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I am submitting herewith a thesis written by Gayle E. Whittaker entitled "The Effects of Crowding on Metamorphosis of Two Species of Anuran Larvae." I recommend that it be accepted in partial fulfillment of the requirements for the degree of Master of Science, with a major in Ecology.

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THE EFFECTS OF CROWDING ON METAMORPHOSIS OF TWO SPECIES OF ANURAN LARVAE

A Thesis

Presented for the

Master of Science

Degree

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Gayle E. Whittaker

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ABSTRACT

Two species of anuran larvae, Bufo americanus and Hyla crucifer, were treated separately for density effects. Tadpoles of comparable size and stage were placed into stackable preparation dishes at five densities of 5, 15, 25, 30 and 40 tadpoles each. The larvae were raised in an environmental chamber to metamorphosis. At metamorphosis the tadpoles were weighed to the nearest 0.001gm. The body length of each individual was measured to the nearest 0.5mm.

A one-way analysis of variance was utilized to statistically test whether density affected the size at metamorphosis or the time in days to metamorphosis. The null hypothesis of no density effects was accepted after the analyses of variance of body weight at metamorphosis, body length at metamorphosis and time to metamorphosis for B. americanus proved to be non-significant. Density effects on H. crucifer metamorphosis were impossible to measure because mortality terminated the experiment before any metamorphosed individuals were produced. Survivorship on day 15 for each species was compared and it was found that the densities of 25 and 40 H. crucifer larvae had significantly higher survivorship than did B. americanus larvae of the same densities.

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CHAPTER I

INTRODUCTION

The effects of crowding are manifested in several ways. In tadpoles the main effects of high densities are reduced body size, decreased growth rate and shorter life spans. Over the years, two schools of thought have developed as to what causes the crowding effects in tadpoles. In the 1930's several investigators (Adolph, 1931; Rugh, 1934; Lynn and Edelman, 1936) asserted that a spatial factor was the main cause of crowding effects. The spatial factor is the space a tadpole is able to move without encountering another tadpole. These investigators recognized that there was some chemical inhibition but that it was of limited importance.

Richards (1958) discovered an alga-like cell in Rana pipiens larvae which she believed acted as an inhibitory agent in crowded conditions. Richards' study prompted several other investigations (Rose, 1958, 1960; West, 1960; Richards, 1962; Akin, 1966; Licht, 1967), all of which supported the hypothesis that chemical inhibition was the primary mechanism causing crowding effects. However, the alga-like cell was proven not to be the inhibitory agent by West (1960) and Akin (1966). These workers found the cell was not an universal characteristic of tadpoles. In fact, its presence was not a constant feature in all populations of Rana pipiens larvae.

Recently, the spatial factor explanation of density effects has been revived by the work of Gromko et al. (1973) and John and Fenster (1975). Both groups of investigators concluded that the

crowding effects were the by-products of physical interactions between tadpoles. Besides the physical space factor, the presence of a psychological space factor was demonstrated by John and Fenster (1975).

All of the above studies were performed in the laboratory. A third group of investigators (Brockleman, 1969; Wilbur and Collins, 1973; DeBenedictis, 1974; Wilbur, 1977a, b) conducted experimental field studies. In a field study the effect of a single factor is confounded by synergistic effects. Keeping this in mind, all of the above workers concluded that density effects were primarily the result of competition for food. No general concensus, thus, has been reached on the mechanism causing causing crowding effects.

Most crowding studies have been concerned with the effects of density on growth rates. Metamorphosis has either been treated secondarily or not at all. Exceptions to this trend are the studies of Lynn and Edelman (1936) and Wilbur (1976, 1977a) which dealt specifically with metamorphosis. Metamorphosis is a complicated process through which a tadpole adapted for one life style transforms into an adult adapted for another. Any factor or factors such as crowding which act on a tadpole population can directly or indirectly affect metamorphosis and this, in turn, affects the adult frog population.

