

Ecological Interactions of Frog Larvae at a Seasonal Tropical Location in Thailand

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ABSTRACT—To determine the adaptive strategies frogs utilize to exploit tropical seasonal environments, a 10 month study of tadpole ecological interactions was undertaken at the Sakaerat Experiment Station, located approximately 250 km NE of Bangkok.

The temporal distribution patterns of larval species occurrence for several ponds show the following: 1) all the species have seasonal reproductive cycles, which are correlated with the unavailability of aquatic habitats during the dry season; 2) the greatest number of species using ponds as larvae correlates with the first time that the aquatic habitats retain water long enough for the larvae to complete metamorphosis; 3) patterns of larval species occurrence in response to the same environmental stimuli are varied; and 4) the occurrence of larval species in any single pond seems due to chance.

Food analyses and behavioral observations are compared with niche analyses of overlap based on larval species abundances. Food differences do not add any information to that obtained from occurrence patterns in characterizing larval niches.

The frog fauna at Sakaerat divides the total environment spatially and temporally at several levels. The most distinctive partitioning of the environment occurs between the wet (14 species) and dry (3 species) season breeders. The rainy season breeders subdivide the available aquatic environment by: 1) utilizing different ponds within the total environment, 2) occupying a single pond at different times, and 3) dividing up the living space within a pond spatially, rather than by selecting different food categories.

All species for which data were gathered have short larval life periods which correlate with the uncertain aquatic habitat due to sporadic rainfall.

All of the ponds had a much greater larval biomass at an early time rather than at a later time. Perhaps by having a period of larval activity at the beginning of the wet season, newly metamorphosed frogs are assured of a favorable period of growth before having to survive the dry season. Alternatively, the period of heavy larval usage may occur at the beginning of the pond cycle to avoid heavy predation.

The single physical factor of rainfall distribution regulates anuran reproductive patterns in tropical areas characterized by a pronounced dry season. The more northerly the environment, the greater the number of physical factors which control the anuran reproductive patterns.

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INTRODUCTION

The least understood period of life in frogs is the larval period, particularly for tropical forms. Yet it is this period in the life history when selection is probably strongest. In order to better understand the biology of amphibians, and in particular, to attempt to discern the major selective forces operative in the amphibian-reptile transition, we must learn more of the population dynamics of larval amphibians in tropical situations.

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The purpose of this report is to describe the ecological interactions of the frog larvae at a seasonal tropical location and to determine the adaptive strategies frogs utilize to exploit a seasonal tropical environment. The following ecological interactions are described: seasonal distribution of larvae and calling adults; seasonal variation in larval biomass; length of larval life; larval food; larval microhabitats and behavior; observed causes of embryonic and larval death. Larval niches have been analyzed elsewhere (Heyer, in press).

DESCRIPTION OF THE STUDY SITE

The main study was undertaken at the Sakaerat Experiment Station, Amphoe Pak Thong Chai, Changwat Nakhon Ratchasima, Thailand. The site is approximately 60 km S of Khorat (Nakhon Ratchasima), a provincial capital, and approximately 250 km NE of Bangkok. The experimental station lies on the foothills (300-500m) adjacent to the Khorat Plateau. The foothills are the base of a low mountain range which separates the central valley of Thailand from the extensive Khorat Plateau.

The climate is monsoon in nature, the pronounced dry season extending from October through February. A typical year has two wettest months, May and September, with September representing the height of the monsoon. Thunder showers occur from March through June; from July through September the rains are more of the enduring kind. Rainfall for 1969 was 1363.1 mm. January, February, and the following December had 15.3 mm of rain total. The wettest months were September, with the maximum total, 453.0 mm, and March with a total of 152.9 mm.

The site has two extensive forest types, a dry evergreen forest and a fire-climax deciduous dipterocarp forest. The dry evergreen forest is a 2-stories forest with an undergrowth layer. The top-story trees are 20-35 m high and are composed of mostly *Hopea ferrea* and *Shorea sericeiflora*. The second-story trees are 5-17 m high and consist of *Memecylon sp.*, *Hydnocarpus ilicifolius*, *Walsura trichostemon*, *Aglaiia pirifera*, and *Lagerstroemia calyculata*, together with saplings of *Hopea ferrea*. The rather dense undergrowth layer is 2.5-3.5 m high. Average horizontal visibility on the ground is 18 m. (Information on dry evergreen forest from unpublished report by Smitinand, Chaiyanand, Nalamphun, Santisuk available through the courtesy of the Applied Scientific Research Corporation of Thailand.) The deciduous dipterocarp forest is a single story forest with a ground cover of grasses and fire resistant shrubs, herbs and cycads. Fires are almost an annual event due to the habits of the people who farm the region.

Data were collected from a series of ponds in different situations on the site (names in parentheses refer to nomenclature as used throughout rest of text): A) from a temporary pond system near the main highway at the site entrance in land cleared for agriculture (Highway Ponds), B) a series of temporary ponds resulting from removal of "laterite" for road fill in the deciduous dipterocarp forest (Laterite Pits), C) an artificially contoured permanent pond filled by a small natural spring in partially cleared dry evergreen forest within the living quarters compound (Dam Stream), D) two naturally occurring temporary ponds in the dry evergreen forest (Met Shack and Station 78 ponds), and E) a seasonal stream coursing through the dry evergreen forest (Huai Pae). Limited comparative information was also gathered from two other streams in different types of dry evergreen forest. The first was approximately 30-40 km S of Sakaerat in another seasonal stream (Forestry Station Stream), and the second was in the Khao Yai National Forest, descriptively another seasonal stream, but with some water running at all times of the year. The ponds are individually described later.

MATERIALS AND METHODS

Larvae were collected with a dip net. Because of the mesh size, larvae of the smaller microhylid species may not have been captured until they were 2 to 3 days old. Quantitative

sweeps were taken only at the Dam Stream. These consisted of a biweekly series of 5 sweeps taken at the same places; 3 at the surface, 2 on the bottom. The entire contents of the dip net for each sweep were emptied into a plastic bag together with some pond water. The samples were then taken to the laboratory where formalin was added to each plastic bag. After at least one day, the bag contents were sorted, and larvae of each sweep were placed into individual vials filled with 10 per cent formalin.

For all other situations, the only difference was in the manner of collecting the larvae. At each pond, series of sweeps were made covering all microhabitats, and samples of each species were placed in a single plastic bag for each collection time. Each individual of rarer species was kept; a sample of each of the common species was kept. Samples were taken whenever other duties would permit, usually a minimum of 1 sample per week when water was present in the pond.

All vials were shipped to the laboratory in the U.S. where the contents of each vial were identified and counted by species, staged according to Gosner's (1960) scheme; in the cases where there were large numbers, samples of 10, 25 (usually) or 50 specimens were staged, and data for the entire lot were then extrapolated. In the case of the Dam Stream samples, volumes were taken of each species for each sweep as a measure of biomass. Volumes were taken by displacement of 10 per cent formalin in either 10 or 25 ml graduated cylinders. Just prior to determining displacement values, the larvae were placed on paper towelling to remove most of the surface moisture. The study sample comprises 8470 larvae.

Gut samples were taken from 2 or 3 specimens of each species from each pond where samples were adequate. In the case of 3 species, *Glyphoglossus molossus*, *Microhyla heymonsi* and *Polypedates leucomystax*, additional tadpoles of different size classes were examined. For each larva examined, the stage, head-body length, and gut length were recorded. At the beginning of the sampling, wet mount microscope slides were prepared from material from the fore, mid, and hind-guts. This was reduced to sampling the fore and hind-guts only. The first 20 objects recognizable as distinct entities were recorded as to broad taxonomic groupings and the minimum and maximum dimensions of the objects were recorded by use of an ocular micrometer. The broad taxonomic groupings used were: Arthropods, Nematodes, Diatoms, Filamentous Algae, "Protozoans", and Other. The Protozoan category included anything that any of the 3 of us involved in the data taking thought might be a protozoan. Statistical procedures are discussed where appropriate.

All of the species discussed herein have been described and figured elsewhere (Bourret, 1941; Heyer, 1971, a,b; Pope, 1931; and Smith, 1930).

SEASONAL DISTRIBUTION OF LARVAE AND CALLING ADULTS

The Dam Stream

The pond was a 3 level 2 X 15.5 m rectangle, much like an inverted 3-step insect pinning block. The average water depth of the first step (4.5 m long) receiving the small inflow from the spring was 0.2 m, the average depth of the second step 0.4 m (6.5 m long) and the average depth of the third step 0.6 m (4.5 m long). When we first arrived (22 February 1969), standing water was present only in the third portion of the pond. After the first heavy thunder shower (35 mm on 13 March), water was present in all 3 steps and the level usually did not vary over 15 cm during any month. Water temperatures were taken with a constant recording thermometer in the deepest portion of the pond during the latter 5 months of the sampling period. The temperatures were constant, ranging from 18 to 29 C; the largest fluctuation occurred in the 2 week period of 11-27 December from 18 to 24 C. No diel pattern is evident in the tracings.

A log book was kept of the observations made at the Dam Stream. Every one to 3 evenings, calling activity of adult frogs and observations of larvae were noted.

This study pond was the only site observed on the biological preserve that had fresh standing water prior to the March thundershowers. During the extremely dry period of late February and early March, adults of 3 species of frogs were frequently observed at the pond: *Microhyla inornata*, *M. pulchra*, and *Chirixalus vittatus*. None of these species called. After the first March rain, these species were never observed again. Apparently, the individuals were congregating around the available water even though the particular habitat was unsuitable for breeding purposes.

Calling activity.—Ten species were heard calling over the course of the study period (Fig. 1). Three species, *Bufo melanostictus*, *Microhyla heymonsi*, and *Ooeidozyga laevis* were calling prior to the first rains in March. Two species called but no eggs or larvae were collected: *Chirixalus nongkhorensis*, which was heard often between 21 May and 23 July; and *Calluella guttulata*, which on two separate occasions a single individual was heard calling (data not on figure). One species demonstrated a strict correlation between calling and mating. On the evening of 13 March, just after the 35 mm rain, a group of *Glyphoglossus* called, mated, and covered the pond with eggs. This species laid another mass of eggs 5 days later. In all the other species, calling predated egg or larval capture. *M. heymonsi* males were heard two days prior to collecting a larval sample. However, that calling record was 20 days in advance of any new egg masses being recorded for that species. Intervals between first recorded calls and first collected eggs or larvae varied widely: *Bufo melanostictus*, 17 days; *Microhyla butleri*, 66 days; *Microhyla ornata*, 7 days; *Ooeidozyga laevis*, 24 days; *Rana nigrovittata*, 19 days; *Polypedates leucomystax*, 40 days; and *Chirixalus nongkhorensis* called sporadically for 65 days with no apparent egg deposition at this pond. In summary, the calling period is much longer than the period of amplexus. The only exception is *Glyphoglossus molossus*, in which apparently both sexes are reproductively ready and respond in similar fashion to the same environmental stimulus. For the other species, either 1) the female of the species is responsible for determining the actual breeding span within a much broader calling period, or 2) the male has a warming up period prior to emitting a "hot" call which attracts females.

