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Field Studies of Breeding Spotted
Salamanders, *Ambystoma maculatum*,
in Eastern Missouri, U.S.A.

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Abstract

The breeding migration of a population of *Ambystoma maculatum* was studied for six seasons at a hilltop site in eastern Missouri, U.S.A., by use of the drift-fence, drop-can technique. Immigrant females were larger than males and underwent a three-fold greater reduction in mass during breeding. The male to female ratio averaged 1.86:1.0. The initiation and cessation of immigration and emigration were variable, with movement to and from the pond tending to occur in pulses. Males immigrated earlier than did females during large immigrating pulses. Spermatophores were deposited 2 or 3 d prior to egg deposition and hatching occurred approximately one month later. Immigrants and emigrants were most frequently captured at the heads of valleys around the pond perimeter. Males appear to be more consistent in the use of migratory pathways than are females. Most immigrants apparently traveled 172 m or less. Intrapopulation competition can explain many of the migratory characteristics of this species.

The spotted salamander, *Ambystoma maculatum*, is widely distributed within the deciduous forest area of the eastern United States and Canada (Anderson, 1967). The broad geographic range and extensive literature on this species make *Ambystoma maculatum* a prime target for comparative ecological studies. Topics which have been investigated include: (1) general biology (Andrews, 1897; Finneran, 1951; Gordon, 1968; Hillis, 1977; Husting, 1965; Peckham and Dineen, 1954; Smallwood, 1928; Wright, 1908; Wright and Allen, 1909); (2) migration and orientation: (Baldauf, 1952; Blanchard, 1930; Shoop, 1965, 1967, 1968); (3) sexual selection (Arnold, 1976); (4) growth, larval survivorship and metamorphosis: (Dempster, 1930; Kaplan, 1979, 1980; Pough, 1976; Shoop, 1974; Whitford and Vinegar, 1966; Wilbur, 1976; Wilbur and Collins, 1974); and (5) symbiotic relationships: (Cargo, 1960; Hutchison and Hammen, 1958; Ward and Sexton, 1981; Wilbur, 1972).

The study reported here is a descriptive summary of the annual migration of breeding adults to a woodland pond in east-central Missouri over the six breeding seasons from 1974 to 1979. The emphasis is upon: (1) the length and mass of immigrants and emigrants; (2) the sex ratio; (3) the temporal pattern of the breeding migration; (4) the constancy of the migratory pathways; and (5) terrestrial dispersion.

Location and Methods

The study area, Salamander Pond, is situated on a hilltop covered by a second-growth forest of oak and hickory on the 800 h Tyson Research Center of Washington University in western St. Louis County, Missouri, U.S.A. This area is near the northern periphery of the range of *Ambystoma maculatum* in Missouri (Anderson, 1967). The pond was constructed in 1965 and has never completely dried. Salamander Pond (Fig. 1) forms a slight crescent approximately 45 m long and 5 to 8 m wide. At high water, the surface area is about 350 m². Maximum depth originally was approximately 1 m in 1965, but the accumulation of organic debris reduced the maximum depth to 0.6-0.8 m by 1979. The surrounding terrain is hilly, ranging from about 235 m in elevation at the pond to about 180 m in surrounding lowlands. The oak-hickory forest is recovering rapidly from extensive cutting which ceased in the mid-1940s (Zimmerman and Wagner, 1979).

The site originally was a low, moist spot accumulating water temporarily. Although spotted salamanders were found on the Tyson Research Center prior to the excavation

of the pond, eggs from another pond were used to stock it in 1966. The newt, *Notophthalmus viridescens*, was also introduced. The following amphibian species invaded: *Ambystoma tigrinum* (initially very rare), *Rana catesbeiana*, *R. blairi*, *R. utricularia*, *Hyla crucifer*, *H. versicolor*, *Pseudacris triseriata*, *Acris crepitans* and *Bufo americanus*. Fish and aquatic turtles are absent, and snakes are scarce.

Salamanders were collected in numbered drop-can traps buried at intervals along both sides of the drift fence (Fig. 1) made of hardware cloth with a mesh of 0.6 cm. The cans (15 cm in diameter and 17 cm deep) were kept partially filled with water to prevent desiccation of the salamanders. In 1975, '76 and '77 the fence extended completely around the pond (Fig. 1). In 1974 only one segment was in place; this unit paralleled the span delimited by traps 4 and 17 (Fig. 1). In 1978 and '79, the complete fence was removed and replaced with two 15 m long sections which extended across known migration pathways. The first (fence A) was tangential to the eastern end of the pond at trap 18 of 1975-77. Fence B was parallel to cans 13, 14, and 15 of the same years, but was located 10 m northwest of the pond. In 1979, two other drift fences were placed across valleys serving as known migratory pathways. The first, fence C, stretched completely across the valley floor and lower hillside at a point 172 m east of fence A. The second, D, was erected across a valley 82 m northwest of cans 1-6 of 1975-77.

Visits to the cans were made at least weekly prior to the onset of migration, at least daily during migration, and terminated when no salamanders were captured during the preceding 7-14 days. Thereafter the fence was left in place but the cans were inverted. On each visit the date, time, and the location of capture, and sex of each individual salamander were recorded. Animals not taken to the laboratory for measurement were released within 4 h of removal from the traps. Immigrants were released in the pond nearest the can of capture; emigrants were released outside the fence in the leaf litter at a distance 10 m perpendicular to the capture site. The snout-vent length (SVL) and mass of those animals taken to the laboratory were recorded to the nearest mm and g, respectively. The animals were returned to the field within 24 h. Not all of the migrants were captured in the three years the pond was completely fenced. Deer sometimes knocked down portions of the fence, some salamanders climbed over intact fences, and raccoons occasionally killed animals buried along the fence. Losses due to our handling of the salamanders were well below one percent.

The deposition of spermatophores and of egg masses relative to other migratory events was recorded in 1978. Twelve bricks (20 x 10 x 5 cm) were placed on the pond bottom as deposition sites for the spermatophores. The bricks were checked daily for new spermatophores. Qualitative estimates of spermatophore deposition elsewhere in the pond were also made. Twelve horizontal wooden dowels (92 cm long and 1 cm in diameter) to serve as deposition sites for egg masses were suspended beneath the surface by two vertical supports. On six of the dowels the masses were left until the eggs hatched. On the remaining 6 rods egg masses were removed on the day after deposition.

