

Structure of Relationship between Fitness Components in Life History of *Rana arvalis*: 1. Dynamics of Reproductive Effort and Its Components

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Abstract—The influence of dates of metamorphosis, size at metamorphosis, and number of emerged juveniles on the reproductive characteristics and female body size were studied by group-marking of postmetamorphic *Rana arvalis* individuals of three generations. The frogs under study emerged after metamorphosis from the breeding pond and their adults were recaptured in the same pond after 3–7 years. The maximum body size, egg size, and reproductive effort were revealed in the females born in 1991. This generation is characterized by the maximum size at metamorphosis and the minimum number of emerged juveniles. At the same time, similar variations in the mean annual values of body length, fecundity, and egg diameter were revealed in females of different generations. The differences between the generations of 1989 and 1990 are less pronounced, despite the similar size at metamorphosis and about the same initial number of juveniles. An increase in the female fecundity and egg diameter (but not in reproductive effort) with age was the general trend for each generation. Mature females originating from early juveniles were, on the average, significantly younger than late juveniles of the same generation. Most of females from the group of late small-sized animals reproduced for the first time after 4th wintering, i.e. one year later than other groups. The groups distinguished within generation differed in reproductive characteristics only slightly. In the early-large female group, a positive correlation between the size at metamorphosis and rates of growth and maturation was revealed.

One of the basic problems of evolutionary ecology is the evolutionary stability of the phenotypic structure of natural populations, which implies the unaccounted for inefficiency of the natural selection. The approaches to its solution are the following. (1) It might be assumed, that traits possessing adaptive value have no additive component of genotypic variation (Falconer, 1981). This approach is incorrect, because in the course of selection with respect to other traits the mechanism of genetic determination is modified, and a trait having no own additive component of variation in its initial state, may acquire such a component (Kreslavsky, 1991). (2) Another approach postulates the existence of a counterbalance of selective vectors acting in various stages of life history, so that their resultant influence on the general fitness may be zero (Severtsov, 1990). Unfortunately, it is very difficult (if at all possible) to confirm that selective vectors of different directions completely compensate one another, since neither the number of acting selective vectors, nor the degree of nonlinearity of their interaction is known. (3) Moreover, the existence of a negative feedback between the adaptive value of a phenotype and the accuracy of its reproduction is allowed

for. Such a feedback inevitably arises if the phenotype, which possesses the maximum adaptive value, has no ontogenetic mechanism of its own reproduction (Cherdantsev *et al.*, 1996). In the theory of catastrophes (Arnold, 1983) this is named the principle “fragility of the good,” since a good phenotype must simultaneously satisfy to several ecological requirements, and it is more difficult to construct such a phenotype, than that satisfying each of these requirements separately. Probably, this is the main reason why the natural selection is inefficient.

The brown frogs are the convenient object for studying this problem, since they are characterized by variability of size on the completion of metamorphosis and dates of juveniles' emergence to land. These phenotypic traits, on one hand, are determined by preceding larval stage of their life cycle, and, on the other, can lead to difference in reproductive characteristics and survivorship of adults. The high variability of these larval characteristics has been revealed both between generations and within separate groups in a given generation, e.g., among juveniles emerging from the same pond (Ishchenko, 1982; for a review, see

Lyapkov, 1995b). At the same time, the larger size at metamorphosis and the higher development rate, determining the earlier dates of juvenile emergence to land, frequently lead to higher survivorship till the beginning of the first wintering and to higher juvenile growth rate (for a review, see Lyapkov, 1995a). However, in the case of a high number (and density) of emerging juveniles this advantage is not detected. In addition, it usually remains unknown as to how frequently this advantage is preserved in later stages of the life cycle, i.e. after first wintering. The variability of the above-mentioned characteristics of larval development may cause the differences in survivorship during the period from emergence to land till maturity and then, till each successive reproduction. The differences may also arise in reproductive effort and in its components (fecundity, egg size, and female body size: for a review, see Cherdantsev *et al.*, 1997), and, as a consequence, in the net rate of reproduction, which is the index representing the age-specific survivorship and fecundity and commonly used to evaluate the fitness (Pianka, 1978).