The greatest number of species heard on any single night was 7. Calling activity was greatest the 3 to 4 month period following the first March rains. Calling activity was noticeably reduced from September onwards.

Larval occurrence.—*Microhyla heymonsi* larvae were present at the initiation of the study and in all months of the year except December. From March through November, two peaks of population density are apparent (Fig. 2); one in April and May, the other in July and August. The larval occurrence of *M. heymonsi* was the closest to an aseasonal pattern of all the species observed.

Ooeidozyga laevis were calling prior to the first major thundershower of 13 March and the single stage 35 larva collected on 21 March suggests that the species was present as larvae prior to the first sample collected of that species. The same situation might obtain for *Rana nigrovittata*, as in both species the larvae are bottom forms, seldom seen by an observer looking from above the water surface, and neither was ever sampled in large numbers. Larvae of *O. laevis* were collected for 6 consecutive months beginning with the March sample. No *O. laevis* larvae were collected during September or thereafter.

Four species of larvae have a pattern coinciding with the first major rains of the year: *Bufo melanostictus*, *Glyphoglossus molossus*, *Microhyla ornata*, and *Rana nigrovittata*. Beyond the initial triggering event, each species shows a distinct pattern. *Glyphoglossus molossus* essentially was a single time breeder. Eggs were deposited twice, 5 nights apart. The egg mass and larvae are quite distinctive; it is doubtful whether any further egg masses escaped detection. *Microhyla ornata* also had an abbreviated breeding season, but the two months when larvae were present are represented by a series of egg clutches. The sporadic calling of *Rana nigrovittata* from the end of October to the end of the study period with a single stage 27 larva collected on 17 December suggests a dry season breeding period as does the following for *Bufo melanostictus*. On 26 December, a large chorus of *B. melanostictus* was heard at a large pond about 50 m from the study pond, and larvae were observed in a garden pool in the living

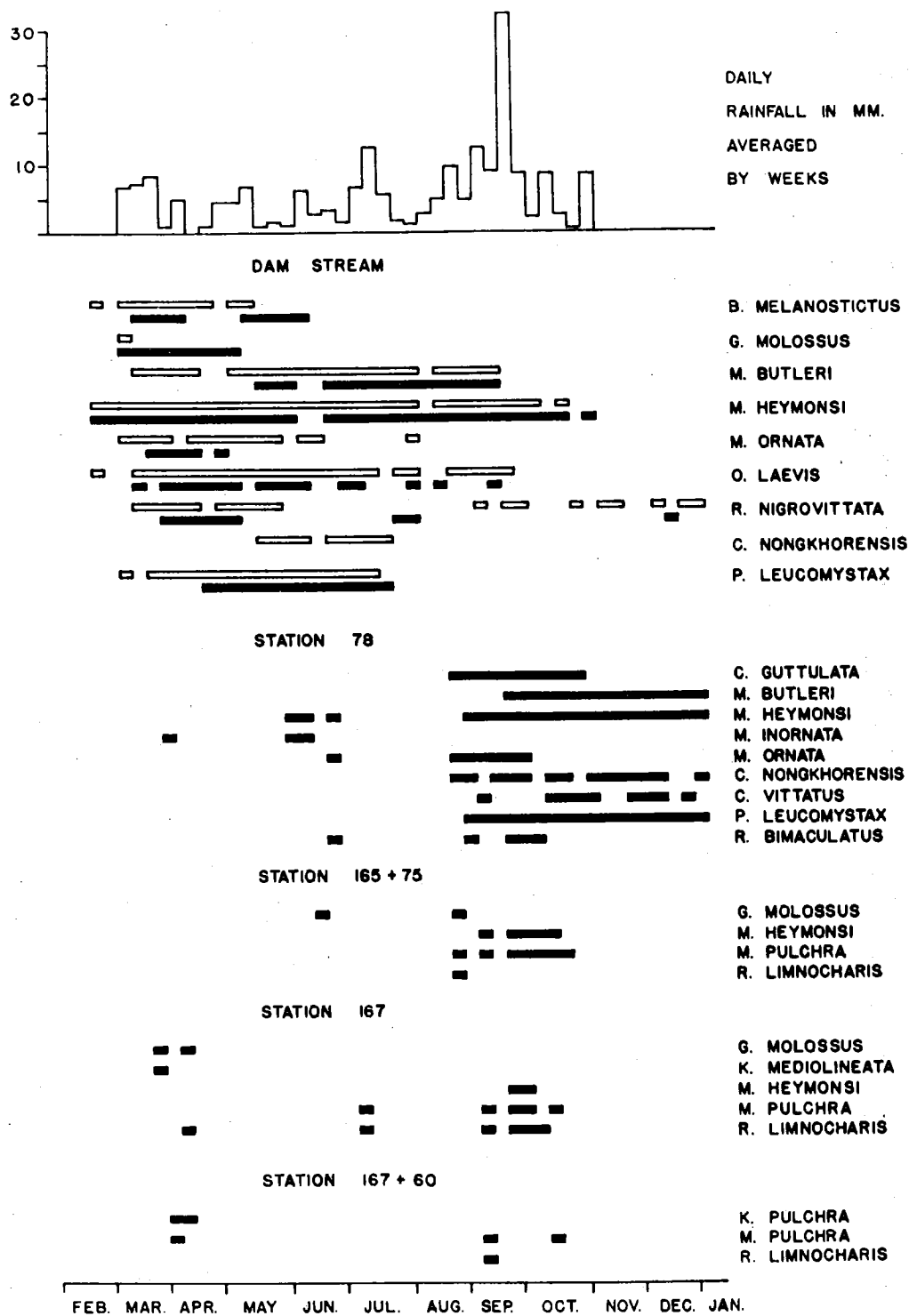


FIGURE 1. Summary of calling patterns and larval occurrence at 5 ponds, Sakaerat, Thailand. Open bars indicate calling males, solid bars indicate larvae.

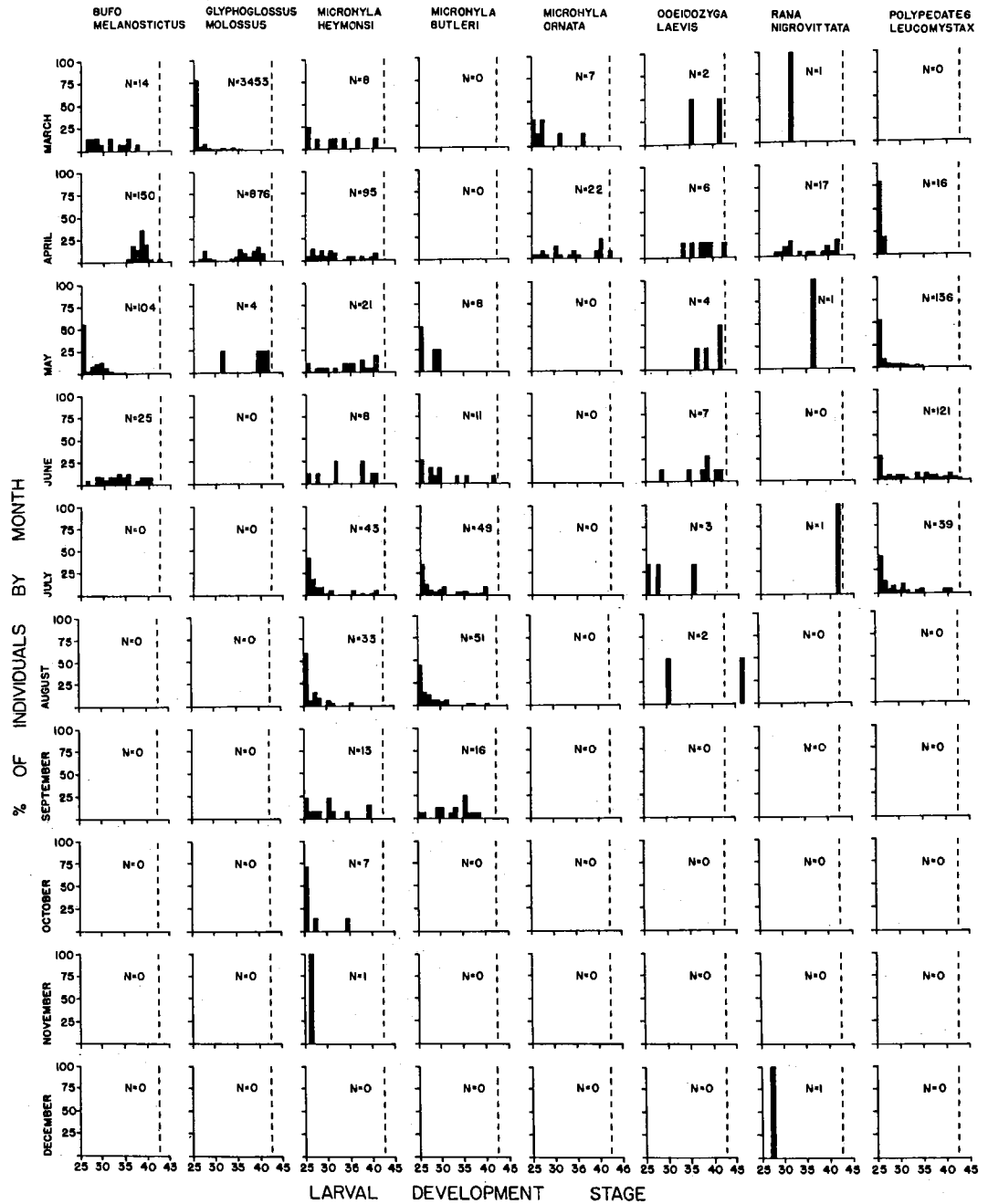


FIGURE 2. Larval population structure each month for the Dam Stream Pond. Stage 25 represents hatchlings, the dashed vertical lines indicate metamorphosis.

compound. *Bufo melanostictus* and *Rana nigrovittata* contrasted in the following: 1) *B. melanostictus* had two major periods of egg deposition and larval development (Fig. 1), whereas *R. nigrovittata* had only one larval peak period (April), and 2) *B. melanostictus* larvae were present in large numbers, *R. nigrovittata* larvae were few in number.

Two species show a pattern of a delay in larval occurrence from one to two months after the first heavy rains: *Microhyla butleri* and *Polypedates leucomystax*. In both species, all larval

development was complete prior to September. *Polypedates leucomystax* were the most obvious, dominant as larvae from May to July.

Station 78, Dry Evergreen Forest

The pond was quite variable in size but during the last cycle averaged about 15 m in diameter, with much of the pond 1 m or slightly greater in depth.

Data were not kept before 5 April 1969, but water and tadpoles were observed once prior to this time. Between 5 April and 14 July 1969, the pond was filled by heavy rainstorms and emptied 4 times. Eggs were deposited each of these times, but the water evaporated before any larvae completed metamorphosis. A heavy rainstorm also filled the pond on 24 August 1969; water was still present in the pond on 2 January 1970 and the water level was decreasing rapidly at that time. The pond would probably not be renewed as January was well into the dry season.

