The relationship among egg size, density and food level on larval development in the wood frog (*Rana sylvatica*)

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Summary. Although inter- and intraspecific variation in egg size among amphibians has been well documented, the relationship between egg size and fitness remains unclear. Recent attempts to correlate egg size intraspecifically with larval developmental patterns have been equivocal. In this study the development of larvae derived from large eggs and small eggs, from a single population in Maryland were compared under a range of food levels and larval population densities. Both food level and density had significant effects on the length of the larval period and size at metamorphosis. However, the response among larvae derived from different egg sizes was not additive. At low densities and high food levels, larvae from small eggs had longer larval periods and a larger size at metamorphosis than larvae derived from large eggs. In contrast, at high densities larvae from small eggs had longer developmental periods but were smaller at metamorphosis than larvae from large eggs. In addition, larvae from small eggs were more sensitive to density irrespective of food level. These results suggest that optimal egg size is correlated with environmental factors, which may explain the maintenance of both geographic and within population variation in egg size commonly observed in amphibians.

Key words: *Rana sylvatica* – Egg size – Development – Density – Food level

Egg size and egg number in amphibians vary among taxonomic groups (Salthe 1969; Salthe and Duellman 1973; Salthe and Meecham 1974; Crump 1974; Wilbur 1977a; Kuramoto 1978: Kaplan and Salthe 1979), among different populations of the same species (Dushane and Hutchinson 1944; Pettus and Angleton 1967; Nussbaum and Tait 1977; Berven 1982a; Howard and Wallace 1985), and among and within females in the same population (Bell 1977; Kaplan 1980; Travis 1983; Crump 1984; Travis et al. 1987). Although the consequence of egg size variation as it relates to fecundity has been well studied both empirically (ref. above) and theoretically (Smith and Fretwell 1974; Wilbur 1977a) only recently have the consequences of egg size variation on fitness, especially within populations, been explored (Kaplan 1980, 1985; Crump 1981, 1984).

Since egg number and size are inversely related in amphibians, most studies relating egg size to fitness have at-

tempted to identify the advantage or larger egg size, since larger egg size results in reduced fecundity. The advantage of large size may be particularly important to anuran larvae. The intensity of competition in amphibian larval populations depends on habitat productivity (food level) and larval density, as well as on larval size distributions. A large body of research on amphibians has clearly documented the effects of competition on growth rates, developmental rates and survivorship (Licht 1967; Wilbur 1972, 1977b, c; Smith-Gill and Gill 1978; Smith-Gill and Berven 1979; Travis 1980, 1981, 1983; Semlitsch and Caldwell 1982; Smith 1983; Petranka and Sih 1986). These studies have shown that larvae at high densities or low food levels grow more slowly, have longer larval periods and are smaller at metamorphosis than those at lower densities and higher food levels. These competitive effects occur either because of exploitation for a limiting resource such as food (Wilbur 1977b; Travis 1984), because of interference from the production of growth inhibitors (Licht 1967; Rose 1960; Richards 1962; Rose and Rose 1965; Steinwascher 1978) or both. Wilbur (1977c) has shown that under crowded conditions larger larvae tend to dominate smaller individuals and monopolize available food. Thus, any initial size differences among larvae resulting from differences in egg size might be magnified, resulting in significantly faster growth rates and shorter larval periods of larvae from large eggs.

The relationship between larval traits, larval competition and egg size is significant since regulation of population size in amphibians is thought to occur largely through density-dependent effects experienced in the larval stage (Wilbur 1980; Smith 1983; Petranka and Sih 1986). Variation in the timing and size at metamorphosis is also thought to influence juvenile survival, female fedundity and male mating success (Martof 1965; Mayhew 1965; Tevis 1966; Wilbur 1971, 1972; Shoop 1974; Collins 1975, 1979; Smith-Gill and Gill 1978; Berven et al. 1979; Travis 1980, 1981; Berven 1981, 1982a, b; Berven and Gill 1983). Thus, variation in egg size may have profound effects at all levels of anuran development and be closely related to fitness.

Any test of the competitive superiority of large individuals should demonstrate two things: 1) larger offspring are competitively superior in a highly competitive situation, and 2) the competitive advantage disappears in less competitive circumstances. Both results are important in developing an understanding of "optimal" offspring size and why it is sometimes advantageous to make more, smaller offspring.