When studying the influence of features of the larval development on the individual general fitness, it is necessary to conduct not only mass juvenile marking, but also subsequent mass capture of adults, among which the proportion of marked frogs is usually very low. Moreover, the proportion of recaptures is much reduced when the first reproduction occurs after several (2–3 as a minimum) winterings. Therefore, the absolute number of recaptured frogs is extremely low, which diminishes the efficiency of such researches. Only several studies of this kind, concerned with a small number of anuran species: *Rana sylvatica* (Berven, 1982, 1988, 1990, 1995), *Pseudacris triseriata* (Smith, 1987), *Bufo woodhousei fowleri* (Breden, 1987, 1988), *B. bufo* (Reading, 1991) and *B. calamita* (Sinsch, 1997a, 1997b), have been reported in the literature. The fraction of recaptured adults was usually extremely low, and in the case of natterjack toad (Sinsch, 1997a) no females were recaptured. In addition, the differences between groups distinguished within generations, have been investigated only by of Berven and Smith.

In 1989–1991 we conducted mass marking of moor frog (*Rana arvalis* Nilss.) juveniles emerging from a breeding pond used by a major part of adults of the population investigated for a long time near Zvenigorod biological station of Moscow University (Lyapkov *et al.*, 2000). Later, during the spring sea-

sons of 1992–1996, we conducted mass captures of adults at by same breeding pond and found among them individuals marked upon completion of metamorphosis. This enabled to study directly the dependence of the age dynamics of female reproductive characteristics (Communication 1), on survivorship and evaluation of general fitness (Communication 2) on the initial characteristics of the terrestrial part of the generation, i.e. on size at metamorphosis, on dates of emergence to land and on number of emerged juveniles. Further, it was possible to reveal, on the basis of such a comprehensive consideration of female characteristics, selective advantages of 1) groups with certain initial sizes and dates of emergence, distinguished within generations, and 2) separate generations as a whole, and also to evaluate the dependence of number of adults on the initial number of the generation and the number of emerged juveniles.

MATERIALS AND METHODS

The newly metamorphosed juveniles were collected near the Zvenigorod biological station of Moscow State University, at an old peat-bog filled with water. This pond is the main spawning place of the investigated *R. arvalis* population. Juveniles were collected using polyethylene drift fences placed at distance of 1–3 m from the bank line of the pond, with a total length of 120 m. Depending on the dates when the juveniles emerged to land, they were assigned to categories of “early” and “late” individuals, with small, medium, and large animals distinguished, depending on body size, within each of two groups. Thus, within generations [in our study the term “generation” means all individuals emerged from an investigated pond in a given year] of 1989 and 1990, all juveniles were assigned to one of 6 phenotypic classes (called hereinafter “groups” for brevity) and were marked with 6 different group markers by cutting off digit phalanx of hind and fore limbs in certain combinations. In 1991, juveniles were marked with only 3 different markers (small, medium and large-sized, without division into early and late). A total of 12113 juveniles were marked in 1989, 4311 in 1990; and 476 in 1991. More detailed description of the marking procedure was given in our previous publication, in which the survival and growth of juveniles in the beginning of their terrestrial life were considered (Lyapkov *et al.*, 2000). In addition, the same group markers were used to specify a particular year of birth. Therefore, the age of each recaptured individual was also determined from its marker.

