

Studies in Larval Amphibian
Habitat Partitioning

W. RONALD HEYER

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ABSTRACT

Heyer, W. Ronald. Studies in Larval Amphibian Habitat Partitioning. *Smithsonian Contributions to Zoology*, number 242, 27 pages, 3 figures, 14 tables, 1976.—Habitat partitioning by larval amphibians was studied in two environments. A two-year study was undertaken at the Chesapeake Bay Center for Environmental Studies and a comparative dry and wet season study was completed at Barro Colorado Island, Panama.

At the Chesapeake site, partial year to year differences in temporal larval habitat partitioning combined with different year to year population sizes indicate: (1) different habitat utilization from one year to the next by the larvae, and (2) different biological interactions involving predator-prey and species associations from year to year.

The stream bed pond habitat on Barro Colorado Island is effectively partitioned by the tadpole community on the basis of space and time. Predation is an organizing factor in the composition of the tadpole community, interspecific competition apparently is not.

This study concludes that competition among tadpoles does not normally occur in nature. Bursts of primary productivity provide superabundant food resources. The habitat partitioning found in tadpole communities reflects the temporal and microhabitat differences associated with the evolutionary life history of each of the species occurring in any pond. Tadpole communities are additive collections of different species, not integrated, interactive superorganizations.

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Introduction

The single goal of this study was to learn more about how habitats are partitioned by larval amphibians. Data were gathered from two very different sites, a temperate pond and a series of tropical stream ponds.

The study of habitat partitioning by larval amphibians has been previously neglected. There are fewer than a half dozen descriptive studies and only 4 quantitative studies (cited in Heyer, 1973). The temperate pond (present study) was followed for two years to study year to year variability in habitat partitioning. The tropical stream ponds, located on Barro Colorado Island, were sampled once during the dry season and once during the wet season to determine the effects of seasonality on habitat partitioning by stream pool larval amphibians.

The studies at the two sites are described separately because the methods and analyses of data are different. Patterns of habitat partitioning evidenced at the sites are then compared. Any patterns of habitat partitioning common to these two environmental extremes should be common to larval amphibia in other environments.

It is necessary to define larval amphibian habitat partitioning as used in this study. The habitat consists of one or more ponds found at a specific site.

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The habitat contains the resources utilized by different species of larval amphibians; different larval species utilize the habitat resources in different ways. The patterns of habitat usage produced by different larval species are manifested as a partitioning of the habitat resources. Larvae may partition the habitat in terms of space, time, or food (among the more obvious categories). Examples of partitioning include: (1) where the habitat consists of a series of ponds at a single site, larvae of a particular species may occur in only a few of the available ponds; (2) within a pond, larvae of a single species may be found only in certain microhabitats or they may utilize only certain kinds of food; (3) two species may use the same pond at different times as larvae. The studies reported herein reveal both space and time habitat partitioning by larval amphibians.

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Chesapeake Bay Area

METHODS AND MATERIALS.—Larval samples were taken once a week from 9 March to 29 June 1974 and from 22 March to 28 June 1975. A sample for 15 June 1974 was not obtained due to illness. An additional sample of 26 July 1975 was taken to determine whether any drastic changes occurred after June, the arbitrarily determined end of the sampling period. In both years, sampling preceded the onset of tadpole occurrence. Samples were taken from a large, shallow pond surrounded by hardwood forest at the Smithsonian's Chesapeake Bay Center for Environmental Studies near Annapolis, Maryland. The common trees in the forest are beeches, hickories, oaks, and tulip trees. Three microhabitats were sampled by dipnet each sampling period. The dipnet had a triangular opening. For the surface samples, the base of the triangle was placed just under the surface of the water. The surface film and about the top 5 cm of water were swept at the grassy edge of the pond where the water was about 30–40 cm deep. The net skimmed the top of the grass. The midwater sample was taken farther from the shore, in about 60–70 cm water, in grassy and open water areas. The net opening was completely immersed, then the net was propelled through the water. Open water areas were emphasized in the midwater sample. The bottom sample was taken in the same general area as the midwater samples, but the grassier areas were emphasized. For the bottom sample, the net was bumped along the bottom. The linear distances sampled for the sweep types were variable, but comparable. Generally, at least a 25 m linear sweep was made for each sample. If the net had an abundance of tadpoles, no further sampling was done in that microhabitat. If few or

no tadpoles were collected, additional sweeps were made. The same microhabitats were sampled each week in the same way both years. The surface, midwater, and bottom sweeps sampled three more or less discrete areas of the pond. The results were of course only a reflection of the dynamics of the populations of the entire pond.

The tadpoles of each sweep type were formalin preserved in separate containers. In the laboratory the samples were sorted and identified to species level. Salamanders were measured by vernier calipers, snout-vent and total lengths measured to the nearest 0.5 mm. Tadpoles were staged (Gosner, 1960). For very large samples (unless all were hatchlings), 50 individuals were staged and the total sweep sample for that species was extrapolated from the staged subset. The 1974 sample is represented by 1182 individuals, the 1975 sample by 2755 individuals. All specimens (total study) are in the collections of the Division of Reptiles and Amphibians, National Museum of Natural History.

TEMPORAL SUCCESSION.—1974 *Pattern:* *Ambystoma maculatum* egg masses were first seen on 16 March, but may have been present (and overlooked) previously. Hatchlings were not collected until 4 May (Figure 1). The previous week, 27 April, an empty salamander jelly case was found in the pond, but no larvae were collected in the sweeps. Many dead egg masses were found in April and May. At the end of June, some of the larvae were metamorphic size.

Ambystoma opacum lays its eggs in the fall. Larvae were present in the pond when sampling started on 9 March. The population demonstrated a synchronous growth pattern (Figure 1). The last larvae, of metamorphic size, were collected on 18 May.

Hyla crucifer hatchlings were first collected on 13 April (Figure 1). Hatchlings continued to be collected through 4 May, indicating a probable breeding season of about a month for *H. crucifer* in 1974. Metamorphic larvae were first collected on 25 May. Only prometamorphic larvae were collected on 8 June. All larvae apparently completed metamorphosis prior to 22 June (no sample available for 15 June). The time spreads of hatchling appearance and metamorphosis are comparable.

Hyla chrysoscelis (not *versicolor*, James Lynch, pers. comm.) were first collected on 1 June (Figure

1). The two larvae collected were both well beyond stage 25. *Hyla chrysoscelis* was not abundant in the pond; sampling error probably accounts for hatchlings not being collected prior to 1 June. Collections of only large larvae on 22 and 29 June suggest that the breeding period for *H. chrysoscelis* ended in early June in 1974.

Rana clamitans were first heard calling on 11 May. Larvae were first collected on 1 June. Larvae were never abundant, but hatchlings were collected through the entire sampling period (Figure 1).

Rana sylvatica larvae were first collected on 6 April. Population growth appeared rather synchronous; metamorphic larvae were last collected on 1 June (Figure 1).

Bufo americanus were collected only once, as hatchlings, on 20 April. Concerted efforts to recollect the species within the sampling areas were unsuccessful for the remainder of the sampling year.

No *Acris crepitans* larvae were collected in 1974.

Tadpoles could be seen easily only in the open water areas of the pond. In 1974, from mid-April to mid-May, *Rana sylvatica* larvae were predominant; the population, estimated visually, appeared to be very large in the open water. After the *R. sylvatica* had metamorphosed, there appeared to be little tadpole activity in the open water areas of the pond.

1975 Pattern: *Ambystoma maculatum* eggs were found on the first sampling time of 22 March. Larvae were not collected until 26 April (Figure 2). Small larvae were collected over a long period, from 26 April to 31 May, apparently reflecting differences in hatching times of the various egg masses. Larvae were present throughout the remainder of the sampling period (Figure 2). Only one egg mass was found in which a noticeable percentage of eggs was inviable.

Very few *Ambystoma opacum* larvae were collected in 1975. Sampling errors apparently account for lack of specimens from the sampling dates of 29 March through 19 April. Larvae were last collected on 26 April (Figure 2).

Hyla crucifer egg masses were first observed on 22 March. Hatchlings were collected from 12 April to 31 May, an 8 week period (Figure 2). Metamorphs were first collected on 31 May and last

collected on 28 June. Judging by the staging graphs and relative numbers (Figure 2), the population had completed, or was in the process of, metamorphosis by 28 June.

Hyla chrysoscelis larvae were first collected on 31 May. The staging graphs (Figure 2) suggest that the breeding period was short and the tadpole growth was synchronous through 28 June.

Overwintered *Rana clamitans* larvae were collected on the first sampling date, 22 March (Figure 2). Calling males were first heard on 10 May, and the first spring hatched larvae were collected on 10 May as well. Early developmental stages of the overwintering larvae were much larger than the same stages of the spring hatched larvae. Larvae were present throughout the entire sampling period.