Previously, I have shown that differences in egg size between high and low elevation populations of wood frogs

accounted for a portion of the observed variation in larval developmental patterns between these populations (Berven 1982b). More recently I have also shown that a substantial amount of variation in egg size exists within populations (Berven 1988). This variation was shown to be correlated with female age at first and subsequent reproduction. In the present study we will examine the relationship between egg size variation (offspring size) and fitness for larvae from a single population, under a range of competitive regimes.

Methods

Thirty *Rana sylvatica* egg masses with egg diameters ranging from 1.50–2.20 mm were collected from a pond (BVII) at the Beltsville Agricultural Station in Prince Georges County, Maryland. A description of the study site can be found elsewhere (Berven 1982a, b). The eggs had recently been deposited (within 12 h) and were between the third and fourth cleavage. Immediately after collection, 3 replicate samples of 10 eggs from each of the 30 egg masses were de-jellied and dried overnight at 40° C and weighed. The remaining eggs were transported on ice to Oakland University in Rochester, MI where they were allowed to hatch in the laboratory.

A total of 252 individuals were haphazardly assigned to one of 18 experimental treatments. The treatments were elements of a $2 \times 3 \times 3$ factorial design. One factor, egg size, consisted of two size categories (large and small) based on the egg dry weights. The large size category consisted of five egg masses with the greatest dry weight (range: 2.01–2.61 mg; $\bar{x} = 2.42 \pm 0.13$ mg) and the small size category consisted of 5 egg masses with the lowest egg dry weight (range: 0.54–0.72 mg; $\bar{x} = 0.69 + 0.06$ mg). Hatching among the egg masses was synchronous and hatchlings within each assigned size category were mixed yielding two populations: one composed of larvae from large eggs and a second composed of larvae from small eggs. A second factor, density, consisted of either 2, 4 or 8 individuals per pan. The third factor, food level, consisted of 3 food levels. The food levels were initially set at 5, 10 and 20 mg but were increased to 20, 40 and 80 mg after 2 weeks. The food was Tetra-min vegetarian fish food weighed to 1 mg precision. The 54 pans were randomized among the shelves. The experiment was conducted in a room maintained at a 12/12 light/dark photo period. The average temperature experienced throughout the experiment was $20 \pm 2.4°$ C. The tadpoles were fed, pans cleaned and water changed three times per week.

Two measurements were made for each larva: (1) the date of metamorphosis, and (2) the size at metamorphic climax. Metamorphic climax was indicated when at least one of the front legs had emerged. The length of the larval period was determined as the number of days from hatching to metamorphic climax. Body size at metamorphic climax was determined by blotting individuals dry and weighing each on a Mettler balance to the nearest mg. The analysis was done using the mean of each replicate to eliminate any bias resulting from the different density treatments. The length of the larval period and size at metamorphosis were log transformed and the assumption of homogeneity of variance among treatment means was satisfied. The analysis of variance (ANOVA) was used to partition the relative contribution of egg size, density and food level, and their interactions, on both the length of the larval period and size at metamorphosis. The ANOVAs were performed using
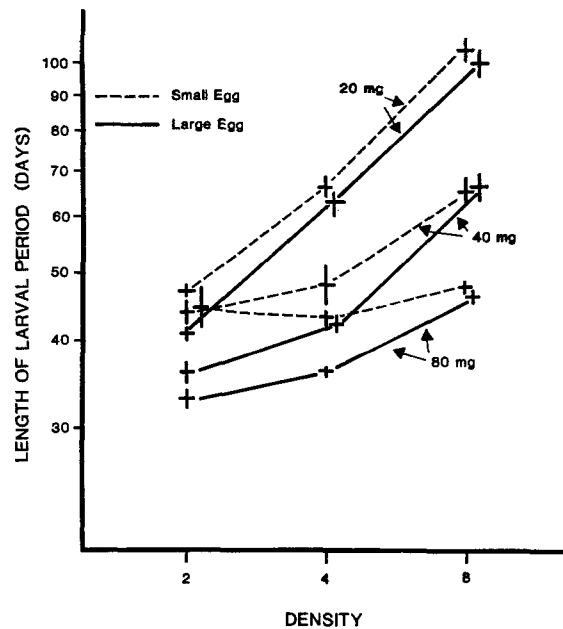

Fig. 1. The relationship among egg size, density, food level and the length of the larval period (note log scale). Each point shown is the mean of three replicate treatments $\pm$ SE. Significant effects are shown in Table 1a

SPSS statistical software following the procedures outlined by Sokal and Rohlf (1981).

