Reproductive Ecology of the Tiger Salamander, *Ambystoma tigrinum*, in Northern Indiana

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Introduction

The tiger salamander, *Ambystoma tigrinum* (Green), is the most widely distributed species of salamander in the world. Seven subspecies range from central Alberta to Saskatchewan to the southern limits of the Mexican Plateau and from Long Island, New York to the Pacific coast of California (7). The subspecies occurring in Indiana, *A. t. tigrinum*, occurs over most of the eastern deciduous forest region except in the Appalachians (7).

Adult *A. t. tigrinum* are terrestrial burrowers except for a short period in late winter when they migrate to ponds to breed. The most detailed life history accounts of *A. t. tigrinum* are by Bishop (2) in New York and Hassinger *et al.* (8) and Anderson *et al.* (1) in New Jersey. There have been no ecological studies on midwest populations.

In 1975, we became aware of a large population of *A. t. tigrinum* breeding in a temporary pond 1 km south of Saint Mary's College. We studied various aspects of the reproductive ecology of this population in 1976 and 1977. Specific aims of the study were to determine numbers and sex ratio of breeding adults, food and growth of larvae, and details of migration of both adults and newly metamorphosed individuals.

Materials and Methods

The study pond is situated in a mowed grassy field. The pond at maximum size is one-fourth ha and 60 cm deep (Fig. 1). Milkweed (*Asclepias incarnata*) and a few red maple trees (*Acer rubrum*), cottonwoods (*Populus deltoides*) and willows (*Salix niger*) grow around the border of the pond. The pond is filled by melting winter snows and rainfall. Water was held until late July in 1976 and late May in 1977. During spring, pH of the pond is 6.8-7.0. *A. tigrinum* is the only salamander breeding in the pond, but anurans *Pseudacris triseriata* and *Bufo americanus* are present. The area surrounding the pond was once an extensive wetland, but human activities have reduced the habitat suitable for *Ambystoma* breeding to the one pond.

In 1975, the first salamanders were noted in the pond on 14 March. In 1976, we visited the pond on 28 February to set up pit traps around the pond, but seining revealed that a considerable number of salamanders were already present—46 were collected in one hour of seining. Pit traps were nevertheless set up and checked daily. These traps were set at 12 compass points about 10 m from the circumference of the pond (Fig. 1). Drift fences from each pit trap diverted immigrating salamanders into the traps. The cans used for traps were 28.0 cm in diameter and 36 cm deep. When it appeared that no more salamanders were

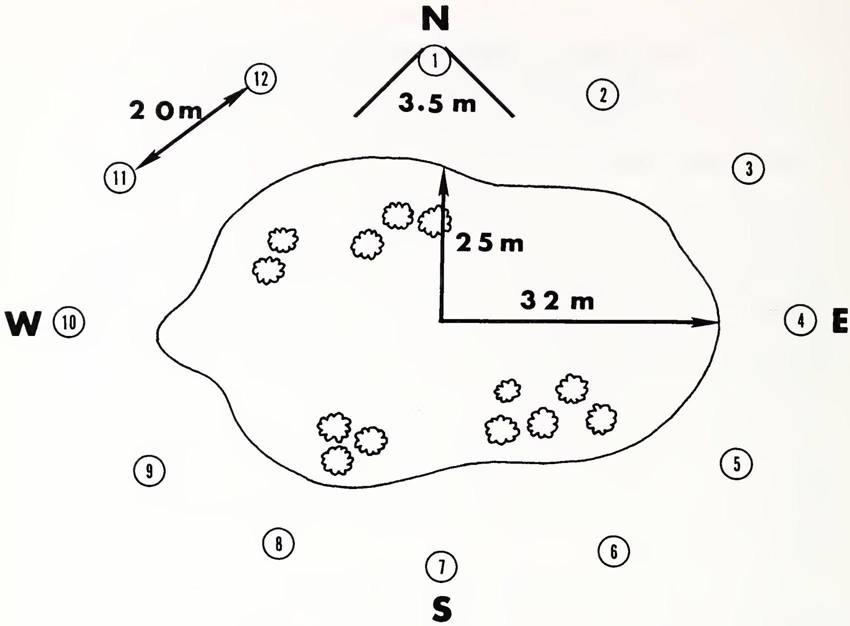

FIGURE 1. *Study pond showing dimensions at maximum size in March, distribution of trees, and placement of pit traps (numbered circles) and drift fences (on trap 1). Not drawn to scale.*

immigrating into the pond, the drift fences were turned on 23 March to sample emigrating salamanders. Additional seining samples were made on 5, 12 and 22 March, and four salamanders were caught by dipnet on 9 March. Seining on 2 April produced no specimens.

Larvae were collected throughout the period of metamorphosis in 1976, and stomach analyses of food items were made. Prior to metamorphosis, traps and drift fences were set to capture the emigrating newly metamorphosed individuals.

