215	0.204
2	SVL	0.087	<u>0.935</u>	0.210	0.272
	Age	-0.024	0.231	0.178	<u>0.956</u>
	Fecundity	<u>0.857</u>	0.481	-0.141	0.047
	Egg diameter	0.104	0.166	<u>0.963</u>	0.183
	E	<u>0.956</u>	-0.117	0.254	-0.054
	Prp. total	0.334	0.240	0.218	0.205
3	SVL	0.032	<u>0.896</u>	0.276	0.345
	Age	0.045	0.287	0.228	<u>0.929</u>
	Fecundity	<u>0.784</u>	0.580	-0.125	0.147
	Egg diameter	0.175	0.189	<u>0.937</u>	0.236
	E	<u>0.948</u>	-0.092	0.301	-0.012
	Prp. total	0.309	0.253	0.223	0.212

with body length reached its maximum in period 3, but I did not find such a relationship for egg diameter and body length. Therefore, some considerable changes were connected with the decrease in numbers. The growth of fecundity at low population size was due to its increased relation with body length. In turn, body length becomes more related to age, as a result of increased annual growth after maturation (see above).

Survival after reaching maturity

Survival of mature females relative to their estimated recruitment (see Methods) considerably varied between periods (fig. 3), and also between cohorts. For example, four- and five-year-old females born in 1982–1986 and 1989 had higher survival than cohorts born in 1990 and 1991. This was most probably explained by their relatively high premetamorphic survival: 1.63 %, 2.56 %, and 7.72 % in 1982, 1983, and 1984, respectively (LYAPKOV & SEVERTSOV 1994), and 1.89 % in 1989 (Lyapkov et al. 2001b). Females of all ages in the cohort of 1991 had the lowest survival (fig. 4). This could be due to low premetamorphic survival (only 0.06 % in 1991) resulting from deterioration of conditions for larval development in the spawning water body (for details, see LYAPKOV 2005a). Female survival was lowest in period 2 (fig. 3), when the mature female number strongly declined, and maximal in period 1, when female numbers were the highest. Thus, the survival did not depend on numbers of mature frogs.

A similar lack of correlation between initial cohort size and survivorship was demonstrated for males (fig. 3). In addition, within each period survival in males of each age

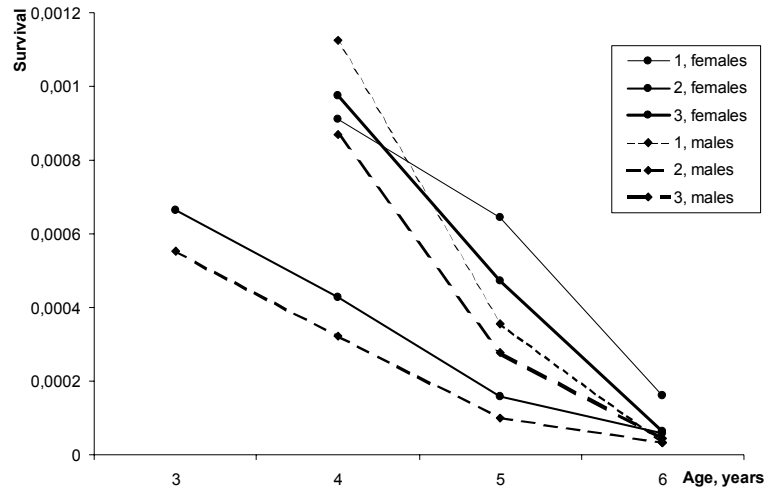


Fig. 3: Survival of adult *Rana arvalis* relative to the initial cohort size. Pooled data on each of three periods (indicated as 1, 2 and 3) are presented.

Überleben adulter Moorfrosche in Beziehung zur anfänglichen Kohortengröße. Zusammengefasste Daten für drei Untersuchungsperioden (angegeben als 1, 2 und 3) werden präsentiert.

was lower than in females (an exception was 4-year-old males in period 1). Lower survival of males after maturation is, apparently, common for most temperate Anura species (see review in LYAPKOV et al. 2007).