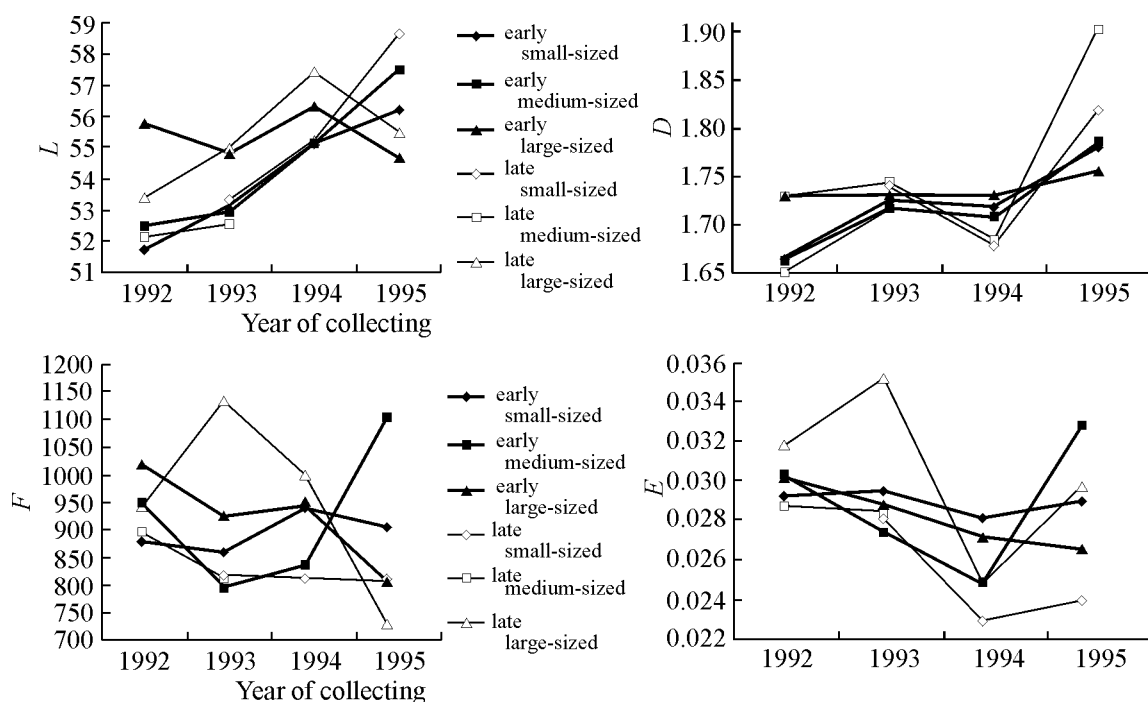


Fig. 1. Age dynamics of reproductive characters of female groups of 1989: L body length, mm; F fecundity; D egg diameter, mm; E reproductive effort; the same in Figs. 2–4.

From 1992 till 1996 we conducted mass captures of adult *R. arvalis* coming to a spawning pond for breeding to find among them the individuals, marked after completion of metamorphosis with group markers in 1989–1991. These recaptures during the breeding period were possible since adults of *R. arvalis* hibernate on land and migrate in mass to spawning pond after wintering. These frogs were also captured with drift fences (total length of about 300 m) located close to bank line and covered approximately 2/3 of the shoreline perimeter. The rest (1/3) of the perimeter was not fenced because it remained frozen and covered with ice and snow at the beginning of migration to the spawning pond. A total of 217 females of 1989 (including 74 small, 34 medium, and 62 large from early groups, and 11 small, 18 medium and 18 large from late groups) and 135 females of 1990 (22, 42, 24, 12, 27, and 8, respectively) were recaptured in 1992–1996. The number of recaptured individuals of 1991 was much lower: only 11 females were recaptured, recognized as medium (9) and large (2). To evaluate the efficiency of captures with drift fences, we also conducted the censuses of all clutches deposited in this pond and compared their number with that of all females captured with drift fences. In 1992, 1993, 1994, 1995, and 1996, the percentage of captured individuals in relation to the total number of spawning females was 48.4, 44.2, 94.0, 69.4 and 34.5 %, respectively.

Therefore appropriate corrections were introduced in the estimating the number of recaptured females. Clutches from recaptured females were obtained in laboratory (most of females were collected *in amplexus*; to single ones males were added in aquaria). The body length and some morphometric characters of females as well as their fecundity and egg diameter were measured by the standard technique (for more detail, see Cherdantsev *et al.*, 1997).

In material processing, Excel 7.0 and a statistical software package STATISTICA 5.0 were employed.

RESULTS AND DISCUSSION

Age dynamics of reproductive characters within the generations of 1989 and 1990

Females of 1989 (Fig. 1). The influence of differences between groups (distinguished by the dates of emergence and the initial size) on the reproductive characters was estimated by one-way analysis of variance (factor “group”) and post hoc multiple comparisons. Among 3-year-old frogs, early large-sized animals outstripped in body length (L) early small- and early medium-sized ones (differences were significant, in both cases $p < 0.01$), and also late medium-sized individuals ($p < 0.01$), but did not differ from late large-sized frogs. (Late small-sized females were not

Influence of age (factor 1), group (factor 2), and its interaction (1×2) on the size and reproductive characteristics of generations of 1989 and 1990 (according to results of 2-way analysis of variance, p is the significance level)