Few calling records of adult males were kept for this pond. Calling was recorded on 5 different nights. In 4 instances, larvae were collected for each of the calling species during the same cycle. In the fifth instance, *Microhyla butleri*, *Ooeidozyga laevis*, *Chirixalus nongkhorensis*, *Polypedates leucomystax*, and *Rhacophorus bimaculatus* were calling on the night of 27 August. Larvae were collected of all but *Ooeidozyga laevis*.

Larval occurrence.—The pond filled on 5 April and dried on 8 April. An egg sample taken and raised proved to be *Microhyla inornata*. The next time the pond filled, it had a wet life of 14 days, from 7-20 June. No larvae were collected, but larvae of *Microhyla heymonsi* and *M. inornata* were observed. The next cycle took place from 25-30 June. Three larval species were collected: *Microhyla heymonsi*, *M. ornata*, and *Rhacophorus bimaculatus*. On another cycle, 11-14 July, eggs were observed, but were not identified, nor were larvae collected (Fig. 1).

The results of the final cycle of larval occurrence which began on 24 August are summarized by biweekly periods (Fig. 3). Three species were present throughout the entire 4.5 month period: *Chirixalus nongkhorensis*, *Microhyla heymonsi*, and *Polypedates leucomystax*. *Chirixalus vittatus* was collected in low numbers over almost a 4 month period; the species may well have been present during the entire period. Three species responded to the heavy rain that filled the pond by laying eggs immediately: *Calluella guttulata*, *Microhyla ornata*, and *Rhacophorus bimaculatus*. Each of these 3 species demonstrate a similar pattern of laying several egg clutches only during the first part of the pond cycle, so that larvae were not present throughout the entire time. *Calluella* larvae were present the first 8.5 weeks, *Microhyla ornata* the first 6 weeks, *Rhacophorus bimaculatus* the first 7 weeks. *Microhyla butleri* larvae did not appear until 5 weeks after the pond was filled with water. One larva collected 29 August, identified as *Kaloula pulchra*, represents the only record for that species at the Station 78 Pond.

Summarizing over the total observation period, *Microhyla heymonsi* appeared to breed at every opportunity. Eggs, larvae, and calling adults were recorded for each wet cycle of the pond. *Microhyla inornata* appeared to breed early in the season and because of the climatic events of 1969 was not successful in bringing any larvae through metamorphosis at Station 78. *Microhyla ornata* and *Rhacophorus bimaculatus* laid eggs in late June and were reproductively successful during the last pond cycle. *Calluella guttulata*, *Polypedates leucomystax*, *Chirixalus nongkhorensis*, and *Chirixalus vittatus* all had larvae metamorphose the first time they laid eggs at Station 78.

Met Shack Pond, Dry Evergreen Forest

The Met Shack Pond was a small temporary pond, averaging about 5-6 m diameter, with the deepest portion about 2/3 m deep. Standing water was present on 17 July when the pond was discovered. Water remained continuously until 24 December, when the pond dried completely. Larvae were never present in any numbers. A series of sweeps from end to end, scraping the bottom, and skimming the surface of the pond never yielded more than a total of 6 larvae. No more than 4 specimens were ever kept per collection date. *Rhacophorus bimaculatus* was present throughout most of the observation period; larvae were collected on 17

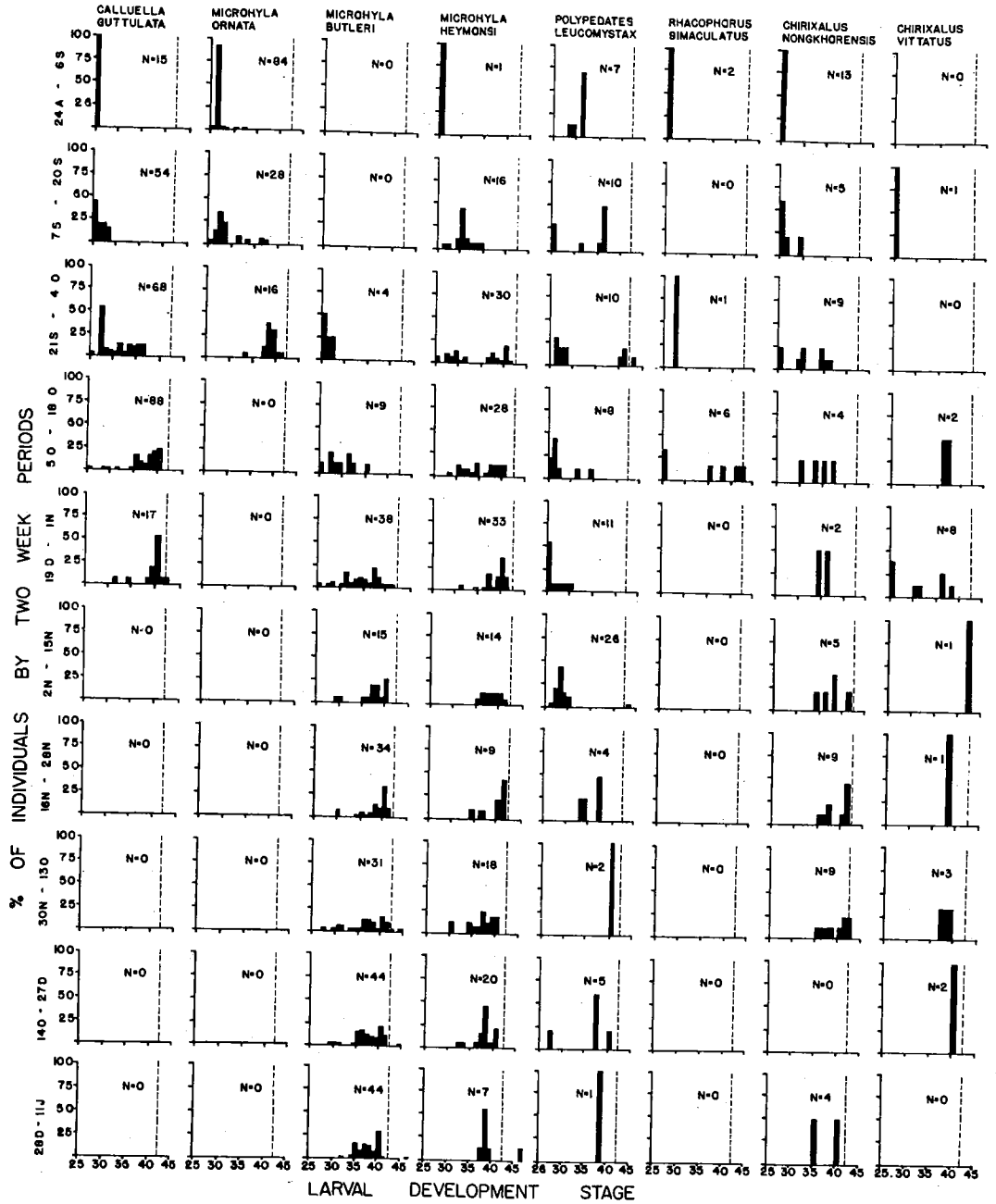


FIGURE 3. Larval population structure each two week period for the Station 78 Pond during the last cycle. Stage 25 represents hatchlings, the dashed vertical lines indicate metamorphosis.

July, 27 August, 10 September, 10 October, 6 November, and 13 November. *Microhyala heymonsi* and *M. ornata* were both collected on 10 September; *M. heymonsi* was collected on 6 November. No larvae were found in any sweeps made from 21 November through 23 December.

Huai Pae, Dry Evergreen Forest Stream

The Huai Pae was one of 3 streams which were surveyed and sampled once each month. The collection and observation of larvae were incidental to the main goals of the monthly visits, but limited information is available. The Huai Pae stream was completely dry except for one watermelon sized water hole when studies were initiated.

On the night of 3 March, 70 adult frogs were collected. With the exception of the minute stagnant pool mentioned above, there was no water and no frogs were breeding. On 22 March, a series of pools were present which contained water at each subsequent observation period. Samples of larval *Kaloula pulchra* were collected on 22 March. Conditions were similar on 12 April, when another series of *K. pulchra* larvae was collected. The records indicate that larvae were present on 10 May, but no samples were taken. On 9 June, the stream bed appeared as though it had been scoured by a flood two nights previous. The pools were searched for larvae—none were seen. On 7 July, *Microhyla heymonsi*, *Ooeidozyga laevis*, and *Rana nigrovittata* were heard calling; larvae of all 3 species were collected from two pools. On 11 July, at a lower section of the Huai Pae, the same species as well as *Polypedates leucomystax* were collected as larvae. On 13 August, 2 *Microhyla heymonsi* were heard calling; 1 *Microhyla heymonsi* and 2 *Rana nigrovittata* larvae were observed. On the nights of 8 September, 6 October, and 8 November, no frogs were heard calling and no larvae were observed. On 8 December 1969 and 3 January 1970, 2 or 3 *Rana nigrovittata* were heard calling but no larvae were seen.

Forestry Station Stream, Dry Evergreen Forest

The first time (26 February) we collected the Forestry Station Stream, the bed was dry; no frogs were breeding. On the next visit, 18 March, there were several small pools in the stream bed. *Kaloula pulchra*, *Ooeidozyga laevis*, and *Rhacophorus appendiculatus* were calling. *Kaloula pulchra* was collected as larvae. This sample comprises the only larval sample from the Forestry Station Stream—no other attempts were made to collect larvae. On the night of 14 April, there was no standing or flowing water in the bed; *Ooeidozyga laevis* and *Rhacophorus appendiculatus* were calling. On 7 May, the bed had shallow pools with a very slight flow of water; *Rhacophorus appendiculatus* was calling. On 5 June, there was slightly more water present than noted at the May visit; *Philautus parvulus* was calling. On 4 July, the bed had a continuous water flow; no frogs were calling. On 8 August, the bed was filled with water; no frogs were calling. On 5 September, the water was at the highest level observed over the entire period; no frogs were calling. On 3 October, the water condition was about the same as during the August visit; no frogs were calling. On 6 November, the water level was about the same as noted for the October visit; one *Rana nigrovittata* was calling. On 5 December, the water was down to a slight flow; several *Rana nigrovittata* were calling. On 1 January 1970, the water level was down from that noted on the December visit; several *Microhyla berdmorei* and *Rana nigrovittata* were calling, one *M. berdmorei* egg mass was observed.

Khao Yai, Dry Evergreen Forest Stream

On 22 May, our first visit to this forest stream, the water was quite low. The following month, the river was a raging torrent. The water level remained high and the current fast through November. In December and January, we were able to wade across the stream and work both banks again. The water level was lower at the end of the study but not as low as when the study was initiated. A single *Rana livida* was heard calling on the night of 14 August. Prior to this date, no frogs were heard, nor were any heard on the two monthly visits following August. On 12 November *Microhyla berdmorei* and *Rana nigrovittata* were calling; one pair of *Rana livida* was observed in amplexus. On 11 December, *Microhyla berdmorei* and *Rana nigrovittata* were again calling; eggs and larvae of *M. berdmorei* were collected from an isolated pool in the flood plain next to the raging stream. On 5 January 1970, one *Microhyla berdmorei* and several *Rana nigrovittata* were calling. Eggs and larvae of both species were observed and a

larval sample of *M. berdmorei* was collected from the same pool that had been sampled the previous month. All *M. berdmorei* larvae collected in both December and January were stage 25-26 larvae, indicating that the December lot of larvae metamorphosed prior to the January sampling time.

