

Structure of Relationship Between Fitness Components in Life History of *Rana arvalis*: 2. Dynamics of Fitness Components

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Received March 3, 2000

Abstract—The influence of dates of metamorphosis (early and late), size at metamorphosis (small-, medium- and large-sized) and number of emerged juveniles on the survivorship and other fitness characteristics of females were studied by counting and group-marking of postmetamorphic *Rana arvalis* individuals of three generations. The females under study emerged after metamorphosis from the breeding pond and were recaptured in the same pond after 3–7 years as adults. Within the generation born in 1989, the survivorship of the group of early juveniles till first and each successive reproduction was higher than in late ones, but within the generation of 1990 this survivorship of early juveniles was lower than in late ones. The survivorship of females of 1990 was higher in comparison not only with the generation of 1989, characterized by smaller sizes at metamorphosis, also with the generation of 1991, characterized by maximum size at metamorphosis. The total number of eggs produced by a given generation was determined by premetamorphic survivorship, and correspondingly by the number of emerged juveniles of a given generation. The net rate of reproduction (calculated on the basis of life-tables) was determined by premetamorphic survivorship to a greater extent than by size at metamorphosis and survivorship till maturity. Within each generation, the net rate of reproduction of a given group was affected rather by its survivorship till each successive breeding than by fecundity. Therefore, in the generation of 1989, the early group had higher net rate of reproduction than the late one. Within the generation of 1990, the relationship between these two groups was inverse. Large-sized (both early and late) groups of 1989 had maximal net rate of reproduction, but these differences were not revealed within the generation of 1990.

On the basis of data on recaptured females, which were marked after the completion of metamorphosis with various group marks according to their size and timing of emergence to land, we revealed relatively weak intergroup differences in reproductive characteristics (Lyapkov *et al.*, 2001). The differences between generations in reproductive characteristics were not always distinct and were affected mainly by variation of these characters between years. At the same time, the distinct differences in survivorship between juvenile groups distinguished immediately at the beginning of terrestrial life (Lyapkov *et al.*, 2000) allow suggest that these differences will persist in later ages. Therefore, Communication 2 is devoted to analysis of differences (between groups within each generation and between generations) in survivorship till maturity and till elder ages, and also in the fitness estimations comprising this survivorship and age-specific fecundity.

MATERIALS AND METHODS

The procedure for obtaining primary data on the basis of adult recaptures was described in detail in Communication 1. For evaluations of the number of

females of each group in each breeding year, a convenient technique for interpretation of the results of recaptures (Caughley, 1977) was used. For analysis of survival dynamics, the proportion of recaptured individuals (relative to the number of those with a given group mark), obtained on the basis of the corresponding evaluations of their number, were calculated. The significance of differences in survivorship (in proportion of recaptures) was estimated by *U*-test. The obtained data made it possible to follow only a separate generation (or group within generation), till its last breeding, but not the offspring produced by a given generation (or group). Therefore, in addition to survivorship, we used as fitness evaluations the conventional group characteristics of population ecology, based on the life-tables of survival and age-specific fecundity, total number of produced offsets (N_0), and net rate of reproduction (R_0).

In addition to the survivorship of adult females, evaluations of the initial number and the number of individuals in each generation that completed metamorphosis are necessary for constructing the life-tables. These evaluations were obtained using the data

on average fecundity and number of clutches deposited in 1989–1991, and also on the censuses of emerged juveniles (Lyapkov *et al.*, 2000). On the basis of constructed life-tables of survival and age-specific fecundity, the total number of offspring characterizing the absolute contribution of a group or of all generation, i.e. eggs number (N_0), and net rate of reproduction (R_0) were calculated (Pianka, 1978; Begon *et al.*, 1986):

$$N_0 = \sum_{x=0}^{T_{max}} n_x m_x;$$

$$R_0 = \sum_{x=0}^{T_{max}} l_x m_x;$$

where n_x is number of individuals (of a given group or generation) of age class (stage) x , T_{max} the maximum age, m_x the average fecundity of age class x , l_x the proportion of individuals that have till age x . As estimate of population number we used the total number of females bred in a given year, equal to the number of clutches deposited in the pond, around which emerged juveniles were collected (see also Lyapkov *et al.*, 2001).

