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Mechanisms Accounting for the Pattern of Fecundity Formation in the Frog, *Rana arvalis* Nilss.

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Abstract—The results of long-term field studies showed that fecundity of female Rana *arvalis* Nilss. frogs may increase on account of an increase in their body length or, alternatively, the shortening of their hindlimbs, with body length remaining unchanged. The type of reproductive strategy is independent of the annual population dynamics, but gradually changes (toward an increased dependence on female body length) with a decrease in the overall number of frogs involved in breeding, which occurs as the result of succession in the habitat studied. The growth of hindlimbs only, without an increase in body length, does not contribute to fecundity but is necessary for normalizing morphological proportions. Hence, fecundity and hindlimb length are the parameters "competing" for the resource provided by the female's body. In general, fecundity (F) as a function of body (L) and hindlimb length (f) may be represented as $F = (F_{max}L)/(L + f)$, where F_{max} is the maximum possible level of fecundity. Morphological proportions of females, rather than their absolute size, are the main parameters determining the dynamics of fecundity; hence, the abstract concept of sizes (as conventially used in ecology) loses its meaning in this case. Hindlimbs may be regarded as the "viability component," and body size, as the "reproductive component." Taking into account that both of these components belong to the morphological structure of the phenotype, it is principally impossible to distinguish between competition of adaptive components for some common resource and their morphogenetic interaction necessary for the maintenance of normal morphological proportions.

INTRODUCTION

The evolution of life cycles has usually been considered as the problem of the optimal distribution of resources between growth and reproduction in a given habitat, with regard to the ontogenetic limitations (Schmalhausen, 1968; MacArthur and Wilson, 1967; Begon *et* al., 1986). The effect of these limitations on the structure of fitness remains unclear. Taking such limitations into account is considered necessary, but only to the extent to which they limit free redistribution of the environmental resource between components of the phenotype. Both adaptationists and their opponents agree on this. The former proceed from the premise that ontogenetic limitations leave sufficient space for selection of various ecological adaptations (for example, see Maynard Smith, 1982), whereas the latter consider the range of "ontogenetically admissible" genotypes to be so narrow that selection has virtually nothing to operate upon (Gould and Lewontin, 1979). Both assume that the redistribution of resources between the components of fitness has no direct relation to the mechanism of their formation during ontogeny.

Allometric relationships are a classic example demonstrating that ontogenetic limitations affect the formation of components of reproductive fitness (Huxley, 1932; Gould, 1966; Shrnidt-Nielsen, 1984; Begon *et* al., 1986). Ecologists rightfully assume that in the case of a proven allometric relationship between fitness-related traits, it is unnecessary to know mechanisms of their development to understand the limitations imposed by allometry on the course of evolution of the life cycle. Suppose, however, that this allometric relationship lacks biological significance, and a common ontogenetic mechanism of interaction between the corresponding traits simply does not exist.

We have reason to believe that the latter applies to the allometric relationship between the components of fitness (primarily fecundity) and body size. In amphibians, corresponding correlation coefficients are extremely variable and usually have low values (Kozlowska, 1971; Koskela and Pasanen, 1975; Kaplan and Salthe, 1979; Kaplan, 1980; Gibbons and McCarthy, 1984, 1986). The dependence of fecundity on body size is possible to approximate by exponential functions, but this approach is arbitrary, and the results are impossible to verify by any additional data. There is one more circumstance that virtually excludes the very possibility of a direct ontogenetic relationship between fecundity and the "somatic" components of the phenotype: variation in fecundity is far greater than variation in body size or any other somatic trait (Lack, 1954). In terms of dynamic systems (see, for example, Romanovskii *et* al., 1975), this means that dimensional characteristics should be regarded as control parameters of the system, whereas fecundity is a dynamic variable. The biological significance of this statement is

Table 1. Mean values (m) and coefficients of variation (cV, %) of analyzed traits in frogs from samples taken in different years from the permanent and temporary (TB) basins

Trait		*L*		*F*		*D*		*E*		*f*		*L/f*	
n	year	*m*	*cV*	*m*	*cV*	*m*	*cV*	*m*	*cV*	*m*	*cV*	*m*	*cV*
75	1987	50.75	6.27	724	24.7	1.69	5.00	0.026	21.8	24.31	9.75	2.10	6.67
		|		|				|					
40	1988	51.89	4.99	910	18.4	1.67	2.99	0.030	15.4	24.99	5.96	2.08	3.85
		|		|		|		|					
82	1989	53.27	4.49	1029	25.2	1.77	3.95	0.038	23.7	25.40	5.67	2.10	4.76
				|		|		|		|			
103	1990	53.86	6.10	926	27.3	1.74	5.17	0.030	22.3	26.10	6.86	2.07	3.86
						|						|	
90	1991	53.90	6.10	988	31.5	1.67	4.79	0.029	29.7	26.50	5.80	2.03	3.45
35	1988TB	$\underline{50.56}$	4.98	839	25.8	$\underline{1.64}$	3.48	0.028	18.2	$\underline{24.16}$	6.17	2.10	4.28
25	1989TB	$\underline{52.04}$	5.15	963	18.9	1.75	3.20	0.037	15.4	$\underline{24.56}$	5.00	2.12	4.72

Note: |—differences between samples taken from PB in consecutive years are significant ($p < 0.05$); underlining shows that differences between samples of the same year taken from PB and TB are significant ($p < 0.05$). (L) Female body length, mm; (*F*) fecundity; (D) egg diameter, mm; (E) reproductive effort: (*f*) femoral length, mm; (*L/f*) the ratio of body length to femoral length.

that changes in body size, leading to changes in the level of fecundity, also modify the mechanism of these changes, i.e., the type of dependence of fecundity on body size. This is equivalent to the establishment of a direct relationship between the mechanisms of ontogenetic development of phenotypic traits and the extent of their contribution to reproductive fitness.

