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BREEDING HABITS AND HABITATS OF THE AMPHIBIANS  
OF THE EDWIN S. GEORGE RESERVE, MICHIGAN, WITH  
NOTES ON THE LOCAL DISTRIBUTION OF FISHES

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INTRODUCTION

THE AMPHIBIAN FAUNA of the northeast and upper midwest of the United States is relatively well-known ecologically. The usual breeding habitats of most species, for example, are often common natural history knowledge, and species may be simply described as breeding in temporary or permanent marshes, ponds, etc. Little attention has been given, however, to two aspects of the breeding ecology of these species:

1. Quantitative information on the degree to which two or more amphibian species regularly utilize the same habitat for breeding. Predictable association of amphibian species in natural communities has important consequences for the evolution of such things as predator-prey relationships, competitive interactions, and life history characters.
2. Data to document the variation in breeding habitats used by individual species within an area. In some species of amphibia, individuals regularly discriminate between temporary and permanent aquatic habitats for breeding. Documenting the consis-

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tency of this discrimination is important for understanding the selective advantage of many characters in amphibia, especially life history characters.

Our knowledge of the natural history of the amphibia of the northeast and upper midwest of the United States (Wright 1914, Walker 1946, Bishop 1941) leads us to reject the idea that amphibian species randomly breed in permanent and temporary aquatic habitats. Regular patterns of association of species with permanent or temporary aquatic habitats have been widely recognized as a general characteristic of the group. In this paper, we quantitatively document several patterns for the amphibia of southeast Michigan.

The following report summarizes observations made from 1968 through 1975 on the breeding habits and habitats of the amphibians found on the University of Michigan's Edwin S. George Reserve and also summarizes studies made by others. Eighteen species have been reported from the Reserve, viz., *Necturus maculosus*, *Ambystoma tigrinum*, *A. maculatum*, *A. laterale*, *A. tremblayi*, *Notophthalmus viridescens*, *Hemidactylium scutatum*, *Plethodon cinereus*, *Bufo americanus*, *Acris crepitans*, *Hyla crucifer*, *H. versicolor*, *Pseudacris triseriata*, *Rana catesbeiana*, *R. clamitans*, *R. sylvatica*, *R. pipiens*, *R. palustris*. Two of these are terrestrial breeders: *Hemidactylium scutatum* oviposits near water, with subsequent aquatic larval development; *Plethodon cinereus* has direct development and does not require water for breeding. The other species all breed in water utilizing temporary and/or permanent ponds, marshes, ditches and similar aquatic environments. Their breeding habits on the Reserve are outlined in the Annotated List of Species presented below, and an analysis of their distribution and co-occurrence in the various discrete habitats we examined is provided. Because fish may prey on some of these amphibian species, this paper also includes an Appendix on the distribution of fishes on the Reserve.

Our observations on the breeding habitats of the amphibia of the Reserve are consistent with studies of these species in the more northern portions of their respective ranges. We identify three general patterns of breeding habitat use in frogs and one in salamanders.

## MATERIALS AND METHODS

## The Study Area

The E. S. George Reserve (Fig. 1), an area of approximately 5 square kilometers, is located in the southwest corner of Livingston County, Michigan, approximately 7 km west of Pinckney, 51 km northeast of Jackson and 39 km northwest of Ann Arbor. The Reserve is in Range 4 east (Michigan meridian), Township 1 north (Michigan base line) and covers Section 19 and parts of Sections 20, 29, and 30 of Putnam Township, and parts of Sections 24 and 25 of Unadilla Township. (This is corrected from Cantrall (1943: 27) (Cantrall, pers. comm.)) Part of Sayle's Lake, approximately 300 m southwest of Southwest Swamp is under the jurisdiction of the Reserve, but populations of amphibians in this lake are only indirectly considered in this study. Since its purchase by Colonel Edwin S. George in 1927, the Reserve has been entirely surrounded by a game fence, originally 3 m high and later raised to 4.2 m. The last fire on the Reserve was a ground fire which swept across the southeast corner in 1926. Since 1930 the Reserve has been maintained as a protected research area under the administration of the University of Michigan Museum of Zoology.

The Reserve lies on the northern edge of an interlobate-morainic region which was extensively eroded by glacial water. With the exception of approximately 20 hectares of high level plain in the north central part of the Reserve, the surface relief is a series of hills, kettle holes, and flat marshland. Roughly three-fourths of the Reserve is dry uplands (about one-third *Quercus-Carya* woodlots and two-thirds old fields) and the remainder is a series of scattered bogs, marshes, and swamps. There are no permanent surface streams. The annual rainfall of 75-100 cm is evenly distributed throughout the year and the frost-free season of 120-210 days (mean = ca. 160 days) generally ends in early October (Visher 1954). More detailed accounts of the physiography, meteorology, vegetation, and history of land use of the Reserve are in Rogers (1942), Cantrall (1943), and Cooper (1958). The paleoecology of the area is documented by a pollen diagram from a glacial lake (Hidden Lake) near the center of the Reserve (Andersen 1954). Sedi-

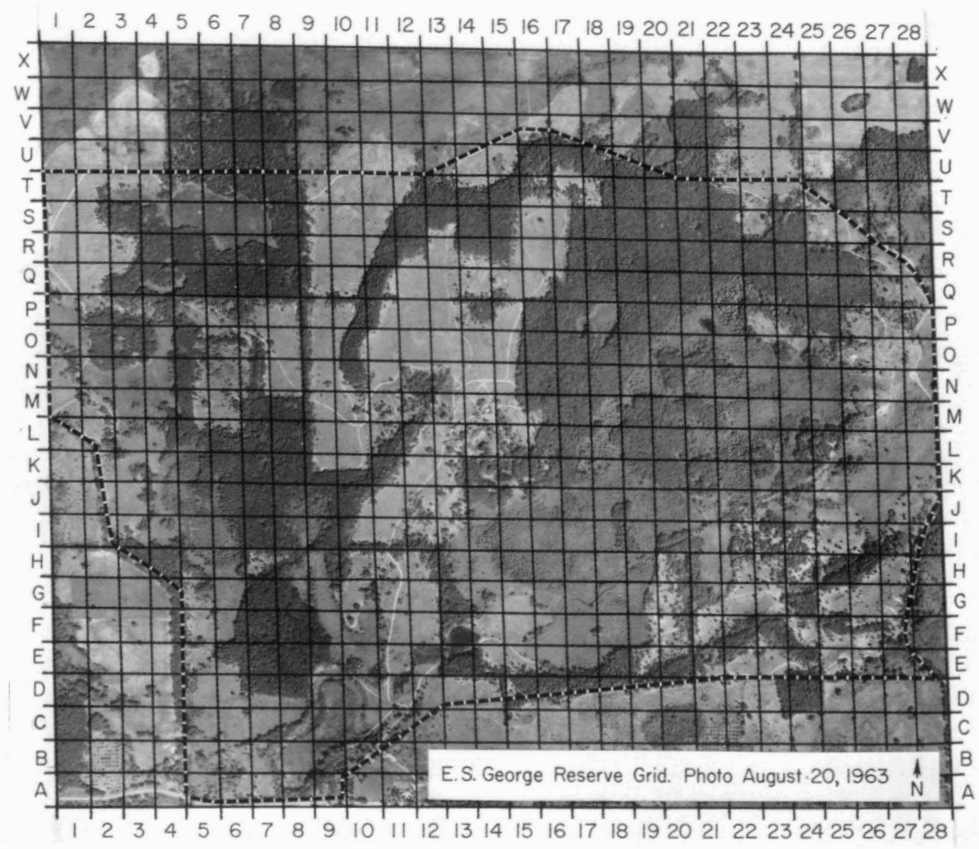


Figure 1. Grid map of the E.S. George Reserve used to locate the aquatic habitats for this study. (This Figure was supplied by, and is the property of, the University of Michigan Museum of Zoology.)