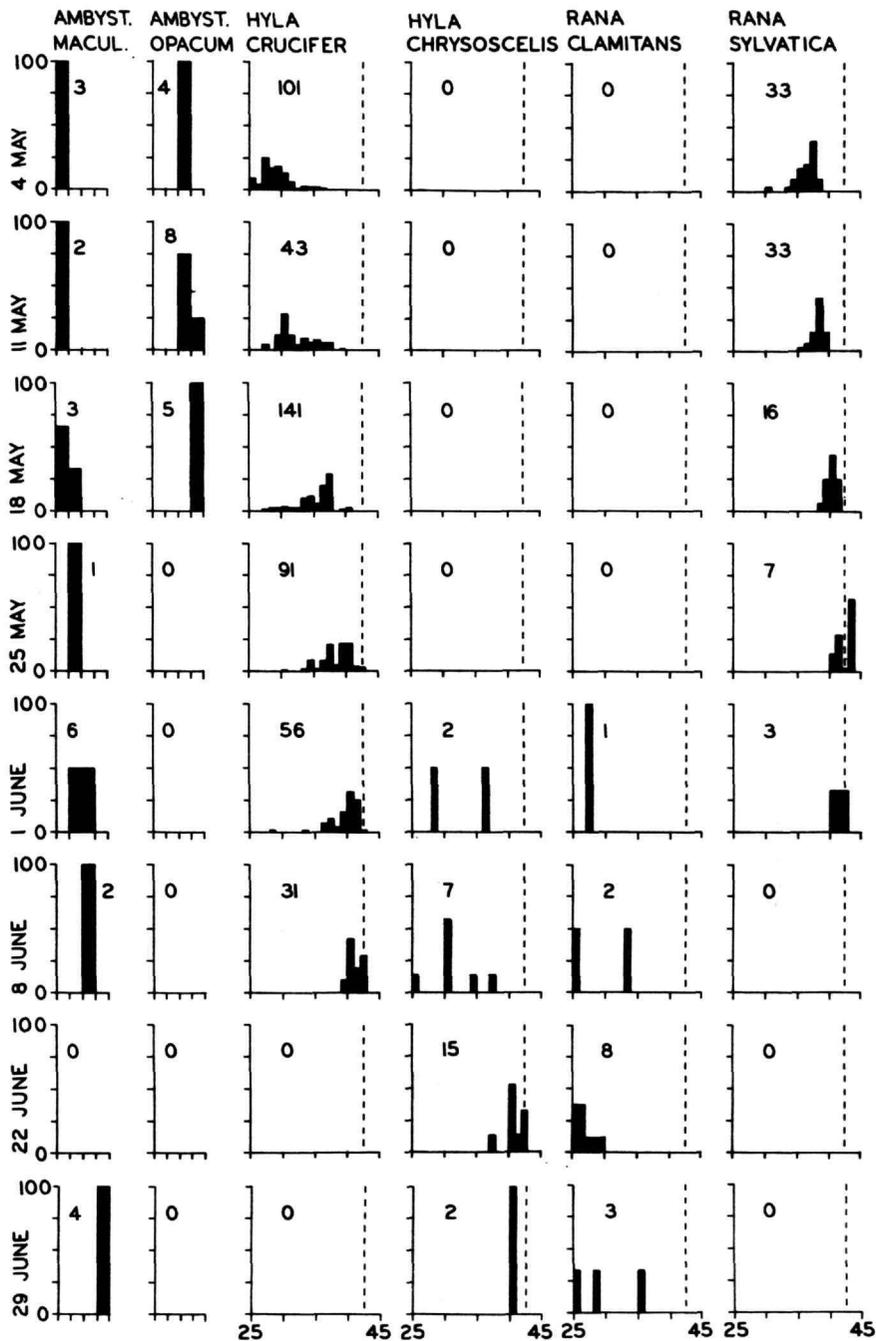
Rana sylvatica eggs were observed on 22 March. Hatchlings were first collected on 19 April and last collected on 10 May. Late prometamorphic larvae were first collected on 24 May and last collected on 28 June (Figure 2).

On 3 May, a calling male of *Acris crepitans* was captured for identification. Calling males were heard on sampling dates from 3 May through 21 June. Larvae were never abundant and were first collected on 21 June (Figure 2).

On 26 July, a sample was taken to determine whether the sampling time span concluding with the end of June was adequate to describe the essential tadpole interactions. Larvae of three species were collected: *Acris crepitans* (6 individuals), *Hyla chrysoscelis* (2), and *Rana clamitans* (18). Hatchlings were collected only of *R. clamitans*. This sample indicated that while larvae were still in the pond, most of the larval activity had concluded before the end of June. No additional species were represented, nor were the species present represented by large numbers.

The sample date of 5 April is notable because no larvae were collected, although they must have been present in the pond (Figure 2). The temperature was cold at the sampling time. The air temperature was 0.4° C, the water temperature 3.4° C, and there was a film of ice on the water. The cold temperature may have caused the larvae, as a behavioral response, to leave the sites they normally inhabited when temperatures were more favorable.

In the open areas of the pond, the predominant



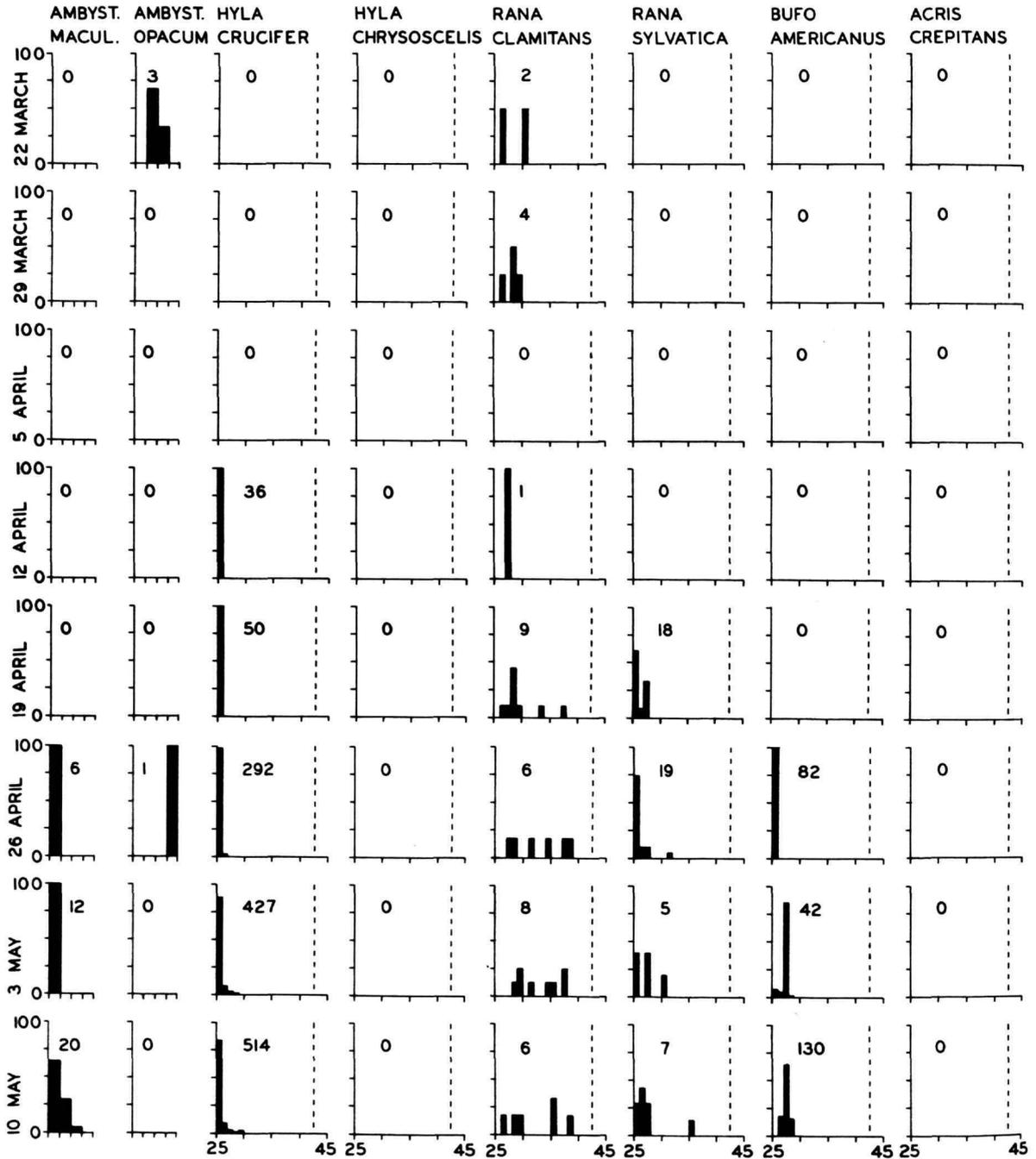
opacum, left to right, ≤ 15 mm, 16–22 mm, 23–29 mm, ≥ 30 mm. Horizontal axes for tadpoles = Gosner (1960) stages. Dashed vertical lines = metamorphosis. Number within each graph = total number of individuals per sample.)

species, estimated visually, was *Bufo americanus*.

Comparison of the 1974 and 1975 Patterns: A comparison of the patterns observed during the

two years produces some striking similarities and striking contrasts (Figure 3).

Each of three species repeated in 1975 the tem-



poral pattern of 1974: *A. maculatum*, *Hyla crucifer*, and *Hyla chrysoscelis* (Figure 3). *Hyla chrysoscelis* not only had the same temporal pattern but also

had consistently low larval densities in both years. The relative numbers of larvae for *Ambystoma maculatum*, as well as for *Hyla crucifer*, were quite dif-

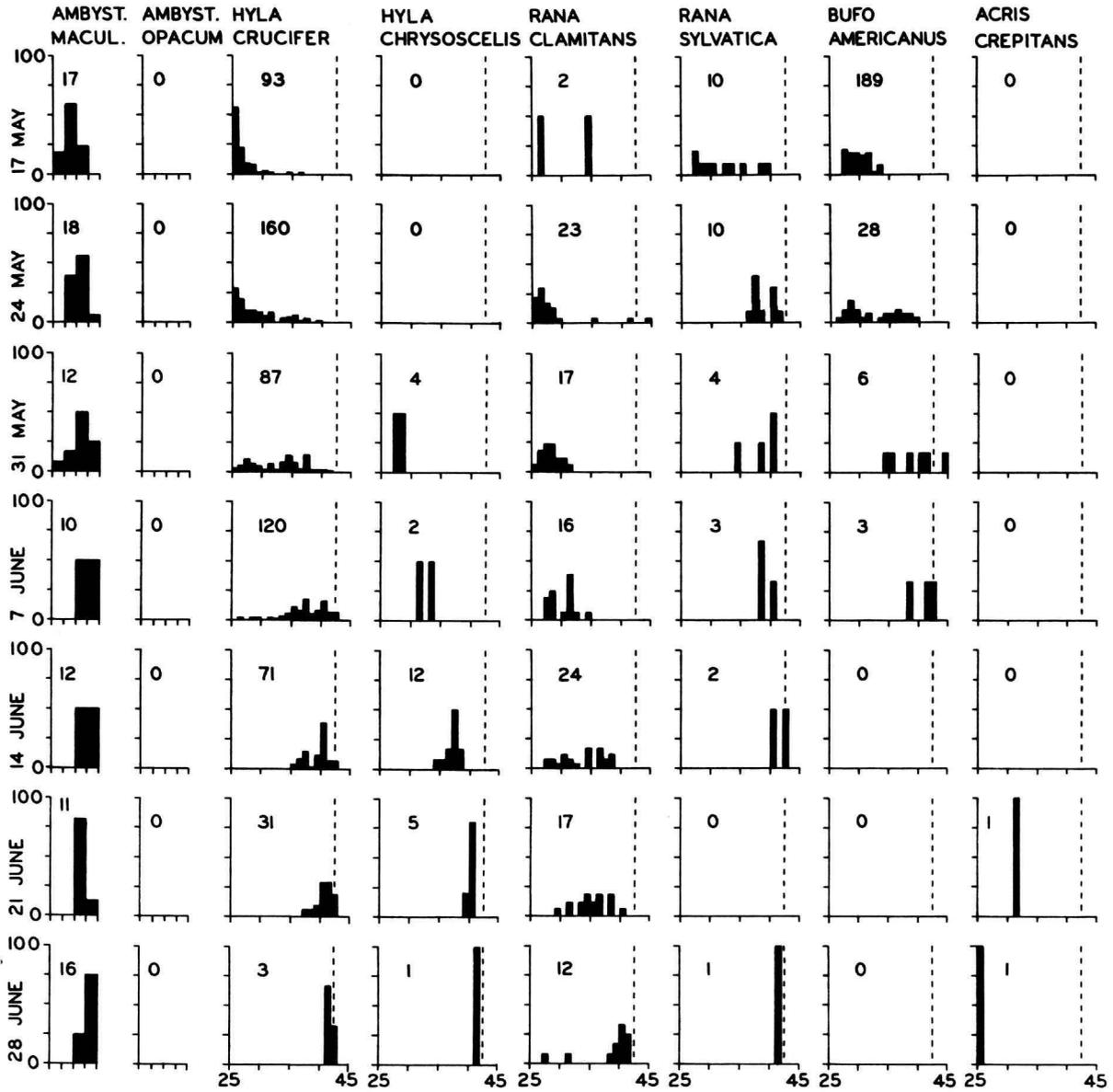


FIGURE 2.—Larval occurrence in 1975 at the Chesapeake site. (Vertical axes are percent of occurrence of each category per sample. Horizontal axes for salamanders = snout-vent size classes: *Ambystoma maculatum*, left to right, ≤ 12 mm, 13–18 mm, 19–24 mm, ≥ 25 mm; *Ambystoma opacum*, left to right, ≤ 15 mm, 16–22 mm, 23–29 mm, ≥ 30 mm. Horizontal axes for tadpoles = Gosner (1960) stages. See Figure 1 for further explanation.)