In this work, we used data from our long-term field experiments (1987–1991) to reconstruct the mechanisms involved in the development of reproductive fitness in the moor frog, ***Rana arvalis*** Nilss.

MATERIALS AND METHODS

Mating ***R. arvalis*** frogs (pairs in amplexus) were captured in their natural spawning grounds in the vicinity of the Zvenigorod Biological Station of Moscow State University. The main spawning ground of the population under study, on which young of the year emerge regularly, is located in a former peat mine abandoned approximately 60 years ago and overgrown with vegetation (subsequently referred to as permanent basins, PB), In 1988 and 1989, we also collected pairs of frogs from various pools in the forest (subsequently referred to as temporary basins, TBs).

Pairs in amplexus were placed in individual aquariums for spawning. Fecundity (F), i.e., the number of eggs per clutch, was determined as described by Surova and Cherdantsev (1987): we measured the volumes of the entire clutch and of its small fragment and calculated the number of eggs in this fragment; the F value was obtained by recalculating this number per total volume of the clutch. Egg diameter (D) was measured under a dissecting microscope fitted with an ocular micrometer, with an accuracy of 0.01 mm. Our previous study showed that, at such an accuracy, differences in the size of eggs within the same clutch were statistically insignificant compared to the interclutch variation in this parameter (Surova and Cherdantsev, 1987); hence, only ten eggs per clutch were measured. Measurements were made during early cleavage, because at later stages eggs accumulate water and increase in size. In females after spawning, we measured the snout–vent length (L) and femoral length (*f*). The age was determined according to a conventional procedure (Smirina, 1972) by counting the number of annual bone rings in the fourth digit of a hindlimb in its serial paraffin sections. The age of females captured in 1991 was not recorded. The reproductive effort (E) was calculated from the formula $E = (FD^3)/L^3$.

In addition to routine statistical treatment of experimental data, we used the method of main components (Jeffers, 1978) and analysis of variance (Scheffe, 1977) to analyze the structure of interactions between the components of reproductive fitness and between morphological traits during the growth of frogs. Calculations were made with the aid of STATGRAPHICS and STATISTICA software packages.

In addition, we used the data on the number of frogs involved in breeding during the last 15 years (1981–1995), estimated by S.M. Lyapkov by taking census of clutches deposited within the home range of the population studied.

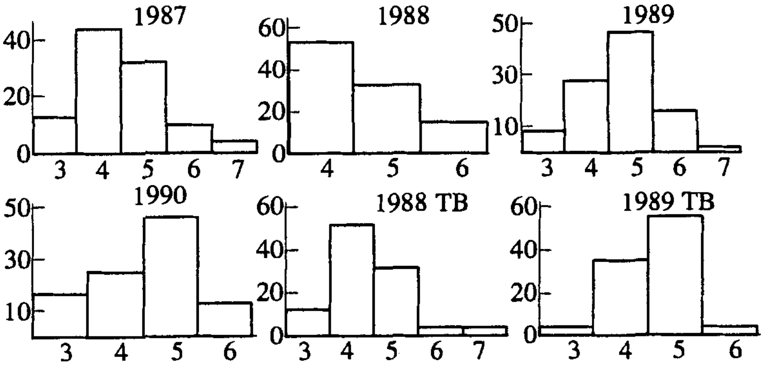

Fig. 1. Age distribution of females in samples taken from 1987 to 1990 from the permanent and temporary (TB) basins. Abscissa shows age of females (years), ordinate shows proportions of females of different age (%).

RESULTS AND DISCUSSION

Long-Term Dynamics of Body Size, Fecundity, and Demographic Structure

We begin with frogs breeding in PB, because only their progeny has a guarantee that individuals surviving the embryonic and larval development will successfully complete metamorphosis and begin terrestrial life. The following chapters of the paper will also deal largely with the data on these frogs, whereas frogs breeding in TBs will be discussed separately.

In 1987, breeding frogs had the smallest body size, the lowest fecundity, and the smallest eggs (Table 1). In the following two years (1988 and 1989). the size and fecundity of frogs increased considerably and, after a small decrease in 1990, reached a plateau (data statistically significant). Changes in the reproductive effort coincided with those in fecundity. The egg size reached a peak in 1989 and decreased by 1991. Body proportions of females, estimated from the *L/f* ratio (Terentjev, 1950), remained virtually unchanged from 1987 until 1989, but in 1990 and 1991 the relative length of hind limbs increased significantly (Table 1).