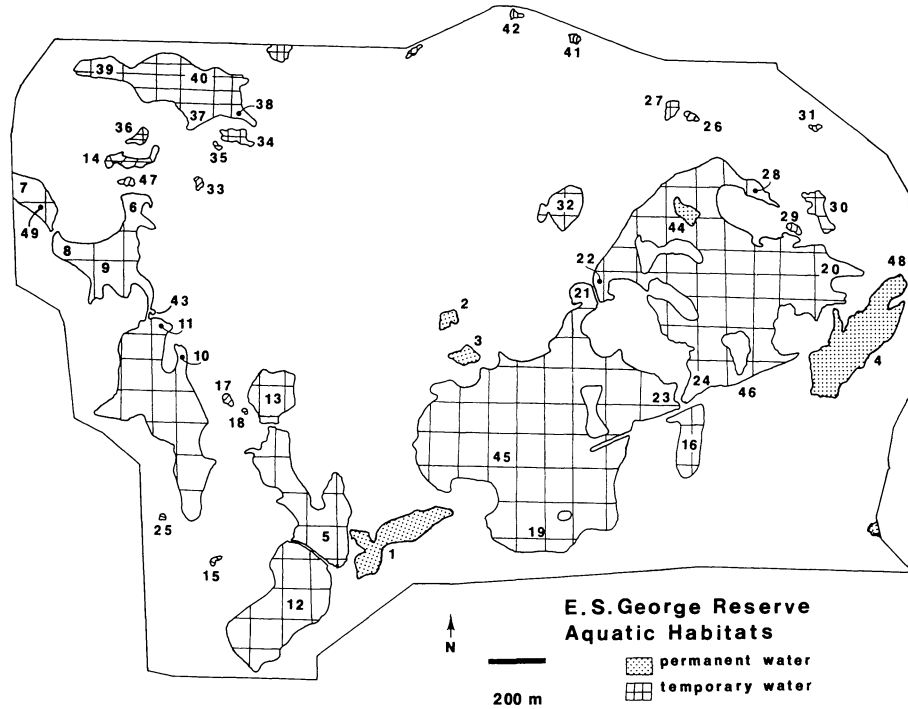


Figure 2. E. S. George Reserve aquatic habitats. Each number represents an individual habitat. Table 1 contains the 1963 E.S.G.R. grid location for each numbered habitat. *Note:* The crosshatching only indicates temporary water and does not correspond to the grid lines of Figure 1.

ments from this lake were dated by  $C^{14}$  methods to  $4550 \pm 500$  years (6.6 m) and  $4670 \pm 900$  years (7.5 m) (Crane and Griffin 1958). Descriptions of several of the aquatic habitats considered in this study (Table 1, Fig. 2) are in Archer (1939), Rogers (1942), Cantrall (1943), Sawyer (1968), and Wilbur (1971b). The present assemblage of amphibians in this area has probably been stable for about 2500 years (Dorr and Eschman 1971; Zumberger and Potzger 1955, 1956).

### Field Procedures

During this study, we identified 57 distinct aquatic habitats on the Reserve and we examined 49 (Fig. 2) for amphibians: 37 for both frogs and salamanders, and 12 for frogs only (Table 1). These habitats are categorized as (a) permanent ponds or marshes, (b) ponds, swamps, or canals which dry in exceptional years, and (c) ponds or marshes which regularly dry by late summer or autumn. Categories (b) and (c) are referred to as temporary habitats.

The amphibian populations were studied by collecting eggs, larvae, and adults at breeding habitats. During the breeding season the presence of male frogs and courting and/or mated pairs of frogs and salamanders was also recorded. Larvae were sampled with seines, dipnets, and minnow traps. Newly transformed individuals were collected around the breeding habitats. All or parts of 10 habitats were fenced to collect migrating adults and juveniles. Fences were constructed of aluminum window screen, hardware cloth, mesh reinforced plastic, or poultry netting. To trap migrating animals, metal cans (11 cm in diameter and 17.5 cm deep) and/or plastic buckets (36 × 25 × 41 cm) were sunk flush with the ground at regular intervals on both sides of each fence. Fences were buried to a depth of 15 cm and depending on the pond and the year extended 45 to 76 cm above the ground. A description of the fences used at a particular pond may be found in Collins (1975).

The following criteria were used to decide whether an amphibian species uses a habitat for breeding: (1) the presence of eggs; (2) the presence of larvae; (3) the presence of transforming animals; (4) the presence of courting or mated adults; (5) the presence of chorusing males. A chorus was any aggrega-

tion of calling males which persisted in a habitat through the breeding season or for several days at a time for discrete intervals during the breeding season. The latter was especially true in *R. catesbeiana* and *B. americanus* which do not chorus continuously through the season. Only the first three criteria were applied in those habitats which are linked with potential sources of eggs and larvae via transport in surface waters. This precaution insured against reporting nonbreeding habitats as breeding sites due to the accidental introduction of eggs or larvae. Presence of a breeding population of a species in a particular habitat is indicated by an asterisk in Table 1.

#### Analytical Procedures

For this study we did not attempt to estimate the numbers of individuals of the various species of amphibians present in any given habitat site; only the presence or absence of a breeding population was recorded. This information was used in a  $2 \times 2$  contingency table to evaluate the degree to which species pairs occurred together at different breeding sites. This simple approach to the analysis of association using data of this sort has advantages (Kershaw 1973), but there are also several sources of possible misinterpretation or statistical error (Pielou 1974: 261). In our analysis, each discrete area of free water used for breeding by a population of amphibians was considered as a distinct habitat site, without regard for its proximity to other sites. Two very closely situated temporary habitats could hold free water for very different lengths of time during a given year and could therefore support different amphibian communities.

The association between each species pair was first measured by the coefficient of association Phi ( $\phi$ ):

$$= \frac{ad - bc}{(mnr s)^{1/2}}$$

where  $a$ ,  $b$ ,  $c$ , and  $d$  are the observed cell frequencies for a  $2 \times 2$  contingency table and  $m$ ,  $n$ ,  $r$ , and  $s$  are the row and column totals, respectively (Pielou 1969: 160). The coefficient  $\phi$  is a special case of Cramér's  $V$  statistic for a  $2 \times 2$  contingency

