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# An Ecological Study of the Spotted Salamander, *Ambystoma maculatum*, and Jefferson Salamander, *A. jeffersonianum*, in West Virginia

Seth J. Myers

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An Ecological Study of the Spotted Salamander, *Ambystoma maculatum*, and  
Jefferson Salamander, *A. jeffersonianum*, in West Virginia

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The Graduate College of  
Marshall University

In partial fulfillment of the  
Requirements for the degree of  
Master of Sciences  
Biological Science

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May 2003

## ABSTRACT

### **An Ecological Study of the Spotted Salamander, *Ambystoma maculatum*, and Jefferson Salamander, *A. jeffersonianum*, in West Virginia**

by Seth Myers

The movements of Spotted Salamanders, *Ambystoma maculatum*, and Jefferson Salamanders, *A. jeffersonianum*, in and out of an ephemeral wetland in West Virginia were monitored for one breeding season using a drift fence lined with funnel traps. Significant movements of *A. jeffersonianum* coincided with rainfall and maximum daily air temperatures reaching a minimum of 5° C. Significant movements of *A. maculatum* coincided with rainfall and maximum daily air temperatures of at least 10° C. *A. jeffersonianum* preceded *A. maculatum* to the breeding site. Males of both species preceded females. The mark-recapture estimate of *A. maculatum* is 67 males and 25 females. The mark-recapture estimate of *A. jeffersonianum* is 11 males and 6 females. *A. maculatum*, considered collectively and by gender, showed an association between entry and exit point ( $P < 0.05$ ). *A. jeffersonianum*, considered collectively and by sex, did not show an association between entry and exit point ( $P > 0.05$ ).

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## Introduction

Spotted Salamanders, *Ambystoma maculatum*, and Jefferson Salamanders, *A. jeffersonianum*, belong to the family Ambystomatidae, commonly referred to as the mole salamanders. Both are similar in length, attaining a maximum total length of 20.3 centimeters (Green and Pauley, 1987), with *A. jeffersonianum* usually more slender than *A. maculatum* (Bishop, 1941). The coloration of the two species is very different. *A. maculatum* has a deep blue-black background with a lighter underside and rounded yellowish spots on the dorsal surface (Fig. 1) (Bishop, 1941). *A. jeffersonianum* is dark gray to brownish gray with bluish gray or silvery flecks on the limbs, sides of the body, and tail (Fig. 2) (Green and Pauley, 1987).

*A. maculatum* is found in southern Canada and much of the eastern United States (Petranka, 1998). It is believed to be statewide in West Virginia, with sightings in almost every county of the state. The known range of *A. jeffersonianum* extends from New York to West Virginia, central Kentucky, and southern Illinois. The exact status of *A. jeffersonianum* in West Virginia is unclear. Although *A. jeffersonianum* is believed to be found throughout West Virginia, sightings have been reported from only a relatively few, widely separated locations. Voucher specimens have been collected from seventeen counties: Raleigh, Hardy, Cabell, Mercer, Greenbrier, Mineral, Wood, Monroe, Harrison, Berkeley, McDowell, Pocahontas, Summers, Pendleton (Green and Pauley, 1987), Wayne, Fayette, and Tucker (Pauley, unpublished data).

Both inhabit deciduous forests during the non-breeding season and can be found under rocks and logs, within leaf litter, in small mammal burrows, and in ground crevices (Petranka, 1998). Douglas and Monroe (1981) found *A. maculatum* and *A. jeffersonianum* to move mean distances of 150 m and 250 m, respectively, from breeding sites during the non-breeding season. *A. jeffersonianum* breed almost exclusively in ephemeral woodland pools and road-rut ponds (Petranka, 1998). In addition to these habitats, *A. maculatum* also utilize permanent ponds for reproduction (Bishop, 1941). The two species often share breeding sites (Thompson and Gates, 1982).

Both species are limited to areas with suitable breeding habitats and therefore patchily distributed (Petranka, 1998). Ephemeral pools and road-ruts, especially, are highly variable in character, and viable breeding habitats are not widely distributed across the landscape (Rowe and Dunson, 1993). Large, disjunct populations may be dependent upon a single breeding habitat. Whenever a single breeding habitat is lost or altered, an entire population and gene pool may perish.