Laterite Pits

The 3 laterite pits for which data were kept had rather common histories. A good thunderstorm would fill them; several successive dry days would dry them. Each pit was no more than 2 m in diameter and 1 m deep when filled with water. The laterite pit at Station 165+75 filled and emptied 9 times. Seven of these 9 times, larvae were present. Only once did the larvae reach metamorphosis, however. Each of the other times that larvae were present, the pond dried. The two pits at Station 167 and Station 167+60 each filled and dried 10 times. In the Station 167 pit, larvae were present 6 of those times; only once did any larvae metamorphose. Larvae were present on 4 different occasions at Station 167+60; no larvae reached metamorphosis at this site. The aquatic life of the pits ranged from 6 to 56 days. Any time a pit dried when large numbers of larvae had not reached metamorphosis, a sun-dried tadpole crust would form where the last pit of water had been. Ants soon devoured the dead tadpoles.

Calling activity.—Call information was recorded when other work coincided with visits to the pits at night. Records are available for 12 nights. On 5 nights there was no calling activity at any of the pits. In only 2 of the 7 instances when frogs were heard calling were the same complement of species calling at all 3 pits; for example, on the night of 17 August 1969, *Microhyla heymonsi*, *Microhyla pulchra*, and *Rana limnocharis* were all calling at each pit. The commoner pattern is exemplified by the night of 7 April 1969 when no frogs were heard at Station 165+75, *Microhyla ornata* was calling at Station 167, and *Microhyla pulchra* and *Rana limnocharis* were calling at Station 167+60.

Calls are not good predictors of presence of larvae of that species, even at a later time period. The available data yield: 1) 7 instances of calling but no larvae of that species collected from that pit during the water cycle, 2) 6 instances of both calling males and larvae recorded from the pit during the same aquatic cycle. With all data pooled, there was still one calling species, *Microhyla ornata*, for which no larvae were sampled from any of the pits.

Larval occurrence.—In some instances, the pits dried before a larval sample was taken. At Station 165+75, *Glyphoglossus molossus* was present the fourth time the pit filled; *Glyphoglossus molossus*, *Microhyla pulchra*, and *Rana limnocharis* were present the seventh time the pit filled; *Microhyla heymonsi* and *Microhyla pulchra* were present the eighth time the pit filled. At Station 167, *Glyphoglossus molossus* and *Kaloula mediolineata* were present the first time the pit filled; *Glyphoglossus molossus* and *Rana limnocharis* were present the second time the pit filled; *Microhyla pulchra* and *Rana limnocharis* were present the sixth time the pit filled; *Microhyla heymonsi*, *Microhyla pulchra*, and *Rana limnocharis* were present the eighth time the pit filled; *Microhyla pulchra* was present the ninth time the pit filled. At Station 167+60, *Kaloula pulchra* and *Microhyla pulchra* were present the second time the pit filled; *Microhyla pulchra* and *Rana limnocharis* were present the eighth time the pit filled; *Microhyla pulchra* was present the ninth time the pit filled (Fig. 1).

During the period from 4 September to 11 October, all 3 pits contained water. Station 165+75 had water from 4 September to 29 October. During this cycle, larvae metamorphosed from two of the pits. Data are sufficient during this period to examine patterns of larval life and growth (Fig. 4). At Station 165+75 *Microhyla heymonsi* were not collected until 13 September; all specimens captured were at stage 25 (Fig. 4). Upon hatching, *Microhyla heymonsi* are so small that they could pass easily through the mesh of the net. Hatchlings were added to the population until 3 October, after which time it appeared that no more eggs were laid in the pond. In spite of young being added to the population during the first half of the pond life, the population did not stabilize, but rather demonstrated a steady population growth until metamorphosis. The same trends hold true for *Microhyla pulchra*, the only difference being that larvae were recorded over a longer period of time (Fig. 4).

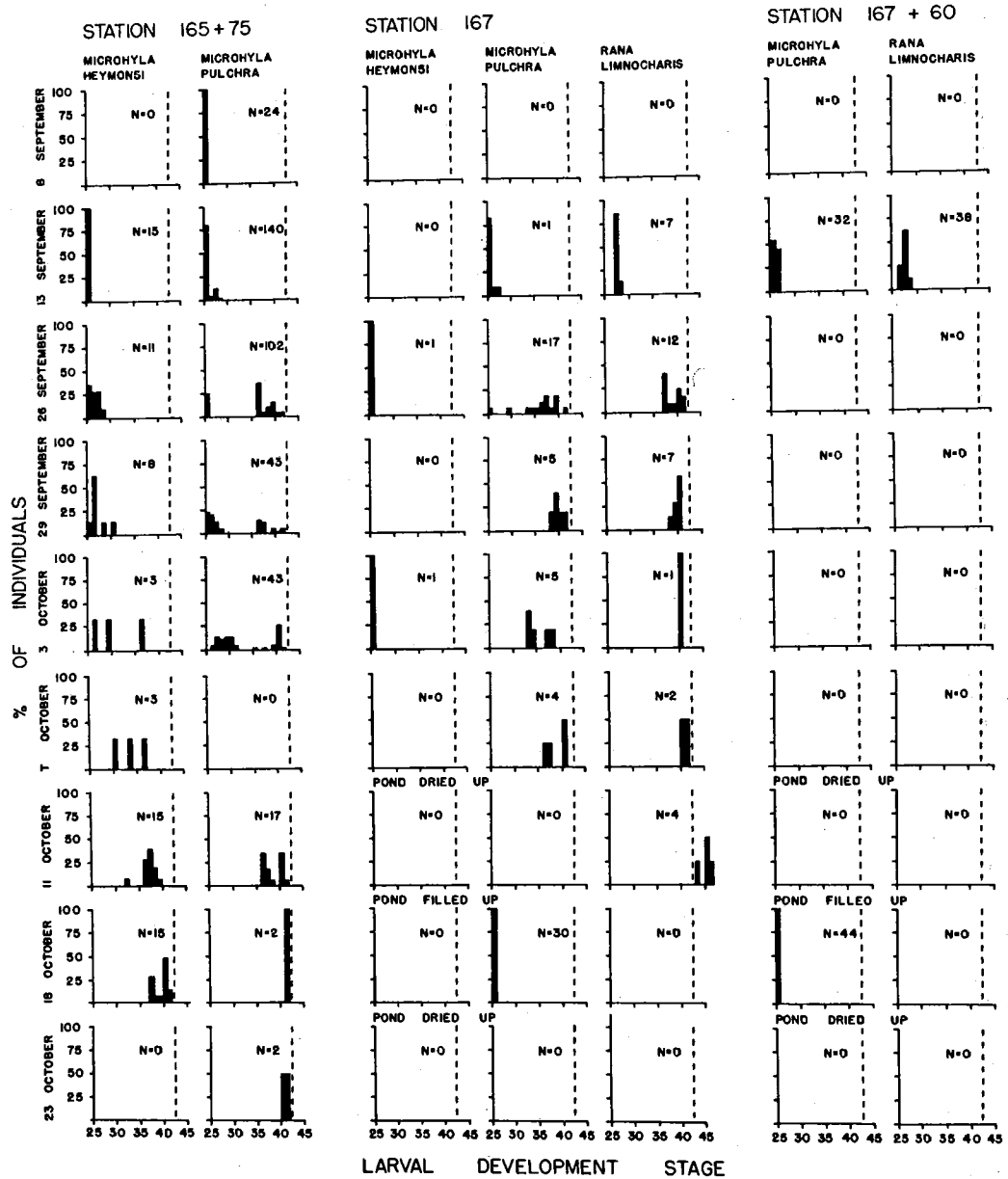


FIGURE 4. Larval population structure each collection date for the Laterite Pit Ponds during the last cycle. Stage 25 represents hatchlings, the dashed vertical lines indicate metamorphosis.

The staging graphs for Station 167 show slightly different patterns (Fig. 4). One individual of *M. heymonsi* was recorded from the pond on each of two occasions. The small larval sample suggests that net contamination may be the source of these larvae, as Station 165+75 was usually sampled immediately before 167. *Microhyla pulchra* were first collected on 13 September, but the presence of stage 27 larvae indicates that hatchlings were present prior to that date. Hatchlings were added to the population as late as 26 September, after which time no more eggs were apparently laid during that cycle. After the pond dried and filled again, a new set of young was collected. *Rana limnocharis* were first collected on 13 September, and like *Microhyla pulchra*, the presence of stages beyond 25 indicates that hatchlings were present before that date. Apparently no new egg clutches were laid, however. On 11 October, the pond

was dry, but newly metamorphosed *R. limnocharis* were abundant in moist places under surface debris.

The staging graphs for Station 167+60 are confusing. Substantial numbers of larvae of *Microhyla pulchra* and *Rana limnocharis* were collected on 13 September. During the rest of that particular cycle, no larvae were collected again. Some catastrophe must have wiped out the larvae. After the pond refilled, a sample of *Microhyla pulchra* was collected.

Highway Ponds

From April through mid-July, sporadic records were kept on the Highway Ponds. From April to June, no particular pond was singled out for study. From June until the end of the study a single, large temporary pond was studied. Few collections were made from April through mid-July. From 23 July through 18 October, larval samples were collected almost once each week.

Calling records.—The few data available show a seasonal pattern. Pooling the 4 records from April and May, the following species were heard: *Microhyla ornata*, *M. pulchra*, *Ooeidozyga laevis*, *Rana limnocharis*, *Polypedates leucomystax*. From June through August (3 recorded observation times) *Kaloula pulchra*, *Ooeidozyga laevis*, *Ooeidozyga lima*, *Chirixalus nongkhorensis*, and *C. vittatus* were heard. In September and October, the following species were heard (based on 2 recorded observation times): *Microhyla heymonsi*, *Ooeidozyga lima*, *Chirixalus nongkhorensis*, and *Polypedates leucomystax*. It is my recollection that *Microhyla ornata*, *M. pulchra*, and *Rana limnocharis* were heard only during the first half of the study period; the two species of *Chirixalus* did not begin calling activity until May or June.