TABLE I  
SPECIES-BY-HABITAT LIST OF AMPHIBIAN BREEDING SITES, THE EDWIN S. GEORGE RESERVE, 1967-1974<sup>1</sup>

Label site number	Type of survey	Permanence of habitat	<i>Hyla versicolor</i>	<i>Ill. crucefer</i>	<i>Pseudacris insularis</i>	<i>Bufo americanus</i>	<i>Rana catesbeiana</i>	<i>R. clamitans</i>	<i>R. pipiens</i>	<i>R. sylvatica</i>	<i>Ambystoma tigrinum</i>	<i>A. maculatum</i>	<i>A. laterale</i>	<i>A. tremblayi</i>	<i>Hemidactylum scutatum</i>	<i>Notophthalmus viridescens</i>
1 <sup>2</sup>	a <sup>3</sup>	PF <sup>3</sup>					ECBLTJSa*	CBLTJSa*			BELTJ*					BLTJ*
2	a	P	CB*			CBE*	JSa	CBLTJSa*			BELTJ*					BLETJ*
3	a	P	CBLT*			CBSa*	BLTJSa*	CBLTJSa*		J	BJELT*					
4	a	PF				CB*	CBLTJSa*	CBLTJSa*	C*						A	
5	a	OF	CB*	CB*	CB*	CBSa*	LJJSa	CBLTJSa*	C*	ECBJ*	E*					
6	a	S	C*	C*	C*	C*		CBLTJSa*								
7	b	S	C*			C*				ECB*						
8	b	O	C*	C*	C*	CB*										
9	a	S	C*	CB*	CB*	CB*										
10	b	S	C*	C*	C*	CB*										
11	b	S	C*	C*	C*	CB*										
12	a	OF	C*	C*	C*	A	CBLTJSa*	ECBLTJSa*	C*	J	B*	E*	B*	B*	B*	
13	a	S	CB*	CB*	CB*	ECBLJ*	J	CBLJSa*								
14	a	O	CBLTJ*	ECBLTJ*	ECB*	ECBLJ*	J	CBLJSa*	CJ*	ECBLTJSa*	BLTJE*	BLTJE*	BLTJE*	BLTJE*	BLTJE*	BLTJE*
15	a	S	J	CJ*	C*	JSa	J	J	J	ECBLTJSa*	BELTJ*	BELTJ*	BELTJ*	BELTJ*	BELTJ*	J
16	a	S	ECBLTJSa*	ECBLTJ*	ECBLTJSa*	JSa	J	CJ*	CB*	ECBLTJSa*	ELTB*	ELTB*	ELTB*	ELTB*	ELTB*	A
17	a	S	ECBLTJSa*	CBLT*	CBT*	JSa	J	J	J	ECBLTJSa*	BELT*	BELT*	BELT*	BELT*	BELT*	
18	a	S		CBT*	CBT*	JSa	J	J		ECBLTJSa*	BELT*	BELT*	BELT*	BELT*	BELT*	
19	b	S		C*	C*	CB*				ECBLTJSa*	BELT*	BELT*	BELT*	BELT*	BELT*	
20	b	S	C*	C*	C*	C*							B*	B*	B*	
21	a	S		C*	C*	ECB*										
22	a	S		C*	C*	ECB*										
23	b	S		C*	C*	C*										
24	b	S		C*	C*	C*										
25	a	S		C*	C*	C*										
26	a	S		C*	C*	C*					L*		L*	L*	L*	L*
27	a	S		C*	C*	C*			C*							



28	a	S		C*	C*	C*		C*		E*	E*	E*	
29	a	S	C*	C*							BEL*	BEL*	BEL*
30	a	S	C*	C*	C*	C*		C*		E*	B*	E*	
31	a	S		C*	C*			C*		E*			
32	a	O	C*	C*	C*	C*		C*					
33	a	S	C*	C*	C*	CB*			L*				
34	a	O		CBLTJ*			J	ECBTJSa*			LE*	LE*	
35	a	S									LE*	LE*	
36	a	O	CBLTJ*	CBLTJ*	EC*	CBLTJ*	J	CJ*	CBJ*	E*	LE*	LE*	
37	b	O	C*	C*		CB*							
38	a	O	C*	C*		CB*				E*	B*	E*	
39	b	S	C*	C*	C*	CB*	C*	ECB*					
40	b	S	C*	C*		CB*							
41	a	S								L*	L*	L*	
42	a	O								B*	E*		
43	a	S									L*	L*	
44	a	P	No breeding amphibian populations recorded.										
45	a	OF	No breeding amphibian populations recorded.										
46	a	OF	No breeding amphibian populations recorded.										
47	a	O	No breeding amphibian populations recorded.										
48	a	OF	No breeding amphibian populations recorded.										
49	a	OF	No breeding amphibian populations recorded.										

<sup>1</sup> *R. palustris*, *A. crepitans*, *N. maculosus*, and *P. cinereus* are excluded from this summary (see text for discussion).

<sup>2</sup> The aquatic habitats listed are those censused during this study. Each habitat number is indicated on Figure 2. The letter and number in parentheses following each name locate the habitat on the 1963 E.S.G.R. grid (Fig. 1): 1. Crane Pond (F-13); 2. George Pond (L-14); 3. Burt Pond (K-14); 4. East Marsh (L-26); 5. Fishhook Marsh (E-10). WEST MARSH (6-11, 43, 49); 6. Northern section near Grunge Pond (0-4); 7. Section northwest of West Marsh Dam (0-1); 8. West Marsh Dam Pond (N-2); 9. Section surrounding north tamarack island (M-3); 10. Section near West Woods Big Pond (J-6); 11. Section near Stream Pond (K-5); 43. Stream Pond (L-5); 49. West Marsh Stream (N-2). 12. Southwest Swamp (C-9); 13. Dollar Swamp (I-8); 14. Crescent Pond (Q-4); 15. Southwest Woods Pond (D-6); 16. Cattail Marsh (H-21); 17. West Woods Big Pond (I-7); 18. West Woods Little Pond (I-8). BIG SWAMP (19-24, 44, 45): 19. Section surrounding Period Island (F-15); 20. Gravel Pit Marsh (N-26); 21. Section southwest of Big Island-Esker Road (M-18); 22. Section northeast of Big Island-Esker Road (M-19); 23. Section southwest of Big Island-R.R. Grade Road (I-20); 24. Section northeast of Big Island-R.R. Grade Road (J-21); 44. Hidden Lake (P-21); 45. Big Swamp Canal (G-16). 25. Willow Pond (F-5); 26. Uzzell's Pond #1 (S-21); 27. Uzzell's Pond #4 (S-22); 28. Red Maple Swamp (Q-23); 29. Ilex Pond (0-25); 30. Old Gravel Pit Pond (P-26); 31. Dreadful Hollow (R-26); 32. Buck Hollow (P-18); 33. Aspen Grove Pond (P-6); 34. Cassandra East Pond (R-7); 35. Cassandra West Pond (Q-7); 36. Star Pond (R-5). CASSANDRA BOG (37-40): 37. Cassandra Bog South (R-6); 38. Cassandra Bog Southeast (R-8); 39. Cassandra Bog West (T-4); 40. Cassandra Bog North (T-6); 41. North Fence Pond (U-18); 42. North Fence Swamp (V-16); 46. Railroad Grade Canal (J-22); 47. Grunge Pond (P-4); 48. Honey Creek (N-28).

Eight Reserve aquatic habitats were not sufficiently sampled during this study to be included in this summary of distributions. These habitats and their E.S.G.R. grid numbers are: North fence fire road pond (T-13), Big Island Marsh (L-20), Northwest Woods Marsh (T-9), four small ponds in grid C-5, and Southeast Marsh (F-27). Each of these habitats, except Southeast Marsh, dries during the summer each year.

<sup>3</sup> C = presence of chorusing males; E = eggs; L = larvae, B = breeding adults, i.e., pairs mated or courting; T = transforming animals; J = juveniles; Sa = subadults; A = adults; O = pond dries in exceptional years; S = pond dries by late summer; P = permanent pond; F = fish present; \* = breeding population; a = surveyed for both frogs and salamanders; b = surveyed for frogs only.

table. Phi is also the square root of Pearson's mean square contingency coefficient with the sign of the numerator preserved. Phi may also be interpreted as a correlation coefficient since it is a special case of the Pearson product moment correlation coefficient computed by representing the classes by numbers (Conover 1971: 180; Pielou 1969: 166). The value of  $\phi$  varies from -1, when negative association between the two species is as great as possible, to +1, when positive association is as great as possible; "as great as possible" means that neither species ever occurs without the other. When the species association is nil, the coefficient is zero. See Conover (1971), Hays (1973), or Pielou (1969) for a discussion of this statistic.

The coefficient  $\phi$  also indicates the direction of association for each species pair. It is possible to test the null hypothesis that the parametric value of  $\phi$  is equal to zero, i.e. that two species are independently distributed with respect to one another; this test is provided by the chi-square test for association in a  $2 \times 2$  contingency table (Conover 1971: 184).

In testing for association between two species, Pielou (1969) notes that two different questions may be asked concerning the random (independent) distribution of two species. The first question is: among the N units examined, for example, the E.S.G.R. aquatic habitats, do two species occur independently of each other? This question assumes the marginal totals of the contingency table are fixed and the question is better phrased: for these marginal totals, what are the probabilities of the various possible sets of cell frequencies, or partitions of aquatic habitats, N? The appropriate statistical test for this question is Fisher's exact test. The values are the probabilities of obtaining a deviation by chance as great or greater than that observed. A low probability ( $< 0.05$ , for this study) is a rejection of the null hypothesis that the two species are distributed independently of one another. The two-tailed probabilities are reported.