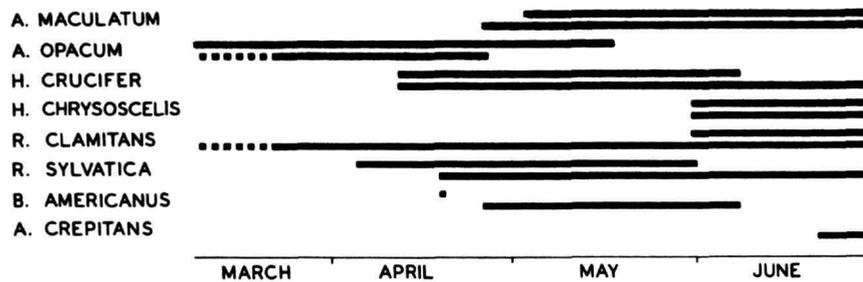


FIGURE 3.—Presence of larvae in the Chesapeake site pond for 1974 and 1975. (Upper line for each species = 1974, lower line = 1975. Dates supplied for which no larvae were collected due to presumed sampling error—see text. Dashed lines = probable presence of larvae prior to initiation of sampling in 1975—see text.)

ferent in 1975 from what they had been in 1974. Although data were not collected on egg masses, visual observation indicated that comparable numbers of *A. maculatum* egg masses were laid in 1974 and 1975. Egg mortality, high in 1974 and low in 1975, probably accounts for the different densities of larval population in the two years. The patterns of *Hyla crucifer* are similar at the onset of both years but different at the end. The data presented in Figures 1 and 2 suggest that the extended breeding season of *Hyla crucifer* in 1975 may account for the larger larval population in that year.

The remaining species show striking temporal and population density differences when the data for the two years are compared. Of these, the most profound differences are found in *Rana clamitans*, individuals of which overwintered in 1974–75, but not in 1973–74. The first appearance of spring-hatched larvae of *R. clamitans* also differs: 1 June in 1974, 10 May in 1975.

In order to understand fully the observed similarities and differences of the patterns of temporal

succession and population density recorded in each of the two years, climatic patterns will have to be examined and analyzed in detail together with the larval data. Long term sampling, over several years, not just two, is necessary to reveal relationships between climate and larval populations. For this reason, these relationships are not examined in this paper. Sampling at the Chesapeake site is planned to continue for the next few years to address these relationships.

MICROHABITAT PARTITIONING.—The numbers of individuals of each species were totalled by type of sweep (Tables 1 and 2) to determine the differences in abundance for each sweep type.

In both 1974 and 1975, *Ambystoma maculatum* individuals were not equally distributed among the three sweep types, more individuals being found in the surface sweeps than in any of the other two sweep types. *Ambystoma opacum* individuals were statistically equally distributed among the three sweep types in both years (based on small-sized samples). Most *Hyla crucifer* larvae were collected

TABLE 1.—Distribution of individuals in microhabitats in 1974 (ns = not significant; * = significant at 5% level; ** = significant at or beyond 1% level)

Species	Surface	Midwater	Bottom	χ^2
<i>Ambystoma maculatum</i> ...	11	2	4	7.88*
<i>Ambystoma opacum</i>	6	3	2	2.36 (ns)
<i>Hyla crucifer</i>	452	47	2	575.81**
<i>Hyla chrysoscelis</i>	6	17	3	12.54**
<i>Rana clamitans</i>	3	4	9	3.88 (ns)
<i>Rana sylvatica</i>	7	121	48	113.67**
<i>Bufo americanus</i>	296	0	0	592.00**

TABLE 2.—Distribution of individuals in microhabitats in 1975 (see Table 1 for key to symbols)

Species	Surface	Midwater	Bottom	χ^2
<i>Ambystoma maculatum</i> ...	59	28	47	10.94**
<i>Ambystoma opacum</i>	0	1	3	3.50 (ns)
<i>Hyla crucifer</i>	882	567	426	174.42**
<i>Hyla chrysoscelis</i>	1	12	11	9.25**
<i>Rana clamitans</i>	1	67	79	72.00**
<i>Rana sylvatica</i>	6	34	38	23.38**
<i>Bufo americanus</i>	4	434	43	705.41**
<i>Acris crepitans</i>	0	1	1	1.00 (ns)

in surface sweeps in both years. However, a statistically greater proportion of the population was collected from midwater and bottom sweeps in 1975 than in 1974 ($\chi^2 = 1727.69$). Most *Hyla chrysoscelis* larvae were collected from the midwater sweep in 1974; in 1975 their concentration was divided equally between the midwater and bottom sweep habitats. In 1974, *Rana clamitans* individuals were statistically equally distributed among all three sweep types, while in 1975, almost all individuals came from the midwater and bottom sweeps. *Rana sylvatica* larvae came mostly from the midwater sweeps in both years. All *Bufo americanus* larvae came from the surface sweeps in 1974, but in 1975 their majority came from the midwater sweeps.

For species represented each year by more than 100 individuals in total and by at least 10 individuals per sweep type, occurrence by size classes of larvae has been determined (Tables 3 and 4). In

1974, statistically more medium-sized *Hyla crucifer* larvae were found in the bottom sweep than expected and statistically more large-sized larvae were found in the midwater sweep than expected (Table 3). There was thus an ontogenetic change in microhabitat preference for *H. crucifer* in 1974. This was also true in 1975 when statistically more large larvae were collected in the bottom sweeps than expected (Table 4). No other species examined demonstrated ontogenetic shifts in microhabitat preference.

The sweep abundance data can be directly related to microhabitat preferences for each species, since the sweeps sampled different microhabitats. As expected, microhabitat preferences were demonstrated for each species for which a total sample size per year was greater than 20 individuals. One would also expect that species would demonstrate the same preferences from year to year. The only species that does not appear to be consistent with this hypothesis is *B. americanus*. However, the entire

TABLE 3.—Occurrence of larvae of two species (adequate for statistical analysis), arranged by size classes, from sweeps in 1974 (size classes of tadpoles = Gosner stage groupings; left of slash = observed figure; right of slash = expected figure based on equal occurrence among sweep types irrespective of size; see Table 1 for key to symbols)

Species	Size	Surface	Midwater	Bottom	χ^2
<i>Hyla crucifer</i>	25-30	235/217	17/21	17/27	5.96 (ns)
	31-36	78/89	7/9	25/11	19.62**
	37-44	139/143	23/14	15/17	6.13*
					31.71**
<i>Rana sylvatica</i>	25-30		34/38	20/15	
	31-36		45/41	13/16	
	37-44		42/40	16/16	
					3.20 (ns)

TABLE 4.—Occurrence of larvae of five species (adequate for statistical analysis), arranged by size classes, from sweeps in 1975 (size classes of salamanders in mm; see Table 1 for key to symbols and Table 3 for further explanation)

Species	Size	Surface	Midwater	Bottom	χ^2
<i>Ambystoma maculatum</i>	≤12	21/15	8/7	6/12	10.79 (ns)
	13-18	11/11	2/5	12/9	
	19-24	16/20	10/9	19/16	
	≥25	11/13	8/6	10/10	
<i>Hyla crucifer</i>	25-30	740/736	502/470	324/358	5.43 (ns)
	31-36	48/55	31/35	38/27	5.82 (ns)
	37-44	94/90	34/58	64/44	19.20** 30.46**
<i>Rana clamitans</i>	25-30		38/35	39/41	1.20 (ns)
	31-36		17/20	26/23	
	37-44		12/12	14/14	
<i>Rana sylvatica</i>	25-30		20/22	30/28	2.61 (ns)
	37-44		10/7	6/9	
<i>Bufo americanus</i>	25-30		368/371	36/32	1.39 (ns)
	31-36		61/59	3/5	

1974 sample was collected in a single, surface sweep which passed through hatching egg strings. The 1975 data doubtless demonstrate the larval microhabitat preferences in contrast to the 1974 information, which may indicate nothing more than the egg deposition sites. *Hyla crucifer*, while demonstrating a preference for the surface sweep microhabitat, showed a shift toward statistically more individuals using the midwater and bottom microhabitats in 1975 than in 1974. This may be due to differences in total population densities for the two years.

The ontogenetic change in microhabitat preferences for *H. crucifer* in 1974 and 1975 is interesting. The data for the two years combined suggest that smaller larvae tend to be in shallow surface areas and as they grow, they move into deeper, more open parts of the pond.

MICROHABITAT METRICS.—Commonly used measures of niche breadth and niche overlap can encompass the factors of temporal and spatial partitioning by the larvae when the measures are based on individual sweeps (see Heyer, 1974, for a previous analysis and justification).

Microhabitat Breadth: The formula used to determine microhabitat breadth is:

$$B_j = \frac{N_s}{N_t} \sum_i p_{ij}^2;$$

where B_j is the microhabitat breadth of species j , N_s is the number of sweeps in which individuals of species j were collected, N_t is the total number of sweeps, and p_{ij} is the proportion of occurrences of species j in sweep i (modified from Levins, 1968).