In 1978, some meteorological variables were measured. Daily rainfall was measured with a rain gauge located in the open within 200 m of the pond. Maximum and minimum air temperatures were recorded from a thermometer placed 1 m above the ground in a shaded area 3 m south of the pond. Maximum and minimum water temperatures were recorded at a depth of 20 cm.

The counts of individual animals within any particular category, and of egg masses

and spermatophores, were treated both as numbers and as frequencies. In the latter case, the frequencies were:

$$\frac{\text{number of items counted for a particular event}}{\text{total number of items in all similar events.}}$$

The temporal aspects of migration were dated by two techniques. The first used the actual date on which a particular event occurred, the second normalized the data by numbering the dates from the beginning to the end of the migratory or emigratory period for any one year serially, e.g., 1 (first day of immigration or emigration, etc.) 2, 3 . . . n (last day). A particular date would be identified by:

$$\frac{\text{number of particular date}}{n} \quad \text{Dates, then, would range from } 1/n \text{ to } n/n \text{ or } 1.0.$$

Results

The numbers of immigrants and emigrants captured during the six breeding seasons are presented in Table 1. A decline in the adult population is evident. The pond was completely surrounded by fencing in 1975 and 1976 when 1001 and 1208 immigrants, respectively, were captured. In 1977, when the pond was still completely fenced, the total number dropped to 629. The fencing in 1978 and 1979 was comparable and the numbers of captured immigrants declined over those years from 373 to 225. This decrease, beginning with the winter of 1976-77, coincided with three successive, extremely cold winters.

Sexual Dimorphism in Body Size. — The Tyson population exhibits a marked sexual dimorphism in body size. The lengths of immigrating adults in 1975 are presented in Fig. 2. The SVL's of males ranged from 6.0 to 8.9 cm (\bar{x} = 7.6 cm). Females were 7.4 to 11.1 cm (\bar{x} = 9.1 cm). The mean SVL (\bar{x} = 9.2 \pm 0.13 cm) of 46 immigrant females in 1974 was significantly different (t_s = 463.47, df = 104, p < 0.001) from the SVL (\bar{x} = 7.91 \pm 0.11 cm) of 60 males immigrants of the same year.

Individuals of both sexes underwent a reduction in mass during the period spent in the pond. Nineteen immigrating females captured on 23-24 Mar 1975 averaged 23.2 g while 20 emigrating females captured on the same night and averaging 16.8 g were significantly different (t_s = 6.54, df = 37, p < 0.001). The mean SVL of the two groups, 8.6 cm for immigrants and 8.8 cm for emigrants, were not different (t_s = 0.9132, df = 37).

Mass losses were much less in the males. The masses of 456 immigrant males of 1975 averaged 15.6 g and the mean weight of 70 emigrants was 13.8 g (t_s = 5.37, df = 524, p < 0.001). There was no significant difference in the SVL of either subgroup, each averaging 7.6 cm.

Sex Ratio. — The ratios of males/females for both classes of migrants are presented in Table 1. Males were more frequently captured than females among immigrants of all six years, averaging almost 2 males for each female over the six year span. Males were also more abundant than females among emigrants in five of the six years. Within each year, the ratio declined from immigrants to emigrants. The major cause of this shift seems to be in the lesser number of male emigrants caught relative to male immigrants. This decline in numbers could be due to one, or a combination of three factors: (1) misjudgement of sex caused by reduction in prominence of secondary sex characters (e.g., enlarged cloacal lips of males and swollen abdomens of females) after breeding; (2) greater mortality rate of males in the pond; (3) greater

ability of emigrating males to climb over the fence. There was no evidence bearing on points 2 and 3. Data indicate that the sex ratio of migrants is not 1:1. A 2 x 6 contingency test showed that the sex ratio of immigrants is not constant year to year ($X^2 = 55$, $df = 5$, $p < 0.001$), but there was no apparent trend ($r = 0.52$, $p > 0.1$).

Temporal Sequence of Migrations. — Table 2 summarizes the data characterizing the seasonal aspects of migration to the breeding pond. The initiation of immigration was quite variable, ranging from 5 Feb. to 20-21 Mar. The earliest males arrived at the pond before or with the earliest females.

The interval between arrival of the first immigrant and that of the modal class averaged 4.5 days for females and 10.7 days for males. The modal class for both sexes coincided in each of the six seasons. The earliest modal date was 19 Feb. and the latest 20-21 Mar. The occurrence of the modal dates of immigrants fell within the span of 11-21 Mar. in four of the six years. Males tended to arrive at the pond earlier than did females during periods of peak immigration (Fig. 3). A statistical test of runs on the more extensive data from 18-19 Mar. 1975 demonstrated that males arrived significantly earlier in the evening than did females ($\mu = 2$, $N_1 = N_2 = 5$, $p = 0.008$).

Immigration terminated at different times over the years. For females, final dates ranged from 30 Mar. until 19 Apr.; for males, the dates varied from 11 Mar. to 23 Apr.

The initiation of emigration of the two sexes occurred on the same night or on two successive nights in three years, but differed by 10 days in 1977 and by 15 days in 1979. Some of the first immigrants left the pond on the same night as their arrival. The modal date of emigrants of both sexes coincided for three of the five seasons for which data are available. For both sexes, there were two or three classes with a frequency $> .20$. Emigration ceased as early as 31 Mar. or as late as 23 Apr. for females; corresponding dates for males were 30 Mar. and 23 Apr.

The immigration season for females averaged 32.3 days and 32.0 days for emigration. Overall, the migration season averaged 37.4 days for females, so that there was extensive temporal overlap between the two directional movements. Analogous values for males were, respectively, 37.5 days, 32 days and 45.6 days.

There was variability in immigration patterns even when time is normalized as in the two years which showed the extremes in immigration patterns (Fig. 4). In 1974, there were a few early male immigrants. Two large pulses of migration occurred, the first at time 0.39 and the second at the time 0.54. Thereafter a few immigrants entered the pond sporadically until near or at the end of the migration period. In 1978 there was a single, large pulse of migrants that entered the pond on the first night. Thereafter, a few immigrants moved in, but none was recorded after time 0.76.