In late January to early March, rising air temperatures and rainfall events trigger adults of both species to emerge and migrate to suitable breeding areas (Douglas, 1979; Blanchard, 1930). Warm temperatures are necessary to release the animals from winter hibernacula and to maintain proper body temperature during migration. Moist conditions during surface activity prevent water loss and subsequent desiccation. Ordinarily, *A. jeffersonianum* precede *A. maculatum* and males of both species arrive earlier than females at the breeding site (Bishop, 1941). Both species exhibit fidelity to certain breeding sites, assumed to be their birthplace, and will bypass other suitable habitats during immigration (Wilson, 1976). The consistency with which individuals return to their natal pond suggests an orienteering ability. After mating, females attach egg masses to structures in breeding pools (Green and Pauley, 1987). The embryonic period of *A. maculatum* and *A. jeffersonianum* is 31-54 and 30-45 days, respectively (Bishop, 1941). The larval period of both species is at least two months and is affected by biotic and abiotic factors within the pool (Petranka, 1998).

As some individuals skip breeding seasons, the number of individuals observed at a breeding location in a single breeding season probably does not include the entire adult population that utilizes the site (Husting, 1965). Although population sizes and sex ratios vary among sites and years, male-biased sex ratios have been consistently reported in the literature and may be due to differences between the sexes in annual survival, age to maturity, or breeding frequency (Husting, 1965; Wacasey, 1961).

Researchers have studied *A. maculatum* and *A. jeffersonianum* at specific breeding locations and gained knowledge of the environmental conditions coinciding with breeding migration, temporal patterns of breeding migration, breeding population size and sex ratio, and orientation ability of the animals. A

common method for gathering information about ambystomatid breeding populations is to completely surround a breeding habitat with a drift fence barrier and place traps adjacent to the fence's inner and outer surface (Storm and Pimentel, 1954). By capturing a high proportion of animals entering and exiting, this method provides a quantitative description of the reproductive migration and population of animals utilizing a breeding location. Previous to the present study, a drift fence study of *A. maculatum* and *A. jeffersonianum* had not been carried out in West Virginia.

**Objectives:**

1. Determine dates of arrival and exit from the study pool as well as length of time spent in the study pool for each species collectively and by gender
2. Determine meteorological conditions coincident with immigration and emigration for each species collectively and by gender
3. Determine patterns observable in reproductive migration for each species collectively and by gender
4. Determine if individuals of each species (males, females, and pooled) enter and exit the study pool at or near the same point, indicating orientation ability
5. Determine the size and sex ratio of the breeding populations in entirety and over time

## **Materials and Methods**

### ***Study Site Description***

The study site is an ephemeral pool located within Beech Fork State Park, near the town of Lavalette, in Wayne County, West Virginia (Fig. 3). The pool is located at an elevation of 224 m on a hillside bench of a west-facing slope of approximately 30°. The pool is directly bordered to the west by a clear-cut right-of-way and to the north, south, and east by a mixed-deciduous forest composed mostly of white oak, American beech, and sugar maple. The shoreline and area immediately around the pool (< 5 meters) are relatively open and contain several small muscle wood, American beech, and white oak trees. Surrounding vegetation provides thick canopy closure and shade during the spring and summer. The bottom surface of the pool basin is soft mud covered by a thick layer of partially decomposed leaves and is strewn with many logs and dead branches. In late winter, water from melting snow and rain enters the pool as diffuse surface and subsurface run-offs. When filled, the pool is a nearly symmetrical oval with an average length of 17 m and width of 6 m (Fig. 4). The maximum depth recorded during this study was 58.5 cm. A channel at the southern end of the pool is the lowest point of the basin and is the outflow point for excess water. The pool typically dries during late summer. The pool is approximately 100 m from the nearest roadway and, aside from the nearby right-of-way, is free of signs of human disturbance. Vertebrate animals encountered at or known to inhabit the pool include: Marbled Salamanders, Spotted Salamanders, Jefferson Salamanders, Red-spotted Newts, Wood Frogs, Northern Green Frogs, Northern Spring Peepers, Eastern Box Turtles, and Eastern Gartersnakes.

## ***Drift Fence and Funnel Trap Design and Construction***

Salamanders were collected with a drift fence/funnel trap array which completely encircled the study pool. Animals attempting to enter or exit the study pool encountered the fence and were directed into funnel traps positioned adjacent to the fence. The design of the drift fence array is shown in Figures 5 and 8. The entire drift fence array was 19.5 m long and 8.7 m wide and composed of 14 individual fence sections (numbered 1 to 14 in Fig. 8), each 3.6 m long. When viewed from above, the drift fence was a bilaterally symmetric eight-sided polygon with two sides of 14.4 m and six sides of 3.6 m. The pool was at the center of the drift fence array and the individual fence sections were approximately equidistant to the shoreline. The fence sections were placed along the top of the pool basin above the expected maximum water level to avoid inundation, although this was not possible in the vicinity of the pool's outflow channel. The distance of each fence section to the shoreline normally ranged from 1 to 3 m.

Four funnel traps designed to sample terrestrial salamanders were placed in association with each individual fence section, one at each end of the fence section on both the inside and outside surface of the fence. Figure 9 shows an individual fence section and associated funnel traps with each of the four traps numbered.