It should be noted that the source of relatively low survival of adult frogs until their first breeding may not only be due to premetamorphic, but also low postmetamorphic survival caused by relatively late maturation. A comparison with the ecologically similar *R. sylvatica* confirms this conclusion: in southern populations, females reach maturity after the first or second hibernation, and the survival of one- or two-year-old females averages 0.0119 and 0.0043, respectively (BERVEN 1990), whereas the survival of three-year-old females (0.00048) is close to that observed in *R. arvalis* (0.00066).

Survival estimates for female *R. arvalis* from the Talitskii region (ISHCHENKO 1999) are close to our estimates for five-year-olds, but higher than those for older individuals. A higher frequency of six-year and older females reflects a longer life span in this population, where the season of activity is shorter than in the Moscow province. There is also some indirect evidence that the survival of older individuals is higher in northern or mountain populations. This concerns primarily higher frequencies of older frogs, and higher maximum age reported for *R. arvalis* (ISHCHENKO 1999, LYAPKOV 2005b), as well as *R. temporaria*, *R. macrocnemis* and *R. amurensis* (ISHCHENKO 1999).

The results of censuses of emerging metamorphs in 1982–1984 years, as well as metamorph censuses combined with group marking (1989–1991), allowed the direct estimation of postmetamorphic survival in six different cohorts. Among males and females of the 1989–1991 cohorts, survival was maximal in males of 1991, until the age of five years (fig.4). However, in the cohorts of 1989 (3- and 4-year-old frogs) and 1990 (all ages), female survival was higher. The joint sample of all cohorts revealed a higher male survival in ages of 3 and 4 years due to high survival of the 1991 cohort, and a higher female survival from the age of 5 (fig. 4).

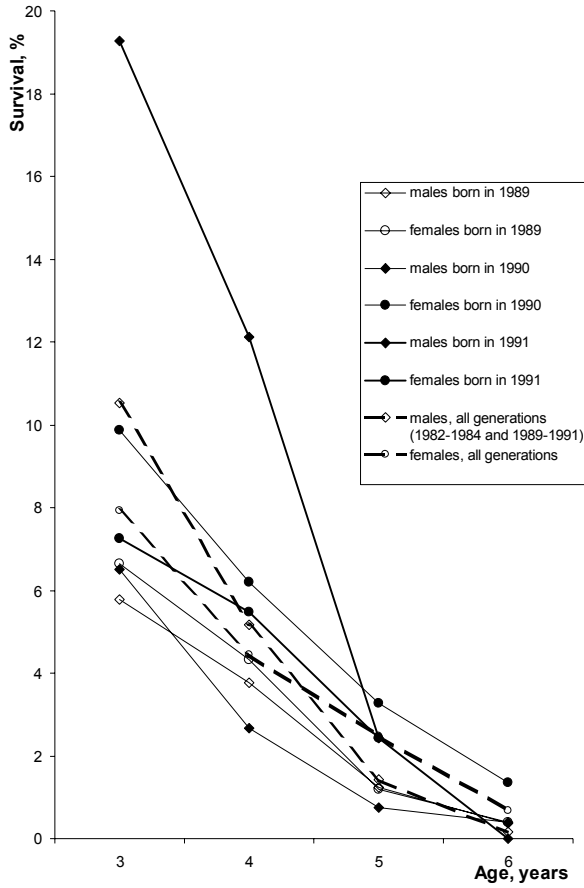


Fig. 4: Survival of adult *Rana arvalis* relative to the number of emerged metamorphs of a given cohort. The data on cohorts born in 1989–1991 and the pooled data are presented.
Überleben adulter Moorfrösche im Verhältnis zur Anzahl metamorphosierter Tiere einer gegebenen Kohorte. Daten über Kohorten, die 1989–1991 an Land gingen und zusammengefasste Daten werden präsentiert.