Larval occurrence.—The data are sufficient to tabulate larval occurrence on a present-absent basis for a series of 10 samples (Table 1). A few patterns are evident from the data table

TABLE 1. Larval occurrence at the Main Highway Pond

	17 June	23 July	9 Aug.	30 Aug.	5 Sept.	13 Sept.	27 Sept.	4 Oct.	11 Oct.	18 Oct.
<i>C. guttulata</i>		X								
<i>G. molossus</i>	X		X	X	X					
<i>M. butleri</i>						X				
<i>M. heymonsi</i>	X	X	X	X	X	X	X	X	X	X
<i>M. ornata</i>			X				X			
<i>M. pulchra</i>	X	X	X	X	X	X				
<i>O. lima</i>	X					X	X			
<i>R. limnocharis</i>	X			X	X					
<i>P. leucomystax</i>	X	X	X	X	X	X	X			
<i>C. nongkhorensis</i>					X					
<i>C. vittatus</i>			X		X	X	X	X		

and from field notes. *Microhyla heymonsi* was present in each of the samples. Several species were present only during the first part of the cycle, from April through September. Water was present in the pond until the end of the observation period in early January 1970. During early October, many sweeps had to be made to obtain any larvae. On 18 October, only a single *Microhyla heymonsi* was collected from numerous sweeps. This data was the last time any larvae were collected, though the pond was swept on a regular basis through 6 November after which no more samples were attempted.

Intersite Comparisons

The following aspects of the seasonal distribution of larvae appear to hold for all situations studied and would be true for any climatic cycle at Sakaerat.

All the species have seasonal reproductive cycles. This is correlated with the unavailability of aquatic habitats during the dry season. The one species which demonstrates the most opportunistic breeding strategy, *Microhyla heymonsi*, still demonstrates a definite seasonal pattern of occurrence (Figs. 1-3).

There appear to be two peak periods when the greatest numbers of species were present as larvae at Sakaerat, March-May and late August-early September (Fig. 1). These peak larval usage times correlate with types of aquatic habitats. The March-May peak occurred at the only permanent pond studied, the Dam Stream. The second peak occurred at the Station 78 and Laterite Pit ponds, which are all temporary ponds. Although no data were gathered, it was obvious in the field that some change occurred in the soil moisture in the last part of August. Prior to this, all rainwater would be immediately absorbed by the soil. Leaf litter would be dry an hour after a heavy rain; pools where rain water collected would disappear quickly. Starting at the end of August, the soil appeared saturated with water. The leaf litter was damp, ponds which started to recede would be replenished by a light rain. It was at this time that larval metamorphosis occurred in the temporary ponds in the deciduous dipterocarp and dry evergreen forests. The greatest numbers of species using ponds as larvae thus correlate with the first time that the aquatic habitats remain permanent in the sense that the pond will remain long enough for the larvae to complete metamorphosis.

Patterns of larval species occurrence in response to the same environmental stimuli are varied. Comparisons of events at the Dam Stream and the last cycle at Station 78 show that some species bred immediately so that larvae were present almost as soon as the pond formed. Some species did not breed immediately. Each species was present as larvae over a slightly different span of time (Fig. 1).

The pattern of calling and larval occurrence in any single pond seems due to chance. The Laterite Pits were nearly identical in size, construction and material. They were side by side (all within 165 m of each other) in the same vegetation and all drew from the same species pool. Each pit pond was unique in its assemblage of calling species or larval occurrence at a given time, however.

Mr. Karl Frogner made collections of larvae at Sakaerat during June, July, and August of 1968. Most of the collections were made along the Huai Pae; some samples were taken from temporary pools in the dry evergreen forest and alongside the highway in agricultural areas. Ten species are represented in the Frogner collections. One species, *Rana pileata*, was not collected in 1969, although many adult and juvenile *R. pileata* were collected in both years. The rest of the species are common to both collections. With the exception of *R. pileata*, the collections of 1968 coincide with habitats, species, and general collection dates for 1969. From the limited data made available by the Frogner collections, it appears that the larval events of 1968 were similar to those recorded in 1969.

SEASONAL VARIATION IN LARVAL BIOMASS

Larval biomass for the Dam Stream Pond was estimated by determining the volume of each species of larvae for each sweep. The total biomass of each species per month was then divided by the total number of sweeps per month to arrive at a figure of average biomass per species per sweep for each month. The sum of all species per month was also determined. The results are plotted on semilogarithmic coordinates (Fig. 5). The total pattern is very seasonal with the greatest volume of larvae occurring after the first heavy rains, followed by a steady decline in biomass during the remainder of the study period. Two species contributed most heavily to the biomass of larvae using the pond: *Glyphoglossus molossus* and *Polypedates leucomystax*. The population density peaks of these two species were temporally separated. All species show a pattern of a population peak, with 3 species showing a pattern of major and secondary peaks. *Microhyla heymonsi* has a pattern most closely approaching a steady state biomass condition, but the fit is not good.

During the peak month, April, there was an average of 4.33×10^{-5} cm³ of tadpole in each cm³ of water. Extrapolated to the entire pond, there was an average standing crop of

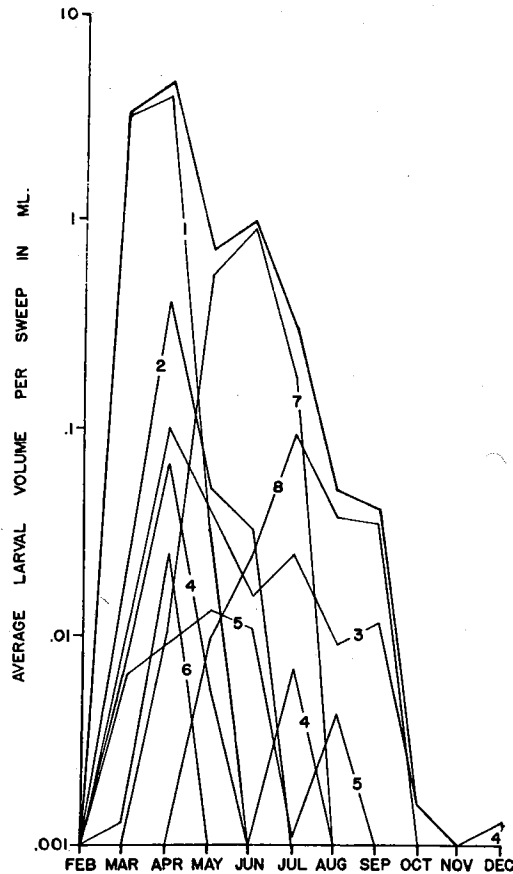


FIGURE 5. Estimation of larval biomass for the Dam Stream Pond. Outer envelope represents sum of individual species. 1=*Glyphoglossus molossus*, 2=*Bufo melanostictus*, 3=*Microhyla heymonsi*, 4=*Rana nigrovittata*, 5=*Ooeidozyga laevis*, 6=*Microhyla ornata*, 7=*Polypedates leucomystax*, 8=*Microhyla butleri*.

ing 33 days after the first rains. The estimate for *R. nigrovittata* is further suspect because the species appears to be a dry season breeder.

Indications of minimum length of larval life can be projected from the collections taken at Station 78. Because the estimates are based on collections at post-hatching and pre-metamorphic stages, and because of the irregularity of sampling, the estimates have an error of \pm one week: *Calluella guttulata*—50 days, *Microhyla butleri*—26 days, *M. heymonsi*—25 days, *M. ornata*—28 days, *Polypedates leucomystax*—33 days. A questionable estimate of 45 days for *Rhacophorus bimaculatus* is based on a stage 42 larva collected on 10 October; as no post-hatching larvae were collected, the date of 24 August was used as the earliest time possible. *Rhacophorus* is of interest because it is the largest larval species collected at Sakaerat and would be expected to have the longest larval life. Data are not adequate to estimate larval life length for either species of *Chirixalus*.

Data are available to estimate minimum larval life for two species from the Laterite Pit Ponds. Estimates are based on the date the pond filled and stage 41-43 larvae. Station 165+75, *Microhyla pulchra* 23 days; Station 167, *Microhyla pulchra*, 23 days; *Rana limnocharis* 23 days.

537.11 cm³ of larvae during April. Intuitively, these numbers appear low and may indicate that the sweeping method under-estimates larval populations.

The same pattern of greatest larval density early in the pond cycle was observed qualitatively during the final cycles at the Station 78 and Highway ponds. No quantitative sweeps were taken to substantiate these observations, but during the last 2-3 months of observation, even though the ponds contained a considerable volume of water, there were noticeably fewer larvae in the water.

LENGTH OF LARVAL LIFE

Reliable data on minimum lengths of larval life from the Dam Stream Pond are available for *Bufo melanostictus*, 27 days; *Glyphoglossus molossus*, 27 days; *Microhyla heymonsi*, 22 days; *Microhyla ornata*, 29 days. For these species, egg masses were identified when laid and the dates of earliest emergence were noted. For *Microhyla butleri*, the estimated larval period was determined by the first collection of stage 25 larvae and the date of emergence, 28 days. In the case of *Polypedates leucomystax*, larval life was estimated by captures of stage 25 and 43 larvae; 28 days. The lengths of larval life for both *M. butleri* and *P. leucomystax* are probably accurate within a day or two of the actual values. Estimates for *Ooeidozyga laevis* and *Rana nigrovittata* are less precise. Both initial dates are based on the first rains of the season as the earliest date for egg deposition. *Ooeidozyga laevis* were seen emerging 27 days after the first major thunder-shower, *Rana nigrovittata* were observed emerg-

Data on variance of time to metamorphosis are available for only two species, *Glyphoglossus molossus* and *Bufo melanostictus*. Eggs of *Glyphoglossus molossus* were deposited on two nights, 14 and 19 March, only at the Dam Stream. Newly metamorphosed froglets were observed to emerge from the pond over a span of 33 days, 9 April to 11 May. The first population of *Bufo melanostictus* in the Dam Stream Pond resulted from a single laying or at the most a series of layings separated by no more than two consecutive nights. The strings of eggs were observed on 15 March. All had hatched by 17 March. On 8 April, no *Bufo* were seen emerging. On 9 April, many *Bufo* were emerging, both day and night. On 10 April, *Bufo* were still emerging, but the majority had already left the pond. On 11 April, virtually all of the *Bufo* had emerged, and by 12 April, there were no *Bufo* in the pond. The vast majority of *Bufo* transformed in 2 days; all had emerged within a 4 day period.

LARVAL FOOD

In order to determine whether different size classes and/or different species feed selectively on different food items, one should examine specimens collected in the same sweep from a pond with a homogeneous supply of known food. No samples of pond water from the different microhabitats where the larvae were occurring were taken. Thus a detailed statistical comparison of different food items recorded from preserved larval guts in this study would be meaningless.

As far as I know, no rates of passage of items through the digestive tract have been performed on any of the species in this study. It seems reasonable that the time is comparable to that found in other studies. Savage (1961) found food passed through the gut of *Rana temporaria* on an average of 6.25 hours, with one time of 4.75, and a tadpole of *Bufo bufo* passed food through the gut in 3.75 hours, remarkably fast rates.

The items recorded in the gut also include parasites and non-food material. The purpose of this portion of the study was to determine whether any noticeable differences occur among the larvae with respect to their feeding habits and items ingested. Thus it is not critical that only food items as such be analyzed from the gut.