Construction of the trapping system was completed by January 24, 2002. The drift fence was constructed of thick, black plastic sheeting with a width of 40 cm. Plastic sheeting was attached to the then frozen ground with sod staples and held upright and perpendicular to the ground by closely spaced wooden stakes. The final height of the fence was approximately 30 cm. The funnel traps are composed of small buckets and four-sided, open-ended funnels constructed from hardware cloth (Figs. 6 and 10). The narrow end of each funnel was inserted into a 10 cm by 10 cm opening cut into the bottom of an 8.7 liter bucket. Funnels were attached to the buckets with plastic fasteners (zip ties). The opening at the narrow end of the funnel within the bucket was approximately 7 cm from the sidewall and 9.7 cm from the floor of the bucket. While in use,

bucket lids were held in place by elastic bands. Each funnel trap was laid on its side at the end of an individual fence section with one edge of the funnel flush to the ground and another to the drift fence (Fig. 6). Funnels were attached to the ground with sod staples placed through the hardware cloth and to the drift fence by either stapling funnels to a wooden stake placed on the opposite side of the drift fence or wiring funnels to the drift fence. Animals which enter the wide end of the funnel may pass through the narrow opening of the funnel and fall into the bucket. Once there, they cannot easily reach the opening of the funnel, the only entrance or exit point of the trap, and are detained in the bucket. A section of fencing (Fig. 9 - Fence Section Divider) was attached to the edge of each funnel opposite the drift fence and extended away from the drift fence meeting a similar section of fencing attached to the funnel of the closest trap on the same side of the fence. The fence section divider diverted the approaching animals away from the sides of the funnel traps and into an open funnel. A moist sponge was placed in the bucket of each trap to prevent desiccation of the animals trapped. Repairs were made and debris removed from against or atop the drift fence and traps, as needed, during daily inspection of the study site.

### ***Animal Collection***

Beginning January 24 and ending April 18, 2002, the funnel traps were examined for trapped animals once each morning between 08:00 and 12:00. Additional visits were made during evenings with favorable migration conditions. Funnel traps surrounding the study pool were checked immediately upon arriving at the site, beginning with traps attached to fence section 1 (Fig. 8) and proceeding clockwise around the pool in ascending numerical order. Trapped animals were placed in a plastic bag for holding prior to processing. To reduce handling time and stress, animals were examined and released before continuing to the next trap. Each animal captured was identified to species and sex, measured, weighed, and marked. This information and also the funnel trap of capture, the fence section corresponding to this funnel trap, and the side of the fence the animal was captured on (inside or outside the drift fence) were

recorded for each animal. After examination, captured animals were released at the center of the fence section opposite the side of capture, allowing them to continue on their intended migration path.

### ***Sex determination, measuring, and weighing***

*A. maculatum* and *A. jeffersonianum* are very distinct from each other. Therefore, no special method was needed in identifying them to species. Male *A. jeffersonianum* and *A. maculatum* were distinguished from females by the distinctive cloacal swelling which signifies a male in breeding condition. Female *A. jeffersonianum* and *A. maculatum* were distinguished from males by either a lack of cloacal swelling or the presence of eggs visible through the abdominal wall. Prior to measuring, salamanders were immobilized and held straight by placing them in a notch cut into a block of foam and applying steady pressure from both sides. The distance from the tip of the snout to the posterior angle of the vent and the distance from the tip of the snout to the tip of tail were measured with dial calipers in increments of 0.1 millimeters. Salamanders were placed in a small bowl and weighed to the nearest 0.1 g with a portable digital Ohaus scale.

### ***Animal Marking Technique***

To track individual movements, salamanders encountered during the study were given a unique mark with the Visible Implant Elastomer (VIE) system manufactured by Northwest Marine Technologies. This marking system utilizes a UV-reactant elastomer (two-part epoxy) that is injected immediately beneath the animal's skin using a small hypodermic needle. The elastomer remains viscous for several weeks when stored below freezing but hardens within 24 hours at temperatures above freezing. The mark becomes permanent after the elastomer hardens and the animal's skin heals. Three colors of elastomer were used during this study: red, orange, and yellow. A maximum of four marking locations were used per animal. With three colors and four marking locations, 255 unique combinations are possible. The four marking locations used are as follows:



beneath the tail posterior to the cloacal opening; underside of the right, upper hind leg; underside of the left, upper hind leg; and underside of the right, upper front leg. As the elastomer is UV-reactant, all animals encountered were checked for the presence of a previously administered marking with a handheld UV light supplied with the kit. No animals were observed to suffer adverse reactions to the elastomer during the study. In a few cases, the marks were lost or migrated within the body and mark identification was difficult or impossible.