Character	Factor	Born in 1989		Born in 1990	
		<i>F</i> -test	<i>p</i>	<i>F</i> -test	<i>p</i>
<i>L</i>	1	7.32	<u>0.00</u>	14.51	<u>0.00</u>
	2	1.52	0.20	1.43	0.24
	1×2	1.49	0.13	0.78	0.59
<i>F</i>	1	1.61	0.19	0.50	0.61
	2	0.22	0.93	0.19	0.91
	1×2	1.41	0.17	0.55	0.77
<i>D</i>	1	12.77	<u>0.00</u>	38.59	<u>0.00</u>
	2	1.57	0.18	0.69	0.56
	1×2	1.78	0.06	0.58	0.75
<i>E</i>	1	6.81	<u>0.00</u>	4.97	<u>0.01</u>
	2	0.34	0.85	0.55	0.65
	1×2	1.35	0.20	0.55	0.77
All characters combined	1		<u>0.00</u>		<u>0.00</u>
	2		0.45		0.84
	1×2		0.09		0.99

For the character codes, see text. The p -values lower than 0,01 are underlined.

* The results of multivariate analysis of variance.

included in analysis design, since only one female of this group was captured after 3rd wintering.) The same significant differences in *L* were observed in 4-year-old females ($p = 0.026$, $p = 0.044$ and $p = 0.023$, respectively). However, no significant differences were revealed in older females (5 and 6 years).

The differences in fecundity (*F*) were observed most rarely: among 3-year-olds, early large-sized females outstripped only early small-sized ones ($p = 0.042$); among 4-year-olds, late large-sized females outstripped early medium-sized frogs ($p = 0.045$); and among 5- and 6-year-olds, no differences were revealed. Significant differences in *F* were revealed rarely because this character is subject to the highest variability (coefficient of variation in a pooled sample was 24.6 % in 1989, and 23.6 % in 1990), owing to the lability of mechanisms of its development (for more detail, see Cherdantsev *et al.*, 1997). At the same time, the pattern of dependence of *F* on *L* was about the same within each group (both of 1989 and 1990), with the correlation coefficients not too high (no more than 0.695), but significant.

The variation of average egg size (*D*) among 3-year-olds corresponded to differences in *L*: in early large-

sized females, *D* was larger than that in early small ($p < 0.01$) and the early medium-sized frogs ($p = 0.029$), and in the late average-sized frogs ($p = 0.025$). However, no significant differences in *D* were revealed among the older females (4, 5, 6 years).

In reproductive effort ($E = FD^3/L^3$) no significant intergroup differences were revealed for any of the age groups.

The multivariate analysis of variance of whole set of these characters revealed significant differences within 3-year-olds ($p < 0.01$); however, no differences were observed within each of the older ages.

For the generation as a whole, the influence of the age was stronger (significant for each character, except *F*), than that of intergroup differences (non-significant for each trait separately, and for the combination of these, see table, generation of 1989). For *L* and *D* this can be accounted for a tendency toward increase in the average values with increasing age (see Fig. 1) till the age of 5 years (*L*) or 6 years (*D*). As regards the significant influence of age on *E*, a stable tendency toward decrease in this complex characteristic was revealed in majority of groups (except in early medium-