Analyzing the age of reproductive females (1987–1990), we found that they begin to participate in breeding at the age of three years and cease to reproduce at the age of six years; the modal age at the peak of population size is four years. During the study period, the mean age of females involved in breeding remained statistically similar, but in 1989 (the year of peak fecundity) the proportion of five-year-olds increased significantly (Fig. 1). We found only one female that successfully spawned at the age of two years and few reproductive females aged over six years (the oldest frog was nine years old), but excluded them from analysis.

Thus, the comparison of samples taken in different years provides evidence for a high plasticity of both morphometric parameters and components of fitness. In fact, each breeding season brings out a new pattern of values taken by traits studied. Hence, pooling samples of different years and averaging the corresponding data, as is common in ecological studies (Begon *et* al., 1986). is inadmissible in our case, both for formal reasons and in essence.

On the other hand, seasonal fluctuations provide a background for relatively long-term changes, which retain their trend for more than two consecutive seasons. These are (1) an increase in the absolute body size, age (specifically, an increase in the proportion of five-year-old females), and fecundity during the period from 1987 to 1989 and (2) relative stabilization of body size and fecundity in the following years, with a concomitant shift in body proportions resulting from an increase in the relative length of hindlimbs.

The fact that long-term changes in body size more or less correlate with those in fecundity may suggest the existence of a common allometric relationship, resistant to seasonal fluctuations, between these traits. It is easy to demonstrate, however, that any allometry is lacking. When we approximated the function *F*(*L*) by the exponential function $F = aL^b$ and evaluated the result by the least squares method (using STATISTICA software), the error was enormous (mean-square deviation of about 10^4). We failed to find any elementary function sufficiently suitable for approximating the empirical dependence. Such a result is understandable, because variation in fecundity is almost by an order of magnitude higher than that in body size (mean variation coefficients see in Table 1).

At the same time, all samples demonstrated the following trend. On the plane (F, L), the empirical points (individuals) were distributed in such a way that the curve showing the regression of F with respect to L for the small females was obviously steeper than that for the large females. We confirmed this finding when approximating the empirical distributions by two linear functions with domains defined according to a visible difference in the shape of *F*(*L*) curves for small and large females. The arbitrary boundary between small and large frogs naturally shifted depending on the sample. Thus, females classified as small in 1987 had body

Table 2. Coefficients of allometric dependence b (from $y = a \times x^b$) of fecundity ($y = F$) and the sum of body length and femoral length ($y = S$) on body length ($x = L$), and coefficients of linear correlation between F and L for small (SM) and large (LA) females (see text)

Trait	Coefficient	Year						
		1987	1988	1988 TB	1989	1989 TB	1990	1991
L, *F*	*b*	1.08	1.79	3.20	2.10	2.84	1.74	1.94
	corr	0.27*	0.47*	0.64*	0.40*	0.74*	0.27*	0.40*
L, *S*	b	1.04	0.98	0.97	0.91	0.86	0.97	0.93
	corr	0.95*	0.97*	0.96*	0.94*	0.96*	0.98*	0.98*
L, *F*	*corr*							
SM		0.29*	0.43*	–	0.34**	–	0.37**	0.37**
LA		−0.44	0.20		0.19		0.29	0.05

Note: (TB) temporary basin.
* $p < 0.05$; ** $p < 0.01$.

size below 54 mm; in 1988, below 53 mm; in 1989, below 55 mm; in 1990, below 56 mm; and in 1991, below 56 mm. The positive correlation between *F* and L was statistically significant only in small females (Table 2). In this table, we did not include the data on TBs because the corresponding samples were too small to divide females into two groups.

Thus, the general trend is that the dependence of fecundity on body size in females disappears as the latter parameter increases (or reaches a certain threshold level). Bannikov and Denisova (1956) obtained similar data on R. *arvalis* many years ago. Hence, the mechanisms determining fecundity of frogs appear to be fairly complex and principally nonlinear. We will discuss them in the following sections.

Interaction between Components of Reproductive Fitness and the Pattern of Fecundity Formation

Variables directly related to reproduction are apparently reproductive effort E, fecundity *F*, body length L, egg size D, and age *T*. Figure 2 shows their distribution in the space of the first and second main components. In the sample from 1987, L, D, and T are closely related to one another and contribute only to the first main component, whereas E and *F* contribute only to the second main component. Hence, we can distinguish two independent processes: changes in fecundity and reproductive effort ("generative growth") and the annual increment in the egg size and body size ("somatic growth").

In samples from the following years (1988–1991), the relationship between L, D, and T gradually weakens, and identification of the somatic and generative growth as different processes becomes possible only with respect to the second main component, because their contributions to it are opposite in sign. As for the first main component, the dominant process is generative growth, but variables characterizing the somatic growth (primarily L) also contribute to it. Thus, the positive relationship between the somatic and generative growth is possible only when the somatic traits (including egg size in our case) can change independently of one another.

As the variable characterizing the size of gametes (D) falls within the space of somatic growth in all samples, only fecundity can serve as the measure of "expenditure for reproduction." The reproductive effort in this case is a formal variable lacking biological significance. Fecundity has two intrinsically independent sources, and one of them (the generative growth) is "guaranteed" and independent from the body size of a female. This means that both small and large frogs have a sufficient internal resource for developing a certain minimal fecundity (if fecundity in 1987 is taken as a minimum). An increase in body size may provide an additional source of fecundity, but only on the condition that it is excessive in relation to a certain minimal annual increment correlating with an increase in egg size. The positive correlation between the somatic and generative growth appears against the background of an increase in body size, and the "excess" expended for improving fecundity may result from the positive allometric relationship between body weight and length, described for many anuran species (Jorgensen, 1981).