### ***Environmental Data Collection***

On-site environmental data were utilized in conjunction with meteorological data collected at a NOAA weather station located at the Huntington Tri-State Airport approximately 21 km northwest of the study pool. Precipitation was monitored on-site daily via two metric rain gauges placed in a clearing 75 m from the study pool. Depth of the study pool was monitored with a water level indicator placed at the area of greatest depth (Fig. 8 - point A). Minimum and maximum water temperatures at the study pool since last observation were measured each day with two thermometers placed approximately 60 cm below the water surface at points B1 and B2 in Figure 8. Daily soil temperature at time of observation was measured with two soil thermometers placed 3 cm beneath the soil surface at point C in Figure 8. Two handheld pH meters, calibrated each day, were used to record daily water pH values. Observational data including cloud cover, current meteorological conditions, and amount of ice on the study pool surface were also recorded daily. Meteorological data collected at the NOAA weather station and utilized during this study are minimum, maximum, and average air temperature and amount and type of precipitation.

## ***Statistical Analyses***

### **Population Structure**

The size and sex ratio of the composite breeding population (entire population of animals utilizing the pool during the study) of each species was determined using two different methods. The first is a raw census method in which all first captures were counted. The second method, adopted from Beneski et al. (1986), allows a correction for animals that crossed the fence without being captured. Assuming all animals released into the pool also exited the pool during the time frame of the study, the following equation represents the probability that an animal was captured while exiting the pool.

$$\text{Trapping Efficiency} = \frac{\text{\# of marked individuals captured exiting pool}}{\text{\# of marked individuals released into the pool}}$$

Next, the total number of marked and unmarked animals observed exiting the pool was divided by the trapping efficiency to estimate the total number exiting the pool. Sizes and sex ratios of the functional breeding population (population size and structure within the pool each day) were determined using the raw census method. All procedures were carried out separately for males and females to allow for differences in catchability.

Sex ratios of the composite and functional breeding populations of each species were tested for difference from 1:1 using a chi-square goodness-of-fit test (degrees of freedom = 1, significance level = 0.05).

Snout-vent length, total length, and mass measurements are presented in the form of frequency histograms grouped by species and gender. The two-sample t-test was used to determine if the mean size measurements of the sexes differ significantly.

## Orientation

Since the fence is continuous, it was possible to count the number of fence sections between entry and exit points in either a clockwise or counter-clockwise direction. It was assumed that the funnel trap a study animal was found in indicated the fence section the animal attempted to breach before becoming captured. A value of zero indicates that capture occurred while entering and exiting the study pool in traps on opposite sides of the fence in association with the same fence section (Fig. 9). A value of one indicates that the animal attempted to exit through the fence section on either the right or left of the fence section first encountered. The drift fence array is composed of 14 sections (Fig. 8) and the maximum number of fence sections between entry and exit point counted in the shortest distance is 7. For this study, the smaller of the two possible distances was determined for each study animal. These values were grouped by species collectively and by gender. Observed means were calculated from these values. The mean distance between entry and exit point given random orientation, to which the observed mean is compared, is calculated by the following equation given by Shoop and Doty (1972):

$$\text{Expected mean} = \frac{1(0) + 2(1) + 2(2) + 2(3) + 2(4) + 2(5) + 2(6) + 1(7)}{14} = 3.5$$

The preceding equation is based on the idea that, after entering the drift fence array, an animal has 14 possible exit routes. The denominator represents these 14 trials. The numerator is the sum of the distance between entry and exit of all possible combinations of entry and exit point for the 14 trials. The range (0-7) of possible distances in number of fence sections between entry and exit point is in parentheses and a coefficient outside the parentheses represents the number of possible combinations that will provide the distance in parentheses. The

observed mean and the expected mean were compared using the one-sample t-test.

The ability of ambystomatid salamanders to enter and exit breeding areas at or near the same point has been investigated by many workers using drift fence studies similar in design to the present study (Phillips, 1989; Shoop, 1965; Stenhouse, 1985). The principal difference between the present study and others is the method of animal capture used and consequent differences in data analysis. In previous studies, a continuous drift fence was erected around the pool and drop cans (animals fall into these and are detained) were sunk flush to the ground adjacent to the fence in pairs on the inside and outside surface opposite each other. The rocky soil of the present study site precluded the installation of drop cans. Instead, funnel traps were placed equidistantly along the interior and exterior surface of the drift fence (Fig. 6). In studies utilizing drops cans, the distance in number of drop cans between fence encounters is often used as a measure of orienteering, with zero indicating captures in drop cans in the same position but on opposite sides of the fence (Phillips, 1989; Shoop, 1965; Stenhouse, 1985). A slightly different tact was taken in the present study. Drop cans are bidirectional traps, capturing animals directed toward the trap by either the left or right adjacent fence section. It is possible that a salamander encountering the fence may turn away from the closest drop can and travel a greater distance to become captured in the next sequential drop can. This is equally likely to occur in either direction, effectively canceling the effect. Funnel traps used in the present study are unidirectional, only capturing animals that travel into the funnel opening in a certain direction (Fig. 9). Animals that encounter a fence section between two funnel traps may turn left or right but will still become captured in one of the funnel traps associated with the fence section. Therefore, the number of fence sections between fence encounters was used as a measure of distance. In Figure 9, an animal captured in Trap 2 during entrance and Trap 3 during exit is considered to have encountered the same fence section and the distance between fence encounters is zero.