The use of the generalized characteristic R_0 is due to the fact that solely the survivorship can not completely characterize the fitness of a given group or all generation. For example mass marking of the *Pseudacris triseriata* juveniles emerging from one pond demonstrated that individuals breeding for the first time at the age of 1 year had the same survivorship till second breeding, as in individuals breeding for the first time at the age of 2 years (Smith, 1987). At the same time, it is obvious that in twice breeding females the characteristic R_0 must be higher. The use of additional characteristic, total number of offsprings (N_0), is accounted for the fact that the differences in this parameter (both between groups within one generation and between generations) were stronger than the difference in R_0 , which is due to differences in the absolute number of juveniles of different groups of the same generation or of different generations. Thus, the contribution of a given group to the next generation will be determined rather by its relative number than by the net rate of reproduction (R_0). In other words, N_0 represents an analogue of absolute fitness (Falconer, 1981) of a given phenotypic class or all generation.

It was revealed that not all females were ready for reproduction at the age of 3 years (Lyapkov *et al.*, 2001). Therefore, for making the real estimation of the

average fecundity, the average fecundity of breeding females of this age was multiplied by a correction factor. We calculated this correction factor as the proportion of the total number of 3-year-old females (Caughley, 1977) relative to the number of breeding 3-year-old females. The value of this proportion varied between different groups from 0.38 to 0.55 and was much less only in late small-sized individuals (0.28 in the generation of 1989 and 0 in 1990). It should be noted that there are no generally accepted methods of interpretation of the results of recaptures of adult amphibians in breeding ponds, including the complicated cases, similar to ours (for a review, see Gill, 1985). Nonetheless, we consider it necessary to use the indicated correction factor, since it expresses the real fact of breeding of only a part of 3-year-old females. In addition, as our preliminary calculation demonstrated, it can essentially affect the values of N_0 and R_0 .

RESULTS

Age Dynamics of Fitness Components of Groups within the Generations of 1989 and 1990

Survivorship

Females of 1989 (Fig. 1). Among the 3-year-old females the late small-sized individuals were characterized by minimum survivorship (significantly different from that for all other groups), and the late large-sized ones were characterized by maximum survivorship (non-significantly different only from early large-sized and late medium-sized ones). In their turn, early large-sized females survived better in comparison with early and late small-sized ones. In further aging (i.e. among 4- and 5-year-olds), significantly higher survivorship persisted only in late large-sized individuals, and lower survivorship, in late small-sized ones, and all remaining differences, detected in the 3-year-old females, became non-significant. Among the oldest females, the late large-sized individuals still survived slightly better than those in all other groups (Fig. 1); however, the absolute survivorship values in all, without exception, groups were very low. The low survivorship of the adult females of the late small-sized group corresponded to the low percentage of recaptures of juveniles of this group dispersed during the summer of 1989 (Lyapkov *et al.*, 2000). The advantage in survivorship of individuals with larger initial size was also recorded in *Pseudacris triseriata* (Smith, 1987).

Females of 1990 (Fig. 1). Among the 3-year-old females early medium-sized ones were characterized

by minimum average survivorship (significantly different from that in early large-, late small and late medium-sized ones). All remaining groups did not differ significantly among themselves. Among the 4-year-olds the highest survivorship was in late small-sized ones (significantly different in this regard from all early groups), which, as already mentioned (see Lyapkov *et al.*, 2001), bred in this age for the first time, since they were characterized not only by small initial size, but also by late dates of emergence. However, if the groups are compared in survivorship till first breeding, the advantage of 4-year-old late small-sized females is revealed only in comparison with 3-year-olds early medium-sized ones (see Fig. 1). The remaining groups did not differ significantly among themselves in survivorship till first breeding, which coincides with the results of mass marking of juveniles and recaptures of adult *Pseudacris triseriata* on spawning pond (Smith, 1987). The survivorship of 4-year-olds late groups was also higher than in each corresponding early group. As in 3-year-olds females, among 4-year-olds, all late groups did not differ among themselves. Among a 5-year-olds females the survivorship of late small-sized and late medium-sized ones was higher, than that in each of early groups. In addition, late small-sized females survived better than late large-sized one. All these advantages persisted also in the 6-year-olds females.