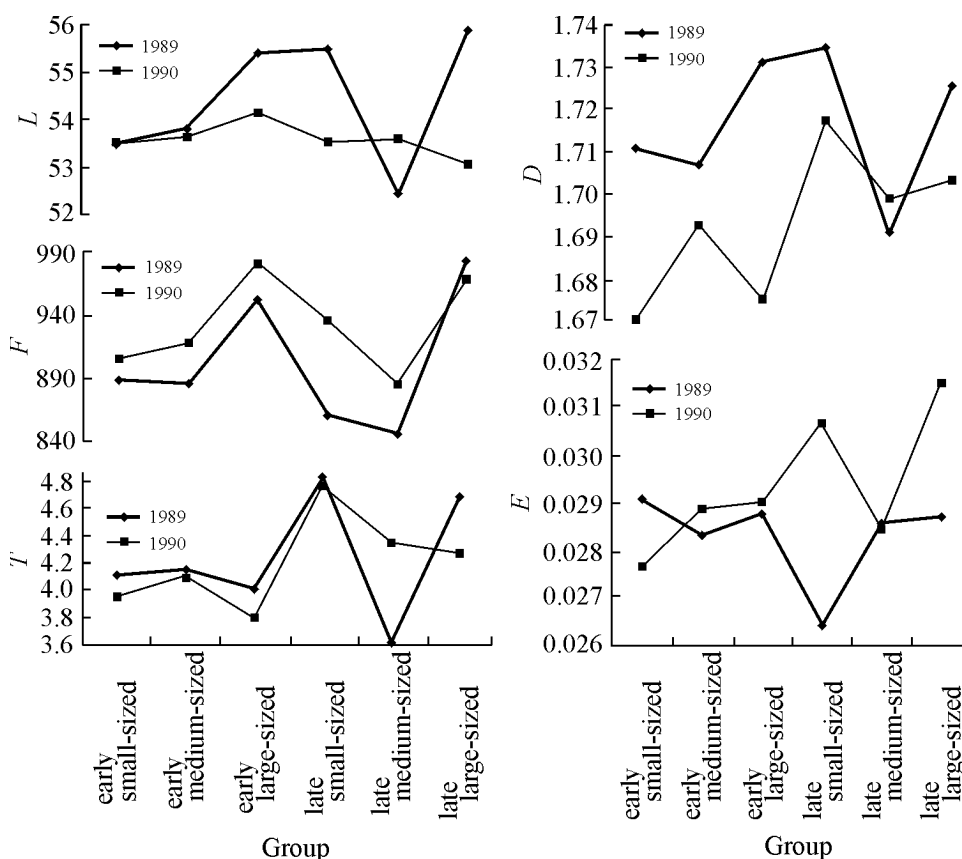


Fig. 2. Group means of reproductive characters and age of female of 1989 and 1990. The lines connect the groups of the same generation. T the age (years).

sized frogs see Fig. 1). E is determined mainly by fecundity. The reason is that in females, starting to spawn at the age of 4 and later the fecundity is lower than in females, that can reproduce already at the age of 3.

In evaluating the influence of the factors “group” and “age”, scarce data on 7-year-old frogs and the late medium-sized group were excluded from analysis (see Fig. 1). All these data can be included in analysis when only a single factor—“group” is considered, i.e. the age dynamics is disregarded. In this case, the influence of the “group” on L is significant: L of early and late large-sized frogs was larger, than that of early small-, early medium- and late medium-sized individuals (Fig. 2). The L value of late small-sized frogs was significantly larger, than that of early small- and late medium-sized animals. To these differences in L corresponded not so distinct (non-significant) differences in D and F (Fig. 3) and, in addition, significant intergroup differences in the combination of all the characters ($p < 0.02$).

At the same time, the distinct intergroup differences in average age (T) of mature females (Fig. 2) were

observed. Since most of late small-sized frogs spawned for the first time at the age of 4, this group was characterized by the maximum average T , and the late large-sized individuals, by an average T close to the maximum value. Each of these groups differed significantly from early small-, early large-, and late medium-sized frogs. Altogether, the late groups were characterized by a significantly higher average T , than early groups.

The nature of intergroup differences in T was most similar to that in L (the correlation between group averages T and L was strong, though non-significant, $r = 0.796$; $n = 6$; $p > 0.05$). A strong (though also non-significant) correlation was observed between average T and D ($r = 0.762$; $n = 6$; $p > 0.05$), too. At the same time, the correlation between L and D was stronger and exceeded the threshold of statistical confidence ($r = 0.946$; $n = 6$; $p < 0.05$), which corresponds to the above-mentioned correlated changes in the average L and D . Therefore on the whole, i.e. with no regard for age dynamics, the revealed intergroup differences in the average age determine the differences in both the body length and the egg size.