In 1977, traps were not used, and all adult salamanders recorded were captured by seining on 26 February; 4, 10, 21 and 29 March; 3, 11, and 15 April. Seining on 24 April produced no specimens.

Each seining effort was an hour. All salamanders were individually marked by toe-clipping. Sex was determined by the presence of swollen cloacal glands in males and the absence of such swellings in females. The snout-vent length (SVL) of all specimens was measured in the field to the nearest mm from the tip of the snout to the caudal end of the vent.

Results and Discussion

Characteristics of the Adult Population

In 1976, 189 (143♂♂:46♀♀) *Ambystoma tigrinum* were captured. Of these, 158 (122:36) were captured by seining, 24 (17:7) by traps, 4 (1:3) by dipnet and 3 (3:0) by both traps and seining. In 1977, 244 (204:40) individuals were captured for the first time by seining. The overall sex ratio in 1976 was 76.7:24.3, and in 1977 it was 84.6:16.4. The operational sex ratio is the ratio of fertilizable females to sexually active males at any one time (6). This varied considerably among samples (Fig. 2). Significance of the sex ratio is discussed after consideration of migratory movements and population size.

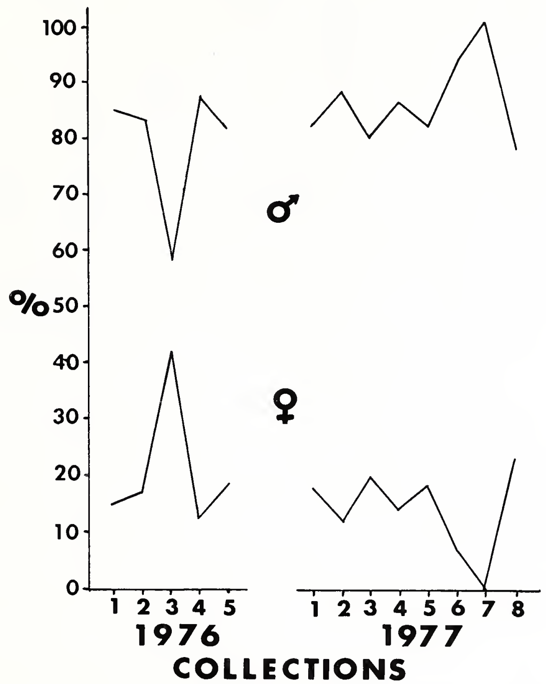

FIGURE 2. *Sequential percentage of male and female* ***Ambystoma tigrinum*** *in 1976-1977 samples.*

Size Relationships.—There was no difference at the 0.01 probability level in snout-vent lengths (SVL) among collections or between males and females (Table 1). Males ranged from 8.1-12.5 cm and females 8.5-12.6 cm SVL. Figs. 3 and 4 show frequency distributions for SVL of all specimens collected in 1976 and 1977 respectively. By inspection, both distributions are normal. It is interesting to note that the mode for 1976 was 10.5 cm, and for 1977 it was 11.0 cm (Figs. 3-4) although mean SVL did not vary much between years (Table 1).

Age classes based on SVL would be hazardous to define. Sixteen specimens originally captured and measured in 1976 were recaptured and remeasured in 1977. The average change in SVL of these 16 specimens between years is +.16 cm, which is probably within the range of measuring error. Growth of adults appears to be too slow to detect age classes by simple field measurements.

Migration of Adults.—Only 14 specimens (7♂♂:7♀♀) were captured in pit traps between 29 February-14 March, 1976, as they immigrated to the pond. Five were in the W trap, 3 in the E trap and the others in traps ENE (1), SES (2),

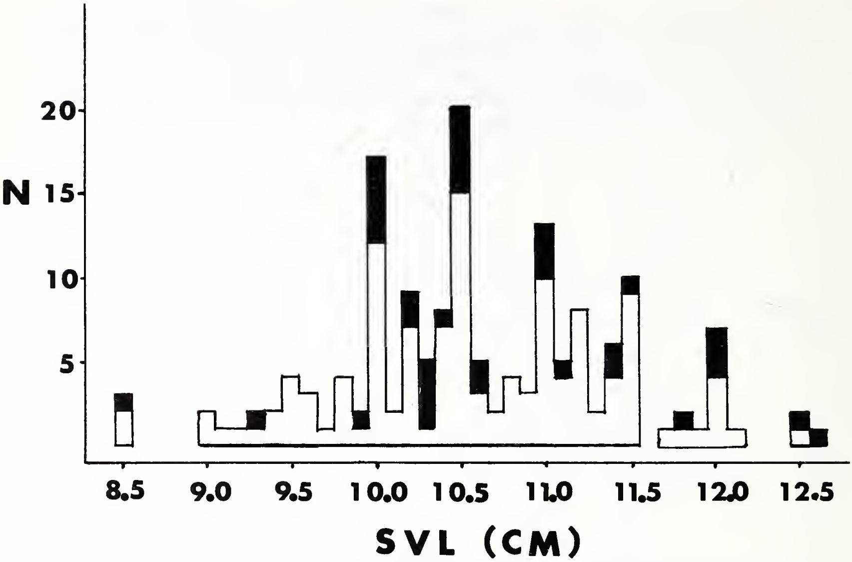

FIGURE 3. *Frequency distribution of snout-vent lengths (SVL) of **Ambystoma tigrinum** males (open blocks) and females (solid blocks) captured by seining in 1976.*