Results

Length of larval period

Both density and food level had a significant effect on the duration of the larval period for individuals derived from either small or large eggs (Fig. 1, Table 1a). Generally, as food level decreased and/or density increased, the length of the larval period increased. However, as indicated by the ANOVA, there was a significant food level × density interaction indicating that the effects of increasing food and decreasing density were not additive (Table 1a). As food level decreased the relative differences in the length of the larval period between density treatments increased (Fig. 1). In general the length of the larval period was more sensitive to changes in food level than to changes in density.

The difference in the length of the larval period between large and small eggs was also highly significant (Table 1a). There was a significant egg size × density interaction indicating that larvae derived from different egg sizes responded differently to the effects of population density (Table 1a). The nature of the interaction can be seen by examing Fig. 1. At the high density treatment (8 individuals) irrespective of food level, the length of the larval period for both large and small individuals did not differ significantly. However, at lower densities (2 and 4 individuals) and higher food levels (40 and 80 mg), larvae from large eggs had significantly shorter larval periods than larvae derived from small eggs (Fig. 1). In contrast the egg size × food level interaction was not significant (Table 1a). Varying the food level had similar effects on the duration of the larval period for larvae derived from both egg size categories (Fig. 1).

Table 1a, b. ANOVA of a) length of the larval period and b) size at metamorphosis

Source	df	MS	Sig level
a Length of Larval Period			
Egg size	1	0.138	<0.001
Density	2	1.169	<0.001
Food level	2	1.003	<0.002
Egg size × density	2	0.034	<0.001
Egg size × food level	2	0.006	NS
Density × food level	4	0.160	<0.001
Egg size × density × food level	4	0.002	NS
Error	36	0.002	
Total	53		
b Size at Metamorphosis			
Egg size	1	0.008	NS
Density	2	0.777	<0.001
Food level	2	0.888	<0.001
Egg size × density	2	0.054	<0.002
Egg size × food level	2	0.001	NS
Density × food level	4	0.032	<0.005
Egg size × density × food level	4	0.020	<0.04
Error	36	0.007	
Total	53		

Fig. 3. A comparison of the length of the larval period between larvae derived from large and small eggs when reared under different densities but the same per capita food level (either 5, 10 or 20 mg). Means shown are based on three replicate treatments and include ±SE
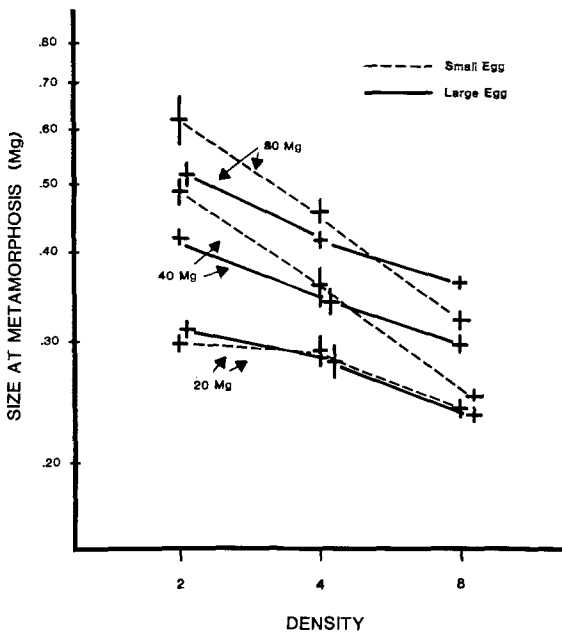

Fig. 2. The relationship among egg size, density, food level and the size at metamorphic climax (note log scale). Each point shown is the mean of three replicate treatments ±SE. Significant effects are shown in Table 1b