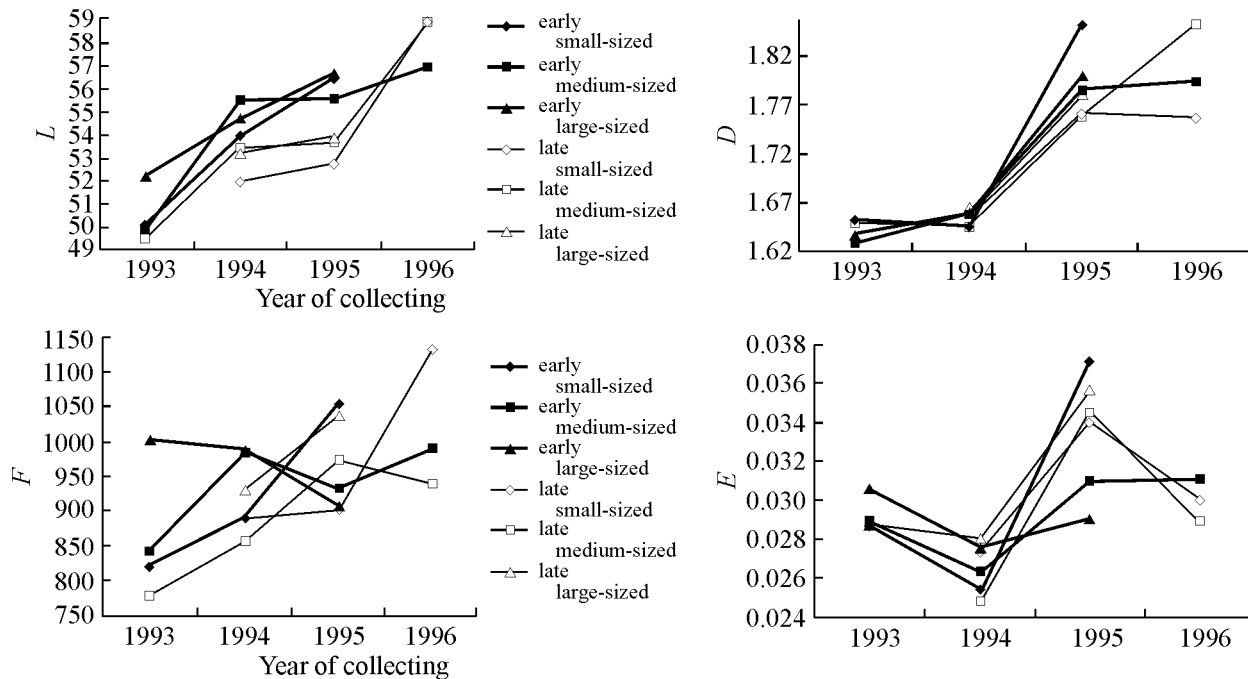


Fig. 3. The age dynamics of reproductive characters of female groups of 1990.

Females of 1990 (Fig. 3). In 1992, only 3 females, which spawned for the first time after 2nd wintering, were recaptured, and, therefore, 2-year-old individuals were not included in the analysis. Among 3-year-old females, the early large-sized animals outstripped the early medium-sized individuals in L ($p = 0.032$). Among 4-year-olds, late small-sized frogs lagged behind all other groups in L (this group differed significantly only from early medium-sized animals, $p = 0.013$). It should be noted that late small-sized individuals of this generation were a unique group, all of whose females reproduced for the first time only after 4th wintering, and despite that, their body size at the age of 4 was the smallest. Among 5-year-old females, the early large-sized animals outstripped late small-sized individuals ($p = 0.027$). Among 6-year-olds, no significant differences in L were revealed.

No significant intergroup differences in F within each of the ages (as in females of 1989) were revealed. No significant differences in D were revealed within 3- and 4-year-olds. Within 5-year-olds, early small-sized animals outstripped late medium-sized individuals ($p = 0.046$), and within 6-year-olds, late medium-sized frogs outstripped the small-sized ones ($p = 0.041$). No significant intergroup differences in E within each of ages were revealed (as in females of 1989). As a result, the multivariate analysis of vari-

ance of a complex of these characters revealed no influence of groups within each of the ages.

On the whole, in females of 1990, the influence of the age on each of the considered traits and on their entire set was stronger, in comparison with the non-significant influence of differences between groups (table, generation of 1990). However, unlike the case of the generation of 1989, the influence of "group" remained non-significant even if the factor "age" was excluded from consideration. Thus, the intergroup differences in females of 1990 were expressed more weakly, than those in generation of 1989.

At the same time, intergroup differences in average age (Fig. 3) were revealed. Late small-sized frogs were characterized by the maximum average T . This group reproduced for the first time at the age of 4 years and differed significantly in T from all groups, except late medium-sized frogs. No significant differences were revealed between all the remaining groups. As also in case of 1989, the average age of the all three late groups was significantly higher than the corresponding average value for early groups. Our results (on both generations) are in general similar to data obtained for the Trans-Uralian population of *R. arvalis* (Ishchenko, 1999): females of the generation characterized by relatively small average size at metamorphosis were on the average older.