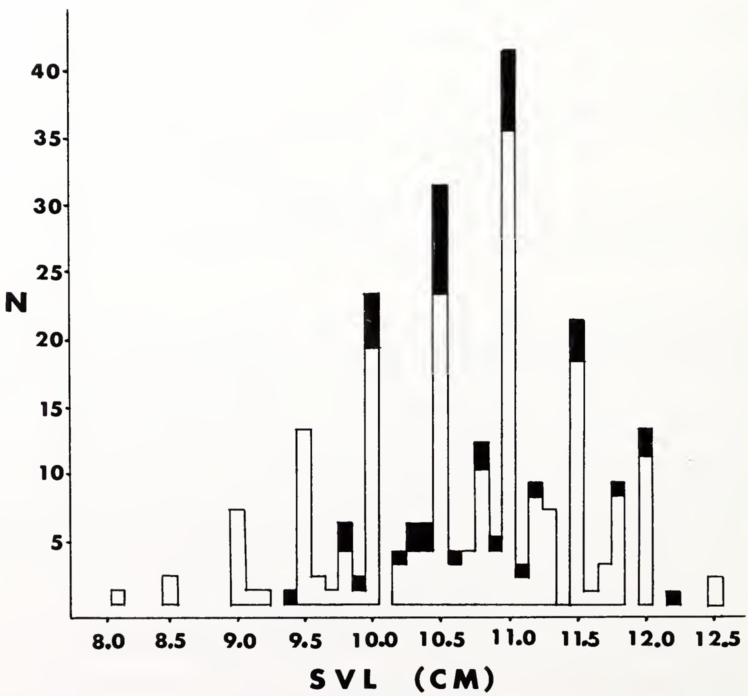

FIGURE 4. *Frequency distribution of snout-vent lengths (SVL) of **Ambystoma tigrinum** males (open blocks) and females (solid blocks) captured by seining in 1977.*

TABLE 1. *Data on snout-vent lengths of* ***Ambystoma tigrinum*** *collected in 1976 and 1977 by seining. Females for a given year were considered as a group separate from males. Data on males from each collection and females for each year were subjected to an analysis of variance. F ratios were nonsignificant at the 0.01 level.*

Date		N	Range	Mean	Var
1976					
	28 Feb	39	8.5-12.5	10.6	0.82
	5 Mar	55	8.5-12.0	10.5	0.53
	12 Mar	26	9.0-12.0	10.7	0.70
	22 Mar	12	9.8-12.1	10.8	0.50
	all ♀♀	39	8.5-12.6	10.6	0.86
			$F_s(4,167) = 0.4890$		
1977					
	26 Feb	22	9.1-12.0	10.8	0.52
	4 Mar	37	9.6-12.0	10.9	0.44
	10 Mar	51	9.0-12.5	10.6	0.80
	21 Mar	63	9.0-12.0	10.8	0.62
	29 Mar	18	9.5-12.0	10.5	0.62
	3 Ap	28	8.1-11.5	10.4	0.79
	11 Ap	25	9.0-12.5	10.7	0.64
	15 Ap	17	8.5-12.0	10.5	0.73
	all ♀♀	44	9.4-12.2	10.8	0.48
			$F_s(8,296) = 1.1507$		

SWS (2) and WSW (1). Two males captured in traps on 1 and 7 March were recaptured in the pond on 12 March.

After drift fences were turned to capture the emigrating salamanders, 13 were collected in pit traps on 29 March. Eleven of these were in traps NEN-ESE,