Microhabitat breadths for 1974 and 1975 are presented in Table 5. When the species are ranked within years by broadest microhabitat width to narrowest, only one species shows the same relative position. *Hyla crucifer* had the broadest microhabitat width both years. Relative to *H. crucifer*, *H. chrysoseelis* had narrower microhabitat widths both years but stood in varying relationship to the other species. The other congeneric pairs, involving *Ambystoma* and *Rana* show reversals of relative rank of microhabitat widths for 1974 and for 1975.

There are no straightforward, powerful, statistical tests to apply to measures based on proportions to determine statistical differences from one year to the

TABLE 5.—Microhabitat breadths (largest/smallest = largest value divided by smallest to determine magnitude of difference from one year to next; see text)

Species	1974	1975	largest/smallest
<i>Ambystoma maculatum</i>	0.0179	0.9711	54.2
<i>Ambystoma opacum</i>	1.3518	0.0194	69.7
<i>Hyla crucifer</i>	6.1109	13.5549	2.2
<i>Hyla chrysoscelis</i>	1.1307	0.0181	62.5
<i>Rana clamitans</i>	0.3293	2.1750	6.6
<i>Rana sylvatica</i>	5.4228	0.2035	26.6
<i>Bufo americanus</i>	0.0156	0.5850	37.5
<i>Acris crepitans</i>	0	0.0003	-

next. For this reason, the larger value is simply divided by the smaller value to determine the order of magnitude of difference from one year to the next. Biologically, there was but a single species that had the same microhabitat breadth for both years: *Acris crepitans* essentially was absent both years. I interpret the differences between microhabitat widths measured in 1974 and in 1975 to be biologically significant for all of the other species.

Microhabitat Overlap: The formula used to determine microhabitat overlap (Horn, 1966) is:

$$ajk = 2 \sum_i p_{ij} p_{ik} / (\sum_i p_{ij}^2 + \sum_i p_{ik}^2);$$

where jk = overlap of species j and k , and p_{ij} is the proportion of occurrence of species j in sweep i . Values range from 0 (no overlap) to 1 (complete overlap). Larval salamanders and larval anurans are in different trophic levels. Tadpoles are primarily herbivorous, while salamander larvae are carnivorous and sometimes eat tadpoles. Co-occurrences in sweeps (which the overlap measure represents in a single value) thus give information on potential predator-prey and competition relationships between salamander larvae and tadpoles. High overlap values are interpreted as the potential (but not necessarily the existence) for predation or competition to occur. Low overlap values are interpreted as indicating that predation or competition is not important.

Overlap values for all comparisons involving salamanders are presented in Table 6. The very low overlap value for 1975 between the two species of *Ambystoma* and no overlap in 1974 confirms previous conclusions (Worthington, 1968; 1969) that

larval *Ambystoma maculatum* and *A. opacum* essentially do not co-occur in the same ponds.

In examining the sweep data for possible predator-prey relationships between the salamanders and tadpoles, the data for all salamanders (in addition to being compared on a species-species overlap with tadpoles) were combined, on the assumption that both species would be potential tadpole predators and it would make no difference to tadpole species x whether it was preyed upon by either salamander species a or b . It is clear from the results (Table 6) that *Ambystoma opacum* potentially is not an effective tadpole predator in the study pond. Almost all potential salamander predation is accounted for by *Ambystoma maculatum*. Two additional generalizations may be drawn from the overlap values. First, potential salamander predation, on all species of tadpoles, was much greater in 1975 than in 1974. The differences involved suggest that salamander predation on tadpoles probably did not have much of an effect in 1974, while salamander predation on tadpoles in 1975 could have been a strong natural selective force. Second, predictions can be made about which species of tadpoles should most likely be affected by salamander predation. In 1974, only *Rana sylvatica* should have had any noticeable predation by salamander larvae. In 1975, *Rana clamitans* and *Rana sylvatica* should have been preyed on extensively by salamander larvae. Such predictions are best treated cautiously until more is known about feeding habits in larval salamanders. For example, the predator-prey size relationships are unknown, but the *Rana* tadpoles become quite large and may escape predation after reaching a certain size.

TABLE 6.—Microhabitat overlaps for comparisons involving salamander larvae (see Table 5 for further explanation)

Pair comparison	1974	1975	largest/smallest
All salamanders - <i>Hyla crucifer</i>	0.0583	0.1879	3.2
All salamanders - <i>Hyla chrysoscelis</i>	0.0603	0.1106	1.8
All salamanders - <i>Rana clamitans</i>	0.0385	0.2920	7.6
All salamanders - <i>Rana sylvatica</i>	0.1111	0.2574	2.3
All salamanders - <i>Bufo americanus</i>	0.0004	0.1565	391.2
All salamanders - <i>Acris crepitans</i>	0	0.0168	-
<i>Ambystoma maculatum</i> - <i>Ambystoma opacum</i>	0	0.0126	-
<i>Ambystoma maculatum</i> - <i>Hyla crucifer</i>	0.0625	0.1938	3.1
<i>Ambystoma maculatum</i> - <i>Hyla chrysoscelis</i>	0.0976	0.1149	1.2
<i>Ambystoma maculatum</i> - <i>Rana clamitans</i>	0.0612	0.2683	4.4
<i>Ambystoma maculatum</i> - <i>Rana sylvatica</i>	0.1163	0.2694	2.3
<i>Ambystoma maculatum</i> - <i>Bufo americanus</i>	0	0.1619	-
<i>Ambystoma maculatum</i> - <i>Acris crepitans</i>	0	0.0168	-
<i>Ambystoma opacum</i> - <i>Hyla crucifer</i>	0.0085	0.0003	28.3
<i>Ambystoma opacum</i> - <i>Hyla chrysoscelis</i>	0	0	-
<i>Ambystoma opacum</i> - <i>Rana clamitans</i>	0	0.0196	-
<i>Ambystoma opacum</i> - <i>Rana sylvatica</i>	0.0224	0.0232	1.0
<i>Ambystoma opacum</i> - <i>Bufo americanus</i>	0.0007	0.0012	1.7
<i>Ambystoma opacum</i> - <i>Acris crepitans</i>	0	0	-

Walters (1975) demonstrated that *Ambystoma* larvae have definite prey preferences among tadpoles when offered a choice; however, she did not include aquatic insects in her experiments. Larval salamanders may prefer insects over tadpoles, even to the extent that tadpoles are not eaten, although available. Anderson and Graham (1967) demonstrated that vertical migration and stratification occur in larval *Ambystoma*. They found that during the evening the larval salamanders leave the sites they have occupied during the day and begin actively feeding. If most feeding is done at dusk, then the overlap values reported here have little or no bearing on the predator-prey relationships of larval salamanders and tadpoles, since all sweeps were taken during the day. Walters (1975) reported diurnal foraging in *Ambystoma* larvae, but had no data to indicate whether most of the foraging takes place during the day or at dusk.

All sweeps were taken when tadpoles were active, so the overlap values represent potential competition when tadpole species-tadpole species comparisons are made. All of the tadpoles in this study have the same gross feeding morphology. Thus, competition may be potentially occurring among all

individuals of all species. For this reason, overlaps have been calculated for each species compared with all other tadpoles in addition to species-species overlap comparisons (Table 7). There is no experimental evidence with which to relate overlap values to potential competition among and within species. Does a value of 0.1062 mean that competition is strong enough so that selection will operate to reduce the overlap? For purposes of this paper, the following common-sense hypothesis will be used to evaluate the overlap values. The range of values from about 0.1 to 0.25 represents the degree of potential competition that the process of natural selection would operate to reduce the microhabitat overlap. Values below 0.1 indicate potential competition is not significant, and values above 0.25 indicate potential competition is significant.

Each of three species had roughly the same amount of overlap with all other tadpoles in 1975 that it had in 1974: *Hyla chrysoscelis*, *Rana sylvatica*, and *Acris crepitans*. Of these, potential competition was a marginal factor only for *Rana sylvatica*, and that for only 1974. For each of the other three species, the degree of overlap with all other tadpole species was different in 1975 from

TABLE 7.—Microhabitat overlaps for comparisons involving only tadpoles (see Table 5 for further explanation)

Pair comparison	1974	1975	largest/smallest
<i>Hyla crucifer</i> - All other tadpoles.....	0.1531	0.3225	2.1
<i>Hyla chrysoscelis</i> - All other tadpoles.....	0.0564	0.0438	1.3
<i>Rana clamitans</i> - All other tadpoles.....	0.0395	0.1519	3.8
<i>Rana sylvatica</i> - All other tadpoles.....	0.1062	0.0679	1.6
<i>Bufo americanus</i> - All other tadpoles.....	0.0096	0.0967	10.1
<i>Acris crepitans</i> - All other tadpoles.....	0	0.0076	-
<i>Hyla crucifer</i> - <i>Hyla chrysoscelis</i>	0.0305	0.0704	2.3
<i>Hyla crucifer</i> - <i>Rana clamitans</i>	0.0204	0.1665	8.2
<i>Hyla crucifer</i> - <i>Rana sylvatica</i>	0.1385	0.1137	1.2
<i>Hyla crucifer</i> - <i>Bufo americanus</i>	0.0146	0.1215	8.3
<i>Hyla crucifer</i> - <i>Acris crepitans</i>	0	0.0074	-
<i>Hyla chrysoscelis</i> - <i>Rana clamitans</i>	0	0.0980	-
<i>Hyla chrysoscelis</i> - <i>Rana sylvatica</i>	0.0336	0.0436	1.3
<i>Hyla chrysoscelis</i> - <i>Bufo americanus</i>	0	0.0215	-
<i>Hyla chrysoscelis</i> - <i>Acris crepitans</i>	0	0.0585	-
<i>Rana clamitans</i> - <i>Rana sylvatica</i>	0.0189	0.2231	11.8
<i>Rana clamitans</i> - <i>Bufo americanus</i>	0	0.1060	-
<i>Rana clamitans</i> - <i>Acris crepitans</i>	0	0.0189	-
<i>Rana sylvatica</i> - <i>Bufo americanus</i>	0	0.1699	-
<i>Rana sylvatica</i> - <i>Acris crepitans</i>	0	0.0232	-
<i>Bufo americanus</i> - <i>Acris crepitans</i>	0	0	-

what it had been in 1974. For *Hyla crucifer*, potential competition was important both years but more significant in 1975. For *Rana clamitans*, potential competition was a factor only in 1975, as it also was (marginally) for *Bufo americanus*. At the community level it would appear that larvae of *Hyla crucifer* are the only ones that would experience potential competition from the rest of the tadpole community on a year to year basis.