An interesting fact is that we observe no significant competition between growth and reproduction when using the female body length as the only parameter characterizing its size. This competition manifests itself only at the level of the second main component in samples taken from 1989 to 1991 (Fig. 2). Hence, either it is actually absent; i.e., only the excessive internal resource is expended for an additional increase in fecundity, or this increase competes with the development (or maintenance) of normal morphological proportions rather than with an increase in the absolute

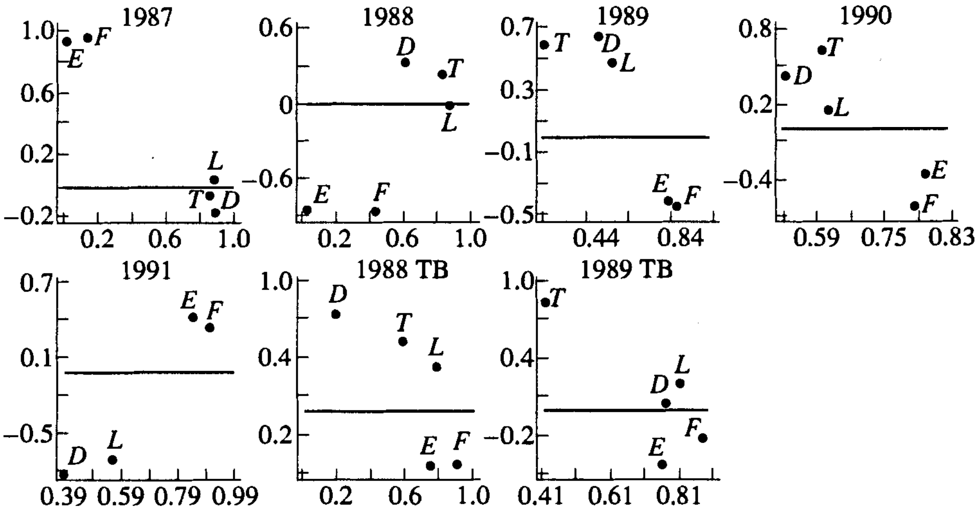

Fig. 2. Distribution of components of reproductive fitness in the space of the first (abscissa) and second (ordinate) main components. For designations of traits, see text.

body size. In the latter case, we may reveal competition by analyzing the relationship between the level of fecundity and the interaction of growth processes that determine body proportions in females.

Relationship between the Patterns of Fecundity Formation and Growth

Intuitively, female body length should be more related to reproduction than hindlimb length. However, the latter parameter is apparently more significant for the survival of frogs (Salthe and Crump, 1977). To analyze the relationship between growth of the body and hindlimbs, we performed the analysis of main components for the following variables: L, f (femoral length), and Uf (Fig. 3).

Theoretically defined variables allow us to distinguish three types of growth: a correlated change in the length of the body and hindlimbs; hindlimb growth without body growth, which implies a negative correlation between Uf and *f*; and body growth without hindlimb growth, which implies a positive correlation between *L/f* and L. In the samples taken from 1987 to 1989, the first and second types of growth fall within the space of first main component (making a positive and a negative contribution to it, respectively), whereas the third type of growth pertains to the second main component. Apparently, the dynamic balance between growth of the body and hindlimbs is lacking: independent positive fluctuations of L are less probable than those off. In biological terms, this means that "normal" growth (i.e., the correlated growth of the body and hindlimbs) may be accompanied by "regulatory" growth, which occurs in frogs with shortened hindlimbs (femurs) and is aimed at restoring the normal relation between body length and hindlimb length.

The negative contribution of Uf to the first main component significantly decreases in the sample from 1990 and disappears in the sample from 1991 (Fig. 3). Note that a decrease in the average Uf value was observed in the same samples (Table 1). Hence, retardation and eventual cessation of the regulatory growth is obviously related to the relative elongation of hindlimbs.

The relation between body length and hindlimb length may also change during the normal growth, provided it is not isometric. It is apparent, however, that the existence of regulatory growth makes the coefficient of allometry impossible to determine accurately. The most accurate method is to use the value of coefficient b from the equation $S = aL^b$, where $S = L + f$. This allows us to avoid the effect of random (nondirectional) independent fluctuations off and L that have no relation to the growth of a frog as an entire organism (Table 2). However, the effect of a directed contribution of the independent hindlimb growth to an increase in the absolute size is not excluded in this way, and, hence, the value of the coefficient is overestimated. Moreover, the degree of overestimation varies depending on the sample: it is relatively high in samples from 1987 to 1989 and low in samples from 1990 and 1991. Data in Table 2 show merely that body and hindlimb growth in samples from 1987 and 1988 were nearly isometric, whereas in samples from 1989 to 1991 the rate of body growth was slightly higher than the rate of hindlimb growth.