In 1974 emigration began late (Fig. 4), at time 0.39. This initial emigration was followed by at least three large pulses. In contrast, there were only two large pulses in 1978, the first occurring at time 0.09 and the second at time 0.47.

Migration and Breeding Activities. — In 1978 we studied the temporal relationships between migration and breeding, and indirectly, time between oviposition of the eggs and hatching, by following the appearance of spermatophores and eggs and the development of the latter. The data, including records of temperature and precipitation, are summarized in Figure 5. Totals of 136 female and 237 male immigrants and of 97 female and 133 male emigrants were captured. Immigration began on the night of 20-21 March when 1.3 cm of rain fell, and the air temperature ranged from 19 to 2°C. Traps were checked at 2245 h and 0130 h when air temperatures were

12 and 8°C, respectively. Water temperature was relatively constant at 7-8°C. A total of 104 immigrant females (frequency = 0.76 of total female immigrants) and 206 immigrant males (0.87) was captured during the night.

Since most adults entered the pond during the first night, only a few were available to enter subsequently. The two largest groups were both females, 13 (0.10) on the night of 22-23 March and 14 (0.10) the night of 23-24 March when rain fell and temperatures were relatively high.

Spermatophores were deposited on the nights of 20-21, 21-22, 22-23, and 23-24 March. The first egg masses ($N = 12$, 0.26) were oviposited during the night of 22-23 March. Other sets (28, 0.60) were laid on the night of 23-24 March. Thus, there was an interval of at least two days between the deposition of the first spermatophores and the appearance of the first eggs. The pond temperature varied between 5 and 14°C during the interval between the initial immigration and the appearance of the second and largest group of eggs.

No fresh spermatophores were observed on the sampling sites subsequent to 24 March. Seven fresh egg masses were tallied at scattered intervals after that date.

Emigration began during 20-21 March, when three females (0.03) and 14 males (0.11) left the pond. The heaviest outward movements were on 23-24 March (55 females, 0.57; 57 males, 0.57) and 5-6 April (22 females, 0.23; 34 males, 0.26). The 23-24 March period coincided with the night when the largest number of egg masses were laid and with heavy precipitation, 3.43 cm. Since no female left on the preceding night when the first eggs were laid, and only 0.30 cm of rain fell, a certain level of rainfall or of moisture may be necessary for emigration to occur. The movement on 5-6 April occurred after the last small flurry of oviposition on the nights of 3-4 and 4-5 April. On 5-6 April, 1.1 cm of rain fell.

Only qualitative estimates of hatching were made in 1978. On 23 April the larvae began hatching although the young remained in the egg mass. Most had hatched by 29 April. Thus, there was an interval of about 31 days from initial egg laying (22 March) until initial hatching (23 April). The water temperature during this period ranged between 3-24°C and averaged 14.1°C with an average maximum of 16.9°C and an average minimum of 11.4°C.

Migratory Pathways. — The tallying of migrants per can-trap permitted analysis of the migratory characteristics of the breeding population. Since no salamanders were individually marked, all analyses were statistical, utilizing the numbers and frequencies of captures per can in 1975 and 1977 when the pond was completely fenced.

No class of salamander (female or male, immigrant or emigrant) of either year was uniformly distributed among the traps. Chi-square tests were performed in which the number of individuals of a specific category (e.g., immigrant females of 1975 captured in cans 1, 2, 3 — 30) were compared to the number expected were captures uniformly distributed about the periphery of the pond. The data for successive pairs of cans were lumped. The chi-square values for all eight tests were highly significant ($p < 0.001$).

The numbers and frequencies of captures in the five most effective and five least effective traps during the two migratory movements are shown in Table 3. The five most effective traps collectively captured 31.5 to 38.6% of the total immigrants, while the least effective traps captured only 1.7 to 3.1% of them. One can, number 14, captured 14.1 percent of all individual immigrant males in 1977. Among salamanders leaving, the five most effective cans registered 36.8 to 46.9 percent of the

emigrants while the five least effective traps revealed values ranging from 0.8 to 2.5 percent of the class. A high of 17.5 percent of emigrant males was recorded from can 3 in 1977.

Certain cans consistently captured large numbers of migrants. Can 9 was the most consistently effective trap, being recorded in six of the eight possibilities listed in Table 3. Other high producers were: 16 (5 times), 14 (4 times), and 3, 4 and 8 (3 times each).

The preceding analyses demonstrate that salamanders tend to enter and leave the pond at certain points. The consistency with which various classes of migrants did so was examined by use of the Spearman rank correlation technique. Cans were ordered from low to high frequencies of capture for each of eight categories, and the r_s value was determined for contrasted pairs of the categories (Table 4). In both years there was a significant correlation between the entry points of male and female immigrants as well as of emigrants, suggesting that both sexes tend to use similar migration pathways within a specific year. There were also significant correlations between the immigrating males and between emigrating males of 1975. The relationship indicates a constancy of pathways for males over the years. The females did not seem to show the same consistency over years, for their correlations were not significant.

Migration Distance. — The two sets of outlying traps provided some information about distance covered by migrants during the 1979 season. A total of five female and two male immigrants were collected at fence C while 62 female and 100 male immigrants were collected at fence A. During the same interval nine female and 17 male immigrants were captured at fence D.

During emigration, 63 female and 130 male emigrants were collected at fence A. Only one female emigrant was captured at fence C while nine female and nine male emigrants were found at fence D. The dates on which most migrants were collected at the outlying fences coincided with the dates for similar classes of migrants at the pondside fences.

Discussion

Our descriptive data will be examined under the supposition that the breeding system is best understood in terms of intraspecific competition: male vs. male, female vs. female and larva vs. larva.

