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Abstract. During the summers of 1961, 1962, and 1963, mass emigrations of *Rana pipiens pipiens* Schreber occurred at the end of the first week in July. The intensity of the movement varied in the three years. Environmental causes for this movement were considered; temperature changes, precipitation or crowding do not seem to be operating. Samples of the tadpole populations were examined and the metamorphic changes prior to emigration are rapid and regular. With final metamorphosis into juvenile frogs, the emigration suddenly begins. It appears to be triggered by internal events related to maturation.

During the evening of 8 July 1961, a massive swarm of juvenile frogs left the waters of Garlock Slough in Dickinson County, Iowa, and moved into the surrounding hills of grass and cropland so that the tall grass was alive with small frogs. They crossed an adjacent highway in such numbers that automobiles crushed a carpet of frog viscera. This emigration continued at a decreasing rate for the next two weeks. Extensive movements of other anurans are known: *Bufo fowleri* (Gunter, 1941), *Bufo americanus* (Blair, 1943), *Scaphiopus hurterii* (Bragg, 1950), *Bufo valliceps* (Blair, 1953), *Rana clamitans* (Martoff, 1953), *Rana pretiosa* (Carpenter, 1954), *Scaphiopus holbrooki* (Pearson, 1955), *Rana catesbeiana* (Willis et al., 1956), *Hyla regilla* (Jameson, 1956). Of these, only the toads appear to display the sort of massive emigrations described in this report on *Rana pipiens pipiens* Schreber.

This phenomenon was an extreme example of an annual event which we also observed in the two succeeding years while at the Iowa Lakeside Laboratory on adjacent Lake West Okoboji. In both 1962 and 1963 the emigrations began on 5 July, reached a peak within a few days and decreased over the next two weeks. During these succeeding years, records were kept of some of the environmental conditions and samples of the tadpole populations were studied during the month preceding the emigration. These samples were staged according to the Taylor and Kollros series (1946) and the stomach contents at different stages were examined. During the emigration period, daily observations were made to estimate the intensity of movement.

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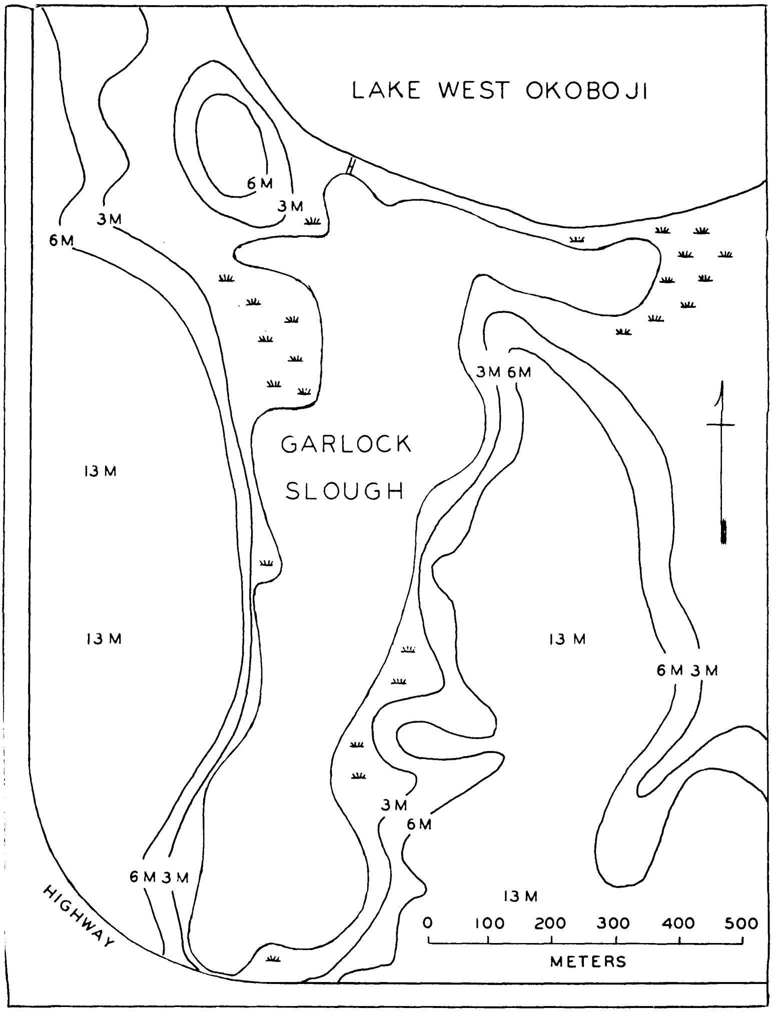

Figure 1. Study site in Dickinson County, Iowa. Three- and six-meter contours and thirteen-meter hills indicated. From State Highway Commission map, 1913.