Size at metamorphosis

Population density and food level also had significant effects on larval size at metamorphosis (Fig. 2 and Table 1b). At low densities and high food levels individuals from both large and small eggs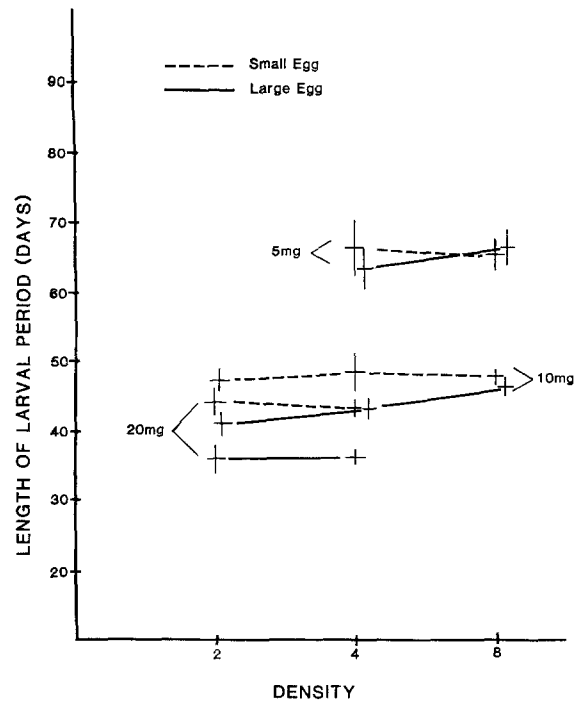 metamorphosed at a significantly larger size than those individuals reared at low food levels and high densities. As was the case for the length of the larval period there was a significant food level × density interaction (Table 1b). At higher food levels (40 and 80 mg) the differences in metamorphic size among density treatments were more pronounced (Fig. 2).

Interestingly, egg size *per se* did not have a significant effect on size at metamorphosis (Table 1b). However, there were significant egg size × density and egg size × density × food level interactions (Table 1b and Fig. 2). The nature of these interactions was primarily due to differences in the response of larvae at the low density and high density treatments (Table 1b, Fig. 2). At low density treatment larvae derived from small eggs metamorphosed at a significantly larger size than larvae derived from large eggs. In contrast, at the high density treatment, larvae derived from small eggs metamorphosed at a significantly smaller size than larvae from large eggs. In general larvae from large eggs were less sensitive to the effects of density and food level than larvae derived from small eggs (Fig. 2).

Density effects independent of food level

To compare the effects of increasing population density independent of food level larvae derived from large and small eggs, the data were analyzed with respect to the per capita food level. Three per capita levels of food availability at either two or three densities (20 mg: 2 individuals/40 mg, 4/80; 10 mg: 2/20 mg, 4/40, 8/80 mg; 5 mg: 4/20 mg, 8/40 mg) were extracted from the original experimental design for further analysis. Both length of larval period and size at metamorphosis were analyzed by a two way analysis of variance for which egg size (large or small) and density were the main effects. Because of the unbalanced nature
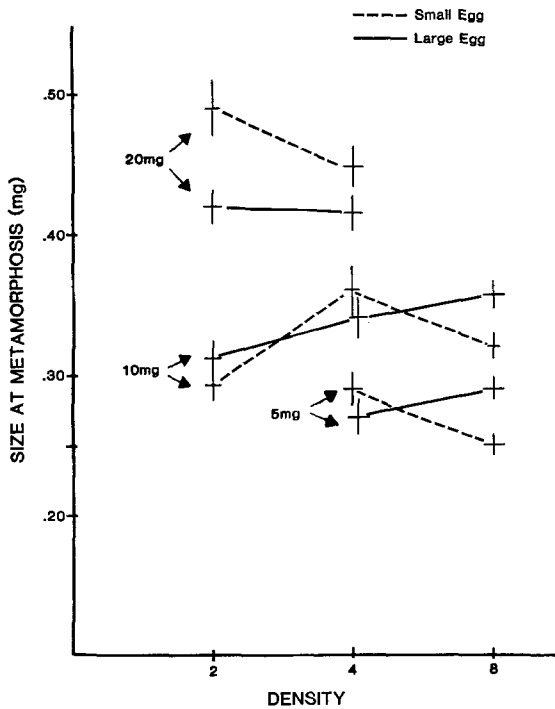
Fig. 4. A comparison of the size at metamorphic climax between larvae derived from large and small eggs when reared under different densities but the same per capita food level (either 5, 10 or 20 mg). Means shown are based on three replicate treatments and include $\pm$ SE

Table 2a, b. Summary of F statistics from the analysis of variances for a the length of the larval period and b size at metamorphosis for 20, 10 and 5 mg per capita food levels. Both the length of the larval period and size at metamorphosis were log-transformed. See text for details of experimental design