Let us consider the probable relationship between the above pattern of growth and the pattern of fecundity formation in frogs. To this end, we combined variables *F, L, f,* and Uf in the space of the first two main components (Fig. 4). In every sample, the first main component characterizes the relation of fecundity to the normal growth (i.e., to the correlated change in L and *f*). This relation proves to be the weakest in samples taken

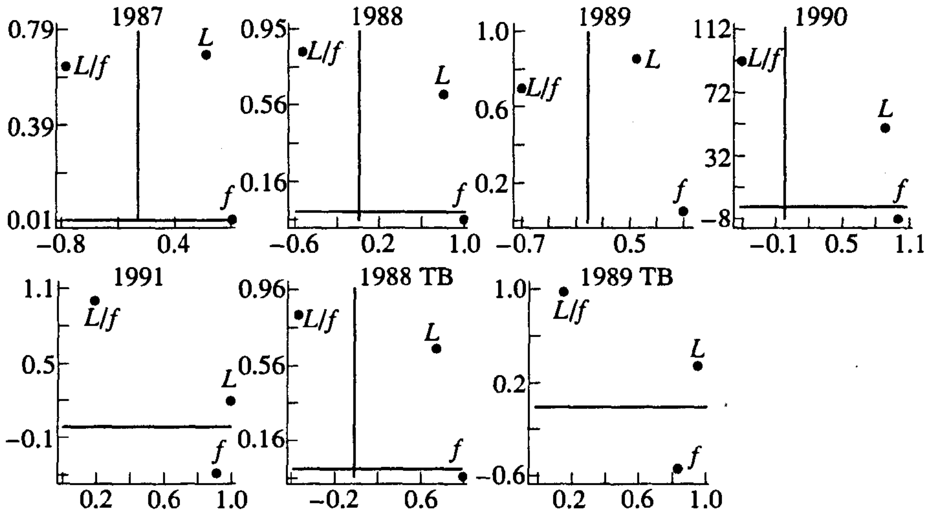

Fig. 3. Distribution of traits characterizing the pattern of growth in the space of the first (abscissa) and second (ordinate) main components. Foe designations, see text.

from 1987 to 1989, in which normal growth was supplemented with regulatory growth. With respect to the second main component, the same samples demonstrate a strong positive correlation between fecundity and the *L/f* value, whereas the total contribution of *L* and *f* is relatively small. Therefore, the second main component characterizes an increase in fecundity accounted for by an increase in the *L/f* value, with the absolute size of a frog remaining the same. If the regulatory growth is virtually lacking, as in samples from 1990 and 1991, the relationship between fecundity and the *L/f* value is much weaker.

Thus, growth and fecundity demonstrate the following relationships. Among frogs with similar body length, those with shorter hindlimbs are more fecund. Hence the mechanism for improving fecundity independently of an increase in the absolute body size: reproduction is provided for by the part of the intrinsic growth resource that otherwise would have been expended for the growth of hindlimbs (femurs). This is the one and only instance of competition between generative and somatic growth. In some samples (e.g., of 1987 and 1988), the role similar to that of the regulatory growth of hindlimbs may belong to an increase in egg size. Thus, if we introduce *D* into the space of traits considered above, the contribution of fecundity to the first main component will decrease to zero in these samples. Therefore, egg size may also increase at the expense of the growth resource that could have been expended for an increase in fecundity.

Another mechanism providing for an increase in fecundity is related to normal growth and is responsible for the existence of a relationship between fecundity and the absolute body size. Note that this relationship manifests itself more clearly when body length increases at a greater rate than hindlimb length, as in samples taken from 1989 to 1991. Taking into account all of the limitations (see above), this formally means that the absolute size may contribute to fecundity only on the condition that the growth of body length relative to hindlimb length demonstrates a positive allometry.

The relative significance of these mechanisms depends on the ratio between regulatory and normal growth, and this ratio, in turn, depends on morphological features of females. Thus, a comparison between samples taken in 1987 to 1989, on one hand, and in 1990 and 1991, on the other, shows that the regulatory growth ceases and, therefore, the correlation between fecundity and body size becomes stronger with an increase in the relative length of hindlimbs. Note, however, that changes discussed here concern only the mechanisms responsible for the formation of fecundity and do not necessarily imply an increase in its level: in samples taken in 1990 and 1991, fecundity was not higher than in the sample taken in 1989.

Females Breeding in TBs

Frogs breeding in TBs have two distinctive features: a delayed breeding period (the onset of spawning in TBs virtually coincides with its cessation in PB) and low reproductive success, because TBs usually dry up before tadpoles enter metamorphosis.

In both samples (1988 and 1989), females from TBs were significantly smaller than females sampled from PB in the same years, but their fecundity was similar (Table 1). The proportion of three-year-olds among females from TBs was significantly higher than in PB (Fig. 1).