## Results

### ***Potential Sources of Error***

Several assumptions were made during data analyses in regard to the mark-recapture and drift fence methods employed. For mark-recapture data, it was assumed that the animals collected are representative of the breeding population as a whole, animals retained their markings during the study, and the marking process did not affect the survivorship or subsequent catchability of the individual (Donnelly and Guyer, 1994). These assumptions were not rigorously tested. However, only four salamanders were recaptured with deteriorated markings and no animals were observed to suffer an adverse reaction to the marking process. For the drift fence component of the study, it is assumed that animals were drawn to the study pool for breeding activity, eliminating the possibility that animals were captured while engaged in activity unrelated to the presence of the study pool (Dodd and Scott, 1994). This seems a reasonable assumption since both *A. maculatum* and *A. jeffersonianum* were observed moving directly into the pool after release. Also, it is assumed that animals which encountered the fence attempted to access the breeding habitat and were not sufficiently disturbed to cause them to vacate the area without being captured, skipping a breeding season (Dodd and Scott, 1994). This assumption is confirmed by observations during the present study of animals encountering the fence and trying to access the study pool repeatedly until being captured. For animals that were captured, it is assumed that capture did not affect future activities, such as duration of stay in the study pool (Dodd and Scott, 1994). It is also assumed that animals captured and released into the pool exited the pool during the course of the study, whether or not they were recaptured. This assumption was confirmed when no animals were found during inspections of the pool carried out immediately before the end of the study.

As stated in the preceding paragraph, loss or alteration of mark combinations used to identify specific animals pose serious problems to mark-recapture studies. This problem was encountered minimally during the present

study and attempts were made to lessen the effect this may have on conclusions drawn from the data. Four *A. maculatum* were recaptured with evidence that their elastomer markings had partially disintegrated and migrated within the body. It was possible to identify two of the animals by comparing the remnants of the mark to the previous mark history for that species. The original marks were then re-administered and the animals were processed as usual and included in the rest of the study. The remaining unidentifiable *A. maculatum* were excluded from all data analyses to avoid mistaken results.

Sampling error in the form of animal trespass is common in drift fence studies (Dodd and Scott, 1994). Animal trespass occurs when the fence is crossed without a capture being made, usually the result of climbing or burrowing activity. For each animal captured and marked during the present study, a profile was created of when and where the individual had been captured by the drift fence/funnel trap array. It is a simple task to determine the arrival day, exit day, number of visits, and total time spent in the pool if an animal was captured each time it attempted to enter or exit the pool. Often, an animal had breached the fence without being captured. This was evident when an animal was first captured while exiting the pool without first being captured while entering. By arranging an animal's capture history chronologically it was possible to detect single trespass events. However, it was not possible to detect double trespass events. An example of a double trespass event would be an animal entering the pool undetected, exiting the pool undetected, and then later being captured trying to enter the pool for the second time. Based upon capture history, this individual is not distinguishable from an animal entering the pool for the first time. The probability of a double trespass event is approximately the square root of the probability of a single trespass event (Trenham et al., 2000). The probability of single trespass events is 1-Trapping Efficiency (Table 5). The probabilities of double trespass events for each species by sex are as follows: male *A. maculatum* = 0.0269; female *A. maculatum* = 0.1325; male *A. jeffersonianum* = 0.184; female *A. jeffersonianum* = 0.04. During data interpretation it was assumed that double trespass events did not occur. For female *A. maculatum* and male *A. jeffersonianum*, the probability of double trespass exceeds 0.05, the probability threshold often accepted arbitrarily during data analysis. This may

cause certain results of the present study which are potentially impacted by trespass to be unreliable indicators of actual phenomenon. The effect of trespass caused data to be scattered among the study animals, with some having complete and others only partial migration profiles. Each analysis was carried out using the data available.

Another potential source of error is the time interval between trap-checking visits. Traps were checked each morning and contained animals that had moved into the traps sometime during the previous 24-hour sampling interval. Consequently, it is not possible to pinpoint when during the sampling interval animals moved into the traps. Measures of day of arrival and departure as well as length of stay in the pool are accurate to plus or minus 24 hours.

