

Ecological Aspects of Amphibian Metamorphosis

Nonnormal distributions of competitive ability
reflect selection for facultative metamorphosis.

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In a single population, larvae of the salamander *Ambystoma maculatum* may metamorphose between weights of 0.24 and 2.34 grams and over a period from 57 to 144 days after hatching (1). In populations of the frog *Rana clamitans* some larvae metamorphose after a larval period of 70 to 85 days; others remain in the pond over winter and do not transform until 335 to 360 days after hatching (2). For a long time the extreme plasticity of amphibian larvae has been recognized by herpetologists as well as embryologists (3), but no synthetic theory of the ecology of amphibian metamorphosis exists.

The endocrine feedback systems between the hypothalamus, pituitary, and thyroid glands that activate and regulate metamorphosis have been modeled (4, 5). These models always contain an ecological black box component of "extrinsic and intrinsic" factors that activate metamorphosis through their action on the central nervous system's stimulation of the hypothalamus. Our work offers a conceptual framework for modeling this black box. Ecological effects on growth rates are discussed and the physiological bases of the initiation of metamorphosis are suggested. This article is limited to the ecology of the larval stage, the period between hatching and metamorphic climax. As a time of rapid, sigmoid growth, frequently intense competition for food, and high mortality, the larval period is probably the stage in which the size of most amphibian populations is effectively regulated (1, 6).

Growth Models for Larval Amphibians

Three salient features of larval growth emerge from field and laboratory studies of both frogs (7, 8) and salamanders (9-12): an initial period of nearly exponential growth, a deceleration, and then a loss of weight at metamorphic climax. The sigmoid growth during the premetamorphic period can be described adequately by several mathematical models (13). The logistic model is unsuited for amphibian studies because algorithms for fitting its parameters require an estimate of some final weight, the upper asymptote. This asymptote may not be attained in amphibians because they often enter the metamorphic stage before the maximum size is reached. Other, more physiologically based models that treat growth as a balance between anabolism and catabolism are popular in fisheries biology, but they require laboratory determinations of metabolic rates and feeding efficiencies (14). A desirable ecological model should have parameters that can be estimated by sampling of natural populations and mark-recapture methods.

The model of normal growth of Laird *et al.* (15) suggests a theory for an ecological model of individual growth. This model treats growth as a balance between two processes: growth in body weight is at an exponential rate, but this rate is damped at another exponential rate. These processes can be justified on physiological and developmental grounds (16). Whatever the mechanism, two expo-

nential processes acting as a control system are represented by Laird *et al.* as a pair of simultaneous differential equations

$$dW_t/dt = \gamma W_t$$

and

$$d\gamma/dt = -\alpha\gamma$$

which have a solution in the form of a Gompertz function

$$W_t = W_0 \exp[(A/\alpha)(1 - e^{-\alpha t})]$$

in which W_t is body weight at time t ; W_0 is weight at time zero; A is the value of γ , the exponential growth rate, at time zero; α is the exponential rate of damping of γ ; and e is the base of natural logarithms. Bertalanffy (17) objects to the Gompertz function because it contains arbitrary constants without physiological meaning. In an ecological model the constants W_0 , α , and A do have reasonable interpretations. The constant A is the value of the exponential growth rate γ at the start of the larval period. The parameters A and W_0 are adaptive characteristics of the species, which can be determined even in the laboratory. The intrinsic growth rate is, of course, temperature-dependent (18).

The value of α , the exponential rate of damping of γ , is determined by both intrinsic factors—in general, physiological rates decrease by some power function of body weight (19)—and extrinsic factors such as food availability, food quality (5, 20), or species interactions (1). The dependence of γ on time will be described by the relation

$$\gamma = Ae^{-\alpha t}$$

The growth curve has an asymptote and a point of inflection that agree reasonably well with most empirical observations of growth in vertebrates (17). The parameters A and α can be estimated by the intercept and slope, respectively, of the regression of the specific growth rate, $(1/W)(dW/dt)$, on t .

If each individual in a population follows the same growth law, the dynamics of the population are simple phenomena. The wide differences in body weight and time of metamorphosis in both laboratory and field populations demonstrate that this is not the case in amphibians (1, 7, 20-22). Two experiments were designed to investigate variation in growth rates. The first involved growth rates of larval salamanders, and the second growth rates

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Table 1. Summary of data for 1971 experiment with *Ambystoma maculatum*; S.D., standard deviation; C.V., coefficient of variation.

Initial density	Time from start (days)	Block-pen	Larvae (N)		Body weight of larvae (mg)				
			Trans-formed before sample	In sample	Mean	S.D.	C.V.	Mini-mum	Maxi-mum
16	20	1-1	0	6	43	7	0.162	36	53
32	40	2-19	0	22	307	82	0.267	157	448
32	60	2-1	11	13	1145	145	0.126	832	1342
32	60	1-19	0	20	921	235	0.255	511	1270
32	80	1-15	14	3	1778	213	0.119	1571	1997
32	80	2-11	18	8	1304	84	0.064	1165	1430
32	100	1-9	3	1	1590			1590	1590
32	100	2-8	23	2	592	110	0.185	515	670
48	20	2-12	0	27	59	18	0.305	18	89
64	20	1-2	0	21	29	26	0.896	8	119
64	20	2-2	0	58	57	18	0.315	28	99
64	40	2-4	0	37	417	103	0.247	217	612
64	60	1-13	3	16	1091	248	0.227	407	1392
64	60	2-16	6	19	640	147	0.229	133	840
64	80	1-17	22	13	966	211	0.218	661	1346
64	80	2-20	15	29	428	84	0.196	232	566
64	100	1-6	14	6	1655	180	0.108	1397	1926
64	100	2-15	23	0					
80	60	2-13	2	29	502	125	0.249	292	709
128	40	1-7	2	94	342	141	0.412	112	699
192	60	1-16	5	135	359	143	0.398	101	674
192	60	2-3	2	118	353	90	0.254	163	622
224	40	1-5	0	107	325	128	0.393	35	666

Table 2. Experimental design and summary of data for 1972 experiment with *Rana sylvatica*; S.D., standard deviation; C.V., coefficient of variation.

