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Experimental Studies on the Dispersal of the Frog, *Rana Pipiens*

RICHARD V. BOVBJERG¹

Abstract. Massive emigrations of the frog *Rana pipiens pipiens* Schreber have been recorded from large sloughs in northwestern Iowa. To investigate the possible ecological causes for this movement, two sets of laboratory experiments were done. A simulated slough was constructed in a large concrete tank and stocked with vegetation and a population of maturing tadpoles. As the time came for the emigration in the field, the experimental population, under the regulated laboratory conditions, had matured and emigrated in a way parallel to the natural situation. In other experiments, emigrations were determined for populations of juvenile frogs, one of which was five times the size of the other. The rate of movement was almost identical in the two groups, suggesting that population pressures do not stimulate movement. The precise correspondence of activity in the artificial slough with that in the field, as well as the apparent density-unrelated response to population density, indicate that the stimuli to this emigration behavior are internal rather than environmental.

In a previous paper (Bovbjerg and Bovbjerg, 1964), crash emigrations of the frog *Rana pipiens pipiens* Schreber were described. Over a three-year period, mass midsummer movements were observed at Garlock Slough, immediately south of Lake West Okoboji in northwestern Iowa. These seasonal movements all started early in July and essentially emptied this large body of water of the juvenile frogs within several days. The emigrating frogs were at, or just prior to, the stage of complete metamorphosis. It was suggested that the stimulus for the emigration behavior was not related to specific environmental factors such as temperature, rainfall, food, or predation pressure. Prior to the movement, density at the margins of the water was very high, which did suggest local, high density as a possible stimulus to emigration.

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This brief report on experimental studies is supplemental to that paper; the natural history, developmental studies, and the citation of the pertinent literature will not be reviewed.

To test the validity of the conclusions based on field data and to explore the role of density in the rate of emigration, two sets of experiments were done in the laboratories of the nearby Iowa Lakeside Laboratory. One experiment, done in two successive years, attempted to simulate the slough situation, but with the maturing tadpoles under defined conditions. The events of the artificial slough were then correlated with the events of the natural slough. The second experiment was designed to test specifically the role of density relative to the rate of emigration. Two experimental populations, one five times the density of the other, were compared in terms of emigration rate.

EXPERIMENTAL PROCEDURES

Experimental Slough. During the summers of 1962 and 1963, experimental populations of 200 tadpoles were grown to maturity in a simulated slough. Figure 1 depicts the concrete tank which measured 4.6 m x 70 cm. One-half of this was the "slough", filled with the natural vegetation and associated invertebrates. A large fluorescent light enabled the algae and vascular plants to be maintained and grown. The well aerated lake water was kept at 6cm depth. In the center of the tank a sand and cobble "bank" was constructed and covered with living strand plants. At the end of the tank a trap collected any frogs which moved up and over the bank.

The rationale of the experiment was simply to collect the emigrated frogs daily, record the numbers and developmental stages, and then to correlate this rate of emigration with that in the field. The frogs were returned to the slough end of the tank each day, density thereby remaining constant.

The tadpoles were collected in mid-June from Garlock Slough at stages varying from X to XXII. The animals placed in the tank were therefore tadpoles rather than juvenile frogs. They matured at a rate corresponding to that in the field, apparently well fed and healthy, with little mortality.

The conditions of existence were very much more regulated than those in the field. Temperatures remained at $20^{\circ} \pm 2^{\circ}$ C. Light was regulated to a day and night of equal length, 0800 to 2000. There was of course no precipitation. No predators were present and a screen protected them from human disturbance. The filamentous algae and plant debris furnished abundant food for the tadpoles, and the insects attracted to the light were ample food for the metamorphosed juveniles.

Density Experiment. To test the role of population density,

two experimental tanks were designed to measure emigration of populations of 10 and 50 juvenile frogs. These experiments were done at the time of field emigration in July. The frogs were from a stock tank of 300 field collected animals in the final stages of metamorphosis, stages XXIV and XXV.

A concrete tank 4.6m by 70cm was divided into two parts by a plank partition (Figure 1). An artificial bank was made of fine-mesh hardware cloth screening, which terminated at a trap. The water was 8 cm deep, and a plank floating in the trap acted as a frog perch. Light was maintained between 0800 and 2000. Water temperature was $21^{\circ} \pm 1^{\circ}\text{C}$. The tank was a barren concrete and screen with no simulation of slough conditions.