Females from TBs demonstrated the prevalence of normal growth (Fig. 2) and a very strong positive correlation between fecundity and the absolute size

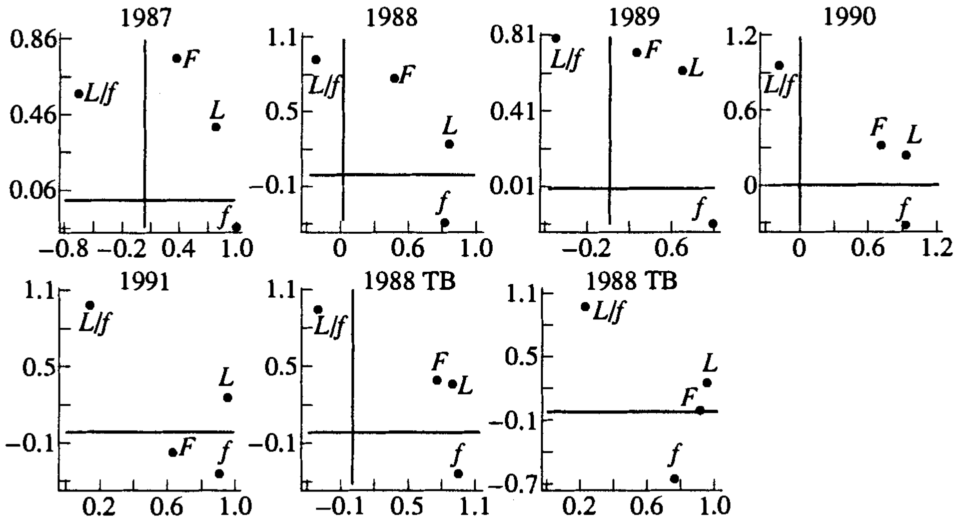

Fig. 4. Distribution of components of reproductive fitness and the traits characterizing the pattern of growth in the space of the first (abscissa) and second (ordinate) main components. For designations, see text.

(Figs. 3 and 4). In other words, mechanisms determining the structure of fecundity in these frogs are very similar to those in females sampled from PB in 1990 and 1991. Therefore, the main distinctive feature of females from TBs is that a decrease (1988) or complete cessation of regulatory growth (1989), with all of the consequences they produce, occur against the background of a relatively small absolute size of these frogs.

Because of low (virtually zero) reproductive success, females breeding in TBs do not form a separate population. Their distinctive features provide evidence for no more than the existence of a relationship between their proper morphological development (because of delayed breeding or, conversely, high energy of somatic growth) and the choice of spawning ground. It may well be that gathering in TBs is characteristic mainly of frogs spawning for the first time (independently of their age), in which homing has not yet developed. Moreover, some frogs from TBs should have accumulated more fat allowing them to prolong wintering. A delayed exit from hibernacula, occurring when vocalization of males in PB has already ceased, implies a greater probability of breeding at random sites, i.e., in TBs.

Probable Effects of Population Dynamics

The data considered so far applies mainly to the ontogenetic mechanisms accounting for the pattern of fecundity formation. In fact, we discussed the individual reaction norm, i.e., the limits of variation in this mechanism as they would have been in an individual capable of living several lives under different environmental conditions. The problem at the population level—why this mechanism is observed in a given group of individuals and in a given year—has not yet been addressed.

Strictly speaking, the available data do not allow us to answer this question, because field observations on marked frogs are necessary for this (we intend to describe them in the next publication). At the same time, to gain better understanding of the mechanisms responsible for fecundity, it is principally important to estimate the ontogenetic plasticity of analyzed traits, which determines the rate of their response to changes in the environment. The degree of plasticity is possible to estimate (roughly, of course) by relating changes in these mechanisms to population dynamics and fluctuations of environmental conditions.

During the period from 1981 to 1991, the number of breeding frogs fluctuated over a four-year cycle (Fig. 5) and, at the same time, gradually decreased (probably as a consequence of succession in PB). The absence of any relationship between fecundity and the absolute body size, observed in 1987, coincided with the peak phase of the population cycle, whereas the positive contribution of body size to fecundity (with both parameters increasing simultaneously) manifested itself against the background of a decrease in population size. Note that at the reverse phase (a population increase in the period from 1989 to 1991), the positive correlation between fecundity and body size did not decrease but became even stronger.

Thus, there is no direct relationship between population dynamics and the "choice" of the pattern of fecundity formation. A certain trend observed in this population—the appearance and subsequent improvement of a correlation between body size and fecundity, and changes in morphological proportions of females—is apparently associated with a gradual decrease in the overall number of breeding frogs. Studies on *R. temporaria* and *R. arvalis* frogs showed that mortality at larval stages (Severtsov and Surova, 1979; Severtsov, 1986) and during the first year of terrestrial life (Berven, 1990; Lyapkov, 1995) depends on population density; hence, a decrease in density is equivalent to a change in the type of habitat in the way promoting an increase in body size (Begon *et al.*, 1986). According to our observations performed from 1988 to 1995, the number of young of the year emerging from PB significantly decreased from year to year. Therefore, the load of population density on juveniles of the first (critical) year of life gradually decreased; i.e., the conditions for their growth progressively improved, providing the possibility of accumulating a certain excessive growth resource. This eliminated competition for the resource between growth and reproduction and subsequently led to a positive correlation between them.

Such a change of reproductive strategy exemplifies a relatively slow response to the modified environment, and it is apparent that rapid types of response exist as well. To reveal them, we grouped females with respect to the year of breeding, age, and generation (females born in a given year) and compared the first group with the second and third by means of two-way analysis of variance (hierarchic scheme, mixed model; see Scheffe, 1977). The year of breeding, i.e., the environmental conditions in the last summer before the current breeding season, proved to have a significant effect on *F*, *E*, and *D*, but the effect on *L* was insignificant. By contrast, the effect of age on *F* and *E* was insignificant, whereas that on *L* and *D* was significant. Finally, the effect of generation on any parameter lacked statistical significance.