Initial density	Time (days)	Pen	Survivors (N)	Sample size (N)	Body weight (mg)				
					Mean	S.D.	C.V.	Mini-mum	Maxi-mum
50	10	14	8	8	32	5.9	18.6	20	37
50	15	29	44	44	59	10.1	17.1	37	84
50	20	25	0						
50	25	34	33	33	328	62.8	19.2	199	463
50	30	35	25	25	554	155.6	28.1	318	881
50	35	24	10	10	846	183.4	21.7	608	1180
50	40	8	26	26	853	237.0	27.8	253	1212
50	45	30	25	25	692	204.6	29.6	162	990
50	50	16	9	9	832	112.5	13.5	705	1018
75	50	32	13	13	852	238.5	28.0	542	1177
100	20	22	10	10	194	48.8	25.1	129	281
100	40	4	13	13	1171	239.5	20.5	660	1000
100	50	19	10	10	853	142.1	16.7	695	1098
125	50	36	67	67	521	127.8	24.5	225	728
150	45	17	6*	6	1275	277.6	21.8	995	1757
150	10	20	17	17	24	5.8	23.7	16	42
150	15	3	41	41	81	8.9	10.9	57	97
150	20	13	124	119	248	38.6	15.6	112	339
150	25	28	74	74	179	44.5	24.8	103	381
150	30	2	90	90	515	138.8	27.0	120	760
150	35	27	80	80	377	98.0	26.0	87	584
150	40	18	25	25	1393	26.6	9.6	1192	1656
150	45	12	0						
150	50	10	56	56	513	109.9	21.4	380	769
300	20	5	?	30	121	20.3	16.8	82	156
300	40	6	131	131	563	161.8	28.8	114	937
300	50	1	184	182	466	129.8	27.9	202	832
600	20	21	292	164	210	49.6	23.5	58	310
600	40	11	3	3	1722	198.2	11.5	1495	1861
600	50	15	283*	283	270	88.0	32.4	120	561
1200	15	26	504	200	49	10.9	22.1	16	83
1200	20	7	899	162	88	19.2	21.7	30	139
1200	30	31	377	322	119	36.1	30.4	38	267
1200	40	9	768	330	108	58.2	54.1	33	742
1200	45	33	347	347	158	75.6	47.8	33	610
1200	50	23	513	197	80	33.3	41.6	30	213

* These pens were damaged so that the actual densities may have been lower or the number of survivors greater than the sample sizes suggest.

of larval frogs. In these experiments, populations with different initial densities were raised in screened enclosures in a natural pond. Replicate populations were sampled at regular intervals between hatching and completion of metamorphosis.

Experimental Populations

During 1971 and 1972 larvae were raised at specific initial densities in screen enclosures (7 meshes per centimeter; 2.44 meters long, 0.61 meter wide, and 0.61 meter deep) in a natural pond. The effects of the initial density of a population (that is, the number of individuals in the enclosure at the start of the experiment) on the ecology of metamorphosis were studied. Experiments were started by introducing an exact number of eggs (1971) or hatchlings (1972) into the enclosures (23, 24). After the hatchlings were introduced experimental populations were undisturbed until they were destructively sampled on predetermined dates. Throughout this article "days since hatching" will refer to the time since the experimental stock, which is a random sample of the available hatchlings, was introduced into the enclosures at the start of the experiment (23). Our experimental densities encompassed the range of densities we have estimated in natural populations (1).

Earlier experiments (1) suggested a set of models that were used to design the following two experiments. Populations of the salamander *Ambystoma maculatum* were raised at ten initial densities in a replicated complete block experiment for variance analysis. Twenty populations with specific initial densities were the experimental treatments randomly assigned to enclosures (pens) in each of two replicated blocks. (Ten densities would be undisturbed except to remove juveniles and five pairs of densities would be destructively sampled at 20-day intervals.) The pens were placed in Burt Pond (25) on 4 May 1971. Hatchlings were introduced on 5 May. Unfortunately, a counting error was made and the wrong pens were sampled on days 20 and 40. This error ruined the symmetry of the experimental design but fortuitously added information about the course of competition in high-density pens. The error was recognized and the sampling procedure modified on days

60, 80, and 100 (Table 1). The results for the populations that completed metamorphosis will be the subject of another paper (26).

In 1972 a 36-treatment experiment tested the effect of eight initial densities on the survival, growth, and developmental rates of tadpoles of the wood frog, *Rana sylvatica* (Table 2). Recently hatched larvae (23) were introduced into the experimental enclosures on 25 April. The larvae were randomly mixed before counting so that each had an equal probability of being assigned to selected combinations of eight initial densities and nine sampling dates. The treatments were randomly assigned to experimental enclosures arranged linearly from west to east on the south edge of the pond.

On the predetermined dates complete censuses were taken by sampling, first with a dip net and then by pulling the pens ashore and passing the mud through a sieve. All survivors were counted and then weighed to a precision of 1 milligram. The largest samples of *R. sylvatica* were subsampled after they were counted because mortality and weight losses during the time that would have been required to individually weigh the entire sample would have biased the estimates.

Figure 1 presents size-frequency histograms of larval *R. sylvatica* sampled 50 days after hatching from pens that contained one of eight initial densities.

ties of larvae. Fifty days after hatching is in the period when the first tadpoles are undergoing metamorphic climax. After this time transformed froglets are no longer a component of the larval population. Two effects of density are apparent. There is a negative, exponential relation between median body size and initial density, and the populations with the highest initial densities have a strongly skewed distribution of body sizes. In the high-density populations only a few individual frogs enter the range of body sizes obtained in the low-density populations, and no animals were in climax stages of metamorphosis.

The development of this negative-exponential decrease in body size and increase in skewness, which has occurred consistently in our other experiments with larval amphibians, can be explained by comparing the change in body size distributions with time in populations started at different initial densities. In the populations with a low initial density (Fig. 2) there is a rapid increase in body weight until some animals enter metamorphic climax and start dehydrating body tissues and absorbing gills, tail fin, and other larval tissues. There is an increase in variance but no obvious skewing in successive samples. At an intermediate density there is a more gradual increase in size until day 40 when many tadpoles enter metamorphic climax (Fig. 3).