Salamander Pond has a maximum surface area of 350 m^{-2} . In 1976, the year of the greatest number of immigrants, there were 868 males and 340 females in the pond, yielding densities of $2.48 \text{ } \delta \text{ m}^{-2}$ and $0.97 \text{ } \text{f} \text{ m}^{-2}$ of pond surface over the entire season. A more realistic estimate of functional density is derived by determining the accumulative frequencies of immigrants minus emigrants as shown in Figs. 4a, b, and Fig. 5. For example, on 22-23 March 1979, 83 percent of all females and 79 percent of all males were in the pond. If this maximal frequency is extrapolated to maximal abundances, one can project that in some years there might be as many as 686 males (868×0.79) and 282 females (340×0.83) in the pond simultaneously. Functional densities could be as high as $1.96 \text{ } \delta \text{ m}^{-2}$ and $0.81 \text{ } \text{f} \text{ m}^{-2}$. Such densities set the stage for severe intraspecific competition, between males for females, females for oviposition sites and larvae for food.

Male-Male Interactions. — In all years, immigrant males outnumbered females by roughly 2:1 (Table 1). Other workers (see Hillis, 1977, for a brief review) have

demonstrated the same disparate ratio. This sexual imbalance suggests that males are in intense competition for a limited resource, the females, and Arnold (1976) has documented the male-male tactics used to reduce the likelihood of a rival inseminating a female once the animals are in the pond. S. Hazen (personal communication) found that 6% of the spermatophores deposited in Salamander Pond in the 16-25 March, 1984 period were multiple spermatophores which resulted from rival males capping each other spermatophores with their own as described by Arnold (1976). Such intense male-male competition suggests that it would be sexually advantageous for a male to arrive at the breeding pond as early as is physiologically possible. The competitive situation faced by later-arriving males can be visualized by the case of the tardy immigrants of 1978 (Fig. 5). The last egg masses were deposited at the survey sites on 3-4 April (2 masses, frequency = 0.04) and 4-5 April (1, 0.02). Presumably, the females had been mated at least two days earlier, on 1-2 April or 2-3 April. Eight males (0.03) entered the ponds on the night of 2-3 April, when about 0.38 of the breeding males were still in it. The late comers probably shared very little in the success of the final breeding bout. From the earliest studies (Wright and Allen, 1909) until this one (Table 2 and Fig. 3), the arrival of greater numbers of males prior to females is well documented.

The several tactics by which early arrival is attained occur between arousal from hibernation and entrance into the pond. The first one is that immigration begins at the earliest possible time, and this time seems to be set by the co-occurrence of a ground thaw, certain minimum air temperatures, rain and overcast or nighttime conditions (Baldauf, 1952; Blanchard, 1930; Hillis, 1977; Peckham and Dineen, 1954; Whitford and Vinegar, 1966). Douglas (1979) has suggested for *A. jeffersonianum* in Kentucky that males have lower thresholds than do females for the stimuli initiating immigration. However, the coincidence of these environmental factors is extremely variable year-to-year, so there can be great discrepancies in the temporal occurrence of immigration (Table 2). Favorable constellations of these stimuli occur occasionally in December, but no salamanders have ever been trapped during those periods.

A second tactic is that animals do not immigrate over long distances. Thus, only two male immigrants were collected in 1979 at fence C, 172 m down valley from the eastern end of the pond, but 100 males were collected at the pondside fence at the head of the valley.

Thirdly, males tend to enter (and exit) at specific points along the pond periphery (Table 3). These entry points are frequently associated with valleys which would tend to funnel immigrants towards the pond, reducing travel time. Shoop (1965) found that spotted salamanders entered the breeding pond at particular points and that many individuals left the pond at the same location at which they entered it.

Female-Female Interactions. — In some years as many as 409 females immigrated (Table 1). If one assumes an average of 125 eggs per females (Bishop, 1943), a total of 51,000 eggs could be deposited, with an initial density of 146 eggs m^{-2} of pond surface. Wilbur (1972) utilized initial densities of 32 and 64 eggs of *A. maculatum* in his experimental enclosures which measured 60 cm wide \times 240 cm long for densities of 22.2 and 44.4 larvae m^{-2} respectively. His highest density was 0.3 as great as the maximal density postulated for Salamander Pond. His data indicated that a decrease in larval survivorship was a function of increased density although survivors grew rapidly. Larger larvae presumably are at a competitive advantage over smaller ones (Dempster, 1930; Shoop, 1974; Wilbur and Collins, 1974). It would

be advantageous for each female to oviposit as early in the breeding season as possible to give her offspring a competitive advantage (Wilbur & Collins, 1974). Early oviposition could be penalized by the eggs being frozen.

The behaviors of females seem to conform to this expectation. While they do not arrive as early as the males during a particular immigration episode (Figure 3), nor travel as consistently along specific migration routes (Table 4), they do arrive at the pond in bursts (Table 2).

The reduced likelihood of larval survival for progeny of females arriving late at the pond seem to preclude long distance travel by the females. The data from outlying fence C and peripheral fence A seem to support this contention since only five immigrating females were collected from the former fence but 62 were captured at the latter one.

Other evidence suggests that most females during any one year immigrate from no greater distance from the pond than can be covered by travel during one night under maximally favorable environmental conditions. However, in other studies (Husting, 1965) as well as in this one (Table 2), it is common to observe bursts of immigrants. Several logical explanations can be given to account for such bursts: (1) females live at different distances from the breeding ponds and, even under favorable conditions, the distant ones need more time for travel; (2) females hibernate in different microhabitats and are presumably stimulated to migrate at different times; (3) immigration may be interrupted by a change in the weather; (4) individual differences to stimuli initiating immigration; (5) a combination of the above. Each of these explanations probably operates at times and masks the idea that most breeding females must be close to the pond at the beginning of immigration. The evidence for the idea comes from calculating Kendall rank correlations (τ) and Spearman rank correlations (r_s) for the frequency of the modal class for each of the six years versus the date on which that event occurred. The positive correlations are just at the limit of acceptance ($\tau = 0.60$, $P_{0.05} = 0.068$; $r_s = 0.81$, $P_{0.05} = 0.829$). Probably the later in the season the modal class occurs, the higher will be the frequency of that class. For example, in 1974, the modal class (0.35) immigrated on 19 Feb. while in 1978, the modal class (0.76) immigrated on 20-21 March (Table 2). Thus, given favorable conditions over an entire night, as would be more likely to occur later in the year, most females arrive en masse, supporting the idea that most start within one night's travel of the breeding pond. Males do not demonstrate this same tendency ($r_s = 0.19$, N.S.).