Per capata food level	Results of anova		
	Main effects		Interaction
	Egg size	Density	Egg size × density
a Length of Larval Period			
20 mg	$F_{(1,8)} = 61.7^{***}$	$F_{(1,8)} = 0.76$	$F_{(1,8)} = 0.36$
10 mg	$F_{(1,12)} = 20.2^{***}$	$F_{(2,12)} = 3.1$	$F_{(2,12)} = 2.9$
5 mg	$F_{(1,8)} = 0.53$	$F_{(1,8)} = 0.14$	$F_{(1,8)} = 0.84$
b Size at Metamorphosis			
20 mg	$F_{(1,8)} = 3.2$	$F_{(1,8)} = 12.6^{**}$	$F_{(1,8)} = 10.5^{**}$
10 mg	$F_{(1,12)} = 0.11$	$F_{(2,12)} = 3.8^{*}$	$F_{(2,12)} = 0.67$
5 mg	$F_{(1,8)} = 0.60$	$F_{(1,8)} = 0.19$	$F_{(1,8)} = 6.7^{*}$

$* < 0.05; ** < 0.01; *** < 0.001$

of this design, the analysis was carried out separately for each per capita food level. The results for length of larval period are summarized in Figs. 3, 4 and Table 2a. Although egg size differences were present at the 20 and 10 mg per capita food levels, there were no significant density effects indicating that density effects other than food limitations, did not contribute to the variation in the length of the larval period. Furthermore, the lack of any significant egg size by density interaction indicated that both populations of larvae responded similarly to differences in density independent of food level. In contrast, for the size at metamorphosis there were both significant density effects as well as egg size by density interactions (Fig. 4, Table 2b). Of particular interest were the interactions present at 20 and 5 mg per capita food levels. In general, increasing density had a relatively small effect on larvae from large eggs, whereas similar changes in density (even though the per capita food level was constant) resulted in dramatically smaller metamorphic size of larvae derived from small eggs.

Summary

In summary, the analysis of variance demonstrated that both food level and population density had significant effects on the length of the larval period and size at metamorphosis. In addition, the response between larvae derived from large and small eggs was not additive. At low densities and high food levels, larvae from small eggs had longer larval periods but metamorphosed at a larger size than larvae from large eggs. In contrast, at high densities larvae from small eggs tended to have somewhat longer larval periods and a smaller size at metamorphosis than larvae from large eggs. Larvae from small eggs were also far more

sensitive to the effects of population density, irrespective of food level.

Discussion

Previous studies which have examined the relationship between egg size and larval developmental patterns in amphibians have been equivocal (Kaplan 1980, 1984, 1985; Travis 1983; Crump 1984; Travis et al. 1987). For ambystomatid salamanders, Kaplan (1980) found that intra-populational variation in egg size correlated with differences in developmental rates and growth rates of larvae to the feeding stage. More recently he showed that differences at the feeding stage are maintained until metamorphosis (Kaplan 1985). In contrast similar studies on anurans have resulted in very different conclusions. Although Crump (1984) found that a positive correlation existed between egg size and hatchling size in the tree frog, *Hyla crucifer*, larger hatchlings did not have a higher survival, maintain a size advantage or metamorphose more quickly than smaller hatchlings. Similarly, Travis (1983) found no consistent relationship between egg size and the growth rates and size at metamorphosis in another tree frog (*Hyla gratiosa*) or *Hyla crucifer* (Travis et al. 1987).

In the present study clear differences in developmental patterns between large and small eggs were demonstrated. However, these differences were not across all densities or food levels. Rather the ability to detect differences in metamorphic patterns between larvae derived from large and small eggs was possible only because rearing conditions were varied. Previous studies on anurans have compared the developmental patterns of larvae under "ideal" conditions. Indeed in the present study no differences between large and small eggs could be detected at certain combinations of food and density. This suggsests that similar differences might be detected in other anurans if a wider range of environmental patterns were examined.

The results presented here also differ from similar studies on the California newt (Kaplan 1985). In that study larvae form large eggs metamorphosed in less time and at a larger size than those from small eggs when food was

unlimited, but when food was limited, larvae from large eggs still metamorphosed at a larger size but took longer to do so. Thus a significant interaction between egg size and food level was detected but this interaction differed from the one observed for wood frogs in this study. Previous authors have suggested that the differences between frogs and salamanders may be related to differences in feeding habits (Travis 1983; Kaplan 1985). The nature of the difference will require further study and inclusion of more species before any general conclusions can be drawn from them.