Although feeding morphologies of all tadpoles under consideration are similar, interspecific competition might be most important between certain species pairs. Each of the following species pairs showed the same overlap in 1974 that they did in 1975 (Table 7): *Hyla crucifer*-*Rana sylvatica*, *Hyla crucifer*-*Acris crepitans*, *Hyla chrysoscelis*-*Rana sylvatica*, and *Bufo americanus*-*Acris crepitans*. Among these, only the *Hyla crucifer*-*Rana sylvatica* pair shows an overlap value that indicates potential competition as a factor. All of the other species pair overlap values are very different for 1974 as compared to those for 1975. For the following pairs potential competition is not a factor in either year: *Hyla crucifer*-*Hyla chrysoscelis*, *Hyla chrysoscelis*-

Bufo americanus, *Hyla chrysoscelis*-*Acris crepitans*, *Rana clamitans*-*Acris crepitans*, and *Rana sylvatica*-*Acris crepitans*. For the following pairs, potential competition is significant for only one of the two years: *Hyla crucifer*-*Rana clamitans*, *Hyla crucifer*-*Bufo americanus*, *Hyla chrysoscelis*-*Rana clamitans*, *Rana clamitans*-*Rana sylvatica*, *Rana clamitans*-*Bufo americanus*, *Rana sylvatica*-*Bufo americanus*. Thus, based on the two consecutive years of this study, 8/15 of the total species-species overlaps probably do not have competitive interactions, while in only 1/15 of the species-species overlaps is competition potentially a year to year factor.

DISCUSSION.—The aquatic larval community appears to have distinct temporal patterns each year. Some of the species show the same temporal patterns each year and others show different temporal patterns each year.

Each species of larvae has essentially the same microhabitat preference for the two years.

The analyzed microhabitat breadths reflect temporal and spatial partitioning with population densities, thereby illustrating the comparative habitat utilization each year. The overall picture is that

the total habitat utilization was very different in each of the two years studied and would likely be different every year.

The microhabitat overlap analyses allow insights into the biological interactions occurring in the pond. Overlaps of salamander larvae and tadpoles give indications of predator-prey relationships, while overlaps of species in the same trophic level give insights into potential competition.

Salamander larvae can prey heavily on tadpoles in nature (Anderson, 1968). Even if most prey capture is done at twilight in microhabitats other than those occupied by the salamanders in daylight, the overlap data presented herein exemplify the kinds of relationships that occur between predators and tadpole prey. The overlap data indicate that the tadpole populations in 1974 were in very different predator environments from those in 1975.

The lack of competition between *Ambystoma maculatum* and *A. opacum* in Maryland due to temporal partitioning has been documented and discussed previously (Worthington, 1968; 1969). The role of competition among tadpoles has not been as well documented. Wilbur and Collins (1973) and Brockelman (1969) demonstrated that intraspecific competition among tadpoles may occur at high experimental densities. Brockelman (1969) found no evidence for intraspecific competition in natural pond habitats. De Benedictis (1974) was unable to demonstrate conclusively that interspecific competition occurs in field simulated experiments. An analysis of the available literature suggests that while competition is a theoretical possibility among tadpoles, the densities found in nature fall well below the densities required to demonstrate competition experimentally. For example, comparative figures extrapolated from Wilbur and Collins (1973) and Turnipseed and Altig (1975) indicate a density of 1 tadpole per 192 cm³ of water as being necessary for tadpole competition to occur (based on the results of 300 larvae density runs in Wilbur and Collins' experimental pens), while the greatest recorded tadpole population density found in nature was identified in a pond edge in Mississippi as 1 tadpole per 285 cm³ water (conservative estimate, using 5 cm water depth to Turnipseed and Altig's density/area data).

In order to demonstrate the occurrence of actual competition among tadpoles, it would be necessary

to determine a limiting factor in the environment. Tadpoles are not territorial; many species freely form association groups and/or schools (Wassersug, 1973). Thus, it appears unlikely that space would be a limiting factor. The pond has abundant submerged vegetation and a deep organic silt bottom; all indications are that it is a productive pond and that food would not be limiting. The tadpole species-species overlap values indicate potential competition, not the existence of competition. Most of the overlap values are low, indicating that there is little potential competition within most of the tadpole community. The highest consistent values involve *Hyla crucifer* (Table 7). *Hyla crucifer* has a small tadpole, and although the numbers of individuals may be high, the biomass may not be appreciable, especially compared to *Rana clamitans* and *R. sylvatica*. The overall results of this study indicate that if interspecific competition is occurring, it most likely is occurring between *Hyla crucifer* and *Rana sylvatica*. Until experiments are performed to determine the density levels required to demonstrate competition between these two species, the most reasonable assumption is that competition is not important for these populations at the study pond. The only other overlap value really indicative of potential competition is that of *Rana clamitans*-*Rana sylvatica* for 1975 (Table 7). While individuals of both species were occupying the same microhabitats, the total number of individuals collected were not great: 148 *R. clamitans* and 79 *R. sylvatica*. These numbers came from a reasonable volume of habitat sampled. I conclude that the total densities involved are of such a magnitude that competition was not a factor for *Rana clamitans* and *Rana sylvatica* in 1975. In the absence of any demonstrated limiting factor, the overlap analysis provides no evidence that competition among tadpoles was occurring in the pond in either year. Since the search for evidence of competition produced such generally negative results, it appears that competition was not likely limiting population growth in any of the tadpole species in the study pond. What the overlap values do demonstrate is that the temporal and spatial relationships within the biological larval community were quite different in 1974 from what they were in 1975.

The conclusions drawn with respect to habitat partitioning for the study pond are as follows. An-

nual differences in larval temporal habitat partitioning combined with different annual population densities result in: (1) differential habitat utilization each year by the larvae, and (2) different biological interactions involving predator-prey and species associations each year. Generally low microhabitat overlap values for tadpole species indicate that competition was not regulating the tadpole community, but that larval spatial and temporal distributions effectively partitioned the habitats. Overall, each larval species was in a different environment with respect to natural selection in 1974 from what it experienced in 1975.

Barro Colorado Island

The stream habitats at Barro Colorado Island (BCI) consist of semi-isolated or completely isolated stream bed pools. Sampling was done once in the dry season (11 February to 5 March 1975) and once in the wet season (1–20 July 1975) to determine gross temporal patterns of tadpole occurrence. Sampling procedures were designed to determine how fish (predators) and tadpoles spatially occupy the habitat.

METHODS AND MATERIALS.—Each stream bed pool was measured by length, breadth, and greatest depth. The measured pool was then sampled by a large or small dipnet appropriate to the size of the pond. Presence or absence of fish was noted. Fish were not collected, so the assumption that the fish were all predators probably overestimates the real situation. In the dry season, the presence or absence of tadpoles by species was noted. In a few samples the individuals were preserved for confirmation of identifications. In the wet season, all tadpoles collected were preserved. Efforts were made to collect all individuals in the small ponds. In the laboratory, all specimens were identified, counted, and staged (Gosner, 1960).

RESULTS.—Few larvae were collected in any single pond; for this reason, only the presence or absence of larvae was noted in the dry season. The wet season sampling, in which quantitative counts were taken, probably reflects the same quantitative relationships as the dry season sampling. During the wet season the greatest number of tadpoles collected in a pond was 18, the average number of tadpoles in a pond that had tadpoles was 3.6.

Ninety-seven ponds were sampled in the dry season, 80 were sampled in the wet season (Table 8). The ponds were larger in the wet season ($\chi^2 = 21.17, P < .01$) as might be expected. Fish occurred in a total of 63 ponds, tadpoles occurred in a total of 47 ponds. Fish and tadpoles co-occurred in only 1 pond.

TABLE 8.—Size classes of ponds (volume in m³) sampled by seasons at Barro Colorado Island

Pond size	Dry season	Wet season
1 - 9.....	2	6
0.1 - 0.9.....	22	43
0.01 - 0.09.....	52	24
0.001 - 0.009.....	21	7

Distribution of fish among pond size classes is presented in Table 9. Fish occurred in the larger ponds. This aspect of habitat preference was evident only in the dry season when there were more small ponds available to choose from. During the wet season, when ponds were larger, the fish distribution among size classes of ponds was random.

The distribution of all tadpoles among pond size classes is presented in Table 10. Tadpoles occurred in a random sample of the available pond sizes in both the dry and wet seasons.

In the dry season, tadpoles of *Bufo typhonius*, *Colostethus nubicola*, and *Smilisca sila* were collected from the stream bed ponds. *Bufo typhonius* were collected in only one pond where they were completing metamorphosis. The sampling period included the very end of the reproductive season of *Bufo typhonius*. The *Colostethus nubicola* and *Smilisca sila* larvae were at all stages of development since the sampling period was during the breeding season of these species. Although sample sizes are not large enough for statistical analysis, the raw data clearly suggests that *Colostethus nubicola* occurred randomly in the available ponds during the dry season when small ponds were more abundant (Table 11). The same applies to *Smilisca sila* larvae (Table 12). *Colostethus nubicola* tadpoles were found in 6 ponds where *Smilisca sila* tadpoles did not occur, *S. sila* tadpoles occurred in 7 ponds where *C. nubicola* did not occur, and *C. nubicola* and *S. sila* co-occurred in 8 ponds. The

TABLE 9.—Fish occurrence among size classes of ponds (volume in m³) sampled by seasons at Barro Colorado Island (for χ^2 determination, sample sizes are grouped so that expected values ≥ 5 ; expected values are determined by multiplying percent occurrence of all fish in all ponds by number of ponds sampled in each size category; see Table 1 for key to symbols)

Pond size	Dry season		Wet season		Total	
	Observed	Expected	Observed	Expected	Observed	Expected
1 - 9.....	1	1	2	1	3	2
0.1 - 0.9.....	17	11	7	8	24	23
0.01 - 0.09.....	28	26	6	4	34	27
0.001 - 0.009.....	2	10	0	1	2	10
	$\chi^2 = 9.55^{**}$		$\chi^2 = 2.00$ (ns)		$\chi^2 = 8.37^{**}$	

TABLE 10.—Tadpole occurrence among size classes of ponds sampled by seasons at Barro Colorado Island (for χ^2 determination, sample sizes are grouped so that the expected values ≥ 5 ; expected values are determined by multiplying percent occurrence of all tadpoles in all ponds by number of ponds sampled in each size category)

Pond size	Dry season		Wet season		Total	
	Observed	Expected	Observed	Expected	Observed	Expected
1 - 9.....	1	0	1	2	2	2
0.1 - 0.9.....	2	5	11	14	13	17
0.01 - 0.09.....	10	11	12	8	22	20
0.001 - 0.009.....	8	5	2	2	10	7
	$\chi^2 = 2.69$ (ns)		$\chi^2 = 2.60$ (ns)		$\chi^2 = 2.33$ (ns)	

TABLE 11.—Occurrence of *Colostethus nubicola* tadpoles among size classes of ponds sampled by seasons at Barro Colorado Island (for χ^2 determination, sample sizes are grouped so that the expected values ≥ 5 ; expected values are determined by multiplying percent of occurrence of all *C. nubicola* larvae in all ponds by number of ponds sampled in each size category)

Pond size	Dry season		Wet season		Total	
	Observed	Expected	Observed	Expected	Observed	Expected
1 - 9.....	0	0	0	1	0	1
0.1 - 0.9.....	2	3	3	7	5	10
0.01 - 0.09.....	8	8	8	4	16	12
0.001 - 0.009.....	4	3	2	1	6	4
			$\chi^2 = 8.12^{**}$		$\chi^2 = 5.52^*$	

two species were randomly associated with each other ($\chi^2 = .28, P > .05$).