Douglas (1979) suggested an interesting alternative for *A. jeffersonianum* to the hypothesis that it is advantageous for a female to arrive early at the breeding congress. He argues that female "hesitation" in reaching the pond: (1) decreases, "... the environmental dangers associated with terrestrial migration"; (2) increases the likelihood of encountering a suitor of a superior genotype. Were Douglas' hypothesis correct, the modal class of female immigrants would not coincide with that of the males. Our data (Table 2) show that the modal class of female immigrants coincides with that of the males in each of the six years. The data for 1980, not reported here, also indicate that the two modal classes coincide. Furthermore, in 1975 and 1979 proportionally more females were in the modal class than the males (Table 2). Husting (1965) also observed a coincidence of bursts of immigrating males and females.

Other Male-Female Differences. — Males and females differ considerably in their

energetic contribution to the next generation. An average female loses about 6.4 g of mass (38 percent of the post-breeding weight of emigrants) while an average male loses only about 1.8 g or 13 percent. This loss probably is a rough approximation of the mass of gametes and associated structures deposited in the pond. If this assumption is correct then females contribute about three fold more than do males. Dr. C.R. Shoop (personal correspondence) has pointed out that a better technique for measuring body mass would have been to dry the animals with paper toweling and to remove cloacal fluids by pressure. His comment is well taken but, since all animals were kept wet continuously except when actually being weighed, it seems unlikely that different hydration levels between the two sexes could account for this great discrepancy.

The sexual imbalance of the breeding population still remains an enigma, and the greater energetic contribution of the females may furnish a partial contribution to its solution. Two possible explanations for this imbalance are: (1) each female does not necessarily breed; (2) adult females experience a greater mortality rate than do males (Husting, 1965). The energetic drain can contribute to the first possibility because it might take more than one season to redress the loss (Husting, 1965). It can also contribute to the second possibility because the weakened females are more susceptible to death by any agent.

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Table 1. The numbers of immigrant and emigrant males and females of the spotted salamander, *Ambystoma maculatum*, caught in drop-cans at Salamander Pond, St. Louis County, Missouri, in 1974-1979. The pond was completely fenced in the years 1975, 1976 and 1977.

	Immigrants				Emigrants			
	Male	Female	Total	Sex ratio δ/η	Male	Female	Total	Sex Ratio δ/η
1974	300	128	428	2.34	145	101	246	1.44
1975	592	409	1001	1.45	550	450	1000	1.22
1976	868	340	1208	2.55	496	297	793	1.67
1977	381	248	629	1.54	268	304	572	0.88
1978	237	136	373	1.784	133	97	230	1.37
1979	132	93	225	1.42	174	90	264	1.93
Total	2510	1354	3864	1.86	1766	1339	3105	1.34

Table 2. Summary of the breeding migration of spotted salamanders (*Ambystoma maculatum*) at Salamander Pond, Tyson Research Center, St. Louis County, MO, U.S.A. N.A. = data not available; ? = events occurred but no numbers recorded; the number in parentheses refers to frequencies.

	1974		1975		1976		1977		1978		1979	
	Female	Male	Female	Male	Female	Male	Female	Male	Female	Male	Female	Male
Immigrant N	128	300	409	592	340	868	248	381	136	237	93	132
Date and Frequency of:												
First Immigrants	19 Feb (0.35)	18 Feb (0.01)	7 Mar (0.21)	5 Feb (0.01)	3 Mar (0.03)	3 Mar (0.02)	11-12 Mar (0.75)	5 Mar (0.01)	20-21 Mar (0.76)	20-21 Mar (0.87)	3-4 Mar (0.08)	3-4 Mar (0.22)
Modal class	19 Feb (0.35)	19 Feb (0.46)	18-19 Mar (0.71)	18-19 Mar (0.53)	4 Mar (0.40)	4 Mar (0.70)	11-12 Mar (0.75)	11-12 Mar (0.82)	20-21 Mar (0.76)	20-21 Mar (0.87)	18-19 Mar (0.68)	18-19 Mar (0.50)
Other Immigrant Classes with Frequencies > 0.20	10 Mar (0.25)	21 Feb (0.24)	7 Mar (0.21)	7 Mar (0.39)	8 Mar (0.26) 29 Mar (0.23)	None	None	None	None	None	22-23 Mar (0.23)	3-4 Mar (0.22) 22-23 Mar (0.22)
Last Immigrants	8 Apr (0.02)	11 Mar (0.01)	19 Apr (0.01)	23 Apr (0.01)	30 Mar (0.03)	20 Apr (0.01)	2 Apr (0.01)	29 Mar (0.01)	15-16 Apr (0.01)	15-16 Apr (0.01)	31 Mar (0.02)	1 Apr (0.01)
Emigrant N	101	145	450	550	297	496	304	268	97	133	90	174
Date and Frequency of:												
First Emigrants	4 Mar (0.01)	3 Mar (0.01)	7 Mar (0.01)	7 Mar (0.01)	N.A.	N.A.	2 Mar (?)	12 Mar (?)	20-21 Mar (0.03)	20-21 Mar (0.11)	18-19 Mar (0.08)	3-4 Mar (0.03)
Modal Class	10 Mar (0.43)	10 Mar (0.53)	27 Mar (0.36)	18-19 Mar (0.24)	N.A.	N.A.	19 Mar (0.31) 28 Mar (0.31)	28 Mar (0.51)	23-24 Mar (0.57)	23-24 Mar (0.43)	22-23 Mar (0.53)	22-23 Mar (0.51)

Table 2 (Continued)

Other Emigrant Classes with Frequencies >0.20	29 Mar (0.30)	29 Mar (0.27)	10 Apr (0.28)	27 Mar (0.20) 19 Apr (0.21)	N.A.	N.A.	22 Mar (0.21)	19 Mar (0.20)	5-6 Apr (0.23)	5-6 Apr (0.26)	None	18-19 Mar (0.33)
Last Emigrants	8 Apr (0.06)	8 Apr (0.01)	23 Apr (0.03)	23 Apr (0.05)	N.A.	N.A.	20 Apr (0.01)	30 Mar (0.01)	15-16 Apr (0.03)	23 Apr (0.01)	31 Mar (0.07)	12 Apr (0.01)
Days between:												
First & Last Immigrants	48	21	43	77	27	48	22	24	26	26	28	29
First Immigrant and Modal Class	0	1	11	41	1	1	0	6	0	0	15	15
First & Last Emigrants	35	36	47	47	N.A.	N.A.	39	18	26	34	13	25
First Emigrants and Modal Class	6	7	20	11	N.A.	N.A.	7	16	3	3	4	19
First Immigrants & First Emigrants	13	13	0	30	N.A.	N.A.	1	7	0	0	15	0
First Immigrants & Last Emigrants	48	49	47	77	N.A.	N.A.	40	25	26	34	28	43

Table 3. The five most and the five least effective can-traps for capturing spotted salamanders in 1975 and 1977. "Can" refers to the number of the can, "No." to the number of salamanders trapped during the appropriate seasons and "Freq." to the frequency of capture of salamanders in a particular can.