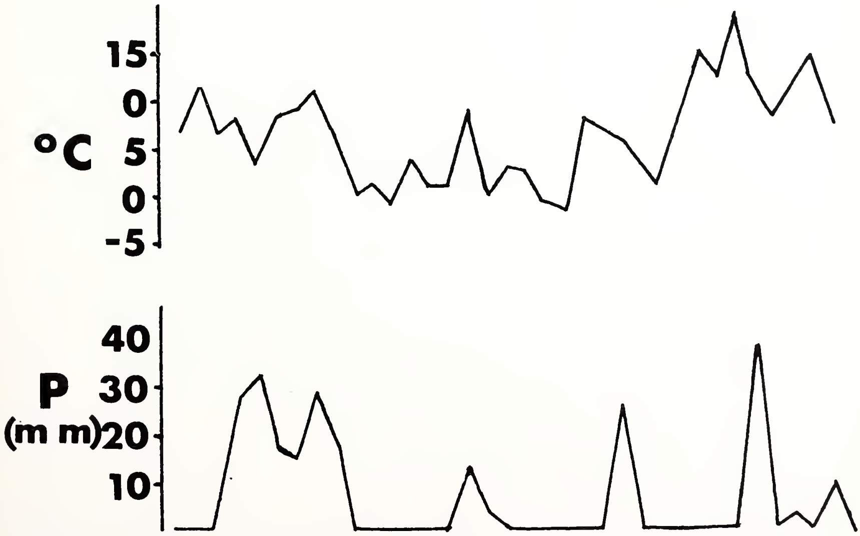

FIGURE 5. *The relation of mean temperature (°C) and precipitation (P) to numbers (N) of adult* ***Ambystoma tigrinum*** *captured in pit traps in 1976. Those captured on 30 March were emigrating individuals; the rest were immigrating to the pond.*

and the remainder were in traps N and WSW. These 13 salamanders were all males. One individual had previously been captured in the pond on 28 February, 5 and 22 March.

The relationships among adult migration, mean daily air temperature and precipitation are shown in Fig. 5. Migration was correlated with periods of precipitation. Temperature appears to show less relation to migratory behavior aside from the fact that rainfall was generally associated with a decrease in temperature.

We found no evidence of a fall migration of salamanders to the breeding pond as suggested for *A. tigrinum* by Duellman (5) in Michigan and Smith (14) in Illinois. The pond is dry in late fall and appears as a tree-line depression in the field. The first immigrating salamanders arrive during or immediately after periods of bitter cold weather, but the highest population concentrations are not found until the air temperature is in the 8-16 C range (Fig. 6).

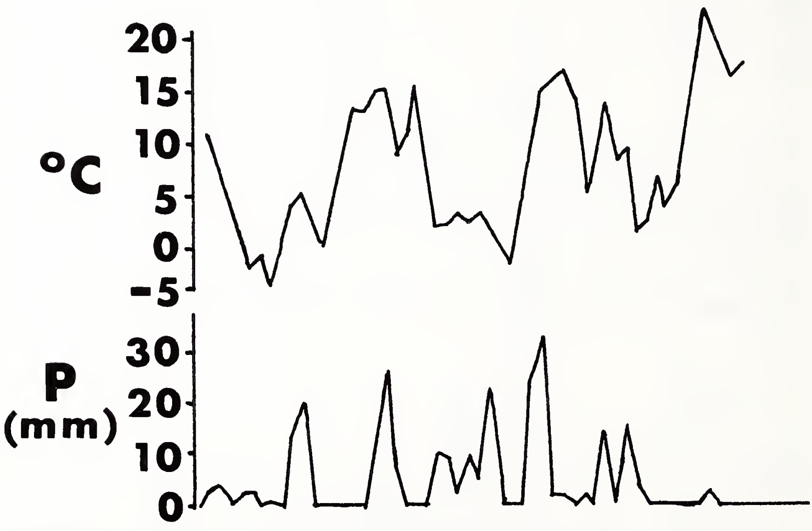

FIGURE 6. *The relation of mean temperature (°C) and precipitation (P) to Petersen population estimates (N) for samples of* ***Ambystoma tigrinum*** *obtained by seining in 1977.*

Recaptures.—In 1976, 11 specimens (5.8%) were recaptured within the breeding season. Ten were recaptured once, and one male was recaptured three times. Two of the 10, both males, were initially captured in pit traps and subsequently recaptured in the pond. Of the 10 recaptured once, three were females. Four of the males and two of the females were recaptured one collection after initial capture, and three males and one female were recaptured two collections later. The specimen recaptured three times was captured in the first seining collection on 28 February and recaptured in the pond on 5 and 22 March. Its final recapture came in a trap on 29 March. Thus this male, captured in the first and last samples of 1976, spend the entire breeding season in the pond.

Eighteen specimens (9.5%) captured in 1976 were recaptured in 1977. One was subsequently recaptured in 1977 three times, six were recaptured twice and 11 were recaptured once. Three (16.7%) of the 18 specimens were females. This percentage is similar to the overall sex ratio and indicates that some if not most female *A. trigrinum* breed annually.

There was a correlation between dates when some of these 18 specimens were initially captured in 1976 and initially recaptured in 1977. Thus two specimens originally collected on 28 February, 1976 were recaptured on 26 February, 1977, and two others originally captured on 12 March, 1976 were recaptured on 10 March, 1977. However, two specimens originally captured on 5 March, 1976 were not recaptured until 3 and 11 April, 1977. Other dates are not as close or disparate as these examples. Synchronic comparisons between 1976 and 1977 are hampered or invalidated by the extreme weather differences between the two years. The winter of 1976 was relatively mild while the winter of 1977 was the coldest on record. Salamanders arrived at the pond both years in later February, but they remained at the pond longer in 1977 (maximum until 24 April) than in 1976 (maximum until 31 March).