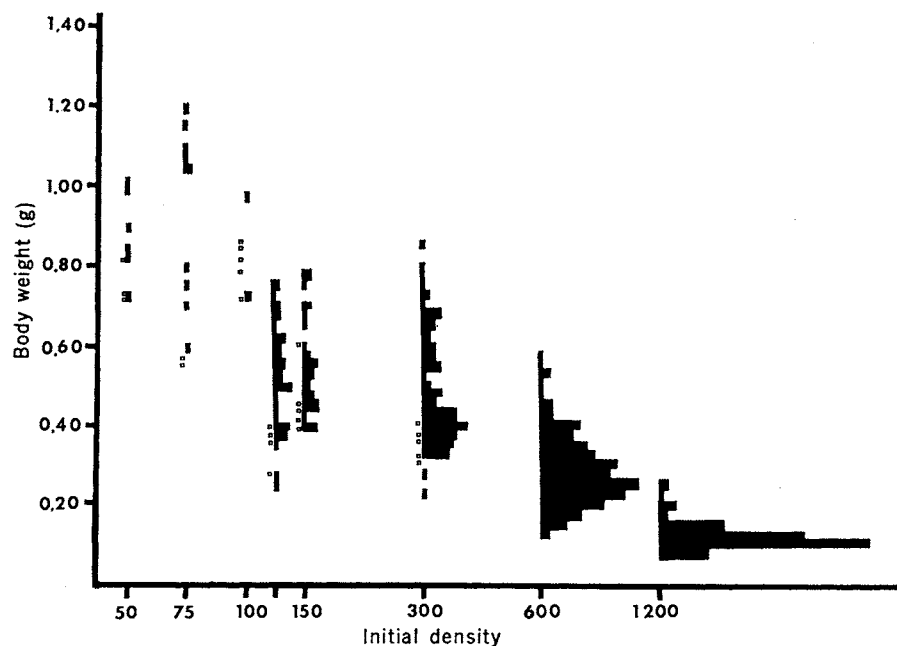


Fig. 1. Frequency histograms of body weights of *Rana sylvatica* larvae (solid symbols) and froglets (open symbols) of various initial densities, 50 days after the start of the experiment. Note the geometric scale of the abscissa. The sample sizes and descriptive statistics are in Table 2.

At a very high initial density (Fig. 2) the effect of competition becomes obvious. The median changes very slightly; only a few larvae are growing as rapidly as larvae at low densities. The distribution becomes increasingly skewed as a few larvae grow to sizes that are within the range of metamorphosing animals. We interpret these results as evidence of competition for

food in our experimental populations.

The data from the experiment with *Ambystoma maculatum* in 1971 show similar results (Table 1). At 60 days after hatching, when some larvae had metamorphosed, the negative, exponential relation between body weight and initial density is accompanied by a positive skewing of the body size distribution (Fig. 4). Figure 5 shows how

the skewing developed at a moderate density. Two of the highest-density pens (128 and 224 larvae) have weakly skewed distributions (Fig. 6) 40 days after introduction. In order to further explain the effect of density on growth we must return to a discussion of the mechanics of growth and the theory of individual growth curves.

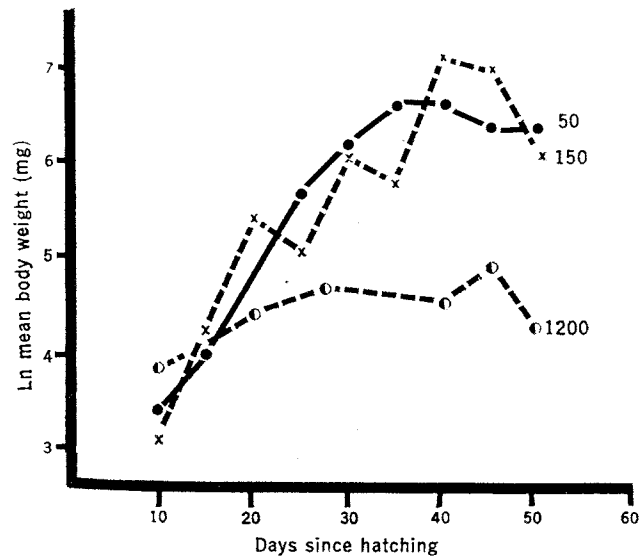
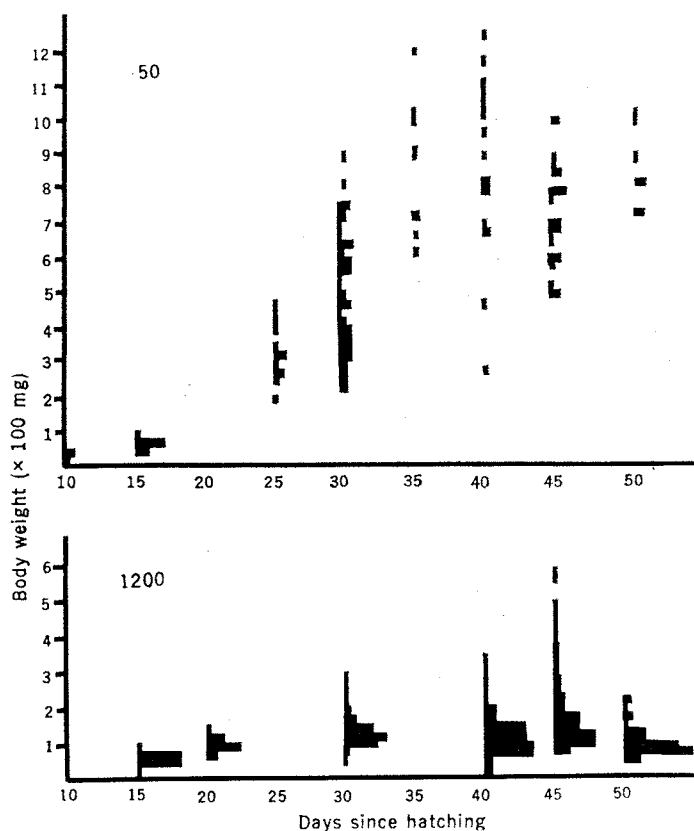


Fig. 2 (left). Frequency histograms of body weights of *Rana sylvatica* larvae in replicate populations of initial densities of 50 or 1200 larvae, at selected times after the start of the experiment. Note the development of skewness in the pens with density 1200 and the rapid overall growth in the low-density pens. Fig. 3 (right). Growth curves of *R. sylvatica* larvae in replicate populations of three initial densities (50, 150, and 1200), at selected times after the start of the experiment. See Table 2 for sample sizes and descriptive statistics.