		1975						1977					
		Most			Least			Most			Least		
		Can	No.	Freq.	Can	No.	Freq.	Can	No.	Freq.	Can	No.	Freq.
Immigrants		16	38	.093	30	4	.010	14	35	.141	29	2	.008
Female		13	30	.073	12	2	.005	9	22	.089	19	2	.008
		3	30	.073	15	1	.002	24	16	.065	18	2	.008
		9	29	.071	25	0	.000	28	15	.060	21	1	.004
		4	29	.071	24	0	.000	25	15	.060	2	0	.000
		$\Sigma = 156$	$\Sigma = .381$		$\Sigma = 7$	$\Sigma = .017$		$\Sigma = 103$	$\Sigma = .315$		$\Sigma = 7$	$\Sigma = .028$	
Male		9	53	.090	21	6	.010	14	35	.092	20	4	.010
		16	45	.076	26	5	.008	4	33	.087	15	4	.010
		13	43	.073	28	4	.007	9	31	.081	22	3	.008
		4	43	.073	25	0	.000	8	24	.063	2	1	.003
		11	40	.068	24	0	.000	7	24	.063	21	0	.000
		$\Sigma = 224$	$\Sigma = .380$		$\Sigma = 15$	$\Sigma = .025$		$\Sigma = 147$	$\Sigma = .386$		$\Sigma = 12$	$\Sigma = .031$	
Emigrants		16	43	.096	29	3	.007	3	43	.141	24	1	.003
Female		8	42	.093	24	3	.007	17	23	.076	23	1	.003
		14	31	.069	13	3	.007	12	20	.066	1	1	.003
		19	28	.062	28	2	.004	20	17	.056	29	0	.000
		9	27	.060	30	0	.00	15	17	.056	28	0	.000
		$\Sigma = 17$	$\Sigma = .380$		$\Sigma = 11$	$\Sigma = .025$		$\Sigma = 120$	$\Sigma = .395$		$\Sigma = 3$	$\Sigma = .009$	
Male		16	50	.091	28	2	.004	3	47	.175	23	1	.004
		14	41	.075	26	2	.004	15	25	.093	22	1	.004
		6	38	.069	27	1	.002	17	18	.067	29	0	.000
		9	37	.067	24	1	.002	16	18	.067	26	0	.000
		8	36	.066	30	0	.000	11	18	.067	24	0	.000
		$\Sigma = 202$	$\Sigma = .368$		$\Sigma = 6$	$\Sigma = .012$		$\Sigma = 126$	$\Sigma = .469$		$\Sigma = 2$	$\Sigma = .008$	

Table 4. Summary of Spearman rank correlations between frequencies of captures in can-traps of selected classes of migrating spotted salamanders, *Ambystoma maculatum*. There are 28 degrees of freedom for each test. t_s = Student's t ; P = two-tailed probability; Im = immigrant; Em = emigrant; N.S. = not significant.

Contrasted Classes	r_s	t_s	P
Im ♀ 1975 vs. Im ♂ 1975	0.80	7.06	.001 = 3.674
Im ♀ 1977 vs. Im ♂ 1977	0.71	2.66	.02 = 2.467
Em ♀ 1975 vs. Em ♂ 1975	0.92	12.57	.001 = 3.647
Em ♀ 1977 vs. Em ♂ 1977	0.67	4.78	.001 = 3.647
Im ♀ 1975 vs. Im ♀ 1977	0.05	0.26	N.S.
Im ♂ 1975 vs. Im ♂ 1977	0.49	2.97	.01 = 2.763
Em ♀ 1975 vs. Em ♀ 1977	0.34	1.92	N.S.
Em ♂ 1975 vs. Em ♂ 1977	0.46	2.74	.02 = 2.467