Colostethus nubicola, *Centrolenella fleischmanni*, and *Physalaemus pustulosus* larvae were collected in the stream ponds in the wet season. All stages of larvae were present indicating the sampling period was within the breeding season of all three

species. *Physalaemus pustulosus* larvae were collected in 6 ponds, in 1 pond it was the only species collected, in 1 pond *Physalaemus pustulosus* co-occurred with *Colostethus nubicola*, in 3 ponds *Physalaemus pustulosus* co-occurred with *Centrolenella fleischmanni*, and in 1 pond *Physalaemus pustulosus* co-occurred with *Centrolenella fleisch-*

TABLE 12.—Occurrence of *Smilisca sila* larvae among size classes of ponds sampled in one season at Barro Colorado Island (expected values are determined by multiplying percent occurrence of all *S. sila* larvae in all ponds by number of ponds sampled in each size category)

Pond size	Dry season	
	Observed	Expected
1 - 9.....	1	0
0.1 - 0.9.....	2	3
0.01 - 0.09.....	7	8
0.001 - 0.009.....	5	3

manni and *Colostethus nubicola*. In the wet season, *Colostethus nubicola* demonstrated a greater occurrence in smaller ponds than expected (Table 11). This preference was evident only in the wet season, when there were fewer small ponds than in the dry season. Over all, *Colostethus nubicola* tadpoles were associated with smaller ponds (Table 11). *Centrolenella fleischmanni* tadpoles were distributed randomly among the pond sizes (Table 13). *Colostethus nubicola* tadpoles were found in 10 ponds where *Centrolenella fleischmanni* tadpoles were not found, *Centrolenella fleischmanni* tadpoles were found in 12 ponds where *Colostethus nubicola* tadpoles were not found, and both *Centrolenella fleischmanni* and *Colostethus nubicola* tadpoles were found in 3 ponds. The two species tend to mutually exclude each other, but the statistical evidence for this is not strong ($\chi^2 = 5.36$, $.1 > P > .05$):

TABLE 13.—Occurrence of *Centrolenella fleischmanni* larvae among size classes of ponds sampled in one season at Barro Colorado Island (for χ^2 determination, sample sizes are grouped so that the expected values ≥ 5 ; expected values determined by multiplying percent occurrence of all *C. fleischmanni* larvae in all ponds by number of ponds sampled in each size category)

Pond size	Wet season	
	Observed	Expected
1 - 9.....	1	1
0.1 - 0.9.....	9	8
0.01 - 0.09.....	5	4
0.001 - 0.009.....	0	1
	$\chi^2 = .11$ (ns)	

HABITAT PARTITIONING.—In terms of habitat partitioning, the habitat is considered as the entire collection of stream bed ponds.

Temporal Partitioning: The habitat is clearly partitioned temporally over a seasonal cycle. Only one species, *Colostethus nubicola*, was present as tadpoles in the two seasonal sampling periods.

Spatial Partitioning: Space partitioning is evident in the total pond system. Of all the ponds with tadpoles present, 68% had but a single species. Where more than one species occurred in a pond, I found no evidence for microhabitat partitioning within the pond. All species were found in the leaf litter that had accumulated in the pond bottoms.

The stream bed tadpole community was effectively partitioning the available habitat on the basis of time and space.

DISCUSSION.—While the effective habitat partitioning evidenced in the BCI stream tadpoles seems to be the product of selective forces acting previously upon the species making up the community, the possible roles of predation and competition invite speculation.

Fish predation in the tropics recently has been hypothesized to be a major organizing factor in tadpole communities (Heyer, McDiarmid, and Weigmann, 1975). Two observations, in addition to the data already presented, are pertinent to the question of possible fish predation as a factor in the BCI study. The single pond sampled in which tadpoles and fish co-occurred had a small surface area, but was a deep crevice pond, in the bottom of which had accumulated a deep layer of leaf litter. The single *Centrolenella fleischmanni* larva collected in this pond was in the deep leaf litter. One of the streams sampled had a weir type dam constructed on it with a pond behind it. Data from this large pond (7 x 6 x 1 m) have not been included herein previously, since the pond is not part of the natural stream bed habitat. In the dry season, fish were in the pond and no tadpoles were collected although *Physalaemus* foam nests were often observed on the periphery of the pond. In early March, the pond was completely drained, and the accumulated silt shoveled out. In the following July, in numerous observations, no fish were seen but a dense tadpole community was present consisting of *Agalychnis callidryas* and *Physalaemus pustulosus*. The data presented herein are consist-

ent with the following conclusions. Fish are effective predators on tadpoles, completely eliminating them from certain pond habitats. The tadpoles have two patterns of occurrence in response to the fish: (1) *Colostethus nubicola* demonstrates a habitat preference, using ponds smaller than those usually occupied by fish; (2) the remaining species apparently exploit the patchy occurrence of fish in the total pond habitat system. That is, tadpoles are deposited in enough ponds so that some of such ponds will be fish free. For such an accommodation to be effective, either a single egg clutch would have to be partitioned among several ponds or the individuals would have to have multiple clutches during their reproductive life. Relative to the anuran species identified in the BCI study, the only clutch deposition patterns available are for *Centrolenella fleischmanni*, in which the male has been shown to fertilize several clutches (data for females unknown, McDiarmid, 1975) and *Physalaemus pustulosus*, in which the female can produce up to four clutches a year with as little as six weeks between clutches (Davidson and Hough, 1969).

The very low numbers of tadpoles collected in the individual ponds strongly suggests that competition is not operating. The existence of many ponds with neither fish nor tadpoles, which appeared similar to the ponds containing tadpoles suggests that there was no competition for space as a limiting factor by itself. It is very difficult, however, to rule out competition (at least intraspecific) for a combination of space and food. In contrast to the many temperate zone temporary ponds that are highly productive, many tropical streams have extremely low productivity (Fittkau, et. al., 1975). No data are available for the productivity of the streams on BCI, but the productivity is probably low, judging by the clearness of the water. Productivity may be higher during the dry season, when tapir feces remain in the ponds rather than being continually flushed from them. Interspecific competition for food resources is not a likely factor, since the species which most often co-occur with each other have very different feeding morphologies. *Colostethus nubicola* larvae have large funnel mouths; the larvae often feed on the surface film. The species that co-occur with *Colostethus* in the same ponds, *Smilisca sila* in the dry season and *Centrolenella fleischmanni* in the wet season, are

substrate feeders with scraping and chewing mouthparts. Each pond, however, may well have limited resources. The tadpoles are certainly capable of moving from pond to pond during rains when the ponds are interconnected. The low numbers of individuals in each pond may represent movement of individuals reflecting competition. The total distribution pattern of larvae would then be a combination of the pond site where eggs were deposited and a radiation to adjoining ponds.

The data and analysis from the BCI study allow the following general conclusions to be drawn. The stream bed pond habitat system is effectively partitioned by the tadpole community on the basis of space and time. Predation is an organizing factor in the composition of the tadpole community, interspecific competition apparently is not.

Other Studies of Larval Habitat Partitioning

Larval salamander population dynamics have been the focus of study by several workers, most notably Anderson and his coworkers (1967, 1968, 1971), Shoop (1974), Wilbur (1972), Wilbur and Collins (1973), and Worthington (1968, 1969). Most of these studies have dealt with predation, competition, survival, and temporal organization of larval salamander communities. Wilbur (1972), combined experimental manipulations and field observations to demonstrate that predation and competition were important factors in the functioning and organization of the larval salamander communities of Michigan.

I am aware of only four studies in which quantitative data were taken to deal with questions concerning habitat partitioning by anuran larvae. Dixon and Heyer (1968) followed a pond in western Mexico for two weeks. Since all microhabitats sampled were combined, no information was available on possible spatial partitioning within the pond. The data strongly indicated temporal partitioning of the habitat by the larvae.

I previously reported on habitat partitioning of the temporary pond environment by the tadpole community for a seasonal tropical site in north-eastern Thailand (1973, 1974). Quantitative sweeps were taken from a series of ponds to determine the temporal partitioning patterns and a series of microhabitat sweeps were taken from a single pond to

determine spatial partitioning within a pond. Gut contents were analyzed to determine any obvious partitioning patterns of the available food resources. The study concluded that the available pond habitats were partitioned by the tadpole community on the basis of time and space, not food.

Calef (1973a) reported on the population dynamics of a single anuran species system in a lake in British Columbia. The study is of interest as it is the only reported study of tadpole population dynamics that covered two years (consecutive) and the study represents an extreme situation in terms of anuran diversity. Calef (1973a) found similar results in both years: almost identical numbers of egg masses were laid in both years and survivorship was essentially the same both years. Food was not a limiting resource; the tadpoles grew at the maximum rate set by the aquatic habitat temperature. The tadpole populations were regulated by predation (primarily salamander).

In an unpublished study, Wiest (1974), reported on a series of ponds in Brazos County, Texas. Wiest quantitatively sampled the larvae of a series of ponds and reported the individual results from four of them. He did not sample for microhabitat differences within ponds. Each of the four ponds had different combinations of species of larvae. Within each pond a temporal succession of species was demonstrated.

The results of all studies that have examined the entire anuran larval communities are similar and consistent with the following conclusions. Habitats are partitioned by space and time, not food. Predation, not competition, has a strong role in controlling and organizing the tadpole communities.

Tadpole Community Organization

A tadpole community is defined as an assemblage of anuran larval species at a single site. Two extreme levels of organization are possible: (1) a community with no interspecific interactions between or among any of the component populations, or (2) a community with either symbiotic relationships that tie the community together, or competition that partitions the community into component parts. With this spectrum of tadpole communities in mind, I have examined the Chesapeake and BCI systems to see what type of community organization they most closely resemble.