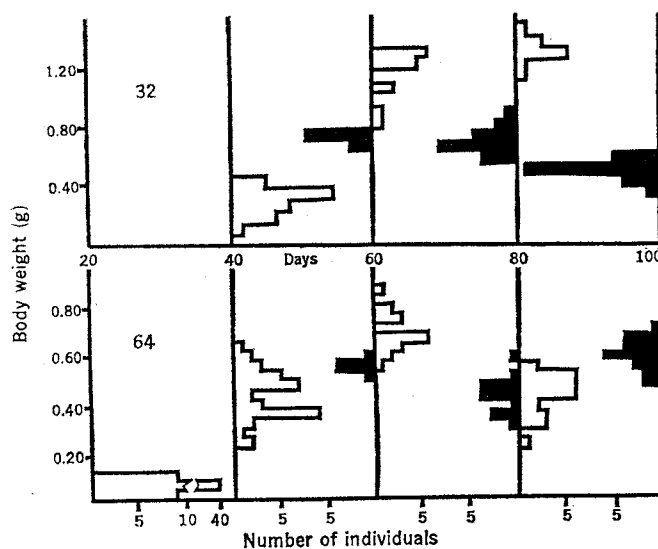
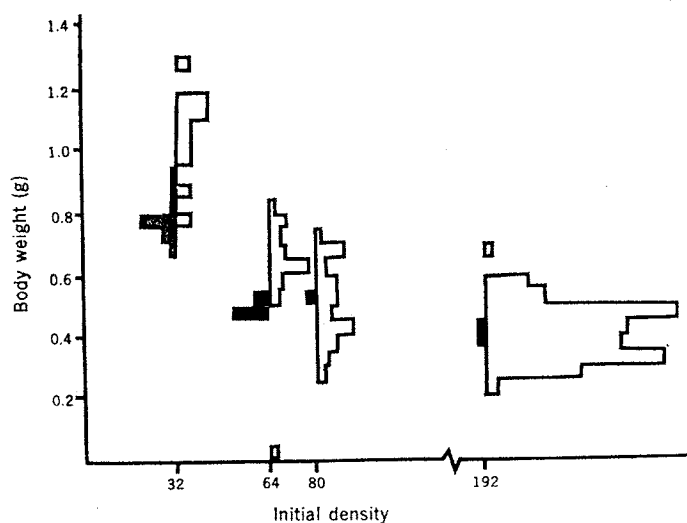


Fig. 4 (left). Frequency histograms of body weights of *Ambystoma maculatum* larvae (open symbols) and transformed juveniles (closed symbols) from populations with selected initial densities, 50 days after the start of the experiment. Fig. 5 (right). Frequency histograms of body weights of *A. maculatum* larvae (open symbols) and transformed juveniles (closed symbols) in replicate populations of initial densities of 32 or 64 at selected times after the start of the experiment. A pen of density 32 was not sampled on day 20. See Table 1 (block 2) for sample sizes and descriptive statistics.

Lognormal Size Distributions

The observed variation of body sizes in our experiments has two major components. Between populations, the effects of density cause an approximately exponential decrease in median body weight, and within populations the distributions of body weights become increasingly skewed as time proceeds. We suggest that this skewing is a consequence of the generation of a lognormal distribution. If the change in body size at any step of a growth process is a random proportion of the previous body size then the process obeys the law of proportionate growth, and body size will tend to be distributed as a two-parameter, lognormally distributed variate, provided the random components are positive, independent deviates having the same probability distribution (27). To generate a lognormal distribution, environmental impulses must have a multiplicative effect on body size rather than an additive effect, which would generate a normal distribution (28). In our application of the Gompertz function a lognormal distribution could be generated by the simple addition of u_i , a normally distributed random deviate with a zero mean, to the exponent

$$W_t = W_0 \exp \left[\left(A/\alpha \right) (1 - e^{-\alpha t}) + u_i \right]$$

This modification only considers variation in the total growth process. Figure 7 demonstrates the linear relation between the standard deviations and the mean body size as growth proceeds in *Rana sylvatica*. The slope of these lines, η , the coefficient of variation, is a useful characteristic of the lognormal distribution. The intercepts are not significantly different from zero, indicating that a two-parameter distribution sufficiently describes the data (27). At the low densities the coefficient of variation is small, but as the distributions become skewed it increases to 0.58 at the highest density. There is no regular pattern to this change, but we suggest that further study might demonstrate a regular increase in η with initial density.

A more mechanistic explanation would assign the variation to one of the model parameters. Variation in A , the growth rate at the start of the larval period, is a real phenomenon, but we suggest that it is an intrinsic variation independent of the density. Larvae raised in isolation and under identical conditions should develop a skewed distribution generated by indi-

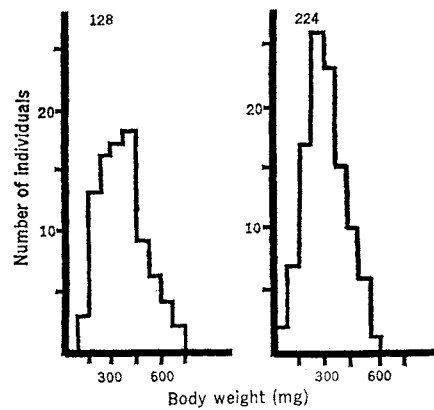


Fig. 6. Frequency histograms of body weights of *Ambystoma maculatum* larvae in populations with initial densities of 128 and 224, sampled 40 days after the start of the experiment. See Table 1 (block 1) for sample sizes and descriptive statistics.

vidual differences in *A*. Ecological factors such as food limitation, other competitive mechanisms, or perhaps growth inhibitors would cause variation in α , the rate of damping of growth. We suggest that variation in this component is the primary mechanism in the genesis of skewed distributions of body sizes in field populations.

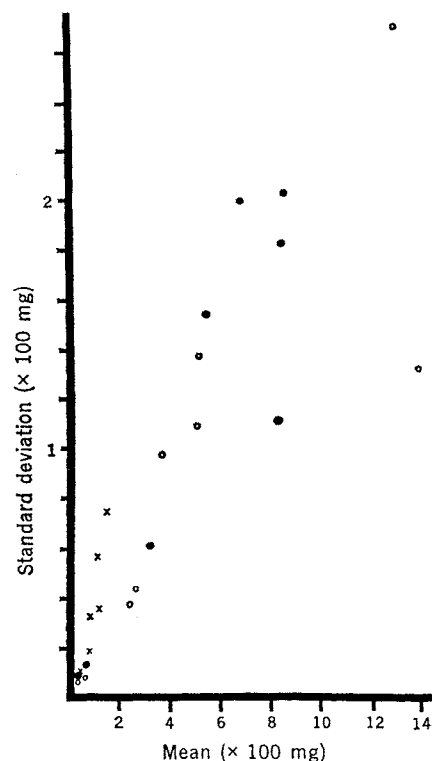


Fig. 7. Standard deviation of body weight as a function of mean body weight for replicate populations of *Rana sylvatica* at three initial densities (closed circles, 50; open circles, 150; crosses, 1200) at selected times after the start of the experiment. See Table 2 for a statistical summary including coefficients of variation.