Thus, environmental factors affecting body length and fecundity of females do not correlate with one another: the rates of their response to environmental fluctuations are different. It is remarkable that fecundity proves to be the most labile parameter (in terms of dynamics, fast variable) immediately responding to living conditions of the last year, independently of the age of a female. In this respect, body length is a stable parameter (slow variable), and egg size occupies an intermediate position.

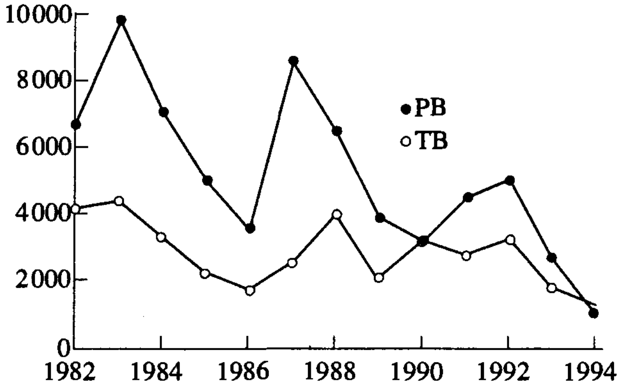

Fig. 5. Female population dynamics from 1987 to 1994. Ordinate shows the number of females breeding in the permanent (PB) and temporary (TB) basins.

Model of Fecundity Formation

The problem is to find a model combining both mechanisms—dependent on and independent of body size—that provide for an increase in fecundity. The basis for constructing this model is the fact that the same growth resource (determined by female body length) can be used to improve fecundity at the expense of hindlimb (femoral) length or, alternatively, to increase the length of hindlimbs at the expense of fecundity. Morphological proportions of females, rather than their absolute size, are the parameter controlling the dynamics of fecundity (the pattern of its formation) and its level attainable at a given body size; hence, the abstract concept of sizes (as conventionally used in ecology) loses its meaning in this case. In a rough but plausible approximation, hindlimbs may be regarded as the "viability component," and body size, as the "reproductive component." Taking into account that both of these components belong to the morphological structure of the phenotype, it is principally impossible to distinguish between competition of adaptive components for some common resource and their "morphogenetic" interaction necessary for the maintenance of normal morphological proportions.

Thus, fecundity and hindlimbs compete for the resources provided by the female body. Assuming that this resource is distributed proportionally (according to the principle of golden section, see Goodwin, 1994),

$$F/F_{\max} = L/(L+f) \quad \text{or} \quad F = (FL)/(L+f), \tag{1}$$

where $F_{\max}$ is the maximum possible level of fecundity.

The dependence of *F* on *L* resembles the saturation curve for an enzymatic reaction, where *L* is the "substrate" and *f* is an analogue of the Michaelis constant, i.e., the parameter determining saturation rate (the lower the *f* value, the higher this rate). In the space (*f*, *L*, *F*), the dependence of fecundity on body and hindlimb length forms a surface that may be regarded as an "evolvent" of saturation curves with different *f* values (Fig. 6). This surface has the following property: linearizing the equation (1) as

$$1/F = 1/F_{\max} + (1/L)(f/F_{\max}) \tag{2}$$

and taking a partial derivative df/dL, i.e., calculating the rate of change in body length with respect to hindlimb length (with fecundity remaining unchanged), we obtain

$$df/dL = f/L. \tag{3}$$

Equations (2) and (3) are not dynamic; i.e., they do not define the law of motion of a system in the space

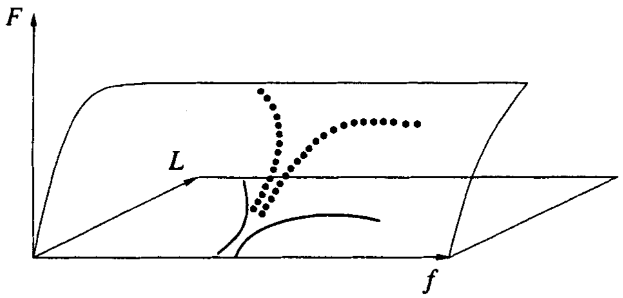

Fig. 6. Model of fecundity formation: the dependence of fecundity on female body length at different values of femoral length, resolved in space. Solid lines show motion on the plane (*L*, *f*) with positive (curve sloping toward *L*) and negative (curve sloping toward *f*) contributions to fecundity; dashed lines show reflection of this motion on the plane *F*(*L*, *f*).

shown in Fig. 6. They only indicate that the regulatory growth (an increase in *f* with *L* remaining constant) causes a decrease in fecundity, and the normal growth (a correlated change in *f* and *L*) can contribute to fecundity only if *f* grows at a lower rate than *L*. This condition is fulfilled in the case of any nonlinear function *L*(*f*) that describes the motion of a system on the plane (*f*, *L*) by the curve sloping up, toward the *L* axis (Fig. 6). In particular, this is possible in the case of a negative allometric dependence of hindlimb length on body length. Thus, this model naturally integrates seemingly alternative mechanisms providing for an increase in fecundity: an increase in the absolute body size, on one hand, and the redistribution of growth resource between the body and hindlimbs without changes in the absolute size, on the other.