The three predominant species collected at BCI are all stream breeding frogs: *Centrolenella fleischmanni*, *Colostethus nubicola*, and *Smilisca sila*. The evolutionary history of each of the three species is distinct. All members of the genus *Centrolenella* for which larvae are known have rheocolous larvae with long, thin tails, bodies flattened dorsoventrally, and a strong body and tail musculature capable of continued, powerful flipping movements. The morphology is typical of larvae adapted to life in running water. Mouthparts consist of a scraping and chewing apparatus. Breeding activities for all species that have been studied coincide with the onset of the rainy season in those areas with seasonal rainfall patterns. *Centrolenella fleischmanni* occurs from southern Mexico to Panama, westward to Ecuador, and eastward to Surinam (Starrett and Savage, 1973). *Colostethus nubicola* larvae resemble *Centrolenella* larvae in body and tail shape, strong musculature, and flipping movements when out of water. *Colostethus nubicola* larvae differ from *Centrolenella* larvae in that the mouthparts form a pronounced funnel, adapted for feeding on the surface film. *Colostethus nubicola* extends from Costa Rica through Panama into western Colombia (Savage, 1968). The tadpole of *Smilisca sila* has a typical pond morphology in contrast to the stream morphologies of the other two species. The body and tail are weakly muscled, the body is globose and the tail relatively short but broad, with high fins. The primitive reproductive pattern for the genus *Smilisca* involves pond larvae (Duellman and Trueb, 1966). *Smilisca sila* has become adapted to breeding in quiet stream bed pools. Such pools predictably exist only during the dry season, which is the breeding season for *Smilisca sila*. The mouthpart morphology is the typical scraping and chewing kind. They are known only from Costa Rica and Panama (Duellman, 1970).

In each of the seasons (dry and wet) there are two co-occurring species in the community composed of the three predominant species. In the dry season, the surface film feeding *C. nubicola* larvae coexist with the substrate processing *S. sila* larvae. In the wet season, the surface film feeding *C. nubicola* larvae coexist with the substrate processing *C. fleischmanni* larvae. The community organization of these three species can be explained in two very different ways. First, it may be that competition for

resources was the source of natural selective forces which led to the morphological divergence of mouthparts of *Colostethus* and the temporal partitioning of the substrate feeding *Centrolenella* and *Smilisca* larvae. The evolutionary result would thus be a competition free, compartmentalized stream bed larval community. The second explanation is that the three species occur as larvae in a community in the way they do because there happen to occur in the same area three species of frogs that have stream breeding adaptations. The organization of the community is due to the way the components coexist, no further evolutionary adjustments being necessary. I favor the last explanation for the following reasons. (1) The associations of the species as larvae appear to be due to similar choices of pond habitats by the three species. If the associations were biologically mediated (e.g., competition) one would not expect the random associations found in this study. (2) The geographic distributions of the species argue against long term, species wide interspecific interactions. Divergence in morphology or temporal use of the habitat would almost have to be a one sided divergence involving only *Smilisca sila*, as it is the only species which throughout its entire range would consistently encounter the other two species. (3) The partitioning of the habitat by the stream tadpole community can be better explained in terms of other features of the life histories of the species involved. The reason that *C. nubicola* larvae have funnel mouthpart stream adapted larvae is likely that the species evolved in an environment characterized by streams lacking standing algal growths or detritus and the food resources were concentrated in the surface film. The reason that *Smilisca sila* breeds during the dry season is likely that the ancestral stock, having a typi-

cal pond life history, became isolated in an area where the only quiet ponds in the environment were in the stream beds during the dry season. The reason that *Centrolenella fleischmanni* breeds in the rainy season is likely because the exposed egg clutches that are placed on undersides of leaves over streams are prone to desiccation during the dry season and rains frequently are needed to insure that the hatchlings reach an appropriate stream habitat.

The same kinds of arguments can be made for the Chesapeake tadpole community. Table 14 presents the major species wide characteristics of breeding habitats and seasons for those species comprising the tadpole community at the Chesapeake study site (data from Conant, 1975; R. I. Crombie and G. R. Zug, pers. comms.). Most of the species have unique combinations of breeding seasons and types of ponds primarily used for breeding. These data suggest that each species has a unique reproductive pattern reflecting the conditions in which that species occurred at the time of its genetic isolation. If interspecific competition had been the major evolutionary force in the habitat partitioning between congeners, their segregation should remain apparent today, although they would no longer be in competition. The essentially complete partitioning of larvae of *Hyla crucifer* from *Hyla chrysoscelis* and *Rana clamitans* from *Rana sylvatica* could be interpreted as competition having occurred between congeneric pairs historically, with natural selection operating to reduce larval interspecific competition. The present almost complete habitat partitioning within the species pairs would be the result of natural selection operating to reduce competition. The alternate explanation of larval habitat partitioning within congeneric

TABLE 14.—Major characteristics of breeding habitats and seasons for species comprising the tadpole community at the Chesapeake site (C = common, r = rare)

Species	Breeding season		Types of breeding ponds				
	Early	Late	Temporary		Permanent		Sluggish streams
			wooded	open	wooded	open	
<i>Acris crepitans</i>		C			r	C	C
<i>Bufo americanus</i>	C		C	C	r	r	
<i>Hyla crucifer</i>	C		C	C	r	r	
<i>Hyla chrysoscelis</i> ..		C	r	r	C	r	
<i>Rana clamitans</i>		C			r	C	C
<i>Rana sylvatica</i>	C		C		r		

pairs seems more plausible. The ancestral stock of *Hyla crucifer* likely was isolated in and became adapted to an environment in which the only available breeding ponds were temporary ones which appeared in the spring. The ancestral stock of *Hyla chrysoscelis* was likely isolated in and became adapted to an environment in which the only available breeding ponds were permanent ones and in addition, the breeding season was associated with late spring and summer warm rains. Similarly, the ancestral stock of *Rana sylvatica* was likely isolated in and became adapted to an environment in which the only available breeding ponds were temporary wooded ponds appearing in the spring. The ancestral stock of *Rana clamitans* was likely isolated and became adapted to an environment in which the only breeding sites were streams and open, permanent ponds and also the breeding season was associated with late spring and summer warm rains. Since the early adaptive histories of the several species, the geographic ranges have expanded and contracted according to major climatological changes so that the species ranges now broadly overlap. Each pond in the species range will have (more or less) some of the major characteristics associated with the primary adaptive pond type of each species. Thus, certain wooded permanent ponds will contain the essential features of the temporary wooded ponds to which *Rana sylvatica* is primarily adapted. When such ponds are encountered, they will be utilized by *R. sylvatica* in the spring, while the same pond may also be used by *Rana clamitans* in the late spring and early summer. The habitat partitioning of the larvae of these two species is thus most likely not a result of biological interactions at the larval stages, but rather a passive reflection of different adaptive reproductive patterns of the species involved. A similar observation may be made for the entire community of frogs utilizing the same ponds. If biological interactions at the larval stage were important in the control and organization of the tadpole community, the interactions would have to be reasonably predictable for natural selection to be effective. The Chesapeake community organization argues against this. Each component species present as larvae was in an essentially different selective environment in each of the two years studied.

Although the role of competition among tadpoles has implicitly (e.g., Wiest, 1974) or explicitly (Wilbur and Collins, 1973) been accorded major importance in the control and organization of tadpole communities, this present study concludes that interspecific competition among tadpoles is not important in the control or organization of tadpole communities. Further circumstantial evidence arguing against significant tadpole competition in nature is relevant to this conclusion. If interspecific tadpole competition had occurred historically, selection should have operated to displace the competing species either with respect to space, time, or feeding morphologies. If this were true, a prediction could be stated that tadpoles with the same feeding morphologies feeding on the same foods within the same type microhabitat should not occur in the same pond at the same time. Data are available from two pond studies which do not support this prediction. For tadpoles with scraping and chewing mouthparts, the best test is to look for co-occurring, similar size larvae belonging to the same genus. Wiest (1974) did not sample for microhabitat differences, but one of the ponds he reported had only one microhabitat. This was pond D, which was a uniform, shallow grassy pond in a heavily grazed pasture. The same larval stages of *Pseudacris clarki* and *P. streckeri*, which have the same mouthparts, occurred together in this pond. The beakless midwater feeding microhylid genera at Sakaerat, Thailand, all have morphologically similar larvae, of the same size, and all feed on the same food in the same way (Heyer, 1973). Three ponds there that had a single uniform microhabitat were sampled. For all practical purposes, the ponds were dirt aquaria. There was no standing vegetation in the water. If competition had been important historically, no two species of any of the midwater feeding genera should have occurred together in these ponds, however, the following pairs did occur together, refuting the importance of the potential for interspecific tadpole competition in nature: *Glyphoglossus molossus* and *Microhyla pulchra*, *Glyphoglossus molossus* and *Kaloula mediolineata*, *Kaloula pulchra* and *Microhyla pulchra* (Heyer, 1973). In another pond which was sampled by microhabitats, *Glyphoglossus molossus* and *Microhyla ornata* larvae occurred in the same sweeps.

Interspecific behavioral adjustments appear to be

rare among tadpoles, indicating that generally, interspecific competition among tadpoles is evolutionarily unimportant. In field experiments, *Agalychnis* larvae occupied the water column and the pond floor when it was the only species present, but when *Hyla rosenbergi*, a bottom dwelling tadpole species, was in the same pond, the *Agalychnis* larvae all occupied the water column (McDiarmid, pers. comm.). Two partially exclusive explanations may account for the type of behavioral shift evidenced by the *Agalychnis* larvae. First, there is competition for space when *Agalychnis* is present with bottom dwelling tadpoles which may occasion a behavioral response by *Agalychnis*: partitioning the habitat to avoid competition. Second, the response by *Agalychnis* may be purely density dependent. Individual *Agalychnis* larvae may occupy the bottom if there are less than a given number of larvae already present on the bottom (including other *Agalychnis* individuals). If there are many tadpoles on the bottom, at least some of the *Agalychnis* larvae will occupy the water column. If all the bottom larvae belong to another species, the results would appear to be habitat partitioning in response to another species, not just other individual tadpoles, but with so little data, it is impossible to choose among the alternatives. Larval behavioral shifts in response to other species appear to be rare, however, and they appear to be part of the total adaptive set of the species that evidences the behavioral switch. Thus the response is completely one sided; there are no accompanying behavioral shifts in other members of the same community. My prediction is that behavioral changes in response to other tadpoles will be found in relatively specialized larvae, such as midwater adapted *Agalychnis*, such behavioral flexibility allowing greater exploitation of the habitat. Thus, when no other bottom dwelling tadpoles are present, *Agalychnis* larvae will utilize the bottom, even though their adaptive morphology is specialized for midwater feeding (Starrett, 1973).

Another factor that would refute larval competition as the origin of temporal partitioning by tadpoles is the following. At the point in the speciation process where reproductive isolation is being reinforced by selection, one premating isolating mechanism that can undergo character displacement is temporal partitioning of the breeding season. If

selection operates to displace the breeding season of two closely related taxa, the larvae would also demonstrate temporal habitat partitioning.