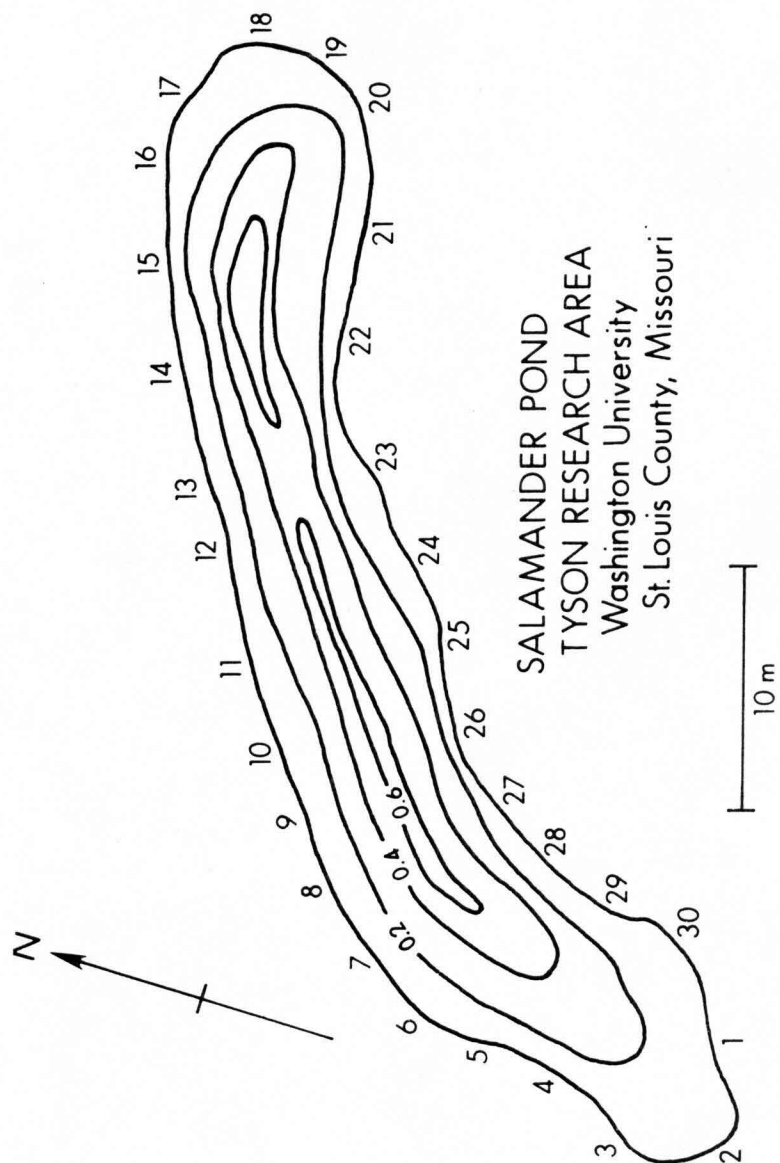


Figure 1. A map of Salamander Pond, Tyson Research Area, Washington University, St. Louis County, MO, U.S.A. as plotted on 26 February, 1975. The depth contours are at 0.2 m intervals, and the two deepest points are 0.62 (m) and 0.61 (m). The numbers around the perimeter indicate the location of the paired drop-cans, one on either side of a drift fence which surrounded the pond in the breeding seasons of 1975 through 1977.

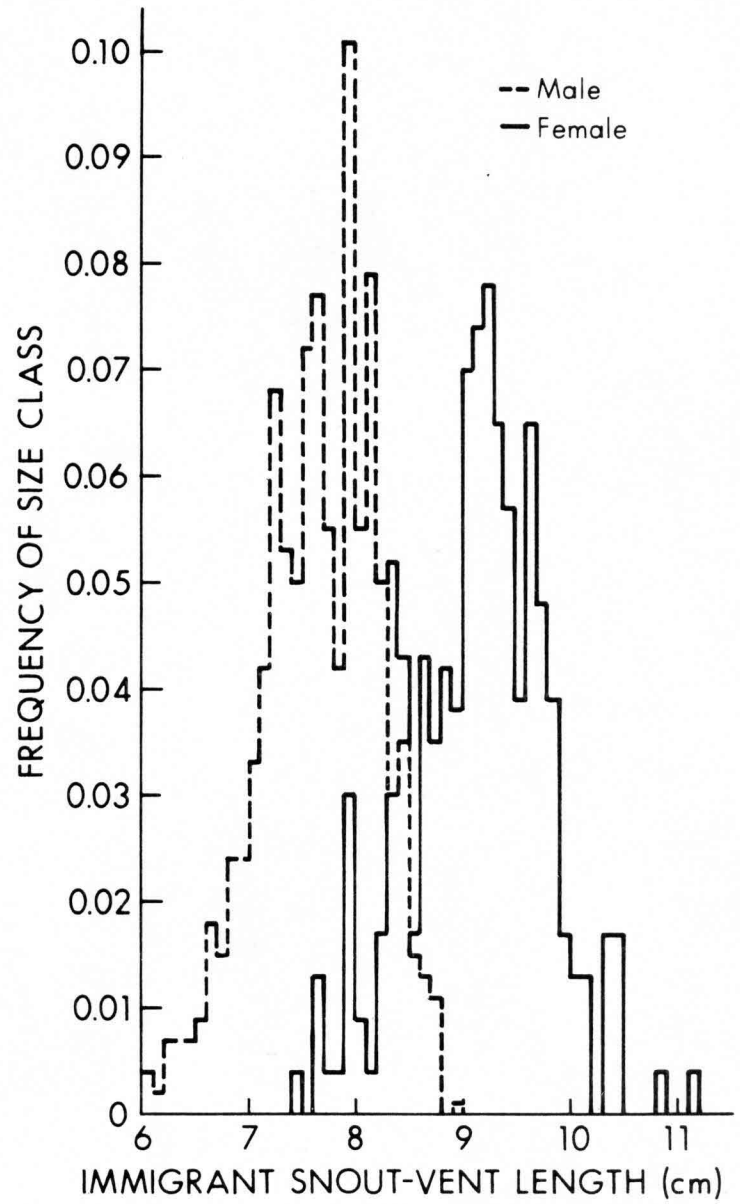


Figure 2. Histograms of the snout-vent lengths of 456 male and of 230 female spotted salamanders immigrating to Salamander Pond in 1975.