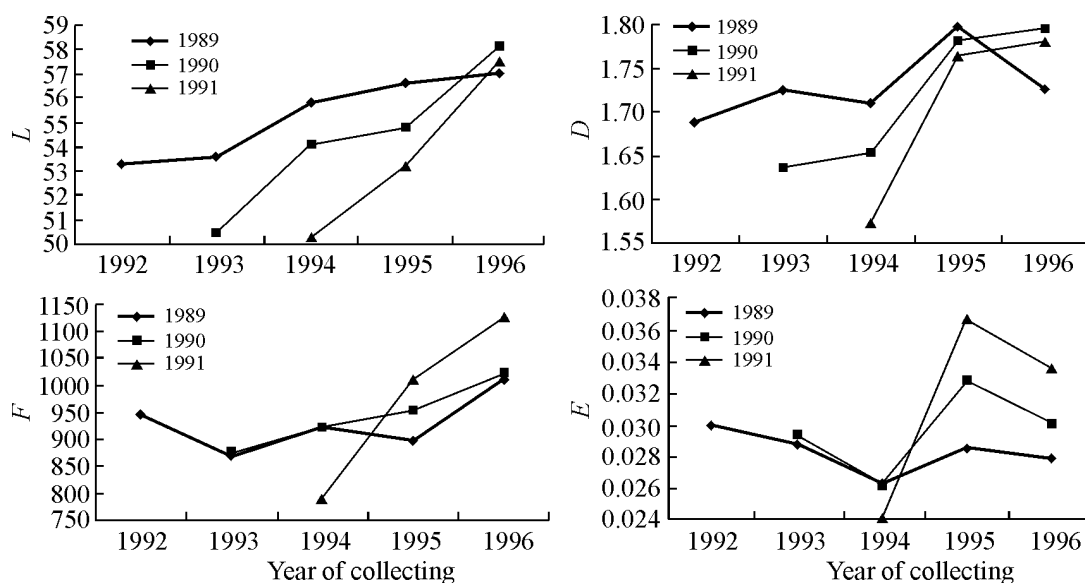


Fig. 4. The age dynamics of reproductive characters of female generations of 1989, 1990 and 1991.

The nature of intergroup differences in T was the most similar to that in D (the correlation between group averages T and D is significant, $r = 0.932$; $n = 6$; $p < 0.05$). However, the correlation between L and T and between L and D were weakly negative (non-significant).

Comparison between Generations of 1989 and 1990

The influence of differences between generations of 1989 and 1990 on each of the reproductive characteristics was evaluated, together with the influence of group and age, by means of three-way analysis of variance (model with fixed effects). Because of the absence of 6- and 7-year-olds in some groups, the levels of the factor "age" were represented only by 3-, 4- and 5-year-old females. Moreover, the late small- and late medium-sized frogs were not included in the levels of the factor "group." The between-group differences exerted significant influence only on L , with no significant interactions of "group" with "age" or "generation" revealed for any character. Only L and D increased significantly with age. This means that no significant increase in F and E was observed with aging (up to 5 years, Fig. 4). No significant interaction of the factors "age" and "group" was revealed for any of the all characters. The influence of the "generation" factor on L was the strongest and was expressed in that 3-year-old females of 1989 were larger, than 3-year-old females of 1990. The interaction "age" \times "generation" was also significant for each of the characters (except F). This interaction was manifested in differ-

ent changes in L , D , and E in females of two generations upon aging (Fig. 4). For example, in females of 1989, the average L between 3rd and 4th winterings increased not so dramatically as in females of 1990. The average D and E decreased between 4th and 5th winterings in females of 1989 and, by contrast, increased in the generation of 1990. In addition, changes in traits similar for different ages (i.e., in different generations), were revealed, which is possibly associated with external conditions in a given year (see Fig. 4). For example, the average L and F in females of 1990 increased relatively fast from 3 till 4 years. During the same period (from 1993 to 1994), the increase in L and F was equally fast in females of 1989 (which were one year older).

To compare all groups of the two generations, we excluded the age dynamics from analysis (Fig. 2). In other words, the two-way analysis of variance, with only factors "group" and "generation" distinguished was applied. Despite the significantly smaller average D (compared with 1989), the groups of 1990 were characterized by larger reproductive effort (E), because of the smaller L and larger F in females of 1990. The allocation of a part of resources to reproduction compensated, to a certain extent, for the lower initial number of juveniles in this generation. One more difference between the two generations was that in most groups of 1990 some decrease in fecundity and, as a consequence, in reproductive effort, too, was observed only at the -years age (Fig. 3). It is possible that the thus maintained relatively high values of E constitute

another mechanism of compensation for lower number of juveniles of 1990.