Total Number of Offspring (N_0)

Females of 1989 (Fig. 2). The higher total number of offspring (N_0) corresponded to more numerous groups of the emerged early juveniles (in comparison with late ones). At the same time, the low survivorship in late small-sized females essentially reduced its contribution to the total initial number of offspring of all generations (compare Fig. 1 and 2). This is accounted by the fact that, if the survivorship of groups were identical, N_0 would correspond to the initial number of a given group (since the groups' average fecundities differ only slightly, see Lyapkov *et al.*, 2001). For the same reason, the contribution of the late large-sized females, characterized by the highest survivorship, was, by contrast, slightly larger than it would be expected, judging only from the of juveniles number of given group. Thus, the influence of the initial size is revealed only by comparison of strongly different groups, i.e. late small-sized juveniles (which were the smallest individuals) with late large-sized ones.

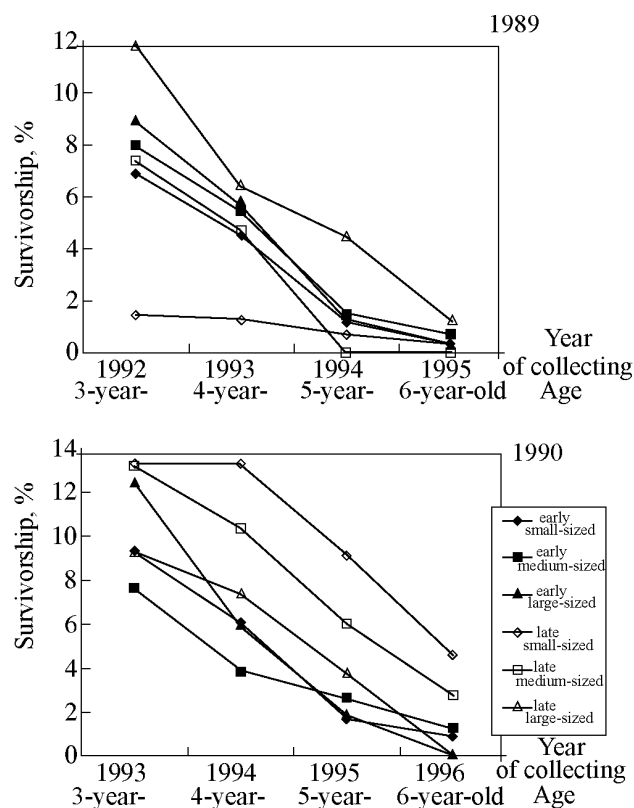


Fig. 1. Survivorship (number of individuals of a given age relative to number of juveniles) of groups of the females of 1989 and of 1990.

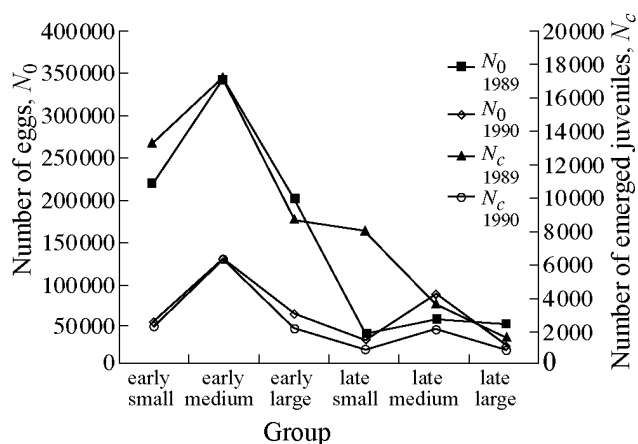


Fig. 2. Number of juvenile groups (N_c) of 1989 and 1990 and total number of their offspring (number of eggs produced in all breeding seasons, N_0) in the corresponding groups of females.

Females of 1990 (Fig. 2). In this generation, more exact (than in generation of 1989) correspondence between values N_0 and the number of emerged juveniles of a given group was observed, since the late groups survived better (than in the generation of 1989). A disagreement was observed only in each of

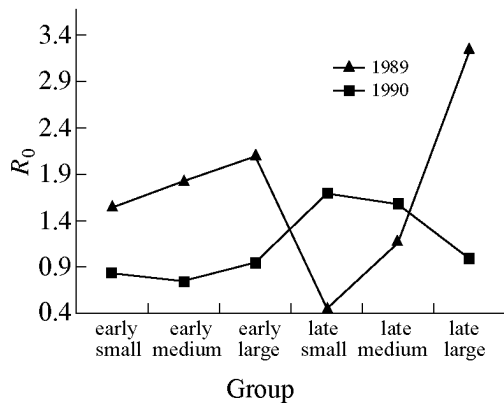


Fig. 3. Net rate of reproduction (R_0) in female groups of 1989 and 1990. The lines connect the groups of the same generation.