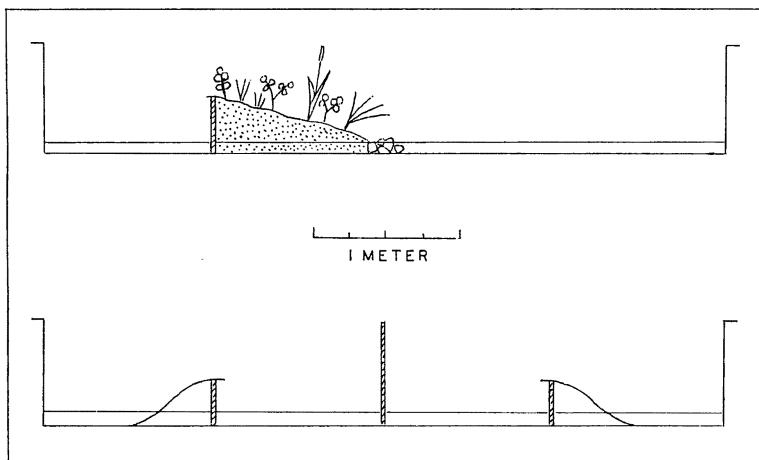


Figure 1. Two experimental tanks. Upper: simulated slough at right, containing 200 tadpoles and aquatic vegetation; sand and cobble "bank" leading to trap at left. Lower; two tanks for density experiments; experimental populations placed at the ends; wire screen ramp to trap in center.

Groups of 10 and 50 animals were placed at each end of the tank twice daily at 0800 and 2000. They were removed from the trap at those times and the numbers of residents and emigrants were recorded. To minimize possible subtle differences in the ends of the tank, the two size groups were rotated daily. Thirty-six experiments were done for each size group; 2,160 position recordings were made. Any one animal was used more than once but not consecutively; it was returned to the culture tank and randomly re-selected. The data show no evidence of conditioned behavior as a result of more than one experimental experience.

RESULTS

Experimental Slough. The emigration rates in the simulated

sloughs of 1962 and 1963 are graphed in Figure 2. For a period of 11 days, during which time the mass movements in the field were occurring, records were kept of the number of frogs removed daily from the trap. The experimental emigrations of the two years correlated closely; experimental emigrations correlated with the movements from Garlock Slough in both years; the developmental stages of the experimental emigrants were identical with those in the field.

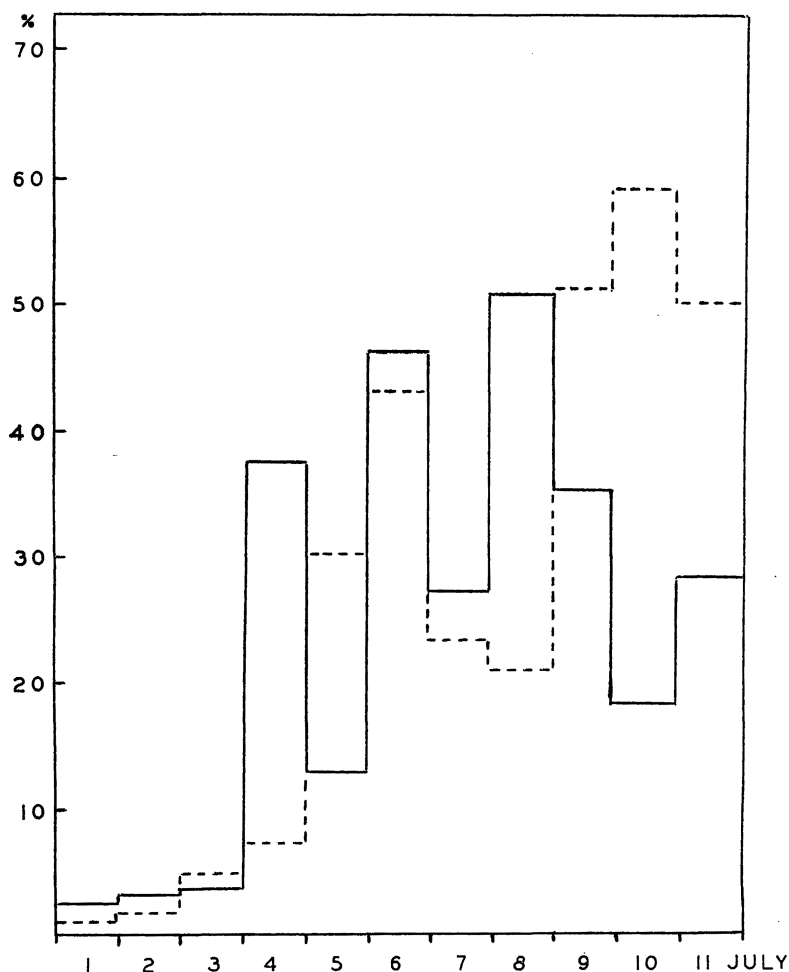


Figure 2. Daily emigration from simulated slough during first 11 days of July 1962 (dashes) and 1963 (lines), expressed as percent of total experimental population.

In 1962 the first laboratory emigrant was recorded on 30 June; this was also the data of the first juveniles leaving the slough.

As the rate of emigration increased in the simulated slough to a peak on 6 July, so also did the rate increase in the field. It is hesitantly recorded that experimental peaks of movement on 6 July and 11 July correspond precisely with peak field movement! In 1963 the first experimental emigrant was again on 30 June. The same sort of increase in rate was noted as in the previous year and again this was correlated with movements in the field. In this second year, however, the peaks of emigration in the field was not as great or as precise as in the previous year.