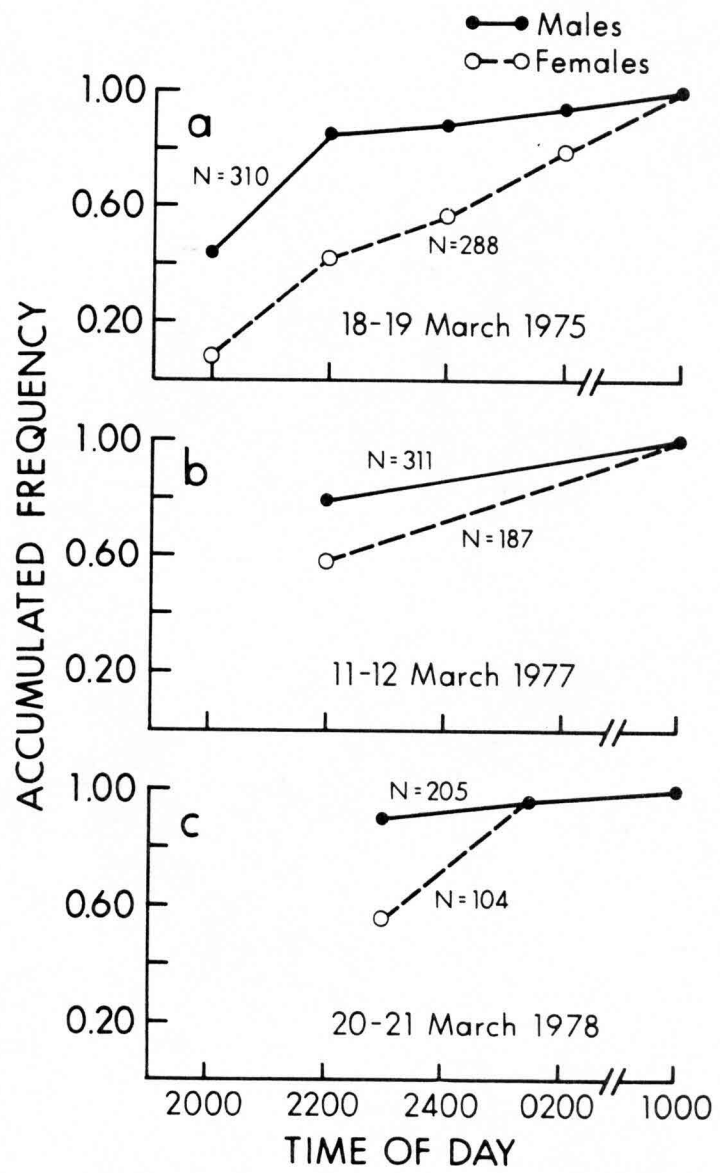


Figure 3. Accumulative frequencies of adults which were censused two or more times on nights of heavy immigration.

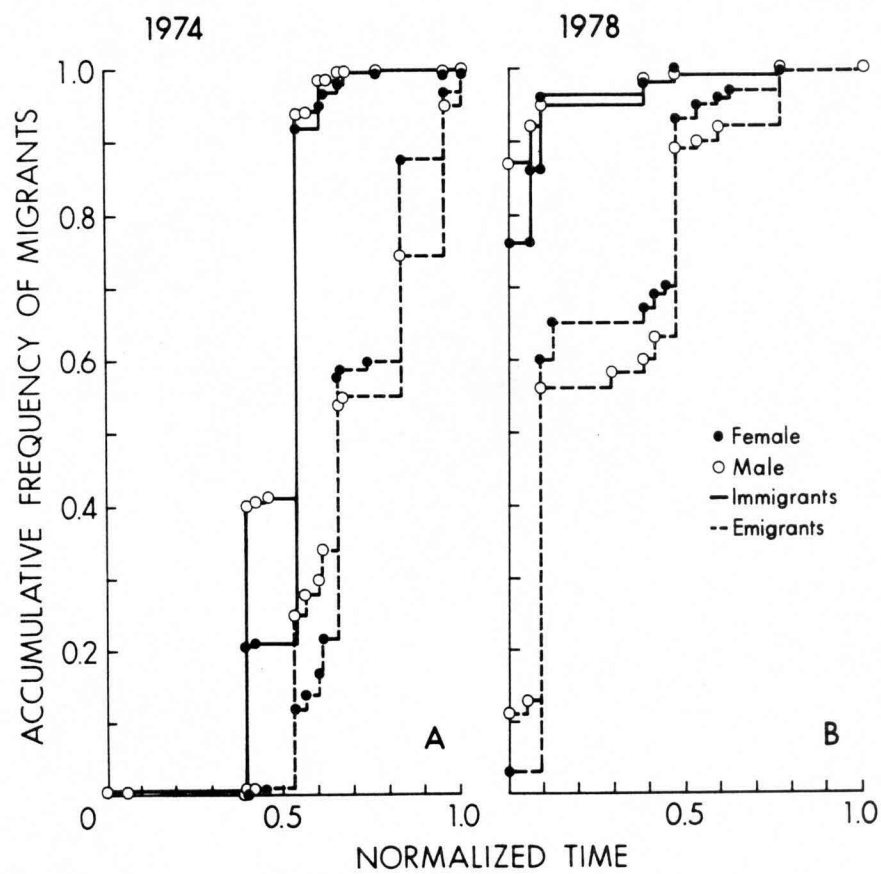


Figure 4. Accumulative frequencies of migrating adult spotted salamanders as a function of normalized time (see text). A = 1974; B = 1978.

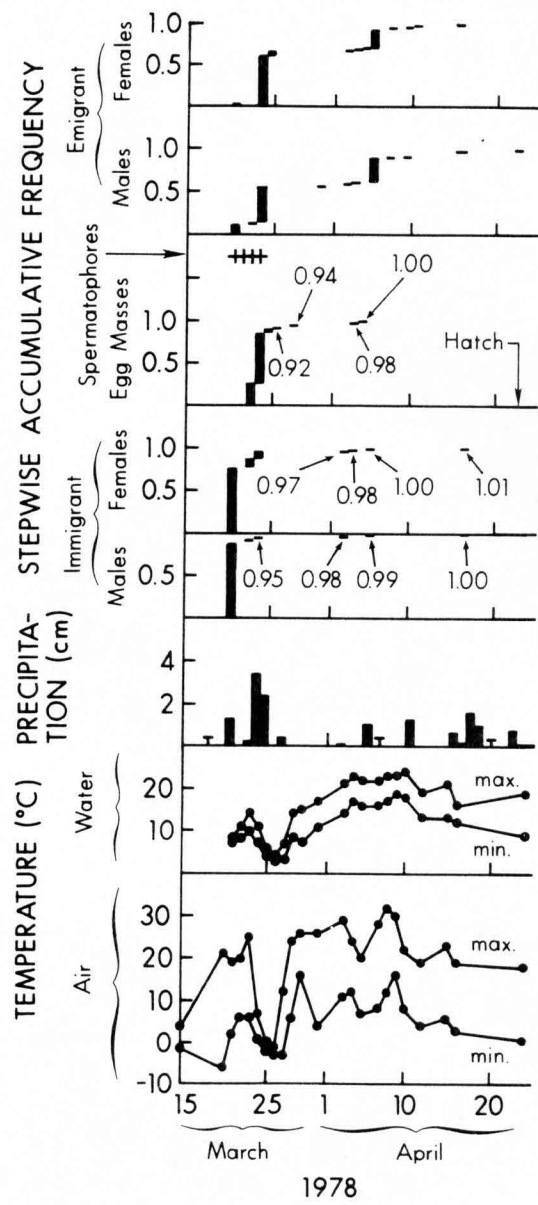


Figure 5. Summary of reproductive and meteorological events during the 1978 breeding season.

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