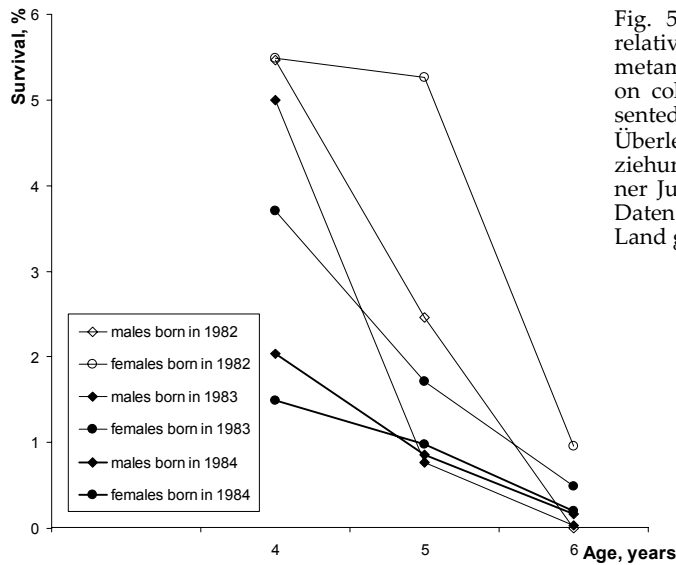


Fig. 5: Survival of adult *Rana arvalis* relative to the number of emerged metamorphs of a given cohort. The data on cohorts born in 1982–1984 are presented.
Überleben adulter Moorfrösche in Beziehung zur Anzahl an Land gegangener Jungtiere einer gegebenen Kohorte. Daten über Kohorten, die 1982–1984 an Land gingen, werden präsentiert.

The survival of both sexes from the 1982–1984 and 1989–1991 cohorts negatively correlates with the number of metamorphs (fig. 5). The maximal metamorph number in 1984 corresponded to their minimal survival, and the minimal metamorph number in 1982 matched with the maximal survival of adult frogs. This relationship was stronger in females ($r_s = -0.714$; $n = 6$; $p = 0.11$) than in males ($r_s = -0.486$; $n = 6$; $p = 0.33$). The revealed sexual differences in survival cause lower frequencies of males older than 4 years, and may cause their earlier first reproduction.

Variation of net reproduction rate and its relationship with population dynamics

It should be noted that the contributions to R_0 of females of different ages within each cohort (tab. 6) generally corresponded to their survival (fig. 3), except for three-year-olds (most of them are not yet involved in breeding). In period 1, four-year-old females made the highest contribution, followed by five-, three-, and six-year-olds. The proportion of three-year-old females breeding for the first time increased considerably in periods 2 and 3, and so did their contributions to R_0 . A different relationship was reported for *R. sylvatica* (BERVEN 1990): among mature females, the highest survival was revealed in two-year-olds and, therefore, their contribution to R_0 constituted 70–90 % in different cohorts.

The highest and lowest R_0 values were represented by cohorts born in 1995 and 1991, respectively (fig. 6). At a low initial cohort size, both high and low R_0 values were observed. During population growth, R_0 gradually decreased, but, limits of population growth (of R_0 value) occurred both at relatively high and low initial cohort size.

Tab. 6: Contributions (%) of female *R. arvalis* with different ages to the net reproduction rate. For each period, the unweighted averages are given.

Beiträge (%) der Weibchen unterschiedlichen Alters zur Nettoreproduktionsrate. Für jede Periode werden die ungewichteten Mittel angegeben.

Generation (year of birth)	Age (years)				
	3	4	5	6	7
1982	10.14	49.89	29.78	9.59	0.60
1983	9.36	41.53	38.91	9.71	0.49
1984	9.68	51.78	31.75	6.42	0.37
1985	7.40	47.76	34.10	10.06	0.69
1986	7.42	44.11	38.84	9.08	0.55
Average for period 1	8.80	47.01	34.67	8.97	0.54
1989	35.84	46.20	13.52	4.44	
1990	29.35	39.47	21.60	9.57	
1991	23.59	51.04	25.37		
Average for period 2	29.59	45.57	20.17	7.01	0.00
1994	26.38	35.99	26.35	5.94	5.34
1995	24.40	52.51	18.12	3.87	1.10
1996	23.10	28.63	38.92	4.99	4.35
1997	29.64	38.82	17.07	8.01	6.47
1998	30.15	66.01	3.35	0.49	
1999	38.78	51.67	8.34	1.21	
2000	29.98	44.43	22.34	3.25	
Average for period 3	28.92	45.44	19.21	3.96	4.32