The correspondence with the data of field observations proves to be fairly rough, largely because hindlimb growth is not the only competitor for the growth resource (in the absence of this competition, the resource might have been expended for an increase in fecundity). As noted above, an increase in egg size (*D*) can also lead to competition. In the sample from 1988, this effect is comparable to that of regulatory growth. It may explain the fact that, notwithstanding a relatively weak regulatory growth in this sample (Fig. 4), the contribution of absolute body size to fecundity, estimated with reference to the *D* value (Fig. 3), was only slightly greater than in the sample from 1987, in which the regulatory growth was significantly more intense. Nevertheless, the number of factors potentially competing for the resource is limited, because otherwise they would have been impossible to distinguish.

Consider again the dynamic interpretation of equation (2). According to a common approach to the analysis of nonlinear dynamic systems, a qualitative description of the dynamics of our system will be based on the hierarchy of rates (characteristic times) of changes in its variables (Romanovskii *et al.*, 1975). As noted above, fecundity is the most labile trait which responds to environmental conditions during the period of active feeding that immediately precedes the current breeding season. Hence, as a first approximation, assume that the level of fecundity is determined in the last summer before a given breeding season. Changes in *L* and *f* occur at a lower rate: as body size strongly correlates with age, *L* has insufficient time to respond adequately to seasonal fluctuations of environmental conditions. This allows us to refrain from considering the dynamics of fecundity, assuming that the time required for changes in it is negligible compared to the time required for changes in morphological parameters. Therefore, we assume that the actual motion occurs in the plane (*f*, *L*) and the moving point is immediately reflected on the surface defined by the equation (2).

In a very rough approximation, the motion in the plane (*f*, *L*) might correspond to the allometric dependence *f*(*L*). Such a dependence, however, can pertain only to normal growth of the body and hindlimbs. This type of growth prevailed in samples from 1990, 1991, and, to a lesser extent, from 1988 (Fig. 3); hence, allometry in them may be regarded as actual. These samples demonstrated weak negative allometry of hindlimb growth with respect to body growth (Table 2) and a strong positive correlation between the absolute body size and the level of fecundity, which generally agrees with the predicted (model) data (specific features of the sample from 1988 were described above).

In general, neither allometric nor any other dependence regarding *f* and *L* as mere dynamic variables can describe the dynamic of growth adequately, because they do not take into account the regulatory growth. In fact, we should regard *f* as both a dynamic variable and a parameter of the equation describing an increase in body length. Hence, growth dynamics prove to be principally nonlinear, which makes its reconstruction on the basis of field data impossible. The only fact relevant for our work is that the regulatory growth reduces and sometimes even eliminates the dependence of fecundity on the absolute body size. We may regard growth of this type as an inevitable consequence for an increase of fecundity in females with imperfect morphological proportions (excessively short legs).

CONCLUSION

Modern ecological theory (MacArthur and Wilson, 1967; Pianka, 1970; Begon *et al.*, 1986) regards phenotype as a two-component system comprising the reproductive and survival components, and this is a prerequisite to the concept of *r*/*K*-selection. An analysis of mechanisms determining the pattern of fecundity formation in *R. arvalis* suggests a principally different idea. One of the components of the phenotype—in our case, female body length—is both its structural part (i.e., belongs to the survival component) and an element of the reproductive component. Changes in the reproductive strategy are possible only via changes in the structure of growth, and, conversely, changes in the structure of growth will inevitably lead to the redistribution of resources between growth and reproduction, i.e., to a change in reproductive strategy.

This postulate may be of general significance, because any component of reproductive fitness is eventually a structural and, hence, potentially morphogenetic component of the phenotype. A distinctive feature of *R. arvalis* frogs (and possibly of all anurans) is the role of hindlimbs in the regulatory processes. A similar role may belong to an increase in egg size (Gibbons and McCarthy, 1986). It appears that the model described in this paper is applicable to all cases when (1) the structural elements of the phenotype are possible to differentiate into the survival and reproductive components and (2) the ontogenetic interaction between these components is not reduced to simple linear (e.g., allometric) relationships.

In our case, the obligatory maintenance of a certain proportion between body length and hindlimb length, which most likely affects the survival of frogs, is the only analogue of "ontogenetic limitations" as they are understood by ecologists. Within these limits, direct selection for higher fecundity is equivalent to selection for excessively short legs, i.e., for frogs that use their growth resource for reproduction at the expense of proper morphological structure. Such selection is apparently impossible because of at least two reasons. First, selection for short legs reduces and eventually eliminates the dependence of fecundity on body size; second, an increase in fecundity achieved in this way is inevitable followed by the transition to regulatory growth (probably as soon as in the next breeding season). In essence, an "absolute" increase in fecundity (e.g., as in *R. temporaria* compared to *R. arvalis*) may result only from the episelective effect (Severtsov *et al.*, 1991; Cherdantsev *et al.*, 1996) of changes in the rate and structure of growth or in behavior (e.g., when polycyclic reproduction becomes monocyclic).

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