This variation may have many causes: genetic differences (29), position of the egg in the egg mass (10), physical characteristics of the microhabitat, or chance differences in feeding opportunities (1). The distribution of α 's must be a continuous, positive distribution that is biologically tractable. We have not yet done the necessary experiments of measuring individual growth rates of larvae raised in varying conditions in order to empirically determine the characteristics of the distribution. A gamma distribution of the α 's has the necessary properties, and it can be generated by several biological processes such as convolutions of distributions of feeding opportunities, variations in the quality of food particles, or encounters with interfering competition. In the Gompertz function, as time proceeds from zero to infinity, the value of the exponential term, $\exp\{(A/\alpha)[1 - \exp(-\alpha t)]\}$, goes from a value of 1 to $\exp(A/\alpha)$; hence a variation of the α 's will have an increasingly important, exponential effect on the body weight. The parameters of the body weight distribution of a population will depend on the parameters of the distribution of growth rates.

The initial weight at hatching, W_0 , may also be a random variable. Total body lengths measured from photographs of a sample of *R. sylvatica* used as stock for the experimental populations did not depart significantly from the skewness or kurtosis of a normal distribution. The variation in size at hatching is too small to account for the great variation later in the larval period. In our experiments the eggs hatched within 2 to 3 days so that the advantages of early hatching are minimized, but this factor is probably more important in nature.

Whatever the source of these deviations, the differences between individuals are magnified during the course of competition (6, 7, 12). Larger tadpoles may prevent smaller ones from reaching food concentrations by the currents generated by the tail action of the feeding individuals (6). In some laboratory cultures of frogs, growth inhibitors are produced in the posterior half of the gut of growing larvae (30). The growth rate of smaller tadpoles is reduced or stopped when they eat the feces of larger tadpoles or encounter inhibitory substances in the water. The taxonomic distribution of this phenomenon is not known, but it is not entirely species-specific (31) and has not been reported in salamanders.

Differences in Competitive Ability

Our application of Laird's model is somewhat predestinarian in that it considers α , the damping rate, as a constant which is set at the start of the growth period. In fact competitive relationships may change as food resources change in abundance or availability or as other members of the population die or metamorphose and leave the pond. This effect was investigated by a transplantation experiment in which six cohorts of *Rana sylvatica* larvae were drawn from the survivors of a population with an initial density of 1200 (Table 2, pen 33) when the population was sampled on day 45 (9 June 1972). Two replicates of 20 larvae from each of three size classes (0 to 100, 100 to 200, and 200 to 400 mg) were placed in separate pens in randomly assigned positions within the original block of experimental enclosures. These populations were destructively sampled on 20 June, after 10 days of growth under low-density conditions. All populations increased in body size (Fig. 8) when they were released from the effects of crowding. This ability to recover from a period of density stress is an adaptation that has evolved in response to a transient environment.

In summary, chance deviations in growth rates can generate a skewed distribution of body sizes. In the next section we suggest that at very high densities the median body size is below the presumed minimum required for metamorphosis, and only a few larvae at the upper end of the distribution are able to leave the pond. A possible mechanism for this effect involves size-specific competition. Gibrat's law of firm size distribution in economics states that if environmental impulses act on a growth process affecting all units equally in proportion to their size, a normal distribution of units will be maintained; if the impulses act differentially on each individual a lognormal distribution will develop (32). In our model these impulses are opportunities for growth such as finding food items, encountering growth retarders, or experiencing episodes of interfering competition. Large individuals not only maintain their relative position in the cohort but increase their advantage by being better competitors or producing inhibitory substances to retard the growth of smaller larvae. It is reasonable to assume that growth is a series of such episodes, each con-

tributing as a variable component of the realized growth rate. The relation between the initial density and the form of the distribution is not clear. Within populations, as competition proceeds, both β , the mean, and ω , the variance, of the lognormal distribution increase but η , the coefficient of variation, remains nearly the same, at least at high initial densities. These three parameters are related

$$\eta = \beta/\omega$$

hence it is the ratio between the standard deviation and the mean that is changed by initial density as manifested in intraspecific competition. In the next section a model is developed to predict when metamorphosis will occur.

Metamorphosis Threshold

The rate at which juveniles leave the pond and the distribution of sizes at metamorphosis are the results of individual responses to environmental con-

ditions which determine when metamorphosis is initiated. Figure 9 is a diagrammatic model of this process. The first assumption of the model is that metamorphosis only takes place over a limited range of body sizes. Many environmental factors such as cold or food availability may influence the size at metamorphosis (7, 10, 33). The existence of a definite limit in body size for the initiation of metamorphosis is suggested by the truncated size distributions of recently metamorphosed amphibians in our experiments [(1) and Figs. 1 and 4] and field collections. There is abundant evidence in the embryological literature that b , the proposed lower limit of body size, is determined by threshold responses to the endocrinological mechanisms that initiate metamorphosis. The hypothalamus may act as an internal clock inhibiting the initiation of metamorphosis (34). For example, *R. sylvatica* and *R. pipiens* have a switch mechanism at a critical developmental stage that reverses the effects of inanition on the pituitary (33). Starvation before the early stages of limb development retards metamorphosis, but after this stage starvation accelerates metamorphosis. Adolph's studies (7) on *R. pipiens* suggest that, within certain limits, body size per se has little effect on the onset of metamorphosis, and that a deficiency in body size can be compensated by an increase in age. Adolph's model related the age at which the forelegs emerge to the body weight at the completion of metamorphosis. The earliest possible date of metamorphosis regardless of body size and the minimum size at metamorphosis are constants in his model. As in our model, the lower limit of body size is probably imposed evolutionarily by the low survivability that extremely small juveniles would have.

Our model also assumes that there is an upper limit to body size, $b + c$, that will not be exceeded before metamorphosis. Due to the weight loss accompanying metamorphosis this upper limit will be larger than the observed weight of the largest juveniles (34). This limit may be imposed proximally by threshold or allometric responses of the endocrine system to body weight or organ size (35). Ultimately this upper limit is an adaptation to the certainty of the larval habitat. This represents the body size that takes so long to achieve that the probability of drying of the pond, or the onset of winter, is so great that natural selection has

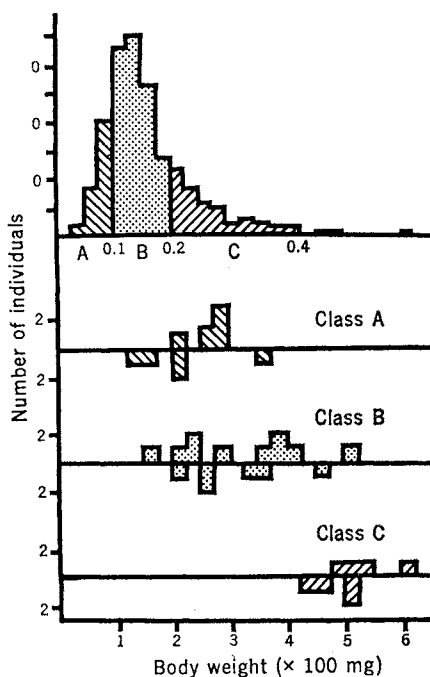


Fig. 8. Frequency histograms of body weights of six populations of *Rana sylvatica* drawn at 45 days after the start of the experiment from a population (Table 2, pen 3) with an initial density of 1200 (upper histogram), and then sampled after 10 days in low-density enclosures. Class A larvae were drawn from the subsample of larvae weighing less than 0.1 g on day 45. Two groups of 20 animals each were allowed to grow for 10 days in separate enclosures (block 1 above the line, block 2 below). Similarly, class B larvae were from the subsample between 0.1 and 0.2 g, and class C larvae between 0.2 and 0.4 g.