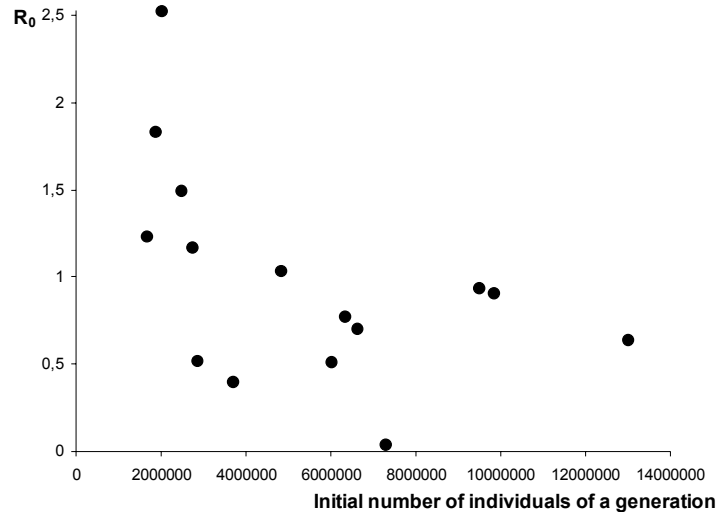


Fig. 6: Net reproduction rate (R_0) and initial cohort size.
 Nettoreproduktionsrate (R_0) und Ausgangsgröße der Kohorten.

High R_0 values for given initial cohort size (in 1995, 1994, 1986, 1984, 1982 and 1983, see fig. 6.) apparently corresponded with density-dependent regulation, while lower R_0 values (in 1990, 1991, 1999 and 2000) were the results of low premetamorphic survival due to density-independent mortality.

Variations in survival rate, body length, and reproductive parameters between cohorts also allowed us to estimate the contributions of each of these characteristics to R_0 . I used data on three-, four-, and five-year-old females (taking into account their maximal contribution to R_0), and calculated rank correlation coefficients between each of the above characters and R_0 , as well as initial cohort size (tab. 7). As expected, the correlation between R_0 and the survival of four- and five-year-old females was significantly positive.

The relatively weak but significant correlation of R_0 with the initial cohort size (tab. 7) indicates a limited amount of density-dependent population regulation. The observed relationship may be caused by a threshold effect, when the growth of the initial number (and density) leads primarily to a decrease in premetamorphic survival; thus, determining the number of metamorphs, it has an indirect effect on female survival, with most females reaching maturity only after the third or fourth hibernation. However in period 3, when there were no high initial cohort sizes, this correlation did not weaken (tab. 7). Moreover, the ponds survey in the middle of June 2001 showed that tadpoles were predated at early larva stages by rotan fish (*Perccottus glenii*) in most parts of main breeding pond (LYAPKOV unpubl. data). These results contradict to the assumption of a threshold effect, and the role of density-dependent population regulation remains open. At the same time, the positive correlation of initial cohort size with the number of females surviving 3 and 4 years indicates the existence of some regulation. The strong negative correlations of the estimated recruitment with body length of three- and four-year-old females and its fecundity suggest a negative influence of the initial population density on somatic growth and reproduction. Thus, an increase

Tab. 7: Relationships between initial cohort size (N_0 , the number of eggs laid) and net reproduction rate (R_0) with average values of body length (SVL), egg diameter (D), fecundity (F), and reproductive effort (E) and female survivorship (surv) of the cohort, and the numbers of mature females survived up to three years (numb₃) and up to four years (numb₄). Subscript indices (3, 4, 5) show female age; r_s is the Spearman rank correlation coefficient.