The Habitat

The study site is in the knob-and-kettle terrain characteristic of recent glaciation. The entire region is dotted with large and small ponds, each with breeding populations of frogs. The substratum is boulder-clay with large gravel beds in the morainic hills. Garlock Slough extends from the southern shores of Lake West Okoboji into the hills of terminal moraine. As seen in the map (Fig. 1) it would appear to be an outwash valley from the lake basin. The adjacent region is a wildlife refuge of the state; it is grassland with one stand of oak on the eastern margin.

The water level of the slough varies with the wet and dry cycles. It is over one meter deep when filled. During seasons of drought, it becomes essentially a wet meadow with watery depressions. The temperatures of these shallow waters reflect air temperatures. Characteristic day temperatures in June are between 20 and 30°C. There is very little stratification; surface water is within 2 degrees of the air and the bottom water 2 degrees less than the surface. The water is well-aerated and clear.

The vegetation is typical of such sloughs with bands of poplar, willow, and the emergent cattails, sedges, and grasses at the margin. The common aquatic plants are found in the water; blooms of *Lemna, Riccia,* and *Wolffia* may cover the surface. This rich vegetation creates a flocculent layer of detritus and large mats of plant material floating at the margin.

The fauna is also typical of such ponds of the region. The plankton is dense as are the amphipods, crayfish, snails, and insect larvae. The vertebrates present include other amphibians, the painted turtle, snakes in the marginal grasses, the muskrat, and water and marsh birds.

The slough is very suitable for the maintenance of very large populations of *R. pipiens.* Food for the tadpoles is very abundant and the grasslands are dense with food for the juvenile frogs. However, many of the invertebrates as well as the vertebrates are predators on both larval and young frogs.

Life Cycle

The reproductive cycle of *R. pipiens* has been well described for Ithaca, N.Y. and Michigan by Wright (1914), Force (1933), Wright and Wright (1949), and Ryan (1953). The climates are similar to that of Iowa and the cycle of the species is very parallel. In New York the emergence from winter hibernation is variable, ranging from early March to mid-April. Spawning occurs in the first two weeks of April. Metamorphosis is complete by the first two weeks of July. Wright (1914) describes the July metamorphosis: ". . . a region may have almost a plague of small meadow frogs." This is an apt description of the movements described in this report. At first frost in October the frogs return to the water to enter the bottom mud in hibernation (Wright and Wright, 1949).

The maturational stages during the month preceding emigration in 1962 are outlined in Figure 2. Large samples of tadpoles were collected at weekly intervals; while a large range in developmental stages was seen, the rate of development appears regular. In the middle of June, tadpoles ranged from 30 to 70 mm in length, with hind limbs ranging from rudimentary to well developed. In the last week of June most of the samples