Of specimens initially captured in 1977, 32 (13.1%) specimens were recaptured in subsequent samples in the breeding season. Four specimens were recaptured twice. Only one female was recaptured within the 1977 collections, and she was recaptured in the subsequent two collections. Of the other three multiple recaptures, one male was recaptured in the following two collections and another was recaptured in the next collection and two collections afterwards. The final multiple recapture was a male initially collected in the first sample on 26 February, recaptured three collections later (22 March) and finally recaptured in the last collection on 15 April. So this individual, as noted for one in 1976, spent the entire breeding season in the pond.

Of the 28 specimens (all males) recaptured once during the breeding season in 1977, 11 specimens were recaptured one collection later, nine were recaptured two collections later, five were recaptured three collections later, one was recaptured four collections later and two were recaptured five collections later.

TABLE 2. *Population estimates (N) based on the Petersen method using 1976-1977 collections of* ***Ambystoma tigrinum*** *obtained by seining. 95% confidence limits were calculated using a Poisson distribution. The percentage of females is the actual value for each sample.*

Date		%♀♀	N	95% CL
1976				
	28 Feb	15.2	787	309-3149
	5 Mar	16.7	770	302-3082
	12 Mar	42.2	360	100-3600
1977				
	26 Feb	18.5	383	130-1913
	4 Mar	11.9	254	138-541
	10 Mar	20.3	1132	444-4526
	21 Mar	13.7	560	191-2796
	29 Mar	18.2	245	84-1227
	3 Ap	6.7	277	94-1387
	11 Ap	0	299	83-2990

Population Size.—Using the formula for the adjusted Petersen estimate of Ricker (13), population size was estimated between successive seining collections in 1976 and 1977 (Table 2). There was considerable variability in population estimates throughout each breeding season, ranging from 360-787 in 1976 and 245-1132 in 1977. In 1976, there were three recaptures between the first three collections and one between the last two collections. In 1977, there were nine recaptures on 10 March from the previous sample on 4 March, but between each other sample and the previous collection there were only two or three recaptures except on 15 April there was only one recapture.

Population estimates are also compared in Table 2 with actual percentage of females (operational sex ratio) per sample. In 1977 the largest population estimate was on 10 March. This sample had the second highest percentage of females (20%) for the season. The highest percentage of females in 1977 was 22.7% for the 15 April collection for which no Petersen estimate can be made, but there were relatively few salamanders left in the pond at that time. Population estimates for 29 March (245), 3 April (277) and 11 April (299) were similar, but on 29 March there were 18% females, on 3 April 6.7% females and on 11 April no females.

The disparate population estimates, low numbers of recaptures and dramatic shifts in the operational sex ratio indicate that there is variable migration among individuals to and from the breeding pond. Only four females were recaptured within a given season, none more than two collections following initial capture. This implies that females do not remain at the pond for an extended period but rather mate soon after arriving at the pond, oviposit and leave the pond. The variation in the operational sex ratio further indicates that females arrive and leave at various times, *i.e.*, there is no synchronic mass migration of females. Most male recaptures were also in the collection following initial capture, but many males were recaptured several collections later, and data on two males demonstrate that they spent the entire breeding season in the pond (see under *Recaptures*). Thus, although individual males remain at the pond for variable periods, males in general stay at the breeding pond longer than females.

Although both males and females act as individuals in their migratory movements, there are definite periods correlated with optimal weather conditions when shifts in population size imply extensive movement within the population. Such periods of mass movement are seen for the 1977 sample in Fig. 6. Population numbers increased dramatically during a period of high precipitation and rising temperature (4-10 March) and decreased during a subsequent similar period (29 March-11 April).

Other methods of estimating population size based on multiple censusing, such as those described by Ricker (13), are inappropriate when there is extensive migration.

The only other estimate of the size of a breeding population of *A. t. tigrinum* was by Anderson *et al.* (1) in New Jersey where they estimated a population of 540 adults in a series of small adjacent ponds. Because of the effects of migration throughout the breeding period, it is hard to estimate the total number of adults in our breeding population, but it could be 1500-2000 individuals.

Interpretation of the Sex Ratio.—Wilson (15) stated that ideally, a parent will not produce equal numbers of each sex but instead make equal investments in them. Female *A. tigrinum* produce and maintain large numbers of eggs and thus assume the greatest physiological burden for reproduction in the sepcies. The evolutionary strategy pursued by this species should be one by which individual females arriving at the philopatric breeding area have the greatest chance of mating, preferably with a superior male. To insure that each female offspring will find a mate, it would be advantageous for an individual to produce more males than females or to at least have all the males aggregated in one area for a period of time.