Die Beziehungen zwischen der Ausgangsgröße der Kohorten (N_0 , Anzahl der abgelegten Eier) und der Nettoerproduktionsrate (R_0) mit der durchschnittlichen Körpergröße (SVL), Eidurchmesser (D), Fekundität (F), Reproduktionserfolg (E) und Überlebensrate der Weibchen (surv) der Kohorte, sowie der Anzahl der reproduzierenden Weibchen bis zu einem Alter von drei (numb₃) und vier Jahren (numb₄). Tiefgesetzte Indices (3, 4, 5) geben das Alter der Weibchen an; r_s = Spearman Rangkorrelationskoeffizient.

Characteristic	n	Correlation with N_0		Correlation with R_0	
		r_s	p	r_s	p
R_0	15	-0.611	0.016		
R_0 (for period 3 only)	7	-0.750	0.052		
SVL ₃	12	-0.741	0.006	0.336	0.286
SVL ₄	14	-0.754	0.002	0.200	0.493
D ₃	11	-0.518	0.102	0.291	0.385
D ₄	12	-0.175	0.587	0.147	0.649
F ₃	11	-0.855	0.001	0.445	0.170
F ₄	12	-0.846	0.001	0.699	0.011
E ₃	11	-0.900	0.000	0.545	0.083
E ₄	12	-0.476	0.118	0.566	0.055
surv ₄	15	-0.221	0.428	0.836	0.000
surv ₅	14	-0.130	0.659	0.653	0.011
numb ₃	13	0.703	0.007	0.104	0.734
numb ₄	15	0.811	0.000	-0.164	0.558

in the initial cohort size exerts an effect on R_0 by causing a decrease in the pre- and/or postmetamorphic survival (fig. 6) and, to a lesser extent, by resulting in a decrease in the body size (and therefore fecundity) of breeding females.

In addition, the calculated numbers of all adult females three years after metamorphosis positively correlates with premetamorphic survival of the corresponding cohort ($r_s = 0.829$, $p = 0.042$; $n = 6$) and with the numbers of emerged metamorphs ($r_s = 0.771$, $p = 0.072$; $n = 6$). The correlation of these two characteristics with the number of all females four years after metamorphosis is also positive: $r_s = 0.886$, $p = 0.019$ and $r_s = 0.943$, $p = 0.005$, respectively (for details see LYAPKOV et al. 2006). These results may be considered as an indirect evidence of the role of premetamorphic rather than post-metamorphic survival in density-dependent regulation.

The rather unstable pattern of population dynamics in *R. arvalis* over all study years may be determined by pond conditions. Breeding in only one relatively large permanent pond provided effective (but not stable) recruitment to the adult population as long as conditions ensured a relatively high premetamorphic survival. Specific demographic features of the studied population are other factors responsible for the unstable population dynamics. The net reproduction rate in *R. arvalis* was generally higher than that in sympatric and partially syntopic population of *R. temporaria* (LYAPKOV et al. 2006). In addition, *R. arvalis* reaches the maximum reproductive value earlier, and the proportion of females that begin breeding at the age of three is almost two times

higher (47 %) than in *R. temporaria* (26 %, LYAPKOV et al. 2002a). This should enable a rapid increase in initial cohort size, particularly of the reproductive part. This pattern was observed in *R. arvalis* in the period of high population size between 1982 and 1992.

The low number of adult *R. arvalis* observed from 1994 onward was determined primarily by a low premetamorphic survival, which was independent of the initial density which constantly remained at a low level. As a result, the terrestrial part of the population was recruited slowly, and the total annual number of breeding females was low. Their abundance did not increase even despite compensatory mechanisms. So, in cohorts born between 1994 and 1998, the survival, age-specific fecundity, and correspondingly R_0 were in general higher than in cohorts born between 1982 and 1991 (LYAPKOV 2005b). However, until 2007, the observed relatively high values of R_0 were apparently insufficient for an increase in numbers.