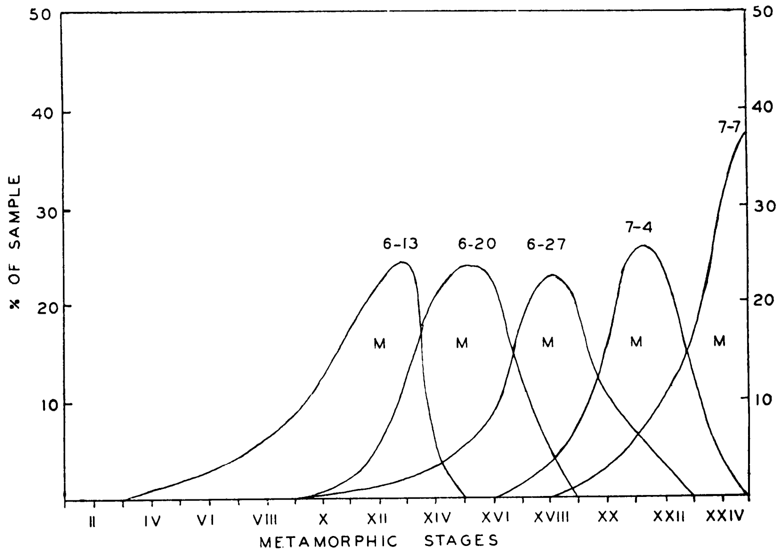

Figure 2. Five samples of approximately 100 frogs taken from Garlock Slough at weekly intervals and at time of emigration in 1962; smoothed curves indicate percent of sample by metamorphic stage (Taylor and Kollros series); M indicates median stage of sample.

contained tadpoles with emerging forelimbs and resorbing tails. In the first week of July the limbs assumed the adult proportions and the tails were diminishing rapidly; the most advanced reached complete metamorphosis by 4 July. By the end of the first week of July the sample was largely of juvenile frogs; some were in the final stages of metamorphosis.

The behavior of *R. pipiens* changes with the changing morphology. Swimming movements of the tail give way to swimming movements of the hind limbs and finally to hopping. Feeding goes from essentially herbivorous to largely carnivorous. In the later stages the tadpoles aggregate in the marginal waters sitting on the mats of vegetation. This appears to be related to changes in breathing and to the mode of locomotion. This shoreward movement has been noted by Noble (1931) and Jameson (1956). The density at the margins of Garlock Slough was estimated at 200 per square meter. Finally exploration of the shores is begun; these preliminary land movements are usually at night and are seldom greater than a meter in extent. When disturbed, these very late-stage individuals dive back into the water instantly. By the first of July the stage is set for the emigration.

Mass Emigration

Of the three annual mass movements observed, only that of 1961 was dramatic. The crash emigration did not command our attention until the evening of 8 July. For two days, the juvenile frogs left the slough and negotiated the surrounding grassy hills in extremely large numbers. A sweep of a dip net would yield several frogs. Just as suddenly, the exodus declined; by mid-July, only an occasional frog was seen in the meadows around the slough.

In 1962 we were alert to the very start of the movement, which came on 5 July with a sparse movement across the road at the south end of the slough. This slow emigration increased in tempo and reached heavy proportions by 11 July. It decreased until another surge occurred on 15 July followed by another on 18 July. By the end of the month all frogs had left the water. The entire period of emigration was longer than that of the preceding year, but less intense.

In 1963, the first obvious movements began again on 5 July. For three weeks a steady but light activity was observed. No one massive peak or even smaller peaks of previous years were noted.

This movement of frogs is very positive and is away from the water in all directions. Just prior to emigration, the presence of a person elicits a fright reaction and prompt retreat to the water; during emigration a person standing in the paths is an island in a current of hopping frogs. Many barriers are surmounted, including deep grass, cultivated lands, roads, fences, and hills of 15 meters in height. While no records were made of the horizontal distance travelled, the road on the west side of the slough, 300 meters from the water, was crossed in large numbers. Movements of over a mile by marked *R. pipiens* have been recorded by Dumas (1964).

This period of observation over three years was clearly one of decrease in total numbers of tadpoles in the slough and one of decreasing intensity of emigration. However, we do not have quantitative data on density nor of the actual numbers moving out of the water.

The Problem of Cause

There remains the problem of what factors, biotic or physical, internal or external, are operating to trigger the emigration and to cause differences among the years. At this time we are unable to offer satisfactory explanations for the differences. We do have data which may rule out some factors and work is in progress to evaluate experimentally some of the factors which may be operating.

The period of study was not one of drought; the basin was filled in all three years. Therefore, volume of water as space for development does not seem to have been an important factor in regulation of numbers.

Temperature might be important in three ways: dictating the time of spring breeding, regulating the rate of development, or triggering emigration. The maximum and minimum daily temperatures are recorded at nearby Iowa Lakeside Laboratory.