## ***Reproductive Migration***

### **Environmental Conditions during Migration**

Weather data obtained from NOAA are summaries of each day (24 hour interval) beginning at 00:00. The 24-hour interval of weather data collection does not match the 24-hour sampling interval of the funnel traps, which were checked each morning at approximately 09:00. Both *A. maculatum* and *A. jeffersonianum* normally migrate during late evening or night (Wilson, 1976). Animals found in the traps each morning were likely captured during the previous night, possibly including captures made prior to 00:00. Therefore, it is instructive to consider weather conditions of both the day and days prior to when animals were found in the traps. Henceforth, the day animals were found in traps is referred to as the day of capture and the day prior to this is referred to as the day preceding capture. The migratory activities of *A. maculatum* and *A. jeffersonianum* and weather conditions of the 2002 breeding season are presented graphically in Figure 11. Each movement period of *A. maculatum* and *A. jeffersonianum* is presented in greater detail in Tables 1 and 2, respectively.

The first and largest inward movement of male *A. jeffersonianum* (January 24) coincided with significant rainfall (1.91 cm) and the highest maximum air

temperatures (16° C) to that point in the season (Table 2). The first female *A. jeffersonianum* observed at the pool was captured on February 7 while leaving, date of entry is not known. Two periods of inward movement of males were detected prior to the capture of this female. The first detected inward movement of female *A. jeffersonianum* (February 11) coincided with no rainfall and minimum-maximum air temperatures of -2° C and 6° C. The immigrant may have been captured prior to 00:00 as the preceding day's conditions were more favorable to migration with 0.71 cm of precipitation and minimum-maximum temperatures of 6° C and 17° C. Each female inward movement was composed of only one individual. The modal class (largest one-day capture) emigrated on March 16 and all *A. jeffersonianum* left the pool between March 16 and 20. Rainfall was abundant during this time and air temperature remained above freezing. Significant movements (> 1 individual) of *A. jeffersonianum* either entering or exiting were confined to periods with soil temperatures above freezing, maximum air temperatures reaching 5° C, and precipitation of 0.4 cm. Weather conditions during the early part of the breeding season fluctuated widely. Periods of immigration initiated by favorable conditions were often interrupted by cold, dry weather, protracting the period of immigration and disallowing synchronous arrival of the breeding population. Prior to the favorable conditions of March 16-20, outward movements were also sporadic and confined to brief periods with rain and air temperatures above freezing.

The first capture of male *A. maculatum* (March 3) coincided with light rainfall (0.05 cm), soil temperature of 2° C, and minimum-maximum air temperatures of -6° C and 11° C on the day of capture. It is possible the immigrant arrived prior to 00:00 as the preceding day (March 2) may have been more favorable to migration with 1.04 cm of rain, soil temperature of 4.5° C, and minimum-maximum air temperatures of 4° C and 10° C. On March 16, the modal class immigrated to the pool. The modal class contained 39% of the total *A. maculatum* breeding population census, 42% of the male census, and 30% of the female census. This was the largest single inward movement of *A. maculatum* (male and female combined). In addition, this was the largest inward movement of male *A. maculatum* and one of the two largest inward movements of female *A. maculatum* (an equally large inward movement of females occurred on March



18). The preceding day (March 15) was the warmest to that point with air temperature reaching 26° C. Rainfall on March 15 (0.3 cm) and 16 (1.55 cm) provided moisture levels sufficient to initiate large-scale migration. The 5-day period from March 16-20 was the longest period of warm weather to that point and received daily rainfall. In total, 77 *A. maculatum* (91% of the total breeding population census) were capture immigrating during this time. The end of all seasonal immigration coincided with the cessation of rainfall on March 20. Most *A. maculatum* entering the pool during this time period remained in the pool 1 to 2 days then migrated into the terrestrial habitat while favorable environmental conditions persisted. Large numbers are seen exiting the pool both 1 and 2 days (March 17 and 18) after the modal class of immigrants arrived at the pool (March 16) (Fig. 11). Significant movements (>2 individuals) of *A. maculatum* either entering or exiting were confined to periods with soil temperatures above freezing, maximum air temperatures reaching 10° C, and precipitation of  $\geq 1.0$  centimeters on either the day of or day prior to capture.