A second question concerning independence of distribution is the following: in the population of aquatic habitats as a whole, are the two species independent of each other? This question no longer assumes fixed marginal totals for the table, but rather assumes that the present sample of N aquatic habitats is a random sample of a large population of habitats, for example, the aquatic habitats in southeast Michigan. The best statistical test for this question is the chi-square test for

independence (Pielou 1969: 164). The appropriate test for independence for each type of  $2 \times 2$  contingency table is discussed in further detail in Conover 1971: 140) and Sokal and Rohlf (1969: 588).

It is argued for  $2 \times 2$  tables (Pielou 1969, Snedecor and Cochran 1967) that, because the continuous chi-square distribution is used to approximate a discrete distribution function, it is necessary for small sample sizes ( $N < 200$ ) to compensate for this inaccuracy by the use of a "correction for continuity" originally introduced by Yates (1934). There is, however, increasing argument against this correction (Conover 1971, Remington and Schork 1970) because its use produces an overly conservative test, i.e., the corrected chi-square fails to reject the null hypothesis as often as it should (the type I error is much lower than desired). Sokal and Rohlf (1969) suggest using the correction for  $25 < N < 200$ .

Biologically, the index of association,  $\phi$ , and the following measures of independence of distribution, the chi square test and Fisher's Exact Test, simply reflect the degree to which two species occur together or fail to occur together, with no implication of cause and effect. In at least one instance, that of *A. tremblayi*, the biological basis for its positive association with *A. laterale* is obvious. For other positive or negative associations, inferences about causation require detailed natural history observations and/or experiments. A positive association always implies temporal overlap for at least the initial part of the breeding season and it implies an overlap in larval developmental periods. A negative association implies non-overlap in these characters.

## ANNOTATED LIST OF SPECIES

### Amphibia, Caudata

*Necturus maculosus*. Mudpuppy.

Mudpuppies are found in Sayle's Lake (R. M. Wiltse, pers. comm.), but this species has not been collected elsewhere on the Reserve. *N. maculosus* is typically found in large lakes or streams.

*Ambystoma tigrinum*. Tiger salamander.

Tiger salamanders live in the upland fields, probably in small-mammal burrows, throughout the Reserve. Large populations breed in Burt and George Ponds. Smaller populations breed in the larger woodland ponds. The larvae are voracious predators and have an important role near the top of a pond food web. The natural history of this species is reviewed by Wilbur (1971b, 1977) and its importance in temporary pond communities was experimentally investigated by Wilbur (1972). Wilbur and Collins (1973) discussed the ecology of metamorphosis, and Duellman (1954) discussed autumn movements in a population near Ann Arbor. Arnold (1976) discussed sexual behavior.

*Ambystoma maculatum*. Spotted salamander.

This species is found in most of the woodlots on the Reserve. Adults are fossorial and are rarely encountered except during the breeding season. Erythrogamous (= yellow) larvae were seined from Southwest Woods Pond in 1971 and 1973, but no adults were ever collected. The natural history of this species has been extensively studied on the Reserve (Arnold 1976; Wilbur 1971b, 1972, 1977; Wilbur and Collins 1973). Husting (1965) constructed a survival schedule for a population near Ann Arbor. Dempster (1930) studied growth rates in another population near Ann Arbor, and Blanchard (1930) and Smith (1907) studied breeding migrations near Ann Arbor.

*Ambystoma laterale* and *A. tremblayi*. Blue-spotted salamander and Tremblay's salamander.

These two species are members of the *Ambystoma jeffersonianum* complex. *A. laterale* is a diploid, bisexual salamander present in many woodland ponds on the Reserve. *A. tremblayi* populations are virtually all triploid females (one large-celled male was collected in the Southwest Woods Pond) and this species is a gynogenetic associate of *A. laterale*. *A. tremblayi* females require insemination by *A. laterale* males to initiate egg development, but the male genome is not incorporated into the egg nucleus. Systematic, evolutionary, and ecological aspects of this relationship have been studied on the Reserve (Uzzell 1964, 1969; Uzzell and Goldblatt 1967; Wilbur 1971a, b, 1972), and near Ann Arbor (Clanton 1934). Using skin transplantation

techniques Wilbur (unpublished data) has shown that among the specimens of *A. tremblayi* collected from the Southwest Woods Pond area salamanders have relationships ranging from presumed genetic identity (complete graft acceptance) to great dissimilarity (mutual graft rejection as rapid as between *A. tremblayi* and *A. maculatum*). *A. laterale* and *A. tremblayi* can be identified at all developmental stages using erythrocyte size (Uzzell 1964; Wilbur 1976a).

*Notophthalmus viridescens*. Red-spotted newt.

Large populations occur in George and Burt Ponds. Populations on the Reserve have a three-stage life cycle: aquatic larvae, terrestrial juveniles (efts), and aquatic adults. Efts dispersing from woodland ponds were frequently caught at drift fences as they left the ponds in the late summer, and entered the ponds in early spring. The length of time spent in the terrestrial stage on the Reserve is unknown. The eft is dull brown and rarely seen in the woodlands.

*Hemidactylium scutatum*. Four-toed salamander.

Population densities are low, but populations are present in several woodland ponds and along the margins of wooded swamps. Populations in eastern Livingston County, near Hamburg, have been extensively studied (Blanchard 1922, 1923, 1933, 1934, 1935, 1936; Blanchard and Blanchard 1931; Branin 1935).

*Plethodon cinereus*. Red-backed salamander.

This species is locally abundant in Washtenaw and Livingston Counties and it is entirely terrestrial. It was recently collected on the Reserve near Cattail Marsh (D. W. Tinkle, pers. comm.).

Three additional species of salamanders occur in Michigan. Populations of *Ambystoma opacum* and *Siren intermedia* are found only in the extreme southwestern part of the state. Several disjunct populations of *Ambystoma texanum* occur in southeastern Michigan. The closest population to the Reserve is near Ann Arbor. Although *A. texanum* does not occur on the Reserve, experimental populations were able to compete successfully with other species of *Ambystoma* in enclosures in Burt Pond (Wilbur 1972).

## Amphibia, Anura

*Bufo americanus*. American toad.

Toads are found throughout the Reserve. The largest breeding populations are in George Pond, Burt Pond, Cassandra Bog, Star Pond, Crescent Pond, and Cattail Marsh. The size of the breeding population of any habitat fluctuates significantly from night to night within a season, and from habitat to habitat between seasons. Brockelman (1968, 1969) examined the effect of larval density and predators on body size and survival in *B. americanus* larvae. The toads were collected in George and Burt Ponds and the experiments were conducted in George Pond. Intraspecific variation in egg size, egg number, and adult survival in Reserve populations are described by Collins (1975). W. Brockelman (pers. comm.) recorded calling toads in Dollar Swamp (1966), but none were heard during this study.

*Acris crepitans*. Cricket frog.

Prior to 1972 there were breeding populations of *A. crepitans* in East Marsh<sup>1</sup> (DeBenedictis 1974) and Southwest Swamp (Wilbur 1971b). The Reserve experienced a drought during 1971. Southwest Swamp dried during late August for the first time since at least 1946, and East Marsh was greatly reduced. No *A. crepitans* called on the Reserve during 1972, nor was there any calling through 1975. The early drying of these otherwise permanent aquatic habitats coupled with low juvenile recruitment and low adult survival probably caused these extinctions (Collins 1975). The population of *A. crepitans* in Sayle's Lake survived the drought.

*Hyla crucifer*. Spring peeper.