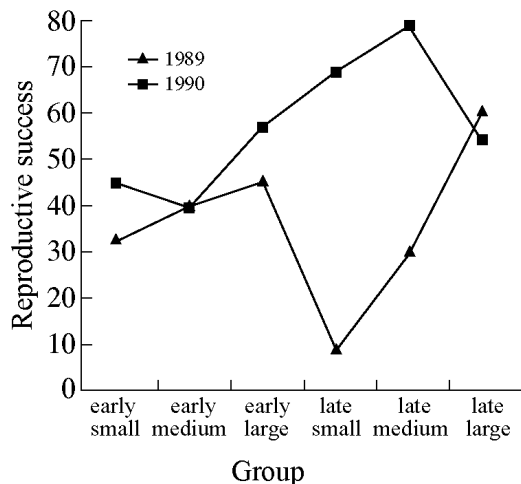


Fig. 4. Reproductive success in female groups of 1989 and 1990. The lines connect the groups of the same generation. For explanations, see text.

late female groups: the values of N_0 did not correspond to the initial juvenile number of these groups, and were slightly higher. The reason is the higher survivorship of the late groups in comparison with early ones (Fig. 1).

Net Rate of Reproduction (R_0)

Females of 1989. The net rate of reproduction (R_0 , Fig. 3) corresponded well to the survivorship level of a given group (Fig. 1). The correlation of the fecundity with the initial size was relatively weak, therefore main contribution to the difference in values of R_0 was made by the survivorship of each of age classes of mature individuals (see formula for calculation R_0 in "Materials and methods"). The average initial size of individuals of a given group also strongly affected R_0 :

both among early and among late groups R_0 was minimal in small-sized females and maximal in large-sized ones. Among all the 6 groups, late large-sized females were characterized by the highest value of R_0 which corresponded to its maximum survivorship. However, the average R_0 value of all early groups (1.79) was 1.8 times that in all late groups (1.01).

Females of 1990. All early groups were characterized by lower R_0 values (Fig. 3), in comparison with the corresponding late groups which coincided with its lower survivorship till age of 4 (Fig. 1). The weakest differences in survivorship of the early and late large-sized females corresponded to the weakest differences in R_0 between these two groups. On the whole, the average R_0 value of all early (0.81) was 2 times less than that of all late (1.60). The generation of 1990 differed from that of 1989 in lower R_0 values in early groups (in comparison with late ones). This difference between generations is not connected directly to the initial juvenile size: both in 1989 and in 1990 early juveniles were larger than late ones. This difference also did not correspond to the number of emerged juveniles: in 1989 the number of early groups was much higher, than that in late ones (Fig. 2); however, early females survived better than late ones. In addition, in contrast to the generation of 1989, in 1990 the number of early juveniles did not exceed so strongly the number of late ones; however, the late individuals survived better than early ones. Thus, the cause of the indicated between-generation differences in R_0 of early and late individuals was the higher survivorship of late females (in comparison with early ones) of the generation of 1990 (Fig. 1).

It is also necessary to note that the revealed differences between two generations confirm the appropriateness of R_0 as a characteristic of the reproduction rate (Begon *et al.*, 1986) of a given group or generation. Alongside with this characteristic, a similar parameter, the average number of juveniles produced by one female, is applied (Berven, 1995). However, the use of another parameter, mentioned in the literature, the so-called "reproductive success of generation" (i.e. the number of eggs deposited by females of a given generation related to the number of females of the same generation at juvenile stage, cited from Ishchenko, 1999), reveals quite other differences between generations. By using this characteristic (Fig. 4), all groups of 1989, except the late large-sized ones, are inferior to the corresponding groups of 1990 (cf. Fig. 3 and 4). This evaluation technique leads to a mistake

since the characteristic “reproductive success of generation” does not take into account the survivorship till completion of metamorphosis. The smaller the number of juveniles of a given phenotypic class or generation (this value stands in denominator of the formula), the higher the “reproductive success of generation”, irrespective of the survivorship till completion of metamorphosis