Conclusions

In this study, sexual dimorphism in body length and growth was demonstrated for *R. arvalis*. Males were larger as a group and in each given age, and grew faster. Also differences in maturation rates were revealed: 2- or 3-year-old males became mature more often and reproduced earlier. Males also had lower survival relative to the initial cohort size, resulting in lower frequencies of older ages in males. These differences are stable despite the gradual increase of male and female sizes, accompanying the mature frog number decrease. These basic sexual differences are in connection with the variation in the degree of expression of size sexual dimorphism in different localities within the species range (see LYAPKOV, 2008).

The long-term study of the *R. arvalis* population revealed the negative feedback between the initial cohort size and its net reproduction rate (R_0). The initial size of the cohort has a negative effect on survival body length and reproductive characteristics in females. Therefore, the increase in initial cohort size influences R_0 in two ways. Lower R_0 values are recorded during periods of decrease in female survival, absolute fecundity (resulting from a decrease in the body length of females of the corresponding age group), and relative fecundity (independent of body size). On the other hand, higher R_0 values should be observed as a result of an increase in the proportion of older females, in cohorts where a relatively small proportion of individuals has reached maturity and spawned for the first time at the age of three years (see also ISHCHENKO 1999). This duality of the mechanisms, involved in the influence of the initial cohort size on R_0 , may be responsible for the soft density-dependent regulation.

The lower diversity of the permanent breeding ponds of the studied *R. arvalis* population and the considerable decrease in premetamorphic survival resulted in a decrease in carrying capacity of the aquatic habitats. Hence, differences in population regulation between the three periods of the *R. arvalis* population are partly in agreement with Wilbur's (1980) model. Before essential deterioration in conditions of premetamorphic growth and development, high carrying capacity was typical for both aquatic and terrestrial habitats. As a result, adult numbers increased to such an extent that in

the main breeding pond high initial cohort size was attained, and, therefore, the regulation operated in both aquatic and terrestrial phases. After the deterioration of conditions for premetamorphic development, the number of metamorphs will be limited by its low premetamorphic survival, while terrestrial habitats remained »unsaturated«. However, population growth was limited even at low density in aquatic and terrestrial phases of the life cycle. The exact causes, conserving this negative relation between initial cohort size and net reproduction rate, are still unclear.

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References

- ALTWEGG, R. (2003): Multistage density dependence in an amphibian. — *Oecologia* 136: 146–150.
- BEGON, M., D. HARPER & C. TOWNSEND (1986): *Ecology: individuals, populations and communities*. — Oxford (Blackwell).
- BERVEN, K. A. (1990): Factors affecting population fluctuations in larval and adult stages of the wood frog *Rana sylvatica*. — *Ecology* 71: 1599–1608.
- CHERDANTSEV, V. G., S. M. LYAPKOV & Y. M. CHERDANTSEVA (1997): Mechanisms of fecundity formation in *Rana arvalis* — *Zoologicheski Zhurnal* (Russian Journal of Zoology) 76: 187–198 [in Russian].
- HELLRIEGEL, B. (2000): Single- or multistage regulation in complex life cycles: does it make a difference? — *Oikos* 88: 239–249.
- HIXON, M. A., S. W. PACALA & S. A. SANDIN (2002): Population regulation: historical context and contemporary challenges of open vs. closed systems — *Ecology* 83: 1490–1508.
- ISHCHENKO, V. G. (1999): *Population Ecology of Brown Frogs from Russia and Adjacent Territories*. — Doctoral Dissertation in Biology, St. Petersburg (Institute of Zoology, RAS).
- ISHCHENKO, V. G. (2003): The measurement of reproductive effort in amphibians — *Russian Journal of Herpetology* 10: 207–212.
- LYAPKOV, S. M. (2005a): A long-term stationary study of demographic and reproductive characteristics of brown frogs as the basis for evaluation of fitness components — *Proceedings of Zvenigorod Biological Station* 4: 170–187 [in Russian].
- LYAPKOV, S. M. (2005b): Geographical and local variation of reproductive and demographic characteristics in brown frogs. In: N. ANANJEVA & O. TSINENKO (eds): *Herpetologia Petropolitana. Proc. 12th Ord. Gen. Meeting Soc. Eur. Herpetol., St. Petersburg, 2003*, *Russian Journal of Herpetology*, 12 (Suppl.): 187–190. — St. Petersburg.
- LYAPKOV, S. M. (2008): Geographical variation of sexual size dimorphism in the moor frog (*Rana arvalis*) in East Europe. — *Zeitschrift für Feldherpetologie*, Supplement 13: 113–120.
- LYAPKOV, S. M., V. G. CHERDANTSEV, E. M. CHERDANTSEVA & A. S. SEVERTSOV (2000): Survival and growth of brown frog juveniles dispersing from breeding pond — *Entomological Review* 81: S167–S180.
- LYAPKOV, S. M., V. G. CHERDANTSEV & E. M. CHERDANTSEVA (2001a): Structure of relationship between fitness components in life history of *Rana arvalis*: 1. Dynamics of reproductive effort and its components — *Entomological Review* 81: S161–S169.