Spring peepers breed in a number of temporary water habitats throughout the Reserve. Large populations breed in open habitats such as Fishhook Marsh, Cattail Marsh, West Marsh, Southwest Swamp, Cassandra Bog, and Crescent Pond. Smaller populations breed in the woodland ponds such as West

<sup>1</sup>This marsh is called Southeast Marsh by DeBenedictis (1974). In fact, Southeast Marsh is a small marsh in the extreme southeast corner of the Reserve (Fig. 1, grid location F-27).

Woods Big, West Woods Little, and Southwest Woods. The natural history of this species on the Reserve is summarized by Collins (1975). Delzell (1958) studied growth and movement in a population located between Dexter and Pinckney, Michigan, approximately 20 km southeast of the Reserve.

*Hyla versicolor*. Gray tree frog.

During the late spring large breeding choruses are found in the open marshes such as Southwest, West, Fishhook, and Cattail. Dense populations may also be found in those woodland ponds with large quantities of emergent macrophytes, such as Crescent and Ilex Ponds. Adults of this species are rarely encountered except during the breeding season when large numbers of chorusing males are easily collected. During the breeding season large numbers of females can be collected moving from surrounding woodlots toward the breeding choruses on rainy nights and one or two nights subsequent. Males call from lily pads and other emergent vegetation, and from small bushes and trees surrounding the breeding ponds. Pairs of frogs were collected in amplexus in the oak-hickory woods surrounding Cattail Marsh. Several of these pairs were as far as 50 m from the chorus and hopping along the forest floor toward the chorus. Intraspecific variation in egg size and clutch size in the Reserve populations is described by Collins (1975).

*Pseudacris triseriata*. Chorus frog.

This is the first species to begin calling in the early spring or late winter. The densest breeding populations are found in open, marshy habitats which are often thickly littered with the dead leaves and stems of the previous year's emergent vegetation. The largest choruses were in Cattail and West Marshes. The natural history of this species on the Reserve is described by Collins (1975).

*Rana catesbeiana*. Bullfrog.

The largest breeding populations of this species are found in Southwest Swamp and Crane Pond. Individual frogs, especially females, move between these populations. Individuals in a larval year class in Crane Pond may require 13-16, or 24-25 months to complete development to metamorphosis (Collins, in

press). The natural history, growth, adult survival and variation in clutch size in Reserve bullfrogs is described by Collins (1975). Emlen (1968, 1976) and Howard (in press) discussed the social structure of the Crane Pond population. Bohnsack (1952) studied an individual using a terrestrial hibernaculum on the Reserve. In early July, 1974, a chorus of bullfrogs was heard for the first time in West Marsh Dam Pond. Six males were collected and marked, but no females were collected. This habitat was formed in 1967 by damming a small stream draining West Marsh. There is also a population of bullfrogs in Sayle's Lake. W. Brockelman (pers. comm.) recorded calling bullfrogs in Dollar Swamp (1966), but none were heard during this study.

*Rana clamitans*. Green frog.

The densest breeding population of green frogs is in West Marsh Dam Pond. A dense population in Burt Pond was destroyed by a winterkill during the winter of 1972-73. In the habitats where *R. clamitans* coexists with *R. catesbeiana*, the green frogs are present in lower numbers, probably as a result of predation by the larger bullfrogs. Bohnsack (1951) described a terrestrial hibernaculum of a green frog on the Reserve. Martof (1952, 1953, 1956) studied green frog populations near Ann Arbor.

*Rana sylvatica*. Wood frog.

On the Reserve wood frogs breed in woodland ponds, or in larger bodies of water with a margin bordered by woods. During the activity season (early spring or late winter to early autumn) adults and juveniles can be collected on the forest floor during or shortly after a rainfall. This is one of the most extensively studied species on the Reserve. Intraspecific larval competition and interspecific larval competition with *Rana pipiens* was examined by DeBenedictis (1974). DeBenedictis (1974) released *R. sylvatica* in East Marsh in 1968 which were originally collected in Emmet County, Michigan and used in his experiments. The ecological effect of wood frog tadpoles on the sympatric species of *Ambystoma* was studied by Wilbur (1972). Intraspecific larval competition was studied by Wilbur and Collins (1973) and Wilbur (1976b). Variation in egg size, clutch size, and population structure is described by Collins (1975).



Terrestrial behavior of a population at Mud Lake Bog, Washtenaw County, is described by Heatwole (1961).

*Rana pipiens*. Northern leopard frog.

Leopard frogs breed in only a few habitats on the Reserve, and none of the populations are presently very dense. Twenty years ago, leopard frogs were abundant on the Reserve and *Rana clamitans* was rare (C. F. Walker, pers. comm.). The relative abundance of these species on the Reserve is now reversed. DeBenedictis (1974) experimentally studied intraspecific larval competition and interspecific larval competition with *R. sylvatica*. In 1969, DeBenedictis (1974) released part of his experimental stock of *R. pipiens* in East Marsh. The original source of these animals was a commercial supplier who collected the animals in Vermont in the spring of 1969.

*Rana palustris*. Pickerel frog.

A single male pickerel frog was heard calling in East Marsh in 1973. There are two specimens in the UMMZ collected on the Reserve in August, 1949, near Crane Pond. DeBenedictis (1974) reported that *R. palustris* was "probably present" in East Marsh during 1968 and 1969. This species is rare.

The only other species of frogs found in Michigan are *Bufo woodhousei fowleri* and *Rana septentrionalis*. *B. w. fowleri* is found in extreme western and southern Michigan. In Michigan, *R. septentrionalis* occurs only in the Upper Peninsula.

Multi-species groups of hibernating amphibians in southern Michigan, and their hibernacula, are described by Blanchard (1933b) and Carpenter (1953). Some aspects of spring migration in amphibian populations near the Reserve were described by Carpenter and Delzell (1951).

## RESULTS AND DISCUSSION

Forty-three of the 49 sites surveyed on the Reserve had breeding populations of one or more amphibian species. Habitat characteristics and breeding data for the species found at each site are presented in Table 1. The number of breeding sites utilized by each species and the number shared with other

species are summarized in Table 2. We have also calculated all of the possible pairwise coefficients of species association,  $\phi$  (Table 2), and the probability of random association for all species pairs among frogs (Table 3), salamanders (Table 4), and frogs and salamanders (Table 5).

### Species Associations

Several species of frogs and/or salamanders often bred in the same habitat on the Reserve (Table 1). Each species exhibited some tendency to be positively or negatively associated with all other species as indicated by the index of association (Table 2). Some species pairs, however, occurred more often than would be expected by chance alone, thereby indicating tendencies to use similar habitats for breeding.

Three groups of positive species associations are recognized for frogs (Fig. 3). Two associations, *H. crucifer*  $\times$  *R. clamitans* and *H. crucifer*  $\times$  *R. catesbeiana*, are significant negative associations (Table 3).

With one exception, *H. crucifer*  $\times$  *R. sylvatica*, the positive anuran associations recognized are based on the results of Fisher's exact test and a chi-square test using the Yates correction factor. The associations between salamanders and salamanders and frogs are also based on these tests. These tests were chosen because of several instances of low expected cell frequencies (Cochran 1954, Lewis and Burke 1949), the relatively small sample sizes for each set of comparisons ( $N = 39, 25, 21$ ), and the number of comparisons made at the chosen level of significance,  $P < 0.05$ . In discussing the problem of interpreting the results of multiple chi-square tests, Cooper (1968) points out the need to be conservative in such situations. Cooper's suggested modification of the level of significance for a large number of multiple comparisons was not used because including the Yates correction factor in the test statistic yields a conservative result. With two exceptions (*H. crucifer*  $\times$  *R. sylvatica* and *H. crucifer*  $\times$  *A. laterale*), the results (Tables 3-5) using Fisher's exact test and chi-square test with the Yates correction are identical for  $P < 0.05$ .