Comparison between Generations of 1989, 1990, and 1991

Survivorship

In 1989, 1990, and 1991, the proportion of emerged juveniles relative to the initial number of generation (i.e., egg number) amounted to 1.89%, 0.70% and 0.06%, respectively (which is most likely accounted to deterioration of larval development conditions in the breeding pond; for more detail, see Lyapkov *et al.*, 2000). Because of the incomparability of the levels of pre- and postmetamorphic survivorship, the survivorship of mature females relative to number of emerged juveniles is shown separately (Fig. 5). The survivorship of the females of each age of generation of 1989 was significantly lower than that in the corresponding ages of the generation of 1990. In all likelihood, this is connected to the smaller initial size of juveniles of 1989 (average body length of early juveniles was 14.47 mm, and that of late ones, 13.24 mm) as compared with juveniles of 1990 (in which the average body length was 16.02 mm and 15.47 mm, respectively), and also to the fact that the proportion of relatively small individuals was higher in 1989. The absolute number was also higher in 1989, which could lead to a stronger density pressure. In addition, the survivorship of the 5-year-old females of 1989 was significantly lower than that in generation of 1991. Thus, the generation of 1990 was characterized by the maximum survivorship, whereas the survivorship of each of ages of generation of 1991 (except for the just mentioned exception) did not differ significantly from the survivorship of the corresponding ages of the generation of 1989, despite the much larger initial size of juveniles of 1991. Although we did not recapture by drift fences around of the breeding pond in 1997, we manually captured adult individuals around the pond and directly at spawning places. Among the collected females, we did not find any marked individual, and this is a good reason to consider that the proportion of females of 1991, which survived till 6 years of age, was close to zero. Thus, the dependence of the adult

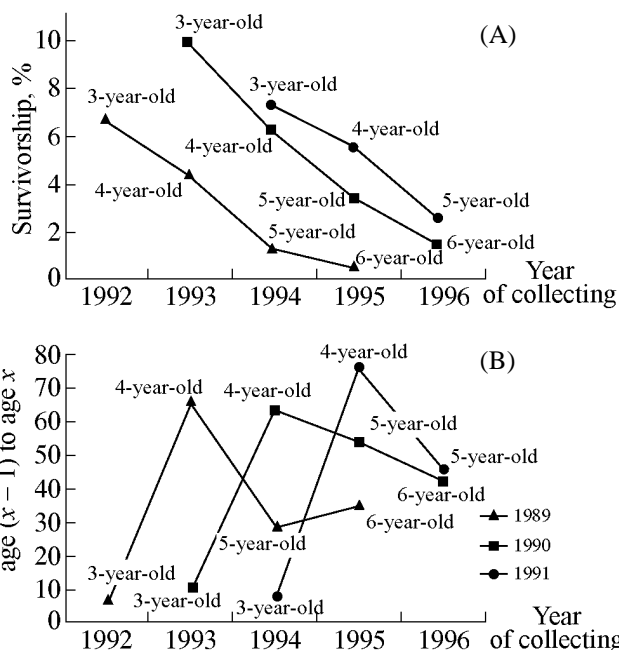


Fig. 5. Survivorship (%) of females of 1989, 1990, and 1991. A number of individuals of a given age relative to number of juveniles; B number of individuals of age x relative to number of those of age $(x-1)$.

survivorship on the juvenile size is essentially nonlinear, so that the influence of the initial size is manifested only in a narrow range of sizes close to minimal value.

The obtained survivorship estimate (relative to number of the emerged juveniles, Fig. 5 a) differs from the data reported in the literature, which we brought together in the table. In females of the *Rana sylvatica*, the species closest to *Rana arvalis* frog, the first breeding occurs after either two winterings (in the lowland population), or after three to four winterings (in the mountain population) (Berven, 1982). To these differences correspond the differences in survivorship, i.e., lower proportion of female recaptures corresponds to longer duration of immature stage (table). The proportion of recaptures in the females from the lowland population of this species corresponds to our data (Fig. 5), despite that of *Rana arvalis* females of the population under study reproduce for the first time one year later. The maximum survivorship (see table) is recorded in *Pseudacris triseriata* females, reaching the sexual maturity also after 2nd wintering (Smith, 1987). At the same time, *Bufo bufo* females breeding first after 4th, 5th, or 6th wintering (Reading, 1991) are characterized by much lower proportion of recaptures. Thus, the revealed distinctions between species or

Published data on the percentage of recaptures of adult *Anura* marked upon completion of metamorphosis