The importance of metamorphosis in overall anuran population dynamics and the lack of studies concentrating on the influence of crowding on this process prompted this investigation. The objective of this research was to determine through laboratory studies whether or not crowding affected size at metamorphosis and/or the time required

to reach metamorphosis. The study is concerned only with density effects and not with the mechanisms behind them. Two species of frogs were tested separately: the American toad, Bufo americanus Holbrook and the spring peeper, Hyla crucifer Wied. These species were chosen because they represent two separate anuran families with differing life styles (Wright and Wright, 1949). Also both species breed at the same time of the year and were readily available. The density effects found for each species were compared.

CHAPTER II

MATERIALS AND METHODS

The Bufo americanus larvae used in this study were obtained from a small creek in Cumberland Gap National Historical Park, near Middlesboro, Bell County, Kentucky. The Hyla crucifer larvae were taken from a water trough on the Holmes Farm in Clax Gap Community, near Harriman, Roane County, Tennessee.

The age of the tadpoles was determined using the staging tables of Limbaugh and Volpe (1957) for B. americanus and of Gosner (1960) for H. crucifer. These tables are illustrated developmental tables which follow anuran development through morphologically distinct stages of embryonic and larval development to metamorphosis. Different staging tables were employed because the Limbaugh and Volpe table is more precise for Bufo larvae whereas Gosner's table is a generalized table more useful for those species for which specialized staging tables are lacking. After the tadpoles were staged, individuals of comparable stage and size were placed into stackable preparation dishes (11.5cm diameter, 300ml capacity) at five densities of 5, 15, 25, 30, 40 tadpoles each. Each density was replicated except for density 25 for H. crucifer which had to be eliminated for lack of sufficient tadpoles. These tadpole cultures will be referred to hereafter as "populations."

The tadpoles were raised in an environmental chamber with alternating 12 hour periods of light and darkness. The temperature range within the chamber was 16-20°C for B. americanus larvae and

18-22°C for H. crucifer larvae. These ranges include the ambient temperature at which the tadpoles were originally collected and are within the temperature range for normal development. Each dish contained 227ml of aerates spring water. Water was obtained from I. C. King Park, near Knoxville, Tennessee. The tadpoles were fed boiled lettuce daily. The water was changed every other day and any excess food or dead individuals were removed daily. High mortality and other problems encountered with the methods will be expounded upon in the discussion.

The emergence of the forelegs was considered indicative of metamorphosis. At this time, the toadlets were removed from the dishes, blotted on paper toweling and weighed in a tared container to the nearest 0.001gm. The body length of each individual was subsequently measured to the nearest 0.5mm.

A one-way analysis of variance (Sokal and Rohlf, 1969) was used to statistically test whether density affected size at metamorphosis or the time in days till metamorphosis.

CHAPTER III

RESULTS

Bufo americanus Results

In the first two weeks of the experiment there was considerable mortality. For this reason, the results were treated in two ways. The data were considered using initial density and also using realized density. Initial density was the original number of tadpoles placed in each dish. Realized density was taken to be the density sustained the longest in any given dish. In other words, after the first two weeks of the experiment the number of tadpoles remaining in each dish was considered the realized density. This type of density has been referred to as "interaction" density by Wilbur (1977a) and "mean crowding" by DeBenedictis (1969). The usage of the realized density was justified by the fact that tadpoles removed from crowded conditions and placed in uncrowded conditions tend to recover from crowding effects (Adolph, 1931). By day 15, which was approximately half way through the experiment, all dishes had reached their realized densities. At that time survivorship was calculated taking into account the initial and realized densities (Table 1). Also, Table 1 contains a day by day account of survivorship for the entire *B. americanus* experiment.

At the end of 35 days all tadpoles had either died or undergone metamorphosis. Table 2 shows the number of days before zero density of tadpoles was reached using initial densities. Table 3 illustrates the same thing using realized densities. The purpose of these tables

Table 1. Daily survivorship data for the Bufo americanus experiment. Day 1 numbers represent the initial density of tadpoles in each dish. The percent survivorship was calculated for day 15.