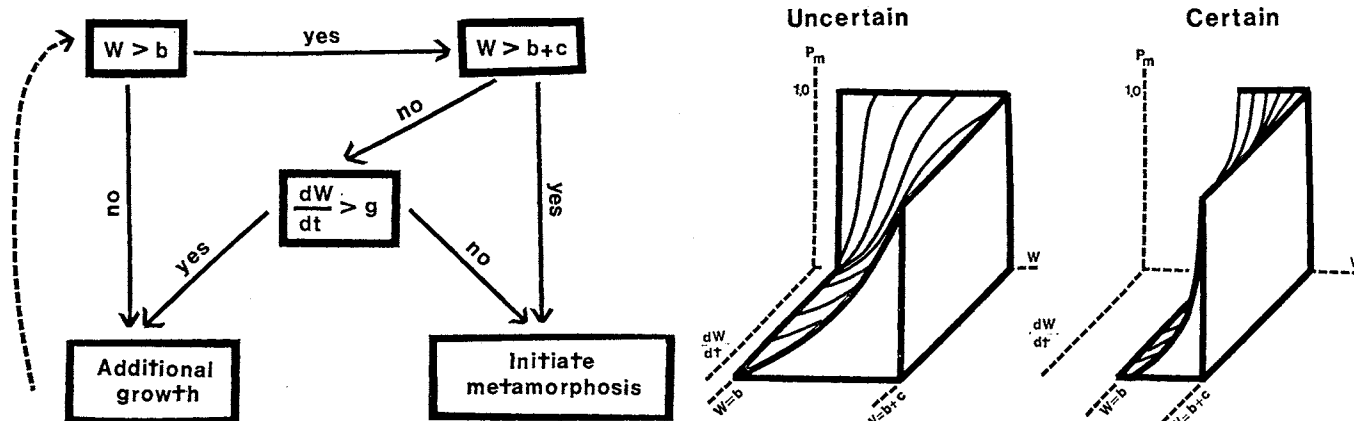


Fig. 9 (left). Hypothetical control process determining the stimulation of the neurohormonal processes that initiate metamorphosis. Constants b and $b + c$ are the species-specific lower and upper limits, respectively, of the body size W at which metamorphosis will occur. Within these limits, metamorphosis is initiated only if the recent growth is less than the value of g , some function of weight. See Fig. 10 for an interpretation of g . Fig. 10 (right). Hypothetical probability of metamorphosis (P_m) surfaces as a function of body size W , recent growth rate dW/dt , and environmental certainty.

avored the initiation of metamorphosis rather than the risk of further growth in the aquatic habitat.

Hence, the limits of body size, b and $b + c$, are physiological constants that have evolved in response to the uncertainty of the larval habitat. The resultant range of body sizes, c , is the phenotypic plasticity of the species. The realized body weight, W , and the growth rate are determined by environmental effects. They are extrinsically determined parameters of our model (36). Between the outer limits of body size, the initiation of metamorphosis will depend on factors other than those related directly to body weight. In the range of body sizes b to $b + c$ there is some evolutionarily "known" probability of successful terrestrial existence if metamorphosis is initiated. We propose that, within these limits, the recent growth history of the individual, in conjunction with body size, determines the switching mechanism (9). If the body weight is small, slightly above b , but the growth rate is rapid, metamorphosis will be delayed in order to capitalize on the growth opportunities in the aquatic habitat. If the body size is small and the growth rate is slow, metamorphosis will proceed. Natural selection has favored the initiation of metamorphosis rather than remaining in the pond and risking predation and the other dangers of the aquatic community. Metamorphosis will occur at smaller growth rates as the body size increases because the advantages of remaining in the aquatic environment are counterbalanced by higher survival or other advantages in the terrestrial community.

We can only speculate on the phys-

iological effect of growth rate on the maturation of the median eminence of the pituitary and the endocrinological initiation of metamorphosis. Perhaps the process of growth itself has a diluting effect on thyroxine, or increases thyroxine metabolism, or perhaps growing tissues have a reduced sensitivity to thyroxine. The reciprocal interaction between thyroxine and prolactin, the effect of this balance on target tissue sensitivity, and the relation between the metabolic roles of prolactin and somatotrophin during the switch from herbivory to carnivory that occurs at metamorphosis in frogs are still incompletely understood (4, 5, 37). A link between our ecological model (Fig. 9) and Etkin's positive feedback model (4) should relate the physiological properties of tissue mass and growth and the biochemical effects of prolactin and somatotrophin on metabolism to feeding opportunities and the neuroendocrine function of the hypothalamus. We have proposed an ecological model of the initiation of metamorphosis which takes as its parameters the ecologically important variables, body size and growth rate. A more complete understanding of metamorphosis may suggest that some aspect of body quality rather than quantity is the critical factor in the initiation of metamorphosis. Our data do not justify further speculation on the nature of these physiological links.

Teleologically, the decision to initiate metamorphosis is an educated (adaptive) guess that the risk of metamorphosis is less than the risk of remaining in the aquatic habitat. We have suggested that the probability of metamorphosis, P_m , at time t is some function

of body weight, W_t , and the recent growth history of the individual

$$P_{m,t} = f(W_t, dW_t/dt)$$

Therefore, since dW_t/dt and W_t are related by the growth law, prediction of the timing of metamorphosis only requires a knowledge of the parameters of the growth curve, which can be estimated by the trajectory of early growth.

The description of the P_m surface is operationally simple, but laborious. A large number of larvae can be raised individually under different and replicated conditions. For each combination of body weight and recent growth history a probability distribution of metamorphosis can be computed. From this array of probability distributions a response surface can be constructed. This response surface reflects adaptations to the uncertainty of the larval habitat, and it should be a characteristic of the species.