The non-significant result for the *H. crucifer*  $\times$  *R. sylvatica* comparison was unexpected because both species bred exclu-

TABLE 2  
 COEFFICIENTS OF ASSOCIATION ( $\phi$ ) AND NUMBER OF COMMON BREEDING HABITATS FOR  
 POPULATIONS OF AMPHIBIANS, E. S. GEORGE RESERVE<sup>1</sup>

	<i>Hyla crucifer</i>	<i>H. versicolor</i>	<i>Pseudacris triseriata</i>	<i>Bufo americanus</i>	<i>Rana catesbeiana</i>	<i>R. clamitans</i>	<i>R. pipiens</i>	<i>R. sylvatica</i>	<i>Ambystoma tigrinum</i>	<i>A. maculatum</i>	<i>A. laterale</i>	<i>A. tremblayi</i>	<i>Hemidactylum scutatum</i>	<i>Notophthalmus viridescens</i>
<i>H. crucifer</i>	.33	.18	.27	.21	.1	.6	.4	.16	.10	.11	.16	.16	.3	.1
<i>H. versicolor</i>	-.09	.22	.14	.17	.2	.11	.4	.9	.8	.4	.7	.7	.1	.3
<i>P. triseriata</i>	.64*	-.14	.27	.18	.1	.6	.4	.15	.9	.10	.12	.12	.3	.0
<i>B. americanus</i>	.10	.37*	.16	.24	.2	.8	.4	.9	.7	.4	.7	.7	.0	.2
<i>R. catesbeiana</i>	-.56*	-.04	-.32*	-.08	.4	.4	.2	.0	.2	.1	.1	.1	.1	.1
<i>R. clamitans</i>	-.52*	.55*	-.20	.14	.54*	.11	.4	.4	.6	.2	.4	.4	.1	.2
<i>R. pipiens</i>	-.05	.18	.09	.15	.38*	.44*	.5	.3	.4	.2	.3	.3	.1	.0
<i>R. sylvatica</i>	.36*	-.003	.44*	-.09	-.28	-.06	.15	.16	.7	.8	.10	.10	.2	.0
<i>A. tigrinum</i>	.02	.43*	.43*	.34	.31	.60*	.46*	.14	.15	.5	.8	.8	.2	.2
<i>A. maculatum</i>	.59*	.42*	.54*	-.34	-.16	-.24	-.02	.23	-.20	.13	.12	.11	.3	.0
<i>A. laterale</i>	.58*	-.31	.14	-.31	-.20	-.14	-.01	.19	-.32	.32	.20	.19	.3	.1
<i>A. tremblayi</i>	.26	-.46*	-.04	-.46*	-.26	-.23	-.07	-.13	-.11	.21	.89*	.18	.3	.1
<i>H. scutatum</i>	.13	-.16	.23	-.43*	.33	.0	.15	.04	.14	.35	.18	.21	.3	.0
<i>N. viridescens</i>	-.79*	.35	-.64*	.08	.33	.34	-.20	-.47*	.14	-.38*	-.43*	-.37	-.14	.3

<sup>1</sup> \* = Associations significantly different from zero,  $P < 0.05$ .

TABLE 3  
 PROBABILITIES OF RANDOM ASSOCIATION OF SPECIES FOR FROGS, EDWIN S. GEORGE RESERVE<sup>1</sup>

	<i>Hyla crucifer</i>	<i>Hyla versicolor</i>	<i>Pseudacris triseriata</i>	<i>Bufo americanus</i>	<i>Rana catesbeiana</i>	<i>Rana clamitans</i>	<i>Rana pipiens</i>	<i>Rana sylvatica</i>
<i>H. crucifer</i>		.68 <sup>c</sup>	.0003	.66	.008	.004	1.0	.06
<i>H. versicolor</i>	.58 <sup>a</sup> .92 <sup>b</sup>		.49	.05	1.0	.0007	.36	1.0
<i>P. triseriata</i>	.0001 .0004	.39 .61		.48	.08	.26	1.0	.01
<i>B. americanus</i>	.53 .86	.02 .05	.32 .53		.63	.48	.63	.74
<i>R. catesbeiana</i>	.0005 .006	.78 .80	.04 .15	.62 .97		.004	.07	.13
<i>R. clamitans</i>	.001 .006	.0006 .002	.21 .39	.37 .59	.0008 .005		.02	1.0
<i>R. pipiens</i>	.76 .72	.25 .51	.58 .97	.36 .68	.02 .12	.006 .03		.63
<i>R. sylvatica</i>	.03 .08	.99 .76	.006 .02	.57 .82	.08 .22	.71 .99	.36 .66	

<sup>1</sup> a = Probability determined using a Chi-square test; b = probability determined using a Chi-square test with the Yates correction factor; c = probability determined using Fisher's exact test (2-tailed probability).

sively in temporary habitats. A positive correlation in the distribution of these two species is indicated by the  $\phi$  value (Table 2). In each of the 16 habitats occupied by *R. sylvatica*, there was at least a small breeding population of *H. crucifer* (Table 1). *H. crucifer* occurred in 17 habitats without *R. sylvatica*, since *R. sylvatica* was restricted to vernal woodland ponds or open temporary water habitats with wooded or partially wooded margins. This suggests that the positive association between *R. sylvatica* and *H. crucifer* is real, and that the marginal lack of significance is a statistical artifact due to the narrower habitat requirements of *R. sylvatica*.

Except for *A. laterale* and *A. tremblayi*, the test hypothesis of random association is accepted for the Reserve salamanders (Table 4). The positive association between *laterale* and *tremblayi* is expected because of the dependent reproductive biology of the latter (see species accounts).

With few exceptions, salamanders and frogs were independently distributed on the Reserve (Table 5). Within the temporary pond community (Table 5), *A. maculatum* was positively associated with *H. crucifer* and *P. triseriata*. The results of

TABLE 4

PROBABILITIES OF RANDOM ASSOCIATION OF SPECIES FOR SALAMANDERS,  
EDWIN S. GEORGE RESERVE<sup>1</sup>

	<i>Ambystoma tigrinum</i>	<i>A. maculatum</i>	<i>A. laterale</i>	<i>A. tremblayi</i>	<i>Hemidactylum scutatum</i>	<i>Notophthalmus viridescens</i>
<i>A. tigrinum</i>		.43 <sup>c</sup>	.16	.67	.59	.59
<i>A. maculatum</i>	.32 <sup>a</sup> .56 <sup>b</sup>		.16	.38	.22	.10
<i>A. laterale</i>	.11 .27	.11 .27		< .001	1.0	.09
<i>A. tremblayi</i>	.57 .90	.29 .57	< .001 < .001		.55	.13
<i>H. scutatum</i>	.49 .94	.08 .25	.36 .87	.30 .75		1.0
<i>N. viridescens</i>	.49 .94	.05 .19	.03 .16	.07 .26	.50 .79	

<sup>1</sup> Statistics are the same as in Table 3.