Attempts to predict the size and timing of amphibian metamorphosis have resulted in two contrasting models. Wilbur and Collins (1973) argue that variation in size at metamorphosis is due primarily to variation in growth rates and that metamorphosis occurs between an upper and lower size threshold depending on recent growth history. Under optimal conditions (high growth rates) larvae should delay metamorphosis until the upper size threshold is reached while under less optimal (low growth) conditions, larvae will metamorphose at the lower size threshold. In contrast, Smith-Gill and Berven (1979) argue that differentiation rate is a better predictor of the timing of metamorphosis and that the size will be largely a function of differentiation rate and environmental factors. Varying degrees of support have been presented for both (Wilbur 1976, 1977b, c; Collins 1979; Dash and Hota 1980, 1983; Travis 1981; Semlitch and Caldwell 1982) while some have produced results which on the whole do not support either (Travis 1983, 1984; Kaplan 1985).

The results presented here are also ambiguous. On the one hand, when food was high and density low, larvae went past their theoretical lower size threshold and metamorphosed at a larger size than when reared at higher densities and lower food levels. However, this hypothesis does not adequately explain the difference observed between larvae derived from small and large eggs. Perhaps larvae from large and small eggs have different size thresholds or measure environmental quality differently. However, the similarity in metamorphic size of both groups at the low food treatment argues against this possibility. On the other hand, the differences in larval patterns between larvae derived from large and small eggs support aspects of the differentiation based model. Larvae derived from small eggs had lower rates of differentiation regardless of the environmental treatments. When food was high and density low, larvae derived from small eggs appeared to grow more for each developmental stage (stage-specific growth rate) than larvae derived from large eggs. In constrast when food was low or particularly when density was high the stage-specific growth was lower resulting in smaller metamorphic size relative to larvae derived from large eggs. Future studies should include simultaneous measures of growth rate and developmental rates to better address these issues.

The presence of a significant interaction between egg size and environmental parameters such as food level and population density also provides important insights in the more general issue of the adaptive significance of egg size variation observed in amphibians and other organisms. Most studies have concluded that larvae derived from large eggs should enjoy an increase in fitness either because of greater initial size, faster growth rates, developmental rates or both (Crump 1984). The advantage associated with producing smaller eggs is thought to lie in the corresponding increase in fecundity (Crump 1984). However, the presence of interactions between egg size and food level and egg size and population density reported above, and in salamanders (Kaplan 1985), suggest that the relative fitness of large and small eggs may actually vary with environmental conditions. Consequently the best combinations of egg size and egg number may vary with the environment. In benign years (i.e. high food or low density or both) the shorter larval period of larvae derived from large eggs may be compensated by the larger size at metamorphosis for larvae derived from small eggs. Thus the contrasting larval patterns between large and small eggs reported here, may produce larvae which have equivalent fitness for that particular environment (Berven and Gill 1983). However, since females producing smaller eggs produce more of them, these females would be expected to have the higher fitness. This is particularly true in wood frogs since those females which produce small eggs also mature a year earlier than individuals producing larger eggs (Berven 1988). In contrast, under more competitive conditions, (such as low food levels or high population densities or both) females producing large eggs would appear to be more fit since under these conditions larvae derived from large eggs not only tend to metamorphose sooner but also at a larger size: both of these effects are correlated with juvenile survival and reproductive success (Berven and Gill 1983). Under these conditions selection may be expected to favor increased egg size over increased clutch size. Given that food levels, populations density and species composition in breeding habitats are known to vary latitudinally, altitudinally, among years and within localities, such environmental variation may be an important factor promoting not only geographic variation in egg size but also an important factor maintaining variation in reproductive strategies within populations.

Kaplan has recently demonstrated that temperature and food level exert a strong influence on both the size and the number of eggs anurans produce (Kaplan 1987). He argues that this sort of environmental sensitivity incurred during oogenesis may be a way that females can deal with an unpredictable pond environment. Similar environmental effects on egg number and size have been demonstrated in wood frogs (Berven 1988). There is also some suggestion that early reproduction and the production of small eggs is correlated with the larval density experienced by those larvae (Berven 1988). These results would tend to support Kaplan's (1985, 1987) contention that environmentally induced variation in reproductive traits may be a type of phenotype plasticity which has evolved to deal with the uncertainity of the larval habitat, which may or may not be predicted during the adult stage when the eggs were produced.

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