The courtship activities of *A. tigrinum* constitute the type of male dominance polygyny involving a lek (6). A lek is a communal display area where males congregate for the sole purpose of attracting and courting females and to which females come for mating. Such aggregations are typified by fairly long breeding seasons, an operational sex ratio skewed towards males, the inability of individual males to control resources necessary for female acquisition and some asynchrony in female mating receptivity (6).

These criteria seem to fit what is known about breeding activities in *A. tigrinum.* The long breeding season, communal mating area, skewed sex ratio toward males and lack of controllable resources are obvious features of this population. Asynchrony of female mating receptivity due to variable migration of females was discussed under *Population Size.* We will comment only on the communal nature of the male courtship display.

Courtship in many *Ambystoma* involves a mass display by males called the Liebesspiel (10). This was described in *A. tigrinum* by Kumpf (9) and O'Donnell (11). O'Donnell (11) stated that courtship begins by males nosing other individuals indescriminate of sex, and such nosing is permitted by both males and females. In *A. maculatum* Nobel (10) stated that such movements involve males turning back and forth over one another and rubbing snouts agains each other's tail or body in a caudo-cephalic direction. Also, the most aggressive males frequently pass under the bodies of others (10).

Females are presumably attracted to males by secretions of the male cloacal glands (9). The female follows the male with her snout applied to the male's vent (9). After the male extrudes a spermatophore, the female settles her vent over it and swims away with the apex of the spermatophore containing the spermatozoa lodged in her cloaca (9). O'Donnell (11) stated that the number of spermatophores is small, and deposition is not necessarily dependent upon presence of females or preceding courtship activities.

Thus *A. tigrinum* fits the lek strategy which explains the skewed sex ratio towards males. If the males of a population remain a long time at the breeding area while females come and go, the operational sex ratio at any one time may be highly skewed towards males. Females have the largest physical investment in the next generation, and nearly all females would be expected to mate successfully. A group of males is more likely to attract a single female than is a solitary male, and a male is more likely to encounter a receptive female when he is in a group (15). However, there may be disporportionate success among males in terms of successful matings. Larger, healthier or otherwise dominant males may mate a number of times while other males do not mate at all (6, 15).

The skewed sex ratio observed in this population may not only be related to sexual differences in length of time spent at the pond, but may also indicate that individuals produce more males than females to insure that each female finds a mate. The mechanics of maintaining such a skewed sex ratio in a dioecious species with a heterogametic and homogametic sex begs more data. The adult sex ratio is a product of three quantities: the ratio at birth, the difference in maturation time between males and females, and differential mortality (15). All three of these quantities can be functions of sexual selection (15). Work needs to be attempted on *A. tigrinum* to see if any of these factors are also responsible for the skewed sex ratio in our population of *A. tigrinum.*

Another explanation for the relatively high number of males in breeding populations of *A. tigrinum* was offered by Anderson *et al.* (1). They suggested that females have a biennial reproductive cycle while males breed annually. Our data do not support this. Of the 18 specimens originally captured in 1976 that were recaptured in 1977, three (16.7%) were females, approximately the proportion one would expect. This indicates that many, if not all female *A. tigrinum* breed annually in this population.

Survivorship.—Blanchard (3) reported that a male *A. tigrinum* raised from an egg lived 11 years in captivity. A female collected as an adult was still in good condition after seven years (3). Oliver (12) reported that an aquatic neotenic larvae of *A. tigrinum* lived 25 years and a transformed adult 16 years. Thus *A. tigrinum* is a relatively long-lived species.

We assume a variable survival rate for *A. tigrinum* throughout the year due to the marked difference in habitat between the aquatic breeding period and the terrestrial mode of life the rest of the year. However, we also assume that natural mortality will be similar among all ages of adults due to similarity of body size, slow growth and known longevity. Ricker (13) gives a formula for determining survivorship (S) based on variable rates as:

$$S = R_1 (M_2) \;/\; R_2 (M_2)$$

where R_1 = number of specimens marked in the first year and recaptured in the second, R_2 = recaptures in the second year, M_1 = number of specimens marked in the first year, and M_2 = number of specimens marked in the second year. Solving this equation for our data gives a survivorship of 71.9% with a variance of .040. This estimate proposes that roughly 72% of the salamanders that bred in 1976 survived to breed again in 1977.

Characteristics of Eggs, Larvae and Newly Metamorphosed Individuals

Hatching and Growth of Larvae.—In 1976, the first eggs were noted in the pond on 2 March and first hatching larvae on 2 April. Clutches were generally attached to vegetation bordering the deeper portion of the pond. Hatching seemed limited to April, but egg clutches in various stages of development were found throughout the month indicating again that females are asynchronous in migrating to the pond. Other workers initiated a detailed study of oviposition in the population in 1977; their results will be reported elsewhere. Our results on larval development are limited to 1976.