TABLE 5  
 PROBABILITIES OF RANDOM ASSOCIATION OF SPECIES FOR FROGS AND  
 SALAMANDERS, EDWIN S. GEORGE RESERVE<sup>1</sup>

	<i>A. tigrinum</i>	<i>A. maculatum</i>	<i>A. laterale</i>	<i>A. tremblayi</i>	<i>H. scutatum</i>	<i>N. viridescens</i>
<i>H. crucifer</i>	.94 <sup>a</sup>	.01	.01	.24	.54	<.001
	.51 <sup>b</sup>	.03	.07	.87	.65	.01
	1.0 <sup>c</sup>	.01	.05	.35	1.0	.01
<i>H. versicolor</i>	.05	.05	.16	.03	.48	.11
	.12	.16	.38	.11	.93	.35
	.09	.12	.31	.09	.59	.23
<i>P. triseriata</i>	.05	.01	.52	.86	.30	.003
	.12	.04	.93	.66	.75	.02
	.08	.02	.60	1.0	.55	.01
<i>B. americanus</i>	.12	.12	.16	.03	.05	.72
	.27	.27	.38	.11	.18	.78
	.20	.20	.31	.09	.09	1.0
<i>R. catesbeiana</i>	.16	.48	.36	.24	.13	.13
	.51	.93	.97	.87	.65	.65
	.48	.59	.43	.35	.27	.27
<i>R. clamitans</i>	.01	.27	.52	.29	.99	.11
	.02	.54	.93	.66	.52	.39
	.01	.36	.60	.54	1.0	.18
<i>R. pipiens</i>	.03	.92	.95	.74	.50	.36
	.11	.66	.56	.71	.91	.91
	.09	1.0	1.0	1.0	.49	1.0
<i>R. sylvatica</i>	.53	.28	.37	.55	.85	.03
	.84	.54	.71	.98	.65	.12
	.67	.39	.61	1.0	1.0	.06

<sup>1</sup> Statistics are the same as in Table 3.

Fisher's exact test and the chi-square with Yates correction are inconsistent for *H. crucifer* × *A. laterale*. However, the marginal significance of the chi-square with Yates correction and the significant pairwise coefficient of association (Table 2) suggest a tendency for these species to be associated. *N. viridescens* × *H. crucifer* and *N. viridescens* × *P. triseriata* are significant negative associations (Table 5). These negative associations are expected because, on the Reserve, *N. viridescens* typically bred in perma-

nent aquatic habitats (Table 1) while *H. crucifer* and *P. triseriata* always bred in temporary habitats.

Certain groups of species regularly bred together. Three groups of frogs (Fig. 3) selected breeding habitats with varying degrees of permanence (Table 1). Group I frogs only bred in temporary aquatic habitats. Group II frogs bred in permanent aquatic habitats, while Group III frogs bred in either permanent or temporary aquatic habitats. Ponds acceptable to frogs in Group I or Group III were suitable habitats for breeding salamanders.

Habitat Selection

Frogs bred in virtually all types of aquatic habitats on the Reserve: four permanent aquatic habitats, nine sites which dried unpredictably (temporary habitat category *b*), and 26 sites

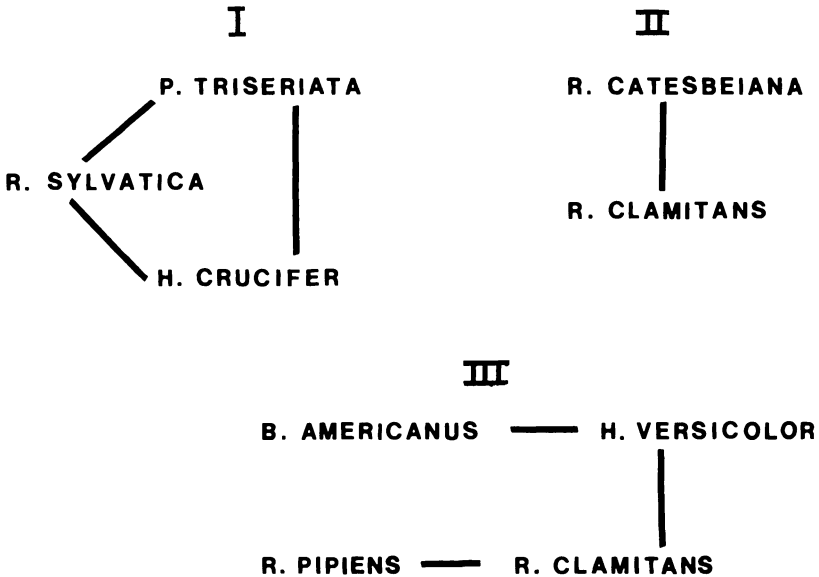


Figure 3. Summary of the significant positive breeding habitat associations for the Reserve frogs. The three species in Group I breed predominantly in temporary aquatic habitats. Species in Group II are largely restricted to permanent aquatic habits. The four species in Group III will breed in permanent or temporary aquatic habitats.

which regularly dried by late summer or autumn (temporary habitat category *c*). Frogs did not breed in ephemeral pools or puddles. Most Reserve habitats with breeding populations of salamanders were to some degree temporary aquatic habitats (Table 1), and there was no significant sorting of salamanders among these habitats (Table 4).

Group II frogs (Fig. 3) characteristically bred in permanent waters. *R. catesbeiana* bred in three permanent habitats and Southwest Swamp which dried in 1971 for the first time since at least 1946. *R. clamitans* was sympatric with *R. catesbeiana* in each site in which bullfrogs bred. *R. clamitans* also bred in five temporary habitats in category *b*. Prior to its extinction on the Reserve in 1971, *Acris crepitans* bred in Southwest Swamp and East Marsh, a permanent habitat. Each of these three species bred in permanent habitats with fish. Bullfrogs and green frogs characteristically bred in open or marshy permanent habitats, while cricket frogs selected permanent habitats with a surrounding marshy area.

In addition to *R. clamitans*, three other species bred in permanent and temporary aquatic habitats: *H. versicolor*, *R. pipiens*, and *B. americanus*. These four species are Group III (Fig. 3). Green frogs and toads were relatively dense in George and Burt Ponds which were permanent habitats with no fish and relatively few bullfrogs. Breeding individuals of these four species occurred sporadically or were absent from Crane Pond and Southwest Marsh, both of which had relatively large populations of bullfrogs and fish. *R. clamitans*, *R. pipiens*, and *H. versicolor* bred in Southwest Swamp (Table 1, habitat 12) with bullfrogs, chorus frogs, spring peepers, and cricket frogs (prior to 1971). Southwest Swamp is a large relatively permanent habitat<sup>1</sup> which afforded a diversity of microhabitats (see Rogers 1942: 34-35 for a detailed description) and accommodated breeding populations of fish and these seven species of frogs. Habitat selection in Group III species did not seem to depend on habitat duration.

*R. sylvatica*, *H. crucifer*, and *P. triseriata* bred in temporary aquatic habitats (*b* and *c* type) that generally dried by late

<sup>1</sup> Portions of Southwest Swamp were predictably dry by late summer or early autumn, while other parts dried only in exceptional years. During the drought of 1971, all areas dried for the first time since at least 1946.



summer or early autumn (with the exception of Southwest Swamp). Many of these *c*-type habitats which did not dry by autumn froze to the bottom during the winter and were functionally temporary for aquatic organisms such as fish and amphibian larvae. Spring peepers and chorus frogs were ubiquitous within these habitat types, but wood frogs were restricted to woodland vernal ponds or open temporary water habitats with wooded or partially wooded margins. Group I frogs typically bred in temporary aquatic habitats.

The breeding habitats selected by salamanders included two permanent ponds, six temporary habitats of type *b*, and 17 of type *c* (Table 1). All of these sites retained water until the end of June in wet years and, with the exception of Southwest Swamp, lacked fish populations. The Reserve salamanders which are aquatic breeders generally utilized either temporary aquatic habitats or habitats that were permanent but uninhabited by fish.

The generalizations presented above concerning the breeding habitats of the Reserve amphibians agree with descriptions of their breeding habitats in other portions of the northern part of the species ranges or, in some instances, throughout the species ranges (see for example: Bishop 1941, 1943, Wright 1914, Pope 1944, Walker 1946, Wright and Wright 1949, Logier 1952).