Some general predictions of the shape of the response surface of species exploiting different habitats might be made (Fig. 10). In stable, permanent habitats most individuals should remain in the pond, regardless of their growth rate, until they reach the optimum size for metamorphosis, the size that has through evolutionary time been optimal for entering the terrestrial juvenile stage. The narrow range of body sizes at metamorphosis will result in great variation in the length of the larval period. Some individuals may require a few months to reach the optimal size, other individuals may require a year. For example, green frogs, *R. clamitans*, and bullfrogs, *R. catesbeiana*, have exceedingly variable larval periods, sug-

gesting a low phenotypic plasticity of body size at metamorphosis (2, 38). These species, which live in permanent ponds, should have a steeply rising response surface and the range of phenotypic plasticity should be small. At the other extreme, species adapted to temporary ponds would have a gradually sloping surface because there has been selection for a facultative timing of metamorphosis depending on the recent growth history of the individual. High probabilities of metamorphosis would occur over a wide range of body sizes as well as larval periods. The maximum body size, $b + c$, would be obtained only if the conditions for very rapid growth were sustained for an unusually long period.

We suggest this probabilistic model as the mechanism that gives rise to the negative exponential relation between body size and initial density during the later stages of larval life (Figs. 1 and 3). The initial density conditions set the growth trajectory that yields a skewed distribution of body sizes as growth proceeds. In low-density populations most larvae have a small damping coefficient of growth and rapidly reach a large body size. Because the growth rate is rapid, metamorphosis is delayed until the maximum larval size is approached. In high-density populations the mean damping coefficient is large and most animals grow very slowly. Only a few individuals with extremely low damping coefficients relative to the mean value have an initial growth advantage, so that they can monopolize the resources and are able to reach the minimum size at which metamorphosis is possible. Because of the slow growth rate imposed by crowding, they metamorphose at a small size which is close to the minimum possible. The remainder of the population cannot catch up and reach the minimum size for metamorphosis before the onset of winter, drying of the pond, or other cause of mortality occurs.

These principles are illustrated by the size at metamorphosis of *Ambystoma tigrinum* in three natural ponds on the Edwin S. George Reserve of the University of Michigan (Fig. 11). In 1972, a summer with nearly average rainfall, the West Woods Pool dried during the third week in August. The Southwest Woods population of *A. tigrinum* was still actively feeding at this time. (The pond dried about 15 September.) The extreme differences between the body sizes of the juvenile salamanders that dispersed from the ponds on 17 August

reflect the different opportunities for growth in the three ponds. Figure 11 is a double-logarithmic plot of body weight against length from snout to vent for the three groups. The groups do not have significantly different slopes, but the differences in elevation of the lines are highly significant ($F_{2,3} = 10.71$, $P < .001$, analysis of covariance). This shows that not only are the mean weights significantly different ($F_{2,14} = 81.1$, $P < 10^{-6}$), but the relation between total weight and body length changes between populations. This is a reflection of the very emaciated condition of the West Wood animals compared to the very robust condition of the nearly adult-sized animals leaving the still productive Burt Pond. *Ambystoma tigrinum* is a species that is most successful in the more permanent ponds on the Reserve (1), but it has the facultative ability to exploit a temporary pond (West Wood). Probably the stunted, emaciated juveniles from the West Wood pond will require a year or two longer to reach maturity (39) than the robust juveniles from Burt Pond.

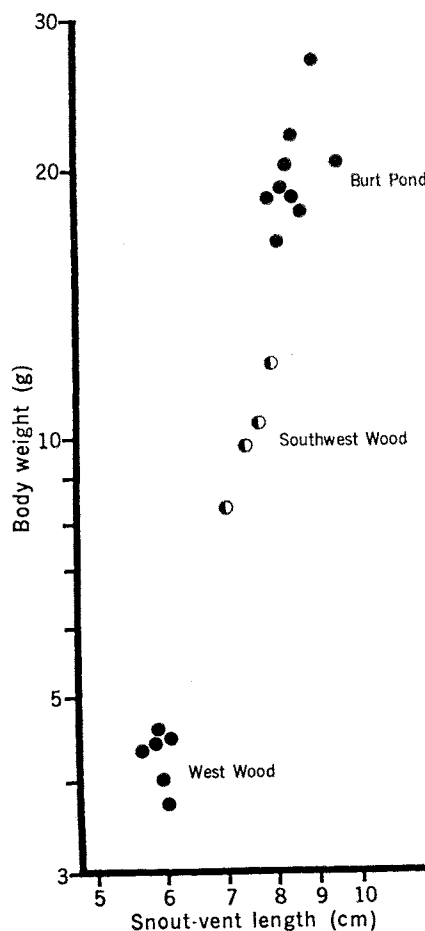


Fig. 11. Body weights of transformed *Ambystoma tigrinum* trapped on 17 August 1972 at three ponds differing in their stage of drying. See text for analysis of covariance.

Evolution of Amphibian Life Cycles

Most amphibians are terrestrial as adults but must return to water to lay eggs and the larval stage must be spent in an aquatic habitat. Extreme modifications of this primitive life cycle involve elimination of either the terrestrial stage (neoteny and paedogenesis) or the free-living aquatic stage (direct development and viviparity). An evolutionary theory of metamorphosis should be able to relate the extremes of evolved life history modes to the ecological and physiological constraints on amphibian life cycles.

Paedogenesis, genetic fixation of larval characters in adults, has evolved convergently in a number of salamander lines. In the evolution of paedogenesis the environmental factors favoring such genotypes include a highly predictable aquatic habitat surrounded by a hostile terrestrial habitat that is arid or unproductive. The extreme examples of adaptation to such an environment are the cavernicolous salamanders (40). The evolution of paedogenesis probably entailed a progressive narrowing of the range of body sizes at which metamorphosis was initiated (Fig. 9). Metamorphosis was probably delayed in conjunction with a progressive increase in the size at which transformation could be initiated and a progressive insensitivity of the hormonal system to larval growth rate (41).

There are some paedogenetic salamanders which are exceptions to this rule of occupying a highly constant aquatic environment. They possess secondarily derived physiological or behavioral adaptations for survival in uncertain habitats (42). These forms have apparently lost the genetic capacity for metamorphosis and must estivate or otherwise remain inactive when the environment becomes hostile to a paedogenetic mode of life.

Neoteny, facultative metamorphosis, occurs in species that are found in permanent aquatic habitats that are occasionally unsuitable for larval growth. There is a continuum between populations in which the vast majority of individuals undergo metamorphosis to populations in which most individuals are permanently larval in morphology (43).