The larvae of this study have 3 distinct mouthpart morphologies apparently correlating with distinct feeding methods. All of the microhylids (*Calluella*, *Glyphoglossus*, *Kaloula*, *Microhyla*) are beakless. The mouth parts are not modified in any way for manipulation of food. A strong buccal pump brings large volumes of water through the buccal cavity; food items are separated out and passed to the gut. The second morphological type has a series of keratinized denticles surrounding a horny beak. This feeding apparatus is used to scrape, chew or cut food items off of a substrate. All members of the following genera have this type of feeding apparatus: *Bufo*, *Chirixalus*, *Polypedates*, *Rana* and *Rhacophorus*. Larvae of the genus *Ooeidozyga* have a terminal mouth, ending in a tube like affair with horny lips and constitute a third type; the mode of feeding is not clearly understood.

Comparison of Gut Lengths

Two types of variation in gut length are expected for larval anurans. In the species which rely on yolk stores for most of their nourishment, such as members of the microhylid genus *Kalophrynus* (Inger, 1966: 135), the gut is quite short. In aquatic frog larvae that depend on capturing food for growth, variation in gut length might be expected to correlate with diet. Shorter guts would indicate primarily carnivorous diets (including soft-bodied protozoans); longer guts would indicate primarily herbivorous diets.

Guts of the preserved larvae proved very difficult to measure accurately. The gut walls were fragile and ruptured as they were straightened out for measurement. In retrospect, gut lengths may be measured more exactly on freshly sacrificed specimens which have not been preserved. The results, although crude and not worthy of detailed analysis for species differences, are at least an approximation and show two trends (Fig. 6). Larval *Ooeidozyga* seem to have the shortest mean gut lengths, although individuals of other species apparently have gut lengths as short as *Ooeidozyga*. The longest gut was recorded from *Rhacophorus*

bimaculatus. This species has the largest and bulkiest larvae of those comprising this study. The remaining data do not indicate other obvious patterns of gut length. Taking additional measurements on more preserved individuals would not drastically alter the pattern as shown on the figure (Fig. 6) and might seemingly add more reliability to finer comparisons than I feel could be justified because of the imprecision of measurement.

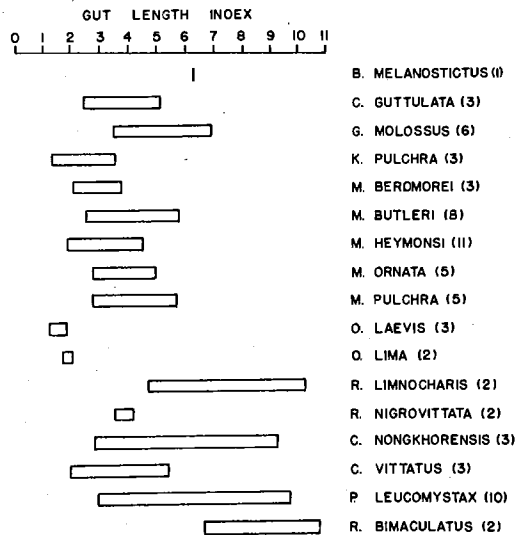


FIGURE 6. Comparative larval gut lengths. The gut length index is the length of the gut divided by the head-body length. Numbers in parentheses indicate number of individuals measured.

Gut Contents

Qualitative analysis.—As stated in the methods, discrete items were placed in one of 6 broad categories. Because the food availability is not known, detailed analysis comparing per cent of food items within and among species is pointless. Previous studies do give an indication of general tadpole feeding ability, however. Farlowe (1928) and Jenssen (1967) found the larvae of *Rana clamitans* to be very general algal consumers. In fact, Farlowe (1928) found that examining the algal contents in tadpole guts was a superior method of determining the species composition of pond algae than were her collecting methods. Dickman (1968) found that larvae of *Rana aurora* strongly reduced the standing crop of lake algae; the dominant filamentous green algae were the most reduced.

Because of the methods used to gather the data, two types of possible food categories were overlooked: bacteria and dissolved organic nutrients. The data are thus biased towards the larger food categories. The interpretations of the results are limited by the degree that bacteria and dissolved inorganic nutrients are important food items for the organisms under study. As far as I know, the importance of these small items as a food source for tadpoles in nature is not known.

Nematodes were recorded for all but 4 species. No attempt was made to identify the nematodes to determine whether they were free living and hence ingested or parasitic in the gut. In at least one species, *Glyphoglossus molossus*, there was an orderly increase of size and complexity of internal organization of the numerous nematodes from the front to the rear of the gut, indicating a parasitic relationship. In some individuals of *Ooeidozyga lima*, *Microhyla butleri*, *M. heymonsi*, and *Chirixalus nongkhorensis*, nematodes were abundant, suggesting the possibility of parasitism. In some individuals of *Bufo melanostictus*, *Rana limnocharis*, *Rana nigrovittata*, *Rhacophorus bimaculatus*, *Chirixalus vittatus*, *Microhyla ornata*, and *Kaloula pulchra*, from 1 to 4 individual nematodes were recorded per gut, suggesting ingestion. Only two species had any arthropod material in the guts: *Kaloula pulchra* and *Microhyla heymonsi*. In two of the 3 guts of *Kaloula pulchra* examined, exoskeletons of larval mosquitoes were identified. In 8 of 14 guts examined of *Microhyla heymonsi*, remains of what appeared to be small mites were recorded. Filter-feeding apparently allows a broader food spectrum than scraping and chewing. Aside from the variations noted above, all the other guts examined had diatoms (except *K. pulchra*), filamentous algae, and protozoans represented in large numbers. Because the food items were not identified to species, there is the possibility that the larvae could be feeding on entirely different species within broad categories. The evidence gathered on scraping and chewing larvae that are indiscriminate feeders (Dickman, 1968 and Farlowe, 1928), suggests that the larval species in this study are basically ingesting the same foods. Intuitively, it would seem that beakless larvae, by the nature of their feeding mechanism could discriminate

particle size, but not composition. With the exceptions of *Kaloula pulchra* and *Microhyla heymonsi*, the species appear to be in potential competition for food when food type alone is considered. The most surprising gut contents were those of *Ooeidozyga* because the contents were the same as those of every other species save *Kaloula pulchra* and *Microhyla heymonsi*. Smith (1916) states that both larval *O. laevis* and *O. lima* are carnivorous, feeding on such items as mosquito larvae and other small tadpoles. The shortness of the gut (Fig. 6) would seem to confirm this statement. The species must be facultative carnivores, however, and be able to operate as omnivores.

Particle size.—Little is known concerning digestive processes in tadpoles. Savage (1961) stated that tadpoles are not capable of digesting cellulose and that much of the contents found in the tract are being passed through undigested. He found that larval *Rana temporaria* could survive on a diet of algae and suggested that the thin walled algae were eaten, the walls having been ruptured by peristaltic action of the gut. Li and Lin (1935) noticed some digestion of euglenoids but not of heavy walled organisms in the hind gut of *Kaloula borealis*. They suggested that *K. borealis* feeds only upon thin walled protozoans and receives no food value from the bulk of the gut contents. Indirect evidence from this study supports the hypothesis that most items passing through the gut are not used for food. An average of each particle was calculated from the maximum and minimum dimensions. The mean particle sizes were determined for the foregut and hindgut samples and compared. If digestion was occurring, the particle sizes in the hind gut should be consistently smaller than in the foregut, assuming the outer cell walls must be broken down in order to digest the cell contents. In comparing all specimens of all species, the average particle size in the hind gut was smaller than in the foregut in 45 (54 per cent) individuals and greater in 38 (46 per cent) individuals. The differences between the two samples are not statistically significant ($\chi^2 = .590$, $P > .05$). Most of the gut contents are being passed through the gut with the cell walls remaining intact.

For the intraspecific and interspecific analyses that follow, only one measurement of particle size is utilized. Three sizes were determined for each particle—the minimum diameter, the maximum, and the average of these two values. In looking over the raw data summaries, each measure demonstrates the same trend. For purposes of detailed analysis, the minimum diameter of the particle as it lies on the microscope slide is the most meaningful measure, since this should be the limiting dimension as the particle passes through the mouth and esophagus into the gut. Particles were often very long in the case of filamentous algae, but the narrow algal width allowed passage through the anterior openings and chambers of the gut. The statistic used for analysis is the average minimum diameter determined for each gut sample.

The minimum dimension of ingested item was related to larval size within species for *Glyphoglossus molossus*, *Microhyla heymonsi*, and *Polypedates leucomystax*. These are the most common larvae in the collection and represent different behavioral or morphological types. Both *Glyphoglossus* and *M. heymonsi* are beakless, but *Glyphoglossus* is a mid-water feeder while *M. heymonsi* feeds upon the surface film. *Polypedates* has the keratinized denticles and horny beak typical of the scraping feeders. The product moment correlation coefficient (Sokal and Rohlf, 1969:499) of head-body length and ingested item was calculated.

For six samples of *Glyphoglossus molossus*, ranging in head-body length from 7.0–10.5 mm, $r = .516$; which is not significant ($t = 1.205$, $P > .05$). For 14 samples of *Microhyla heymonsi*, ranging in size from 4.5 to 8.0 mm head-body length, $r = .273$; which is not significant ($t = .982$, $P > .05$). For 11 samples of *Polypedates leucomystax*, ranging in head-body length from 5.6–14.5 mm, $r = .128$; which is not significant ($t = .388$, $P > .05$).

The particle sizes were compared to determine whether there were any species differences in size of particle ingested. The Student-Newman-Keuls procedure was used to find the significant differences among means (Sokal and Rohlf, 1969: 239-246). Least significant ranges were calculated for a particular level of significance and compared with mean differences among ranks.