## Temporal Patterns of Migration

Table 3 summarizes the migratory movements of *A. maculatum* and *A. jeffersonianum* observed at the study site. Male *A. jeffersonianum* were the first to migrate to the site, arriving on January 24. Female *A. jeffersonianum* followed on February 11. Male *A. maculatum* were captured entering the pool March 3, 38 days after the first appearance of *A. jeffersonianum*. Female *A. maculatum* appeared at the pool on March 16. For both species, males appeared first and initial migratory waves were composed of a higher percentage of males than females (Figure 11). The first large wave of *A. jeffersonianum* (> 1 individual) was 100% male. The first large wave of *A. maculatum* (> 1 individual) was 82% male and 18% female. Median day of first arrival given in Table 3 describes the central tendency of arrival for each species by sex. The chronological order of median day of first arrival parallels the day of first appearance and, from earliest to latest, is as follows: male *A. jeffersonianum*, female *A. jeffersonianum*, male *A. maculatum*, and female *A. maculatum*.

The synchrony of immigration can be described by the span of days necessary for all immigrants to arrive (total and 5<sup>th</sup> to 95<sup>th</sup> percentile range), number of waves of immigrants, median number of days between immigratory waves, and proportion of the total breeding population census entering during peak movement periods. The following data are summarized in Table 3. Male *A. maculatum* were captured entering over an 18-day period during 6 movement periods separated by a median length of 2 days. Female *A. maculatum* were captured entering over a 5-day period during 5 movement periods separated by a median length of 1 day. Ninety percent (5<sup>th</sup> to 95<sup>th</sup> percentile range) of both male and female *A. maculatum* entered the pool during a 5-day period. The modal class, 42% of the male breeding population census, of male *A. maculatum* was captured entering the pool on March 16. Two modal classes of equal size, 30% each of the female breeding population census, of female *A. maculatum* were captured entering on March 16 and 18. Male *A. jeffersonianum* were captured entering over a 52-day period during 5 movement periods separated by a median length of 11.5 days. Female *A. jeffersonianum* were captured entering over a 38-day period during 5 movement periods separated by a median length of 7.5 days. Ninety percent (5<sup>th</sup> to 95<sup>th</sup> percentile range) of male and female *A. jeffersonianum* entered the pool during a 53-day and 34-day period, respectively. The modal class, 33% of the male breeding population census, of male *A. jeffersonianum* was captured entering the pool on January 24. As all inward movements of female *A. jeffersonianum* were composed of 1 individual, each of the 5 inward movements are considered modal classes and contain 16.7% each of the female breeding population census.

The ranks of each species by gender for the immigration parameters given in Table 3 and described in the preceding paragraph are presented in Table 4. The immigratory period of each species by sex is ranked from 1 to 4 (most to least synchronous, ties are indicated by \*\*) based on 5 criteria: TLIMP (total length of immigratory period); 90% IM (length of 5th to 95th percentile range of immigratory period); # MP (number of movement periods); MNDMP (median number of days between movement periods); % MC (percentage contained in modal class).

It is unclear which factor is the clearest indicator of synchrony of immigration. If all factors are weighted equally and the magnitudes of the differences are ignored, the sums of the rankings shown in the far right column of Table 4 are indicative of synchrony (lower numbers indicate greater synchrony of immigration).

As with immigration, the synchrony of emigration can be described by the span of days necessary for all emigrants to exit (total and 5<sup>th</sup> to 95<sup>th</sup> percentile range), number of waves of emigrants, median number of days between emigratory waves, and proportion of the total breeding population census exiting during peak movement periods. The following data are summarized in Table 3. The emigration of male *A. maculatum* took place over the course of 18 days (total and 5<sup>th</sup> to 95<sup>th</sup> percentile range) during 8 movement periods separated by a median length of 1 day. The emigration of female *A. maculatum* occurred over 28 days during 9 movement periods separated by a median length of 2 days. Ninety percent (5<sup>th</sup> to 95<sup>th</sup> percentile range) of female *A. maculatum* exited during an 11 day period. Two modal classes of equal size, 31% each of the male breeding population census, of male *A. maculatum* were captured exiting on March 17 and 18. The modal class, 25% of the female breeding population census, of female *A. maculatum* was captured exiting on March 20. The emigration of male *A. jeffersonianum* took place over 53 days (total and 5<sup>th</sup> to 95<sup>th</sup> percentile range) during 5 movement periods separated by a median length of 4 days. The emigration of female *A. jeffersonianum* occurred over 5 days (total and 5<sup>th</sup> to 95<sup>th</sup> percentile range) during 4 movement periods separated by a median length of 3 days. The modal class, 56% of the male breeding population census, of male *A. jeffersonianum* was captured exiting on March 16. As all outward movements of female *A. jeffersonianum* were composed of 1 individual, each of the 4 outward movements are considered modal classes and contain 16.7% each of the female breeding population census.

The ranks of each species by gender for the emigration parameters given in Table 3 and described in the preceding paragraph are presented in Table 5. The emigratory period of each species by sex is ranked from 1 to 4 (most to least synchronous) based on 5 criteria: TLEMP (total length of emigratory period); 90% EM (length of 5th to 95th percentile range of emigration); # MP (number of

movement periods); MNDMP (median number of days between movement periods); % MC (percentage contained in modal class).