Species	Number of marked juveniles ¹	Percentage (%) of recaptures of adult:		Source
		males	females	
<i>Rana sylvatica</i>	445	11.20	5.80	Berven, 1983, 1990 ²
	3370	25.60	14.12	
	579	32.10	8.90	Berven, 1983, 1990 ³
	20262	11.60	3.90	
	521	6.10	3.50	
	1163	4.80	2.10	Berven and Grudzien, 1990 ⁴
	401	31.40	16.40	
	1001	5.00	2.20	
	4311	7.51	3.99	
		526	14.07	3.80
	122	14.75	3.28	
<i>Pseudactris triseriata</i>	771	50.06	17.90	Smith, 1987
		19.00 ⁵		
<i>Bufo w. fowleri</i>	8539	0.43 ⁶		Breden, 1987
<i>B. bufo</i>	7259	1.13	0.19	Reading, 1991
<i>B. calamita</i>	1709	1.05	–	Sinsch, 1997a, 1997b

¹ The total number of marked juveniles is given; to account for the percentage of recaptures of males or females this number is divided by 2.

² Data on various generations of the lowland population (pond 1).

³ Data on various generations of the lowland population (pond 2).

⁴ Data on various generations of the mountain population.

⁵ Author's evaluation with correction for different ages of maturation of males.

⁶ Samples of males and females combined.

populations can be accounted in general for difference in age of maturation.

Total Number of Offspring (N_0)

The strongest influence on the total number of eggs produced by the whole generation is exerted by the number of emerged juveniles (Fig. 6), which, in turn, is determined by the survivorship till completion of metamorphosis. The maximal value of N_0 of the generation of 1989 (see Fig. 5) corresponded to the maximal values of its survivorship and the initial number. And, by contrast, the survivorship after emergence to land has no essential influence: the intermediate value of N_0 of the generation of 1990 corresponded to the maximum survivorship of the females of this generation (Figs. 5 and 6).

Net Rate of Reproduction (R_0)

Each group of 1990 had lower value of R_0 than the corresponding group of 1989 (except for late small-

sized females of generation of 1989 characterized by the lowest survivorship). The overall average value of R_0 , (obtained by pooling of all groups) for the generation of 1989 was also higher, than that in 1990 (Fig. 7). This difference is not connected directly to either the initial juvenile size, or their survivorship till maturity. As already mentioned, the main reason for such an advantage in R_0 of the generation of 1989, in comparison with the generation of 1990 (and also that of the generation of 1990, in comparison with the generation of 1991) consists in the corresponding strong differences in survivorship till the completion of metamorphosis. The premetamorphic survivorship (the highest in the generation of 1989) makes much greater contribution to the advantage in R_0 than the postmetamorphic survivorship (which was significantly higher in females of 1990 than that in the generation of 1989) and fecundity (which was lower in the females of 1989 than that in 1990 and 1991, see Lyapkov *et al.*, 2001).

DISCUSSION

The Recruitment of the Mature Part of Population and Dependence of Adult Survivorship and Net Rate of Reproduction on Initial Number of Juveniles

Let us outline the results of Communication 1 (Lyapkov *et al.*, 2001) and 2 (this study). The changes in some reproductive and demographic characteristics lead to partial compensation of the decrease in the initial generation number caused by high premetamorphic mortality. For example, owing to the better initial conditions of terrestrial life (because of the relatively low density near a pond), and also to the larger initial juvenile size, there remains a reserve of fecundity increase in any age, without increase in body length of individuals and in egg size, both dependent on age. However, this only refers to an increase in fecundity. The high mortality till metamorphosis does not increase the probability of surviving till the first breeding in survived juveniles. All generalized fitness evaluations depend first of all on the survivorship till completion of metamorphosis, which, in turn, is determined by conditions of a given pond and features of a given year and, additionally, does not depend on density in a wide range of values of the initial number of generation (Lyapkov and Severtsov, 1994).