Days																																		Percent
1	2	3	4	5	6	7	8	9	10	11	12	13	14	15	16	17	18	19	20	21	22	23	24	25	26	27	28	29	30	31	32	33	34	35	Survivorship
5	5	5	5	5	5	5	5	4	4	4	4	4	4	4	4	4	4	4	4	4	4	4	4	4	2[a]	0	0	0	0	0	0	0	0	0	80
5	5	5	5	5	5	5	5	1	1	1	1	1	1	1	1	1	1	1	1	1	1	1	1	0	0	0	0	0	0	0	0	0	0	0	20
15	15	15	15	15	15	15	15	15	15	15	15	15	15	15	15	15	15	15	15	15	15	14	14	14	14	13	13	2	2	2	2	1	1	0	100
15	15	11	11	11	11	11	11	11	11	2	2	2	2	2	2	2	2	2	2	2	2	2	2	2	2	0	0	0	0	0	0	0	0	0	13.3
25	25	5	5	5	5	5	5	5	5	5	5	5	5	5	5	5	5	5	5	5	5	2	2	2	2	2	2	0	0	0	0	0	0	0	20
25	14	14	14	14	14	14	14	14	14	14	14	14	14	14	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	56
30	30	30	30	30	30	30	27	27	27	27	27	27	27	27	27	27	27	27	27	27	27	27	27	27	26[a]	26	24[a]	24	24	24	21	0	0	0	90
30	30	30	14	14	14	14	14	14	14	14	14	14	14	14	14	14	14	14	14	14	14	14	41	41	14	14	13[a]	11	0	0	0	0	0	0	46.6
40	40	40	40	40	4	4	4	4	4	4	4	4	4	4	4	4	4	4	4	4	4	4	4	4	1[b]	0	0	0	0	0	0	0	0	0	10
40	40	9	9	9	9	9	9	9	9	9	9	8	8	8	8	8	8	8	8	8	8	8	8	8	8	8	8	0	0	0	0	0	0	0	20

[a]Decrease due to removal of a metamorphosed tadpole.

[b]Decrease due to tadpole mortality and removal of a metamorphosed tadpole.

Table 2. Days until the Bufo americanus populations reached zero using the initial densities.

Replicates	Initial Density				
	5	15	25	30	40
A	27	35	29	33	27
B	30	27	15	30	29

Table 3. Days until the Bufo americanus populations reached zero using the realized densities. The numbers in the body of the table represent the the days each laboratory population took to reach zero.

Realized Density				
1-2	4-5	8	14-15	27
30	27	29	35	33
27	29	-	15	-
-	27	-	30	-

is to illustrate the variation between replicates. In this case, the variation is in the number of days required for replicate densities to reach zero. The data was further treated to determine the percentage of tadpoles reaching metamorphosis for each population (Table 4). In keeping with the other results, the percentage of metamorphosis was calculated for both the initial density and realized density. Metamorphosed individuals came from four of the ten dishes. The experiment produced a total of seven toadlets. The size of the toadlets at metamorphosis was measured by body weight (gm) and body length (mm) which is comparable to snout-vent length. The time to metamorphosis was also determined using the number of days from the beginning of the experiment until the emergence of the fore limbs. This data is presented in Table 5.

One-way analyses of variance were performed considering both initial density and realized density as the treatments. The analysis of body weight at metamorphosis (Tables 6 and 7) as well as the analysis of body length at metamorphosis (Tables 8 and 9) proved to be non-significant. The null hypothesis of no density effects was accepted. This also proved to be the case for the time to metamorphosis (Tables 10 and 11).

Table 4. Percentage of Bufo americanus tadpoles reaching metamorphosis.

Initial Density	Percent Metamorphosis	Realized Density	Percent Metamorphosis
5	0	1	0
5	40	4	50
15	0	2	0
15	0	15	0
25	0	5	0
25	0	14	0
30	3	14	7
30	10	27	11
40	2.5	4	25
40	0	8	0

Table 5. Data summary for metamorphosed Bufo americanus individuals.

Initial Density	Realized Density	Body Weight(gm)	Body Length(mm)	Days to Metamorphosis
5	4	.135	9	26
5	4	.067	7	26
30	14	.088	7.5	28
30	27	.073	7	28
30	27	.070	7	28
30	27	.078	8	26
40	4	.103	8.5	26

Table 6. Effect of initial density on the body weight of Bufo americanus larvae at metamorphosis: Results of the analysis of variance.