Breeding populations of amphibians were found in at least 43 of the 57 aquatic habitats of the George Reserve recognized for this study. These habitats were either permanent (the habitat always contained free water) or temporary (the habitat was known to dry, at least occasionally). The temporary habitats were either certain or uncertain breeding habitats. The degree of certainty was a function of the length of the larval period of a species within a season and the seasonal variation in the length of time the temporary pond had free water (Wilbur and Collins 1973, Collins 1975, Wilbur 1977). Permanent ponds could also be certain or uncertain breeding habitats. The uncertainty in these habitats was probably a function of the annual variation in the density of predators in a particular pond (Collins 1975). Hence, the degree of certainty in temporary habitats was primarily a function of abiotic factors, while in permanent habitats, biotic factors seemed to be dominant. The anuran associations recognized (Fig. 3) reflect differences in the degree of permanence of the breeding habitats of each species. The

salamanders showed little discrimination among the types of temporary aquatic habitats on the Reserve. Ponds acceptable to anurans in either Group I or Group II were acceptable to salamanders.

The preceding discussion of amphibian associations leads to consideration of the species composition of habitats and the relative density among species within habitats. Knowledge of the length and timing of breeding seasons as well as the length of larval periods results in a clearer understanding of the environmental conditions affecting larval competition and predator-prey relationships.

The three anuran groups did not breed simultaneously. Group I frogs bred in early spring. While some Group I species were still breeding, Group III species began breeding. Frogs in Group II began breeding during the breeding season of Group III several weeks after the end of breeding by Group I frogs. Group II frogs continued to breed after the end of breeding by Group III (Collins 1975).

Reserve salamanders overlapped broadly in breeding season, length of larval period, and habitat selection. Salamanders also overlapped with the Group I frogs which bred in temporary aquatic habitats. Competition and predator-prey interactions among the species utilizing temporary aquatic habitats were demonstrated by Wilbur (1971, 1972, 1976b) and Wilbur and Collins (1973). Group II frogs did not often co-occur with large numbers of other amphibians, but intraspecific competition between larval bullfrogs in Crane Pond affected length of larval period and body size at metamorphosis (Collins, in press). Group III frogs bred after salamanders in sympatric habitats.

The larval period of Group III frogs overlapped broadly the larval period of sympatric frogs from Groups I and II, and sympatric salamanders. DeBenedictis (1974) demonstrated that intra- and interspecific competition affected the body size and time of metamorphosis in *R. sylvatica* and *R. pipiens*. Brockelman (1969) demonstrated that these same variables were affected by intraspecific competition in *B. americanus*. Larval competition and predator-prey interactions within and between sympatric amphibians were a consequence of overlap in larval period. These interactions and the predictability of the aquatic habitat have an important influence on the structure of amphibian communities on the Reserve.

## CONCLUSIONS

There are three types of aquatic habitats on the Reserve, viz., permanent, temporary habitats which always dry by late summer or early autumn, and temporary habitats which may dry in exceptional years. Frogs bred in virtually all habitats on the Reserve and are excluded from only the most ephemeral ponds and puddles. The Reserve salamanders bred only in temporary aquatic habitats on the Reserve or in permanent aquatic habitats without fish.

There are three groups of frogs which regularly occur together on the Reserve. These three groups are correlated with differences in breeding habitat type: (I) *R. sylvatica*, *H. crucifer*, and *P. triseriata* bred only in temporary aquatic habitats. (III) *R. pipiens*. *R. clamitans*, *H. versicolor*, and *B. americanus* bred in either temporary aquatic habitats or permanent aquatic habitats. (II) *R. catesbeiana* and *A. crepitans* characteristically bred in permanent aquatic habitats. *R. clamitans* was always sympatric with bullfrogs in permanent habitats.

Three factors which affect the species composition and relative density of amphibians in any Reserve habitat were predictability of the aquatic habitat, timing and duration of breeding season, and duration of larval period.

## APPENDIX

Notes on the Distribution of Fishes  
on the E. S. George Reserve

The following table indicates the distribution of fishes among habitats on the Reserve. An X indicates that individuals of the species are found in the habitat (See Table 1 for E.S.G.R. grid locations).

There are two main drainage patterns on the Reserve. The primary drainage is in a northeast direction from Southwest Swamp through Fishhook Marsh, Crane Pond, the canal, and East Marsh, with an exit from the Reserve via Honey Creek. The history of this system, including man-made perturbations, is described in Rogers (1942), Mitchell (1964), DeBenedictis (1974) and Wilbur (1975). Honey Creek drains to Portage Lake and the Huron River system.

Habitat location	Fish species						
	<i>Phoxinus eos</i>	<i>Notemigonus crysoleucas</i>	<i>Umbra limi</i>	<i>Ameiurus melas</i>	<i>Culaea inconstans</i>	<i>Esox</i> sp.	<i>Moxostoma</i> sp.
Southwest Swamp	X	X	X				
Fishhook Marsh	X	X	X				
Crane Pond	X	X	X				
Big Swamp Canal	X	X	X	X	X		
Railroad Grade Canal	X	X	X	X	X		
East Marsh	X	X	X	X	X	X	X
Honey Creek	X	X	X	X	X		
West Marsh Stream			X				

The second major drainage on the Reserve is through West Marsh. Water flows north through West Marsh and leaves the Reserve via a marshy area northwest of West Marsh Dam. West Marsh Dam was constructed in 1967, forming a small pond on the southeast side. During the spring and early summer, the flow of water from the southern portion of West Marsh (south of grid K-5) to the northern portion (northwest of grid M-5) forms a temporary stream.

*P. eos*, *N. crysoleucas*, and *U. limi* are widely distributed on the Reserve. *A. melas*, *Esox*, *C. inconstans*, and *Moxostoma* are more restricted in occurrence, and are prevented from invading Crane Pond due to an elbow-shaped culvert at the eastern end of Crane Pond (grid F-14). All fish were eliminated from Southwest Swamp and Fishhook Marsh when these areas dried in 1971. The fish successfully reinvaded these habitats from Crane Pond during 1972 and subsequent years. These three habitats are contiguous, via culverts, at least in the spring of each year.

Occasional migrant fish can be found in Honey Creek, the final portion of the E.S.G.R. drainage to the east. Sunfish (*Lepomis* sp.) enter the upper reaches of Honey Creek and thus the Reserve. An elbow-shaped culvert between Honey Creek and Southeast Marsh restricts sunfish to a very small portion of the Reserve. Permanent establishment of a fish population in the

upper reaches of this tributary is prohibited by the late summer drying of the portion of Honey Creek on the Reserve.

Dr. Reeve Bailey (pers. comm.) found 18 species of fish on the Reserve during a survey conducted between 1952 and 1955. Many of these species were migrants from Honey Creek (the dam and culvert were constructed at East Marsh in 1965), or were species introduced (ca. 1942) by Colonel George. A series of winterkills eliminated the introduced species by 1962 (Mitchell 1964), and the relatively new culvert and dam at East Marsh prevent immigration from Honey Creek. DeBenedictis (1974) reported *Notropis* sp. and *Rhinichthys* sp. from East Marsh, but these species were not collected during our study.

The small stream draining West Marsh to the northwest has a population of *U. limi*, but an elbow-shaped culvert prohibits the entrance of fish to West Marsh Dam Pond. The only additional fish population on the Reserve, exclusive of Sayle's Lake, might occur in Hidden Lake. This habitat has not been sampled for a number of years, and it would not be surprising to find at least *U. limi*.

Sayle's Lake is a large (several acres), permanent, marl lake located approximately 300 m southwest of Southwest Swamp. This lake is enclosed within the boundaries of the University of Michigan Fresh Air Camp, but one-half of the margin of the lake is within the jurisdiction of the Reserve and the lake is therefore available for study. The fish fauna of Sayle's Lake is considerable. There are several species of *Lepomis*, *Micropterus salmoides*, *Pomoxis* sp., *Chaenobryttus coronarius*, *Ameriurus melas*, *Amia calva*, and several other species, none of which are adequately documented. Bailey (1955) lists a number of species of fish collected in Bass Lake, a lake which is ecologically similar to Sayle's Lake and approximately 300 m west of Sayle's Lake. Raymond (1937) described the chemical and physical characteristics, aquatic macrophytes, and plankton of Bass Lake.

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