The frequency distributions of snout-vent lengths of larvae collected in the pond on 29 June and 19 July and of newly metamorphosed individuals caught in traps on 6 and 15 July are shown in Fig. 7. The wide range of larval sizes also indicates an extended period of egg-laying.

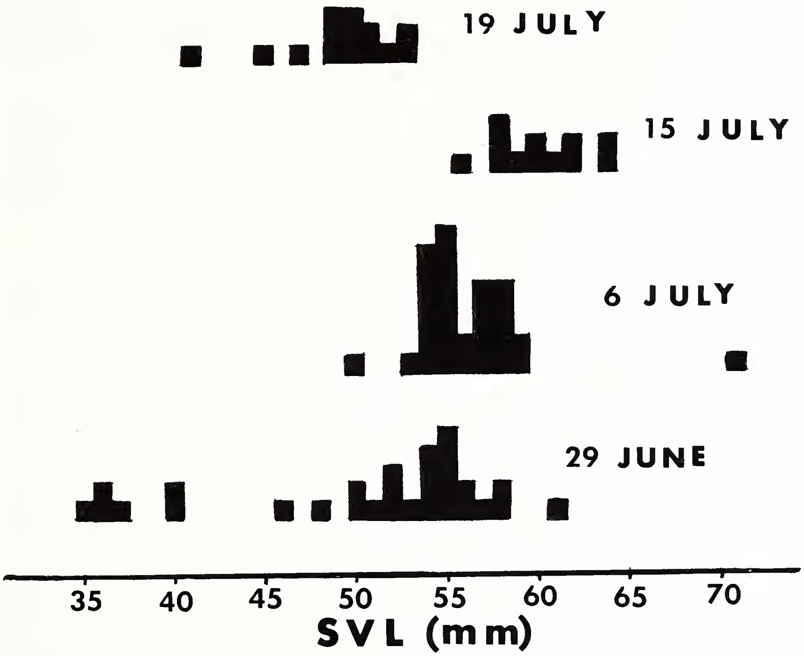

FIGURE 7. *Frequency distribution of snout-vent lengths (SVL) of larval **Ambystoma tigrinum** collected in the pond on 29 June and 19 July and of newly metamorphosed individuals captured in pit traps on 6 and 15 July, 1976.*

Toward the end of July, 1976, as the pond became nearly dry, some specimens collected in pit traps were not completely metamorphosed and still possessed gill stubs. When we visited the pond on the night of 15 July, 200 larvae were actually counted before counting was stopped as many more than that were present. As pond depressions dried, large larvae made no attempts to burrow or cross overland to other depressions still holding water. Since some trapped specimens still retained gill stubs, this suggests that the urge to emigrate is closely correlated with a specific stage of metamorphosis.

The pond dried completely on 20 July, and many larvae were found desiccated. These larvae were apparently from late broods and had not reached a critical stage necessary for emigrating behavior. Most of these desiccated larvae were quite large. Larvae that failed to leave the drying depressions were heavily preyed upon by birds, especially killdeer, bittern and grackles.

In 1977, following a prolonged drought, the pond dried completely at the end of May. No collection was made immediately prior to the drying, and it is assumed that the entire year crop was killed. Such catastrophies may play an enormous role in the dynamics of this population of *A. tigrinum*. The pond is the last suitable habitat for *A. tigrinum* in an area of several kilometers, and many man-made barriers exist in the interim.

The fate of all such ponds in succession is to disapper, but as long as the pond holds water during breeding activities, salamanders are likely to return to the pond for a number of years. The high survival rate for adults (71.9%) and longevity (16 years) indicate that the population could continue for a number of seasons without recruitment from younger classes.

Food Habits of the Metamorphosing Larvae.—In the absence of predator fishes, the larval salamanders were the top predators in the aquatic ecosystem. However, a few large, larval predacious beetles (*Dytiscus*) were observed feeding on larval *A. tigrinum*. Insect predation on small larval *A. tigrinum* was reported by Anderson *et al.*(1).

The larvae of *A. tigrinum* were voracious feeders from the time the yolk was absorbed until metamorphosis was close to completion. The larvae of all ages were primarily carnivorous. Some plant and organic detritus were consumed inadvertently while feeding on animals. Limited quantities of filamentous algae (*Oedogonium, Spriogyra, Zygemia*) were taken when the small larvae fed extensively on individual planktonic crustaceans which were feeding on algal masses attached to rooted plants. Also, organic detritus was found in the stomachs when the larvae fed on certain benthic invertebrates (*i.e., Hyalella*, chironomid larvae) and during the period when small tadpoles (*Bufo americanus*) were preyed upon in large numbers in the warm, shallow (less than 5 cm) edges of the pond.