There are no significant differences among the first 13 ranks (Fig. 7), which include all scraping larvae, both *Ooeidozyga*, and one half of the beakless microhylids. *Microhyla heymonsi*

		C. vittatus	B. melanostictus	R. limnocharis	R. bimaculatus	O. laevis	P. leucomystax	R. nigrovittata	C. nongkhorensis	M. pulchra	M. berdmorei	O. lima	G. molossus	C. guttulata	M. ornata	M. butleri	M. heymonsi	K. pulchra
n _i	RANK	1	2	3	4	5	6	7	8	9	10	11	12	13	14	15	16	17
12	1	o																
3	2	-	o															
8	3	-	-	o														
6	4	-	-	-	o													
8	5	-	-	-	-	o												
24	6	-	-	-	-	-	o											
7	7	-	-	-	-	-	-	o										
6	8	-	-	-	-	-	-	-	o									
12	9	-	-	-	-	-	-	-	-	o								
6	10	-	-	-	-	-	-	-	-	-	o							
4	11	-	-	-	-	-	-	-	-	-	-	o						
15	12	-	-	-	-	-	-	-	-	-	-	-	o					
6	13	-	-	-	-	-	-	-	-	-	-	-	-	o				
12	14	*	-	-	-	-	-	-	-	-	-	-	-	-	o			
16	15	*	-	*	-	-	*	-	-	-	-	-	-	-	-	o		
28	16	-	-	*	*	*	*	*	*	*	*	*	*	-	-	-	o	
6	17	*	*	*	*	*	*	*	*	*	*	-	*	-	-	-	-	o

FIGURE 7. Statistical analysis of particle size among species. Values found significant at the $P=0.05$ level are indicated by an asterisk, values found not significant at the $P=0.05$ level are indicated by a dash. The order of ranking is by order of magnitude of the means of the statistics by species, 1 being the smallest. Because different sample sizes are involved, significant rank comparisons need not be adjacent in the matrix. Fore and hind gut mean minimum particle sizes were used as independent statistics.

and *Kaloula pulchra* ingest significantly different sized particles than many of the other species. Most of the species that *M. heymonsi* and *K. pulchra* differ from are scraping and chewing feeders. In addition, *M. heymonsi* is significantly different from *M. pulchra* and *G. molossus* with respect to particle size; *K. pulchra* is significantly different from *M. pulchra*, *M. berdmorei*, and *G. molossus*. As the largest particles were arthropods, the shift in diet accounts for the significant differences in particle size ingestion. *Microhyla ornata* and *M. butleri* are also significantly different with respect to particle size ingestion from a few other species, none of them with similar feeding types, however. To put the data into perspective, *Kaloula pulchra* larvae were collected in numbers only from small rock pools in the bed of an intermittent stream. They were the only species present in the pools, thus the significance of the differences noted is not as important ecologically as in the other species with significant differences. *Microhyla heymonsi* was collected with *Rana limnocharis*, *Rhacophorus bimaculatus*, *Ooeidozyga laevis*, *Polypedates leucomystax*, *Rana nigrovittata*, *Chirixalus nongkhorensis*, *Microhyla pulchra* and *Glyphoglossus molossus*; *Microhyla butleri* was collected with *Chirixalus vittatus* and *Polypedates leucomystax*; *Microhyla ornata* was collected with *Chirixalus vittatus*. In these associations, differences of particle size ingestion may be an important component in niche differentiation. The overall significance of the matrix, however, is that most of the species are ingesting the same size particles. Only the two species that utilize a different food category (arthropods) differ significantly from many of the other species.

One relationship noticeable in the matrix (Fig. 7) is that the scraping feeders have smaller mean particles in the gut than the beakless feeders. This relationship is more evident when

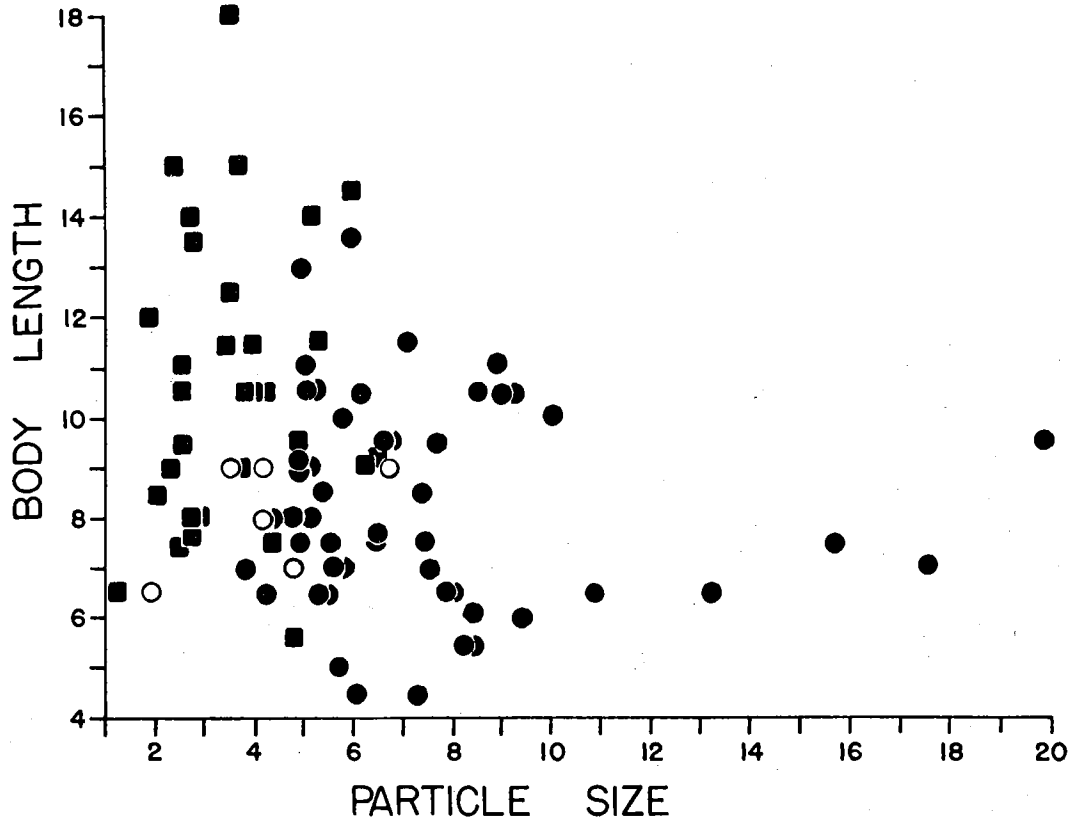


FIGURE 8. Particle size differences among larval feeding types. Squares are scraping and chewing feeders, solid circles are beakless larvae, open circles are *Oooidozyga*.

mean minimum particle size is plotted against head-body length (Fig. 8). In this figure, each point is the mean minimum particle size per individual (fore and hindgut samples combined). The symbols represent feeding mechanisms. The scrapers are evidently breaking down particles with their denticles and beaks prior to ingesting them. This must allow a greater efficiency in feeding, as the larvae can digest the cell contents of the heavy walled particles that are broken down by the mouthparts. Seemingly, scraping feeders would need to process much less food because they would have a much higher efficiency than beakless feeders. If so, the beakless feeders must have some compensatory mechanism. Apparently the mechanism does not involve longer gut lengths. Even though the data are crude, comparative gut lengths demonstrate that if anything, the scraping feeders have longer guts than beakless feeders (Fig. 6). Compensatory mechanisms could involve 1) much faster passage of ingested particles through the gut with digestion of only the soft bodied forms for the beakless feeders, or 2) different amounts of feeding time required. Observations on the scrapers are much more difficult as the mouthparts are not directly observable, but my impression was that the scrapers did not appear to be feeding all the time. Jenssen (1967), among others, indicates that tadpoles with scraping and chewing mouthparts, such as *Rana clamitans*, feed continuously, because every gut examined is full and the respiratory and food gathering systems are combined. No one has examined whether or not feeding rates may be variable, however. The buccal pump of tadpoles may only need to operate at a low rate for respiratory purposes. As food items are brought in during respiration, they are processed, but the passage through the gut may be very slow. However, when the tadpole is actively feeding, the buccal pump might operate much faster, processing

food items through the gut at a faster rate. Studies on *Xenopus* suggest that buccal pump rates are related with food availability (Wassersug, pers. comm.).

LARVAL MICROHABITATS AND BEHAVIOR

Bufo melanostictus were most often observed in large groupings, in contact with the substrate, either on large rocks or on the dirt bottom (Fig. 9, positions 5, 6). Most of the time

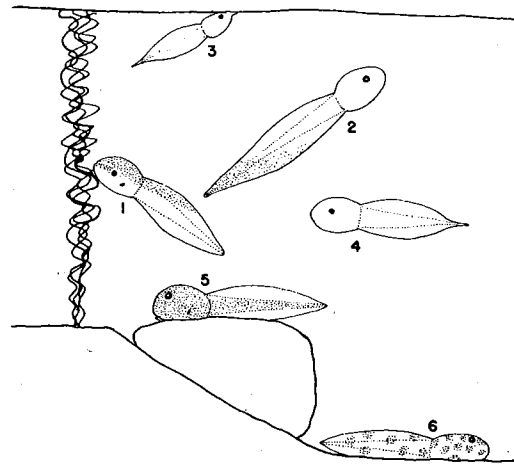


FIGURE 9. Characteristic tadpole positions in a pond.

the individuals were not actively moving about, although swimming individuals were also observed. *Calluella guttulata* larvae were suspended in the water column at an angle (Fig. 9, position 2). The head and body were transparent in the water, the black tails obvious. The larvae seemed to occur in loose aggregations and were most often seen in fairly open water. On 17-19 March, the larvae of *Glyphoglossus molossus* were making vertical migrations in the water. The water was turbid; it was not possible to see whether the larvae went completely to the bottom or not. The hatchlings of 17 and 18 March did not appear to be aggregated. On 19 March, part of the population appeared to be randomly distributed, but the larvae in the shallowest portion of the Dam Stream Pond seemed to form an aggregate. After this time, schools of *Glyphoglossus* were a common sight. On 24 March, the larvae were segregated into different sizes. The size differences between the larvae from the two egg masses laid 5 nights apart were still noticeable at this time. Whether the larvae were single or in groups, they moved around slowly in the open water most of the time. The larvae characteristically maintained an angle in the water column (Fig. 9, position 2).

Almost all the *Kaloula pulchra* larvae were collected from very small rock pools in the bed of the intermittent Huai Pae previous to any flood water in the bed. The larvae were collected at night and appeared active. They were distributed throughout the water column of the aquarium-sized ponds.

Larval *Microhyla berdmorei* were collected from a small (diameter approximately 80 cm) rock pool adjacent to the flowing stream at Khao Yai at night. The larvae were extremely numerous in the pool and appeared distributed throughout the water.

Pope (1931) indicated that larval *Microhyla butleri* in southern China inhabited more permanent pools than either *M. pulchra* or *M. ornata* and that they moved about in schools. At Sakaerat, the larvae were collected only from more permanent ponds. The species was never abundant in the Dam Stream Pond, and the tadpoles did not appear to aggregate there. On 6 June, from 1:00-1:30 pm, 6 larvae were positioned just under the surface vegetation, but they were processing the water and not feeding on the plants. All larvae observed in the Dam Stream Pond were among the aquatic plants in water greater than 20 cm deep. The larvae characteristically were oriented horizontally (Fig. 9, position 4).

More observations were made of *Microhyla heymonsi* larvae than of any other species. The species is beakless with enlarged funnel-lips specialized for surface film feeding (Fig. 9, position 3). The bodies are nearly transparent in the water. The most conspicuous structures are the widely separated eyes which are iridescent bronze in life and a light tail spot, but it is much less noticeable than the eyes. To maintain position, the tip of the tail is moved inconspicuously.

Even when wind was moving the surface water, the larvae maintained a constant position for most of the time. When disturbed by moving objects such as myself, the larvae immediately dropped 2-4 cm under the surface of the water, almost parallel to the surface, and would then very slowly rise to the surface. Other than the sudden drop, there was no obvious movement. Larvae apparently feed continuously on the surface film unless disturbed. One individual fed continuously during a 25 minute observation period until I got tired and left. On another occasion, a larva fed for 3, 1, and 2 minutes continuously. The reason for the interruptions was large particles, approximately 1-2 mm, which were brought in by the feeding currents. When these larger particles touched the funnel, the larva submerged, but just under the surface—not to the depths as when I disturbed them. The feeding currents broke the surface film and smaller particles entered the funnel. Larger particles were spit out for a distance of 1-2 cm from the funnel. The larvae never appeared gregarious. Sometimes the larvae were seen scattered over the entire water surface.