Peculiarities of Generation of 1991

The 4- and 5-year-old females of 1991 were characterized by the maximum average values of F and E (in comparison with corresponding ages in generations of 1989 and 1990, see Fig. 4). However, only the difference in E among 4-year-olds was significant; in all other cases, the differences were non-significant because of the low number of recaptured females of 1991. In 1991, the initial number of juveniles, emerging from the pond upon metamorphosis at maximum size and minimum density (Lyapkov *et al.*, 2000), was the smallest (compared with generations of 1989 and 1990). Therefore, the maximum values of F and E for the generation of 1991 may be regarded as compensation. In addition, in all individuals of 1991, the correlation between F and L ($r = 0.711$) was stronger, than that in generations of 1989 and 1990 (0.505; 0.500, respectively; all correlations significant), which in part compensates for the high tadpole mortality.

Since the influence of intergroup differences was also weak within the generation of 1991, the already used two-way analysis of variance (with only factors "age" and "generation") was applied to compare all the three generations. Including data on the generation of 1991 in this design gave somewhat different results (than in the case when only 1989 and 1990 were compared). The factor "generation" influenced significantly each trait (except F) and the whole set of characters, the factor "age" affected significantly L and D and the whole set of characters. In addition, the interaction "age" \times "generation" influenced significantly each character (except F). This interaction was expressed in a faster increase in D , F , and E in females of 1991 during the period from 3 to 4 years, compared with two other generations (Fig. 4). At the same time, this interaction was also a manifestation of the already mentioned characters, similar for different generations in the same years. For example, from 1995 till 1996, a relatively fast increase in L and F in females of not only 1991 (from 4 to 5 years), but also 1990 (from 5 to 6 years) was observed. In addition, from 1994 till 1995 a simultaneous increase in D in different ages of all the three generations was revealed. The existence of all these synchronous changes means that some warm seasons (in 1993, 1994, and 1995, in our case) were more favorable for all the generations, than those in other years. The importance of abiotic conditions

(temperature and precipitation during the warm season preceding the reproduction) for the development of reproductive characteristics has been noted for a number of temperate zone species: *R. temporaria* (egg size, Cummins, 1986), *R. sylvatica* (fecundity and egg size, age at first reproduction, Berven, 1982, 1988), and *Bufo bufo* (fecundity, Reading and Clarke, 1995).

Let us summarize the results, obtained in this study. With few exceptions, the groups distinguished within each generation differ in reproductive characteristics only slightly because of fundamental nonlinearity of the relation between initial size and dates of emergence of juveniles, on the one hand, and postmetamorphic growth rate and characteristics of mature frogs, on the other. Only for early large-sized individuals which first reproduce at 3 years of age, there is a positive correlation between initial size and rate of growth and maturation. Those females for which the connection between initial size and rate of growth and maturation is weakened or absent, first reproduce at older age. Distinct (and significant) differences in body length and fecundity were revealed between large-sized group and remaining groups within each of the two generations (1989 and 1990). However much more distinctive differences were revealed between frogs of different ages, that is due, in addition to the "normal" age dynamics, also to variation of the conditions of the activity season between years. On the whole, the generations differed essentially in fecundity and in reproductive effort only in that case when the differences in number and size of emerged juveniles were considerable (i.e. generation of 1991 differed from the two previous ones). Presumably, the common reason for the weak differences between the generations of 1989 and 1990 is the comparative similarity of conditions of terrestrial life after metamorphosis. The density of emerged individuals can exert strong influence on dispersing juveniles only at a distance of no more than 200 m from the pond. Moreover, the most density-sensitive juveniles do not migrate farther than 200 m, perishing in the vicinity of pond (Lyapkov *et al.*, 2000). Such a stricter elimination of relatively small individuals must lead eventually to equalization of the survivorship of juveniles initially belonging to different size classes.

However, consideration of separate reproductive characteristics is insufficient for evaluating the survivorship and estimation of general fitness of individuals belonging to different size classes with different dates of emergence, and also to different generations. An

analysis of these components is the subject of our Communication 2.

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