Records of the developmental stages of the emigrants from Garlock Slough were kept; these were almost all advanced metamorphic stages XXIII and XXIV, where stage XXV is the fully developed juvenile. In the simulated slough, the emigrants were the same stages, XXIII and XXIV, predominantly the latter. Since the frogs were returned to the slough portion of the tank from the trap, the proportion of stage XXV increased with time as the population matured.

Density Experiments. Within the experimental design described, there was no significant difference in the rates of emigration between two populations, one of which was five times the density of the other.

The total number of emigrants in 36 trials of the 10-frog population was 315 compared to 45 non-emigrants. A mean of 8.75 frogs moved and 1.25 remained (range: 10-0 to 7-3). Expressed as percent, the ratio of emigrants to residents was 87.5% to 12.5%.

The total number of emigrants in the 36 trials of the 50-frog population was 1,616 compared to 185 non-emigrants. A mean of 44.86 frogs moved and 5.14 remained (range: 50-0 to 37-13). Expressed as percent, the ratio of emigrants to residents was 89.72% to 10.28%.

The comparison based on these 2,160 position recordings, shows 89.72% emigration in the 50-frog populations and 87.5% emigration in the 10-frog populations; a closer correspondence would be suspect. Apparently density is not a factor affecting the rate of emigration.

CONCLUSIONS

The remarkable correlation of development of the tadpoles in the simulated slough with that of those in the field indicates that this developmental rate is relatively unaffected by the minor ecological variants in the field at this time of year. The equally striking correspondence in the time of emigration and the pattern of that movement would seem to validate the pre-

vious conclusion (Bovbjerg and Bovbjerg, 1964) that no single environmental variable acts to trigger the emigration.

In the field, days varied from cloudy to bright and were shortening daily; in the laboratory, light was regulated to constant diurnal patterns and intensity. In the field, precipitation occurred sporadically during the period of movement, but was not related directly to peak periods; in the laboratory there was of course no precipitation. In both the natural and artificial sloughs there was ample food. In the laboratory there was absence of predation. Population densities were equivalent in the two environments. Even with this regulated artificial environment in the absence of possible environmental stimulations to emigration behavior, the population responded in the same manner and at the same times as the field population.

The density experiments would seem to rule out population pressure as a stimulus to movement. In the field, the metamorphosing frogs aggregate densely at the margin of the water. But they do not appear to be interacting negatively to closeness of neighbor. There is no evidence of aggressive behavior or spacing. In the simulated slough and in density experimental tanks, no such behavior was seen. This underlies the density-unrelated emigrations seen in the experiments.

We must retain the notion that this striking emigration behavior in the laboratory, as in the field, is triggered by internal causes related to the complex changes at metamorphosis. What these changes are, whether neural or hormonal or both, are not known. A very profitable area of research is uncovered.

POSTSCRIPT

In our previous report we noted a decrease in the tadpole population during the years 1962 and 1963. We were at a loss to explain this from any local or meteorological conditions over these years. In 1964 the population was reduced to zero. No tadpoles were found after extensive collecting in the entire slough. Many of the usual invertebrates were in reduced numbers as well. We did, however, find large numbers of fish of several species not seen in previous years. A question put to the officials of the Iowa Conservation Commission at Orleans, Iowa, was answered with the suspected but stunning information that truckloads of young fish were stocked in the slough in 1964, a practice increasing in intensity over the last two years.

The wildlife preserve at Garlock Slough is obviously no longer in existence and to that extent at least accounts for the brevity of this report. It had been hoped that a continuing study could

have been made of the frog populations and their migratory behavior in what was an ideal natural situation.

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Larval Development of Four Caryophyllaeid Cestodes¹

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Abstract. Adults of the caryophyllaeid cestodes *Glari-dacris catostomi*, *Hunterella nodulosa*, *Monobothrium hunteri* and *Monobothrium ingens* were recovered from naturally infected fishes. The oligochaete annelid intermediate hosts were experimentally infected with embryonated eggs of these cestodes. Fully developed proceroids were characterized by a scolex similar to that of the adult, also by a cercomer and primordia of reproductive organs.

Caryophyllaeid cestodes are unsegmented helminths possessing a single set of reproductive organs and which vary in length from one to 75 mm. Adults are common parasites of catostomid and cyprinid fishes in North America, but their life cycles are poorly known. Experimental life history accounts of the American species are limited to McCrae (1961) and Calentine (1964, 1965). The present report involves the intermediate hosts and larval development of *Glari-dacris catostomi* Cooper, *Hunterella nodulosa* Mackiewicz and McCrae, *Monobothrium hunteri* Mackiewicz and *Monobothrium ingens* Hunter. The periodicity of the first three species in Iowa fish hosts was presented earlier (Calentine and Fredrickson, 1965). McCrae (1961) studied the larval development of *G. catostomi* and *H. nodulosa*, but certain of my results differ from his findings.

MATERIALS AND METHODS

Adults of *G. catostomi*, *H. nodulosa* and *M. hunteri* were taken from white suckers, *Catostomus commersoni* (Lacépède), in the Iowa River, Franklin and Hardin Counties, Iowa. Adults of *M. ingens* were recovered from smallmouth buffalo, *Ictiobus*

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