Throughout the majority of its range the red-spotted newt, *Notophthalmus viridescens*, has a life cycle involving an aquatic larva, metamorphosis to a terrestrial eft stage, then a return to water and a second metamorphosis to a sexually mature, aquatic adult. In

several areas, including the coastal areas of the northeastern United States, whole populations or portions of populations may bypass the terrestrial eft stage and remain in the ponds as neotenes (44), perhaps because there is selection against the terrestrial efts due to dry, sandy soils. As long as the aquatic environment remains stable the advantages of remaining in the pond and growing to adult size outweigh the advantages of metamorphosis. If the pond begins to dry or there is a succession of dry years the percentage of neotenes in the population drops sharply because the ability to facultatively transform when growth is impossible has been retained.

Some individuals of the Mexican axolotl, *Ambystoma mexicanum*, cannot transform under any environmental stresses, whereas others transform under only slight stress (45). Since this species inhabits Lake Xochimilco, a large, predictable body of water, the initiation of metamorphosis involves a selective balance between the advantages of staying and growing in the lake or transforming and growing elsewhere. Our model predicts that the physiological processes that initiate metamorphosis are related to the recent growth history of the individual (Fig. 9). Animals with an initial growth advantage would remain in the lake and continue to grow. With growth and aging, tissues become less sensitive to stimulation by thyroid hormone (46) and it becomes less likely that the animal will ever transform. The slower growing members of the larval population would metamorphose as an adaptation to escape density-dependent effects of competition with the larger larvae and neotenes. We suggest that the evolutionary basis of neoteny in axolotls, in contrast to *Notophthalmus*, has primarily a demographic (competitive) basis rather than primarily an environmental (drought) basis.

Neotenic populations of *Ambystoma tigrinum* in desert or high-altitude ponds (47) and of *Ambystoma gracile* in high-altitude ponds (48) can be explained by the hostility of the terrestrial environment. Populations of *A. gracile* at high elevations are often completely neotenic. On the plains of France and Italy the newt *Triturus alpestris* metamorphoses, but at high altitudes neoteny is common (49). *Hynobius lich-enatus* (a Japanese salamander) metamorphoses the first year in small temporary pools, but may be neotenic in cold lakes (50). All of these neotenic populations are probably examples of

the progressive loss of sensitivity to thyroxine in populations where the aquatic environment is usually more favorable for growth and maturity than the terrestrial habitat. Metamorphosis as a facultative response to slow growth is probably maintained by selection during the occasional years of unfavorable conditions in the ponds (51).

The last major derivative from the primitive amphibian life history is terrestrial development. Terrestrialism has taken various expressions in the course of amphibian phylogeny (52). The caecilians have aquatic larvae (*Ichthyopis*), terrestrial development without free-living larvae (*Hypogeophis*), and viviparity (terrestrial *Typhlonectes* and *Caecilia*, aquatic *Nectocaecilia*). Among the Caudata some species lay eggs close to the water and the newly hatched larvae must find their way into the stream or pond (*Desmognathus fuscus* and *Hemidactylum*). Among the Anura many species also use this strategy, probably as an adaptation to avoid predation (many Centrolenidae, Hylidae, and Leptodactylidae). Other species are completely terrestrial and their larvae metamorphose before hatching (frogs of the genus *Eleutherodactylus* and the salamanders *Plethodon* and *Aneides*). Many of these species have large eggs and parental care (53). Internal fertilization and selection for rapid development or parental care have resulted in viviparity in the frog *Nectophrynoides* and the salamanders *Salamandra salamandra* and *S. atra* (which gives birth to transformed young).

This diversity of life cycles is a result of the terrestrial radiation of the Amphibia without the evolution of the cleidoic egg. Amphibians have remained dependent on water, but have evolved sensitive phenotypic responses to uncertain environments. The facultative growth and metamorphosis of the temporary pond amphibians used in our experimental populations demonstrate the preadaptations that made evolution of neoteny and paedogenesis possible. Constant montane woodland environments have favored reduction of the variability of size at metamorphosis. In these habitats increased terrestrialism is possible, direct development increases the freedom from aquatic habitats, and parental care permits the reduction of clutch size so that only a few large eggs are laid, each hatching within a narrow range of body size which maximizes survivability in the high-density populations characteristic of these forms (52).

Summary

A synthetic theory of the ecology of amphibian metamorphosis is founded on the observation that the large variation in length of larval period and body size at metamorphosis typical of a particular species of amphibian cannot be directly explained by differences in dates of hatching or egg sizes. It is proposed that as development proceeds, variation in exponential growth coefficients causes a trend from a normal distribution to a skewed distribution of body sizes. The degree of skewing increases and the median of the distribution decreases with increasing initial densities of populations. The relative advantages of the largest members of a cohort may arise from a variety of mechanisms including the production of growth inhibitors, interference competition, and size-selective feeding behavior. These mechanisms result in a nonnormal distribution of competitive ability, a possible source of the density-dependent competition coefficient found in systems with many species (1).

In our model the ranges of body sizes and dates of metamorphosis are determined by a minimum body size that must be obtained and a maximum body size that will not be exceeded at metamorphosis. Between these two size thresholds the endocrinological initiation of metamorphosis is expected to be related to the recent growth history of the individual larva. Species that exploit uncertain environments will have a wide range of possible sizes at metamorphosis. Species exploiting relatively certain environments will have a narrower range. The evolution of neoteny and direct development logically follow from the application of these ideas to the ecological context of the evolution of amphibian life histories. Species that live in constant aquatic habitats surrounded by hostile environments (desert ponds, caves, high-altitude lakes) may evolve permanent larvae genetically incapable of metamorphosis. Other populations may evolve a facultative metamorphosis such that populations are a mixture of neotenes and terrestrial adults. Direct development results from selection to escape the competition, predation, and environmental uncertainty characteristic of some aquatic habitats and is usually accompanied by parental care. The relation between our ecological model and the physiological mechanisms that initiate metamorphosis can only be suggested and it remains an open problem for developmental biologists.

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54. We thank G. Borgia, B. E. Frye, N. G. Hairston, L. Herche, M. Hirschfield, J. Hoogland, A. G. Kluge, P. Sherman, A. Templeton, D. W. Tinkle, and C. F. Walker, who read all or parts of preliminary manuscripts. Their suggestions were always helpful but were not always followed, and we accept responsibility for the errors that remain. H.M.W. was supported by the University of Michigan Society of Fellows, the E. S. George Reserve, and NSF grant GB 8212 for research in systematic and evolutionary biology to N. G. Hairston. J.P.C. held an E. S. George scholarship.