Finally, a theoretical model based on a community analagous to a tadpole community predicts that several phytoplankton cropping species may coexist without competitive exclusion (Smith, et al., 1975).

The available evidence indicates that communities of tadpoles represent nothing more than a collection of species co-occurring as larvae. A tadpole community is not an integrated whole; biological interactions within the community are not important evolutionarily; there is no natural selection operating directly to integrate or partition the community. Similar conclusions have been reported recently in other aquatic communities, involving predatory fish (Mendelson, 1975) and dragonfly larvae (Benke and Benke, 1975).

The Generalized Anuran Life Cycle and Its Evolutionary Maintenance

Wassersug (1975), from a morphological analysis of tadpole adaptive types, proposed that the tadpole stage evolved to exploit the bursts of primary productivity characteristic of temporary ponds. The temporary food resources are exploitable because the tadpole stage is temporary, coinciding with the bursts of primary productivity.

Heyer, McDiarmid, and Weigmann (1975) proposed a model that from an ecological viewpoint presents reasons why the generalized anuran life history should be maintained in temporary ponds during the larval stage. As long as there are temporary ponds with bursts of primary productivity, selection will favor the maintenance of the generalized anuran life cycle which includes the herbivorous tadpole stage. The total environment for which the tadpole stage is adapted is marked by extreme variability and unpredictability. The environment is unpredictable from a climatic-physical aspect. Ponds may be present in a location in one year and absent the next (Wiest, 1974; Collins, 1975). The biological environment varies in the same pond from one year to the next (Chesapeake data). For any species found in a series of ponds, the biological environment varies from pond to pond (Heyer, 1973; Wiest, 1974; BCI data).

One evolutionary response designed to exploit unpredictable environments is to maximize both reproductive effort and genetic variability simultaneously. The amphibian genetic system appears to be well suited to maximize genetic variability in its reproductive effort. Polyploidy is not known to occur in higher vertebrates (parthenogenetic lizards excluded), possibly because the higher vertebrate is a complexly integrated machine that can not function if the genetic controls are changed to any great degree. Having an extra chromosome set may be too much of a genetic change to allow the higher vertebrate cell to function properly. Polyploidy is known for lower vertebrates, including frogs, and could be interpreted to mean that the amphibian cell can tolerate considerable genetic changes and still function. (This argument does not imply that mammals are more highly evolved than frogs. It does imply that frogs have more evolutionary mechanisms available than mammals.) Wilson, Sarich, and Maxson (1974) have shown that closely related species of frogs have much larger genetic differences than similar pairs of mammal species. They assumed constant rates of protein evolution and concluded the frog species are much older than the mammal species. Another interpretation is that many mutations in albumin structure may be deleterious in the homeostatic mammalian system although such can be tolerated in the less well regulated amphibian system. These inferences suggest that compared to the mammalian genetic system, the anuran genetic system is preadapted to, and continually selected for, maintenance of large amounts of variability. One of the reasons large clutch size may be adaptive in frogs is that a wide variety of genotypes can be expressed in every reproductive effort. Some of the genotypes likely would be adaptive in the situation in which any egg clutch was laid, but due to the unpredictability of the pond environments, there is no way for natural selection to operate to select a genotype that will always work best. Natural selection would operate to select those individuals that maximized genetic variability in each reproductive effort. It is not necessary to postulate an increased mutation rate; selection would maintain, rather than reduce, the variability present.

There are no available direct data on the amounts of genetic variation present in a single

large frog egg clutch, but there is circumstantial evidence to suggest that the amount of variation is considerable. Many frog egg clutches brought in from the field and raised under laboratory conditions experience heavy mortality, particularly at three stages: gastrulation, hatching, and metamorphosis. These three times represent periods when different parts of the genotype are activated for the first time. Death may be due to defective genotypes. High genetic variability would account for this high rate of genetic death as many of the combinations are lethal in some egg clutches. Thus, it would appear that the number of genotypes is maximized within a single clutch. The larger the clutch, the more possible genotypes can be exposed and selected in the pond where the clutch is laid.

In addition to the maximizing of individual clutch size, breeding adults should produce multiple clutches in order to ensure reproductive success in an unpredictable environment. Crump (1974) found this to be true for the single gravid female recapture she reported: *Hyla rhodopepla* is a small, pond breeding hylid which produced 2 clutches in 31 days. This is the only known data on tropical pond breeding frogs other than that for *Physalasmus* previously discussed (Davidson and Hough, 1969). To achieve maximum reproductive effort, frogs in the temperate zones could either be long lived, producing one clutch a year, or if short lived, produce multiple clutches in one year. Some species of temperate frogs are known to be long lived, reproducing over several seasons (Collins, 1975). *Rana clamitans* combines long life and the production of multiple clutches within a reproductive season (literature summarized in Collins, 1975). There are no data on number of clutches laid per season by small species; in Michigan, most individuals of small frog species have only one reproductive season, but some individuals breed over at least two reproductive seasons (Collins, 1975). Thus frogs exploiting temporary ponds with large clutch size and multiple clutches would have selective advantages over frogs with smaller clutch sizes and/or single clutches. Salthe and Duellman (1973) demonstrated that, of all the frogs they studied, pond breeding frogs have egg clutches with the most eggs.

The generalized anuran life cycle involving large, multiple clutches with essentially random popula-

tion control at the larval level should occasionally result in great densities of frogs when, due to the random character of tadpole population control, there is little or no tadpole population reduction. Such outbreaks of frogs have been reported in newspapers and at least once in scientific journals (Scott and Starrett, 1974).

In some ways, the situation Calef (1973a) described is not consistent with the conclusions reached in this paper (see "Other Studies of Larval Habit Partitioning" above). The larval population dynamics were very similar in the two consecutive years studied by him. At the northern distributional limit of frog occurrence, one would not expect to find a system where larval population structures are the same from one year to the next. If the larval populations are as stable as the two year study indicates, the simplicity of the system may well account for this stability. There is one species of frog which breeds in permanent water in British Columbia. The predatory salamanders are permanent residents of the lake in which these frogs breed. Calef (pers. comm.) found salamanders in all ponds and lakes where *Rana aurora* bred. The system is apparently in a steady state and predictable; ponds are effectively permanent, predator and prey interaction always occur between the same predator and the same prey. Under these predictable conditions, Calef (1973a) concluded that the biological interactions (predator-prey) control and stabilize the community structure and population density of *Rana aurora* larvae. Calef's study adds support to the hypothesis that modifications of the anuran generalized life cycle only occur in relatively predictable environments (see "Evolutionary Modifications of the Generalized Anuran Life Cycle" below). His study also indicates that not all predictable environments are limited to tropical wet forests.

Selection, Population Control, and the Anuran Life Cycle

The data, analyses, and conclusions presented here are summarized in terms of features of the life cycle where natural selection and population control likely are most effective.

Calling Sites: Competition for calling sites is most evident in those species with long breeding seasons. In those species for which calling sites have been a limiting factor, territoriality has been a common evolutionary response (for example: *Rana clamitans*, Wells, pers. comm.; dendrobatids, Duellman, 1966, Silverstone, 1975; centrolenids, McDiarmid and Adler, 1974). Territoriality involving male calling sites can be an important population control mechanism.

Egg Deposition Sites: Egg deposition sites may be the same as calling sites (e.g. centrolenids, McDiarmid, 1975) or within the defended territory but not identical with calling sites (e.g. dendrobatids, Crump, 1972; Silverstone, 1973). Territoriality may have arisen in response to limited availability of egg deposition sites. Some non-territorial frogs have specific egg deposition sites, the availability of which may control the population size of the species (e.g. some *Phyllomedusa* lay their eggs on leaves of particular species of plants, Pyburn, pers. comm.).

Clutch Size and Number: As discussed above, selection should favor large clutch size and multiple clutches in frogs with generalized life cycles. A most effective population control at this level is climatic uncertainty, such as ponds drying up or egg masses freezing. Egg predation can be important within ponds (Walters, 1975) but unpredictable among ponds or from year to year. In these situations, selection will favor large, multiple clutches.

Larvae: Certain kinds of predator-prey interactions can have an evolutionary effect on type of pond choice by species of frogs. As argued elsewhere (Heyer, McDiarmid, and Weighmann, 1975), for selection to operate, the predator must eliminate, not reduce, tadpole populations. Predation by fish (Heyer, McDiarmid, and Weighmann, 1975) and turtles (Heyer and Muedeking, in prep.) has been identified as a factor that has likely produced evolutionary change in terms of choice of ponds; the smaller, temporary ponds, free of fish and turtles being favored. The relationship between pond size and occurrence of (either, but not both) fish and *Colostethus* larvae in the BCI stream ponds is consistent with this hypothesis.

Salamander and invertebrate predators within

temporary ponds may effectively reduce population sizes (Calef, 1973a; Walters, 1975), but the level of predation usually is variable among ponds or from year to year. In these situations, selection will favor maximizing variability of reproductive efforts; that is, large, multiple clutches will be favored.

Adults: Direct data are not available, but it seems likely that all effective population control occurs in the stages already listed. Competition for resources (other than calling or egg deposition sites) is probably not important. Scott and Starrett (1974) reported on an unusual situation where the number of adult *Agalychnis spurrelli* was several times greater in one area than normally encountered. This suggests that adult frog populations are normally well below the carrying capacity of the environment. Calef (1973a) suggested that if survivorship from juvenile to adult *Rana aurora* were similar to the rate of larval survival, the adult population would be sufficient to maintain the population, but he found adult populations to be 3 to 6 times as large as those needed to maintain the population (Calef, 1973b). Thus, for *Rana aurora*, most population reduction is occurring in the larval stage.

Evolutionary Modifications of the Generalized Anuran Life Cycle

Temporary ponds that are characterized by bursts of primary productivity occur in seasonal environments. The appearance and duration of such ponds is highly variable. By contrast, environments with little seasonality do not have bursts of primary productivity in their ponds, the ponds are long lived, and the biological communities more predictable and stable. In relatively aseasonal, stable environments, selection should operate to finely adapt the organism to the environment. There would not be a selective advantage to maximizing genetic variability within a clutch. In fact, selection should operate to reduce genetic variability to the optimum genotype(s) for the stable environment in which the species occurs. Large clutch size and multiple clutches would not have selective advantages per se. Evolution could operate on other parameters involving smaller clutch sizes that would adapt the life cycle to stable environments, such as parental care, brooding, and increase of yolk per egg, which is a prerequisite for direct development in most frogs (Salthe and Duellman, 1973; also see Heyer, 1975).

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