Source of Variation	DF	SS	MS	F
Among Densities	2	.001	.0005	1*
Within Densities	4	.002	.0005	
Total	6	.003		

*Non-significant at $p < 0.05$

Table 7. Effect of realized density on the body weight of Bufo americanus larvae at metamorphosis: Results of the analysis of variance.

Source of Variation	DF	SS	MS	F
Among Densities	2	.001	.0005	1*
Within Densities	4	.002	.0005	
Total	6	.003		

*Non-significant at $p < 0.05$

Table 8. Effect of initial density on the body length of Bufo americanus larvae at metamorphosis: Results of the analysis of variance.

Source of variation	DF	SS	MS	F
Among Densities	2	1.3	.65	.956*
Within Densities	4	2.7	.68	
Total	6	4.0		

*Non-significant at $p < 0.05$

Table 9. Effect of realized density on the body length of Bufo americanus larvae at metamorphosis: Results of the analysis of variance.

Source of variation	DF	SS	MS	F
Among Densities	2	1	.5	.667*
Within Densities	4	3	.75	
Total	6	4		

*Non-significant at $p < 0.05$

Table 10. Effect of initial density on the time required to reach metamorphosis for Bufo americanus larvae: Results of the analysis of variance.

Source of Variation	DF	SS	MS	F
Among Densities	2	3.86	1.93	2.57*
Within Densities	4	3	.75	
Total	6	6.86		

*Non-significant at $p < 0.05$

Table 11. Effect of realized density on the time required to reach metamorphosis for Bufo americanus larvae: Results of the analysis of variance.

Source of variation	DF	SS	MS	F
Among Densities	2	4.19	2.095	3.136*
Within Densities	4	2.67	.668	
Total	6	6.86		

*Non-significant at $p < 0.05$

Hyla Crucifer Results

After the first two weeks of the experiment there was little mortality in the majority of the dishes. However, in order to permit comparisons with Bufo americanus, survivorship was calculated on day 15 (Table 12).

The total mortality at density 15 occurred on day 11 (Table 12). Five days later complete mortality occurred in the replicate dish at the same density. The remaining populations retained their realized densities except one dish of thirty tadpoles whose numbers dropped to four individuals on day 17. Every population reached zero on day 19. The pattern of mortality suggested that some kind of disease was the causative agent behind the mortality. Other possible causes of mortality such as a mulfunction in the environmental chamber or contaminated food were ruled out because cultures of tadpoles not under study remained alive while the tadpoles in the crowding study died. Fungal contamination was discovered on the walls of the environmental chamber, but there was no determination as to whether or not this accounted for the observed mortality.

Comparison of the Two Species

The initial intent of this study was to compare the various parameters measuring the metamorphosis of each species. However, since the H. crucifer larvae did not survive long enough to produce any metamorphosed individuals the only comparison possible was percentage of survivorship at day 15. The means of per cent survivorship were calculated for each species. These means were then compared statistically using a t-test (Table 13).

Table 12. Daily survivorship data for the Hyla crucifer experiment. Day 1 numbers represent the the initial density of tadpoles in each dish. The percent survivorship was calculated for day 15.

Days																			Percent Survivorship
1	2	3	4	5	6	7	8	9	10	11	12	13	14	15	16	17	18	19	
5	5	5	5	5	5	5	5	5	5	5	5	5	5	5	5	5	5	0	100
5	5	5	5	5	5	5	5	5	5	5	5	5	5	5	5	5	5	0	100
15	15	15	15	15	15	15	15	15	15	0	0	0	0	0	0	0	0	0	0
15	15	15	15	15	15	15	15	15	15	15	15	15	15	15	0	0	0	0	100
25	25	25	25	25	25	25	25	25	25	25	25	25	25	24	24	24	24	0	96
30	30	30	30	30	30	30	30	30	30	30	30	30	30	30	30	4	2	0	100
30	30	30	30	30	30	30	30	30	30	30	30	29	29	29	29	29	29	0	96.6
40	40	40	40	40	40	40	40	40	40	40	40	40	40	39	39	39	39	0	97.5
40	40	40	40	40	40	40	40	40	40	40	40	40	40	40	40	40	40	0	100

Table 13. A comparison of mean percentages of survivorship between Bufo americanus and Hyla crucifer.