The relation between the number of emerged juveniles, R_0 , N_0 , and the survivorship of all three generations indicates the absence of a density-dependent control of the number of a mature part of population. The intermediate (but not the lowest) number of juveniles corresponds to the maximal survivorship in females of the generation of 1990 (Fig. 5), and the values of R_0 and N_0 characterizing the generations as a whole grow with its increasing number (Figs. 6 and 7). The premetamorphic survivorship exerts the strongest influence on the number of juveniles emerged in a given year, but its decrease does not lead to a decrease in mortality after emergence to land. The postmetamorphic survivorship of the generation of 1991 was lower, than that in the generation of 1990, characterized by lower premetamorphic mortality, than that in the generation of 1991. The most possible reason for the absence of such a density-dependent mortality consists that, in fact, the high density affects the emerging juveniles only in the immediate vicinity of the pond (according to our data, within 200 m, see Lyapkov *et al.*, 2000), but not in the process of further dispersal. A similar dependence of the recruitment of the adult part of population and the absence of density-

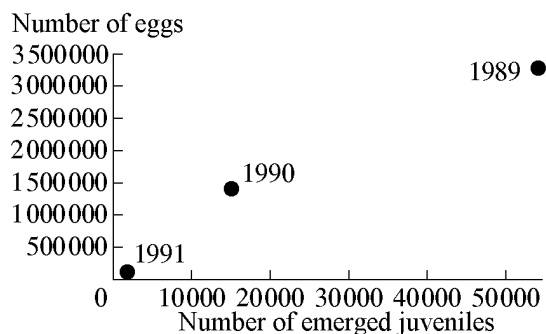


Fig. 6. Dependence of the total number of offspring (number of eggs produced in all breeding seasons) of females of the generations of 1989–1991 on the number of the juveniles of the same generations.

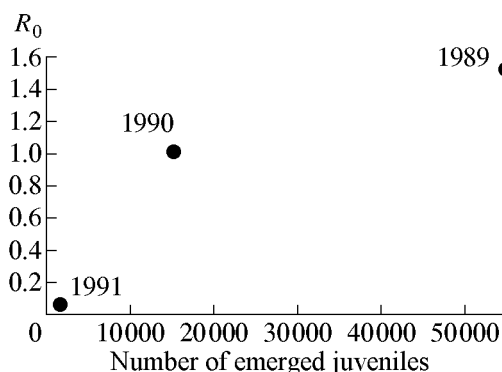


Fig. 7. Dependence of the net rate of reproduction (R_0) of generations of females of 1989–1991 on the number of juveniles of the same generations.

dependent mortality after the emergence to land were revealed in the North American *Rana sylvatica* (Berven, 1990, 1995), a species close to *Rana arvalis*, and also in *Bufo calamita* (Beebee *et al.*, 1996). At the same time, the initial number of earlier generations of the investigated population (Cherdantsev *et al.*, 1997), their premetamorphic survivorship and, correspondingly, the number of juveniles exiting from the main breeding pond (from 17850 to 290270 individuals; for more detail, see Lyapkov and Severtsov, 1994), were much higher than those in 1989–1991. Therefore, the possibility of density-dependent control is not ruled out under conditions of higher initial terrestrial number of generations.

Fitness Evaluations for Females Characterized by Different Size at Metamorphosis and Dates of Emergence to Land

Comparison of early and late individuals. The investigated population as a whole is characterized by higher number of early juveniles, in comparison with

that of late ones, within the same generation (Lyapkov, 1986; Lyapkov *et al.*, 2000). The significantly higher survivorship till the first breeding corresponded to an essentially higher number of early juveniles of generation of 1989 (in comparison with late ones, see Fig. 2). In the generation of 1990 the survivorship of early females till the first breeding was significantly lower than that in late ones, though the number of early juveniles exceeded the number of late ones not so strongly, as in 1989. In other words, the mortality of early individuals does not increase with increasing number (density) of juveniles of a given generation. The reason for the absence of such a density-dependent mortality is the already mentioned limitation of the effect of high density to only the shoreline zone (Lyapkov *et al.*, 2000). In addition, there were no significant differences between early and late females in any reproductive characters within both generations (see Lyapkov *et al.*, 2001). This means also that the development of the reproductive characteristics is not connected with the revealed differences in survivorship between early and late individuals.

The change of net rate of reproduction did not depend on the initial terrestrial density, either: in early individuals of 1989 (characterized by high juvenile number) the value of R_0 was higher, than that in late ones, while in early females of 1990 R_0 was lower, than that in late ones (despite the already noted weaker difference in number between the early and late juveniles). Thus, the situation when the late juveniles emerging to land at low density will have in future (in the adult stage) a selective advantage, is not repeated every year. In other words, there cannot be a permanent advantage of only late juveniles, i.e. there are no preconditions for directional selection for lower developmental rate. At the same time, as already noted, comparison between all the three generations revealed an increase in both number of emerged juveniles and R_0 . Obviously, this occurs because of an increase in the proportion of early individuals, in which (in the case of high total number) R_0 is higher, than in late ones. Therefore, it is possible to assume that, in years of high number of emerged juveniles, early individuals will possess in their further development a selective advantage. However, the number upon completion of metamorphosis is affected not only by the initial density of generation, but also by environmental factors (Lyapkov and Severtsov, 1994). Therefore it will vary between years drastically and unpredictably. In addition, in the situation of a di-