The year 1961 was one of gradual increase in temperature from March to June. In 1962 there was a sudden increase in late April. In 1963 the sudden increase in temperature occurred early, in the last week of March, and warm days continued as a very mild spring. Yet, in each of these diverse years the emigration date was exactly the same. It might be postulated that the single emigration pulse of 1961 and the repeated pulses of 1962 were related to a single and multiple periods of breeding in the early spring. We have no records of the actual breeding dates in the Okoboji region; this lack precludes a conclusion on this point.

The temperatures at the actual times of emigration are remarkably similar for the three years. The June and July temperatures were almost identical; no sudden changes were noted at the times of emigration. Temperature apparently is not a trigger for the sudden movements of the young frogs.

The role of day length as a trigger is critical in the cycles of many vertebrates. The emigration of the frogs here follows the summer solstice by two weeks; our data do not tell us if this is important.

In some other amphibians, terrestrial movements are related to atmospheric moisture and precipitation; the movements of toads from ponds occur in periods of rainfall (Gunter, 1941; Bragg, 1942; Blair, 1953; Carpenter, 1954). This is not true with the frogs of the Okoboji region. The greatest movement was during a five day interval between light precipitations. The lowest rate of movement followed three days of heavy rainfall.

Biotic stimuli to emigration could include food shortage, increase in predation, or population pressure of the metamorphosing frogs themselves. The diet of *R. pipiens* is completely altered in the late stages of metamorphosis. The terrestrial rather than the aquatic habitat is the source of food. Table 1 records the stomach contents of the animals in various stages of metamorphosis.

Filamentous algae are a major part of the diet of the swimming tadpoles. Vascular plant fragments are recognizable in the gut; apparently plant debris is also consumed. During stage XX, rapid changes in the mouth begin and intake of food ceases. A plug of a clear material fills the stomach. With essentially juvenile mouth parts, feeding becomes completely carnivorous. The range of foods found here corresponds with that described by others (Noble, 1931; Knowlton ,1944; Hamilton, 1948). For a week preceding emigration, the feeding habits are those of the terrestrial animal. There is no shortage at any stage in development. Diet change and food shortage would not seem to act as triggers for emigration.

No obvious changes in predation pressure occur which could cause the mass movement from the water. Actually, predation pressure on the frogs increases after they leave the water; birds and snakes are attracted in large numbers by the mass movement onto land.

In Garlock Slough the density of newly metamorphosed frogs becomes very high; the water margins are crowded with hopping animals. The stimulus of overcrowding could be a factor in initiating the emigration. The role that high density plays in this respect has long been considered important to some forms; the idea has recently been reviewed by Wynn-Edwards (1962). However, experimental work in progress indicates that population pressure is not a factor in the movements of *R. pipiens*.

Table 1. Stomach contents of 75 frogs from Stage XVIII to XXV (Taylor and Kollros series)

Stage	Stomach Contents
XVIII Cloacal tailpiece disappearance.	Almost entirely plant material; plant debris, filamentous algae, *Lemna, Riccia*, green plant fragments, occasional ostracod, amphipod.
XIX Skin window to forelimbs.	Entirely plant material, plant debris, filamentous algae, *Riccia, Lemna, Spirodela,* green plant fragments.
XX Forelimbs emerge; changes in mouth begin.	Greatly reduced contents; plant debris, green plant fragments, *Lemna.* Soil particles.
XXI Larval beak gone; rapid changes in mouth.	Many with empty stomachs; others with very little plant material.
XXII Operculum and gills resorbed; tail reduced.	All stomachs empty of food. Replaced by thick, viscous plug.
XXIII Great reduction of tail length.	Entirely animal material, both aquatic and terrestrial in origin; copepods, amphipods, ants, wasps, collembolans. Stomach contents meager.
XXIV Last vestige of tail.	Terrestrial food; land snails, collembolans, beetles, flies, millipedes, wasps, occasional amphipod. Stomach filled.
XXV Juvenile frogs.	Very heavy insect feeding reflected; many types of beetles, flies, collembolans, wasps, spiders. Some fragments of wood, pebbles.

We are left with the notion that the stimulus for emigration is internal and related to the complex of neuro-humoral and morphological changes at metamorphosis. While the trigger appears to be internal, the expression of these changes is behavioral.

May we request that members of the academy assist us in gathering data on these movements to ascertain the extent to which the activities described here are general over the state. We particularly need the dates of spawning in different parts of the state.

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