Few collections of *Microhyla inornata* larvae were made. The species bred in large ponds in the dry evergreen forest, but they also apparently take advantage of small bodies of water. Karl Frogner collected larvae from a water-filled cavity of a fallen tree in the dry evergreen forest in 1968.

Larval *Ooeidozyga laevis* are bottom forms (Fig. 9, positions 5, 6). They were never abundant and usually frequented the bottom of deeper waters during the day and moved into shallow water bottoms at night. Only two observations were recorded. On 8 April 1969 between 9:00-9:30 pm one tadpole was observed on the bottom next to shore in 5 cm of water at the Dam Stream Pond. It remained in one place, but its mouthparts were constantly moving during the observation period. On 21 April 1969 an individual was sighted between 1:30-2:00 pm. When it moved it inched along the bottom in a very methodical fashion. The movement contrasted sharply with the swift darting of *Bufo melanostictus* larvae.

Pope (1931: 483) observed larval *Ooeidozyga lima* in southern China and confirmed Smith's observations (1916) of the species in Thailand. The larvae are sluggish, frequent the bottoms, and make early use of the larval legs. Pope said that the species looks and behaves like a piece of bottom debris, such as a dead leaf. The few specimens collected at Sakaerat were taken from the turbid waters of the Highway Ponds where no larvae could be seen.

Rana limnocharis larvae are bottom dwellers (Fig. 9, positions 5, 6). The larvae were abundant in one of the laterite pits.

Rana nigrovittata larvae also were found on the pond bottoms (Fig. 9, positions 5, 6). They never appeared abundant in the Dam Stream Pond. Larvae were not seen in shallow water in the daytime, but were frequently encountered at night in shore where the water was 5-10 cm deep. The larvae were not active.

Larvae of both *Chirixalus nongkhorensis* and *C. vittatus* were only seen in the net after sweeping the water. They are probably both bottom forms.

Larval *Polypedates leucomystax* were found in a variety of positions and microhabitats (Fig. 9, positions 1, 2, 5, 6). The tadpoles were never observed in aggregations. On 2 May 1969, post-hatching larvae were observed swimming up and down in the water column. The larvae broke the water surface on the ascent. Not all larvae were participating in the vertical migrations, some were swimming horizontally. Larvae were observed to be hanging in the water, apparently filter feeding, scraping aquatic vegetation, and scraping bottom rock surfaces.

Larval *Rhacophorus bimaculatus* were never observed in the ponds where they were netted. The large larvae were not abundant in the samples. They are assumed to be bottom dwellers.

The mid-water and surface forms have laterally directed eyes, the bottom dwellers have dorsally directed eyes. The bottom dwelling *Bufo*, *Chirixalus*, *Ooeidozyga*, *Rana* and *Rhacophorus* all have dorsally directed eyes. All microhylids have laterally directed eyes. Larval *Polypedates leucomystax* have laterally directed eyes which correlates with observations that the individuals spend most of the time in the water column, rather than lying on the bottom.

OBSERVED CAUSES OF EMBRYONIC AND LARVAL DEATH

Whenever convenient, egg masses were counted and scored in the field for dead embryos. The following are percentages of dead individuals per mass. Because microhylids lay floating egg masses one egg thick, the estimates are reasonably accurate. *Glyphoglossus molossus*, 5 per cent, 6 per cent; *Microhyla heymonsi*, 4 per cent, 8 per cent; *M. ornata*, 50 per cent; unidentified microhylids, 2 per cent, 25 per cent, > 50 per cent, < 1 per cent, 2 per cent.

On 24 March, 2 floating egg masses were observed at Station 167 at 11:00 am. During the early afternoon, a thundershower hit the region. When Station 167 was revisited at 4:00 pm of the same day, no eggs were floating. It appeared as though the eggs had been destroyed by the rains.

Many times when the Laterite Pit ponds were just about dried up, the remaining puddle of water would be thick with larvae. On 23 October only two rather late-stage *M. pulchra* larvae were collected from a small body of water at Station 165+75. On 27 October, there was just enough water to sample. The net was full of dragonfly larvae; no *M. pulchra* were present. The data, while far from being conclusive, do suggest that predator populations may build up to the point where they limit the tadpole populations.

The following instances of predation were observed: 1) Members of the fish genus *Monopterus* feeding on microhylid tadpoles. One such fish collected had two microhylid larvae in the gut, 2) A large bellostomatid hemipteran sucking the body juices from a larval *Microhyla butleri*, 3) An adult *Ooeidozyga laevis* feeding on a newly metamorphosed *Glyphoglossus molossus*.

THE ADAPTIVE STRATEGY

The total environment is divided spatially and temporally among the frogs at several levels. The most distinctive partitioning of the habitat occurs between the wet and dry season breeders. Only 3 Sakaerat species breed in the dry season; of these, the most notable are the species which are stream breeders. *Microhyla berdmorei* and *Rana nigrovittata* from Sakaerat and *Rana livida* at Khao Yai breed during the initial part of the dry season when no more floods occur, but while water is still abundant in the streams. The majority of the Sakaerat species (14) breed at the initiation of the rainy season. The first heavy rains appear to initiate reproductive activity in these species, either in triggering mating in adults that are reproductively ready or in stimulating the gonads to begin gamete formation. The rainy season breeders subdivide the available environment by: 1) utilizing different ponds within the total environment, 2) occupying a single pond at different times, and 3) dividing up the living space within a given pond spatially, rather than by selecting different food categories (Heyer, in press).

The frogs appear to share two major adaptations to the environment at Sakaerat. First, all of the species for which data were gathered have remarkably short larval life periods. The average larval life length based on all available data from Sakaerat is 29.4 days. This is a much shorter time than found in frogs of either moist temperate regions (e.g. 4-5 months for *Rana temporaria* in England, Savage, 1961; 3-4 months for *Rana arvalis* in Russia, Shchupak, 1970;) or pond or stream larvae of tropical wet regions (e.g. 39 days for *Bufo biporcatus* in Sarawak, Inger, 1966). The selection for reduction of time of larval life correlates with the uncertain aquatic habitat due to sporadic rainfall. The number of frogs that have the genetic capability to metamorphose after only a 3-4 week larval period is small and may account for the predominance of microhylids of the frog fauna at Sakaerat. As a group, they seem to have shorter larval periods than most other pond frogs. Second, all of the ponds went through a larval bloom. Two causes for this phenomenon could be involved, and the data are not adequate to sort out which may be the more important; A) By having a period of larval activity at the beginning of the wet season, newly metamorphosed frogs are assured of a favorable

period of growth before having to survive the devastating dry season. Larger frogs would certainly have an advantage over smaller frogs in surviving the dry season, and/or B) The larval bloom may occur at the beginning of the pond cycle to avoid heavy predation. The larvae are present in large numbers at a time when predator populations, particularly aquatic insects, are still at an early stage of growth.

In attempting to discern which environmental factor is the most critical to the success of the frogs at Sakaerat, one would have to say the physical factor of rainfall distribution has had the most pronounced effect on the adaptive ecology of the frog fauna at Sakaerat.

Comparison with Other Studies

Few studies on tadpole population dynamics have been reported; of these, none has set out to answer the same questions that this study has attempted to answer. Most other studies have been concerned with anuran reproductive cycles as they relate to calling, mating, and egg deposition. Certain portions of those studies are comparable with parts of the present study. Because of the rarity of these comparative studies, it is worthwhile to consider the most relevant ones individually.

Goh (1962) recorded the overall reproductive cycles of six common frog species at Singapore over a two-year period. Singapore is a wetter environment than Sakaerat and the drier months of Singapore are not as catastrophic to the frog fauna with respect to breeding opportunities as at Sakaerat. Goh based tadpole presence during the months of the year on observation, not collections, so quantitative comparisons are not possible. She demonstrated that each of the species studied was capable of reproduction throughout the year as adults. Her data on tadpole occurrences over the year strongly suggest that there was a seasonal partitioning of the ponds among the species as larvae. Each of the 6 species she studied in detail occurred at Sakaerat. Any differences of reproductive pattern would further attest to the broad niches of the species involved: *Bufo melanostictus*, *Kaloula pulchra*, *Microhyla butleri*, *M. heymsi*, *Rana limnocharis*, and *Polypedates leucomystax*. Goh's study did not concern itself with determining the environmental controls on the reproductive patterns.

Two studies were reported from similar tropical environments in Mexico and Africa. Dixon and Heyer (1968) examined anuran succession in a temporary pond in Colima, Mexico. The environment was characterized by a pronounced dry season. The study was made when the pond filled for the first time at the initiation of the rainy season and was terminated as the pond was in the process of drying. There appeared to be a larval bloom which followed formation of the pond, but a temporal partitioning of the pond among the larvae was also evident. Inger (1968) studied the reproductive patterns of frogs at the Parc National de la Garamba during the end of the dry season and the beginning of the wet season. The environment was characterized by a pronounced dry season. The beginning of the rainy season was marked by sporadic thunderstorms with intermittent drying up of the ponds causing massive larval mortality. A big breeding frenzy accompanied the first heavy rains. As far as the events were recorded at Colima and the Parc National de la Garamba, they exactly parallel the situation at Sakaerat.

Blair (1961) studied the calling and spawning patterns of 7 species of frogs that utilized a single pond which was permanent most years in Texas. The temperate environment was characterized by a pronounced dry season, with sporadic thundershowers being the only source of rainfall. Blair did not collect the larvae quantitatively, but observed a larval bloom in the spring. The breeding patterns were accounted for by a combination of rainfall and temperature interactions. These two parameters apparently controlled the reproductive patterns which included a temporal partitioning of the pond.

Savage (1961) has undertaken the most definite study on the causative external factors on spawn date for *Rana temporaria* in the British Isles. He demonstrated that the triggering climatic factors included a number of interrelated components: altitude, rainfall and temperature in the three month period preceding and including spawn deposition, amount of bright

sunshine, latitude, and longitude. These factors were not interrelated in a simple fashion, but each was important by itself against certain environmental backgrounds. An exhaustive study of many possible climatic factors contributing to spawn dates was not made for Sakaerat because data must be accumulated for many years to make this type of analysis. However, all available evidence points to the overriding effect of rainfall distribution controlling spawn dates at Sakaerat.

The results of this study appear to be valid for other tropical areas characterized by a pronounced dry season as evidenced by similar frog reproductive patterns in similar environments in Southeast Asia, Central America, and Africa. The single physical factor of rainfall distribution regulates the reproductive patterns. In extratropical regions, physical factors are also the most important environmental factors regulating reproductive patterns. Thus in Texas, rainfall and temperature together regulate the reproductive patterns, while in the more extreme climate of England, rainfall, temperature, amount of bright sunshine, and altitude control the reproductive cycles at a given longitude and latitude.

No data are yet available on the role of external factors in regulating reproductive cycles for the most complex frog communities, those of the wet tropical forests.

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