Initial Density	Mean Percentages of Survivorship		t-value
	B. americanus	H. crucifer	
5	50	100	1.67*
15	56.65	50	.10*
25	38	96[a]	3.22**
30	68.3	98.3	1.38*
40	15	98.75	16.45***

[a]Only one sample
*Non-significant at $p<0.05$
**Significant at $p<0.05$
***Significant at $p<0.01$

By referring to Table 13 it can be seen that the densities of 25 and 40 H. crucifer tadpoles had significantly higher survivorship than did B. americanus tadpoles of the same densities.

CHAPTER IV

DISCUSSION

Mortality in the first few weeks of an experiment as occurred with B. americanus has been observed in other crowding studies (Lynn and Edelman, 1936; Wilbur and Collins, 1973; DeBenedictis, 1974). In fact DeBenedictis (1974) noted that he was able to predict which pens would have low survivorship by the second week of the experiment, although he does not specifically state how he made the prediction. Wilbur and Collins (1973) did not discuss the mortality problem within the text of their paper but they did provide a table from which this information could be derived. The total mortality in the H. crucifer experiment illustrated one of the disadvantages of crowded conditions. Allee (1931) pointed out that the transmission of contagious diseases was easier in crowded areas which apparently was the case in the H. crucifer study.

Another major problem with tadpole studies is the variability between replicates. In this study variability appeared in the percentage of survivorship, percentage of metamorphosis and number of days each population took to reach zero. Wilbur (1976) recognized the same problem calling the large variances between replicates "the most salient results of these experiments." Variability among replicates was again observed by Wilbur (1977a, b) while studying both B. americanus larvae and Rana sylvatica larvae. He also noted variation among members of a single population. Wilbur (1977a) attributed the variations to genetic and physiological differences among individuals. Variability concerning metamorphosis among replicates was observed

by DeBenedictis (1974). He observed that replicate pens behaved differently in percentage of metamorphosis and emergence times.

The B. americanus tadpoles in this study metamorphosed in 26-28 days which is in line with the four to six weeks reported by Dickerson (1931) for B. americanus in nature. According to Wright and Wright (1949) the size at metamorphosis for B. americanus ranges from 7-12mm. The range of sizes at metamorphosis noted in this study was 7-9mm which falls within the size range reported by Wright and Wright (1949).

The analyses of variance using the initial densities were non-significant mainly because the highest initial density had such a great amount of mortality that it actually was a very low (realized) density. Lynn and Edelman (1936) observed the same phenomenon as the chamber with the greatest initial number of tadpoles and an early high death rate ranking the chamber in fourth or fifth place in realized density rather than in the first. DeBenedictis (1974) states "The relationship between size at metamorphosis and numbers of survivors is more likely to be strong if most deaths occur early in the history of the pen, when tadpoles are small."

In the B. americanus experiment the highest realized density was 27 tadpoles. This density was not great enough to produce density effects because B. americanus tadpoles are known to form aggregations much larger than this number (Beiswenger, 1975). Also both B. americanus and H. crucifer generally lay their eggs in temporary water sources (Wright and Wright, 1949). This results in a high concentration of tadpoles in a limited amount of water.

The B. americanus larvae collected for this study were in a small creek (ca. 20-50cm wide and 1-5cm deep), which was prone to drying up without adequate rainfall. The tadpoles were observed in several aggregations of approximately 20-30 tadpoles at the time of collection. The H. crucifer larvae were found in an unused water trough which had been filled by rain. The trough was completely dry within three weeks after the tadpoles had been removed.

Considering the life histories of these species, higher densities have to be maintained in the laboratory for crowding effects to be manifested. However to maintain high densities the causes for the early mortality must be found and eliminated. Also the prevention of disease must be emphasized since tadpoles are highly susceptible to disease and disease tends to spread quickly from sample to sample. Finally the problems of variability among replicates continues to plague tadpole studies no matter how stringently the external factors are controlled. A solution or an adequate explanation of this problem must be developed.

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