The size of the animals as prey was a significant selective factor in the feeding habits of the larval salamanders. However, other than swallowable size, there were no species preference for prey. Selection of swallowable prey was directly correlated with abundance. In this respect the natural development and succession of invertebrates in the temporary pond supplied ample food for the population of *A. tigrinum* larvae.

All microhabitats of the pond were inhabited by the larval salamanders at some stage in their development. While the larvae moved primarily on the bottom in search of food, many were observed swimming among rooted plants. Also, they moved into planktonic zones where crustaceans were feeding on filamentous algae and into very shallow water to consume tadpoles.

In the Eubranchiopoda, which characteristically inhabit temporary ponds in early spring, the fairy shrimp population preceded the development of feeding larval salamanders. However, one species of clam shrimp was a significant food item in April. Cladocera, chiefly *Ceriodaphnia* and species of Copepoda constituted major food items. Ostracoda, a few Rotatoria and small immature insects completed the diet of larval salamanders in April.

In May, Rotatoria, mainly *Brachionus,* and water mites, Hydracarina, became important foods. The cladoceran population shifted from primarily

Ceriodaphnia to *Daphnia* and secondarily *Chydorus*. Also, for a period of about two weeks in May large numbers of *Bufo americanus* tadpoles were consumed.

The planktonic organisms remained important food items throughout June and July. However, a variety of insects formed the chief portion of the diet. Dineen (4) reported that larval *A. tigrinum* have dual feeding habits; snapping at the larger organisms when light is adequate and gulping water from a stationary position in order to sieve out plankters when the light intensity is low. Several species of Odonata and Trichoptera were common food items. The most significant families of Hemiptera were Corixidae, Gerridae, Nepidae, and Notonectidae. Coleoptera was represented in the stomachs by Dytiscidae, Hydrophilidae, Belostomatidae and Gyrinidae. Tendipedidae and Culicidae were abundant dipteran foods. Other common summer food included Amphipoda, Oligochaeta and Gastropoda. Very few Hirudinea were consumed by the larvae. Some terrestrial insects were eated by the larval salamanders. Surface feeding was observed on a few occasions in shallow water.

The newly metamorphosed individuals captured in pit traps during emigration contained mainly earthworms and terrestrial insects. However, many of the stomachs were empty.

Emigration of Newly Metamorphosed Individuals.—Traps were set up in June, 1976, and between 6-29 July, 158 newly metamorphosed individuals were caught in the traps. All 12 traps caught some specimens, but 58% were in traps NEN-ESE. The pond dried completely on 20 July, but a heavy rain refilled the pond on 21 July and 35 specimens were caught that day in traps even though there was no evidence of live salamanders in the pond the previous day. After 21 July, no larvae were found in the pond, and only seven were caught in traps. These latter specimens may have fallen into the traps during normal foraging and not have been new pond emigrants. The relationship of temperature and precipitation to numbers of specimens caught in the traps is shown in Fig. 8. Emigration was correlated with rainfall and/or low temperature.

The general easterly preference for migratory movements of newly metamorphosed specimens cannot be explained. To the east are extensive athletic fields bordering a major highway on which dead salamanders have not been observed. To the north is the campus of Holy Cross Junior College and to the south and west are large fields bordering the Saint Joseph River. The grounds-keeper of Holy Cross Junior College mentions the occasional unearthing of specimens while planting trees and doing other work on the grounds.

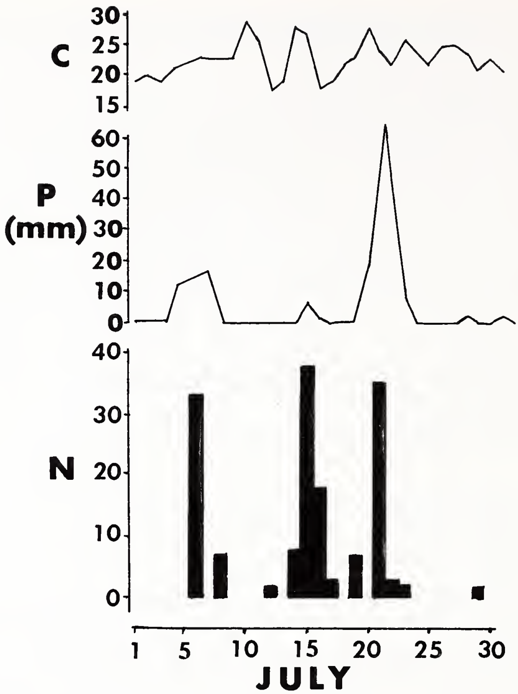

FIGURE 8. *Relation of mean temperature (°C) and precipitation (P) to numbers (N) of newly metamorphosed* ***Ambystoma tigrinum*** *captured in pit traps in July, 1976.*

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