rectional increase of the proportion of early juveniles there would be also a stronger influence of density on their mortality immediately after the completion of metamorphosis (Lyapkov, 1995), at least close to a pond, which, in turn, would reduce the survivorship till the first breeding and would thereby constrain the further increase in R_0 of this phenotypic class. Obviously, it is advantageous to have in such a situation a certain average level of developmental rate and a wide enough norm reaction to a change in the initial number of the generation.

Comparison between large- and small-sized.

Within the generation of 1989, large-sized individuals (both early and late), having achieved the sexual maturity, were characterized by larger body length (L) and fecundity (F), in comparison with average- and small-sized ones. In addition, the survivorship till age of 3 and 4 years correlated positively with the juvenile size: the survivorship of large-sized females (combined sample of early and late individuals) was significantly higher than that in small-sized ones. Both groups of large-sized individuals were also characterized by higher survivorship in elder age and by the maximum value of R_0 . However, the relative number of the initially large-sized juveniles was the lowest (among both early and late individuals) and their contribution to the next generation was also relatively low. In other words, the initial number of large- and small-sized juveniles differed so drastically that, on this "background", distinctions between individuals, belonging to different phenotypic classes, were rather weak. Within the generation of 1990, early large-sized females had advantage only in L (and accordingly, in F), and late large-sized ones only in F and in reproductive effort. At the same time, in this generation the relative initial number of large-sized individuals was also low and, despite the relatively high value of R_0 , the contribution to the next generation was also relatively low. This means that the permanent (i.e., in successive generations) increase in the proportion of individuals completing metamorphosis at large size is impossible. This would lead to their predominance in a population, since their net rate of reproduction is the highest. The most probable reason for such a limitation consists in that large-sized individuals have higher general fitness only in conditions of relatively high percentage of initially small-sized individuals. If the percentage of large-sized individuals became relatively high, their advantage would be lost or, at least, determined not by their initial size, but randomly. So,

in each of generations, the group with the maximum net rate of reproduction does not possess the mechanism of own reproduction in successive generations and, therefore, can not permanently increase its number (or frequency). In addition, among late individuals of the generation of 1990, large-sized ones were characterized by the minimal value of R_0 , i.e. initially large-sized juveniles may have no constant selective advantage at least in late individuals.

It is also necessary to note that the advantage in the initial size of generation as a whole does not determine the advantage in separate fitness components. As already mentioned, the relationship between the average (for a generation) body length at metamorphosis and the adult survivorship is markedly nonlinear, and this survivorship achieves the maximum at some intermediate value of the initial size. Since the fecundity is strongly and positively correlated with the initial size (see Lyapkov *et al.*, 2001), the correlation between the fecundity and adult survivorship also appears to be weak, though positive. It will be also recalled that the premetamorphic survivorship (the highest in the generation of 1989) is not correlated positively with the initial juvenile size. Owing to all these reasons, the selection for larger size at metamorphosis (i.e. for higher growth rate before metamorphosis) is impossible at the level of different generations.

Correlation Between General Fitness of a Phenotype and Accuracy of Its Reproduction

According to our data, the main reason for evolutionary stability of the phenotypic structure of the populations consists in that there is no mechanism of ontogenetic development of the structure of the relationship between fitness components, and there is no selection aimed to create such a mechanism, either. This conclusion is supported by the above-mentioned results: essentially nonlinear dependence of the survivorship of adult females on the initial juvenile size, weak (though positive) correlation between survivorship and fecundity and absence of a mechanism for reproduction of differences in such phenotypic characters as size at metamorphosis and number of a given juvenile size group. All these factors make higher the probability of origination of a negative correlation between the accuracy of reproduction of phenotypic characters and their contribution to the general fitness.

ACKNOWLEDGMENTS

The study was financially supported by the Russian Foundation for Basic Research, project nos. 94-04-

13770-a and 99-04-48502; Foundation "Leading scientific schools," project no. 00-15-97863, and Foundation "Universities of Russia," project no. 991771.

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