- LYAPKOV, S. M., V. G. CHERDANTSEV & E. M. CHERDANTSEVA (2001b): Structure of relationship between fitness components in life history of *Rana arvalis*: 2. Dynamics of fitness components — Entomological Review 81: S170–S179.
- LYAPKOV, S. M., CHERDANTSEV, V. G. & E. M. CHERDANTSEVA (2006): Regulation of population numbers in the *Rana arvalis* frog according to the results of long-term observations on the same population — Entomological Review 86: S226–S239.
- LYAPKOV, S. M., V. G. CHERDANTSEV & E. M. CHERDANTSEVA (2007): Sexual differences in growth rate and survivorship after metamorphosis in *Rana arvalis* — Zoologicheski Zhurnal (Russian Journal of Zoology) 86: 501–517 [in Russian].
- LYAPKOV, S. M., M. B. KORNILOVA & A. S. SEVERTSOV (2002a): Structure of variation in reproductive characteristics of *Rana temporaria* L. and their relationship with frog size and age — Zoologicheski Zhurnal (Russian Journal of Zoology) 81: 719–733 [in Russian].
- LYAPKOV, S. M., M. B. KORNILOVA & A. S. SEVERTSOV (2002b): Demographic characteristics and population dynamics of *Rana temporaria* L. — Zoologicheski Zhurnal (Russian Journal of Zoology) 81: 1251–1259 [in Russian].
- LYAPKOV, S. M. & A. S. SEVERTSOV (1994): Effect of the initial number of a generation on the numbers of metamorphs, their size, and dates of emergence in *Rana temporaria* and *R. arvalis* — Zoologicheski Zhurnal (Russian Journal of Zoology) 73: 97–113 [in Russian].
- MANTEIFEL', Y. B. & V. A. BASTAKOV (1989): Amphibians of the lake Glubokoe reserve: numbers and specific behavioral features — Proceedings of Conference on the Herpetofauna of the City of Moscow and Moscow Region: Amphibians and Reptiles, Moscow, 1987: 70–80 — Moscow (Moskovskoe Obshchestvo Ispytateley Prirody) [in Russian].
- MARUNOUCHI, J., T. KUSANO & H. UEDA (2002): Fluctuation in abundance and age structure of a breeding population of the Japanese brown frog, *Rana japonica* Gunther (Amphibia, Anura). — Zoological Science 19: 343–350.
- TARKHNISHVILI, D. N. & R. G. GOKHELASHVILI (1999): Spatial structure and regulation of a population of the brown frog *Rana macrocnemis* in Georgia. — Herpetological Journal 9: 169–145.
- VERSHININ, V. L. (2002): Ecological specificity of amphibian populations. — Advances in Amphibian Research in the Former Soviet Union. 7: 1–161.
- VONESH, J. R. & O. DE LA CRUZ (2002): Complex life cycles and density dependence: assessing the contribution of egg mortality to amphibian declines — Oecologia 133: 325–333.
- WILBUR, H. M. (1980): Complex life cycles — Annual Review of Ecology and Systematics 11: 67–93.