As with immigration, it is unclear which factor is the clearest indicator of synchrony of emigration. If all factors are weighted equally and the magnitudes of the differences are ignored, the sums of the rankings shown in the far right column of Table 5 are indicative of synchrony (lower numbers indicate greater synchrony of emigration).

*A. maculatum* remained in the pool a shorter period of time than *A. jeffersonianum*. The median length of stay was 2 days for male and 1 day for female *A. maculatum*. The median length of stay was 33 days for male and 24 days for female *A. jeffersonianum*. The minimum and maximum length of stay and 5-95 percentiles, given in Table 3, parallel the median length of stay and are from shortest to longest: female *A. maculatum*, male *A. maculatum*, female *A. jeffersonianum*, and male *A. jeffersonianum*.

Order of exit for each species by gender parallels the order of arrival. Based on day of first exit, male *A. jeffersonianum* were the first to depart the pool (January 25), followed by female *A. jeffersonianum* and male *A. maculatum* (March 16), and finally female *A. maculatum* (March 17). The median day of last exit gave slightly different results and, from earliest to latest, is as follows: male *A. jeffersonianum*, female *A. maculatum*, and female *A. jeffersonianum* and male *A. maculatum*.

The length of the breeding season, from first immigrant to last emigrant, for each species by sex is shown in Figure 12. Male *A. jeffersonianum* (54 days) were present for the longest period in the pool followed by female *A. jeffersonianum* (38 days), male *A. maculatum* (31 days), and female *A. maculatum* (29 days).

The number of visits was similar among the species and sexes. Male and female *A. maculatum* visited the pool a range of 1 to 3 times with 1 visit the median and modal class. Male and female *A. jeffersonianum* visited the pool 1 to 2 times with 1 visit the median and modal class.

## ***Population Size and Structure***

The sizes and sex ratios of both the composite and functional breeding populations were determined. The composite breeding populations are a summary of all animals utilizing the site during the study. The size of the composite breeding population was determined for both species by raw census (simple count) and by a mark-recapture method which adjusts for animals evading capture (Tables 6 and 7). The functional breeding population is the total number of animals in the pool at any one time and changes as animals enter and exit the study site. The sizes of the functional breeding population were determined by the raw census method. Implementation of the mark-recapture technique to estimate functional breeding population size was not possible as only the overall, and not cumulative, trespass rates are knowable. Similar to population size, sex ratios of the breeding populations were described overall (composite sex ratio) and per day (functional sex ratio). Composite sex ratios were determined using the raw census and mark-recapture population estimate. As with functional breeding population size, functional sex ratios were determined by raw census.

For the composite *A. maculatum* breeding population, the raw census is 65 males and 20 females, and the mark-recapture population estimate is 67 males and 25 females (Table 7). For the composite *A. jeffersonianum* breeding population, the raw census is 9 males and 6 females, and the mark-recapture population estimate is 11 males and 6 females (Table 7). The composite sex ratios of *A. maculatum* given by the raw census and population estimate are 3.25:1 and 2.68:1 (male:female), respectively (Table 8). Sex ratios by both methods are significantly different from a 1:1 ratio ( $P < 0.05$ ). The composite sex ratio of *A. jeffersonianum* given by the raw census and population estimate are 1.5:1 and 1.83:1 (male:female), respectively (Table 8). Sex ratios by both methods are significantly different from a 1:1 ratio ( $P < 0.05$ ).

For both species, the sizes and sex ratios of the functional breeding populations each day are presented in Figs. 13-16. Quantitative descriptions of

the functional breeding populations at peak sizes are given in Table 9. The *A. maculatum* functional breeding population peaked sharply and then decreased at a slower rate (Fig. 13). This fluctuation in functional breeding population size was caused by differences in the rate and onset of immigration and emigration and by the emigratory modal class of both male and female *A. maculatum* containing fewer individuals and occurring several days after the immigratory modal classes (Table 3). The two female *A. maculatum* appearing to occupy the pool after April 18 are assumed to have evaded capture while emigrating (Fig. 13). They are included in the graph because it is impossible to know when they breached the fence. The *A. jeffersonianum* functional breeding population also experienced a peak, although not as sudden as in *A. maculatum*, followed by a drop in numbers (Fig. 15). This fluctuation in functional breeding population size is caused by differences in the rate and onset of immigration and emigration and by the emigratory modal class of both male and female *A. jeffersonianum* occurring after the immigratory modal classes. The one female appearing to occupy the pool after April 18 is assumed to have evaded capture while emigrating from the pool. The functional sex ratios of both species were highly skewed toward males during the beginning of breeding activity (Figs. 14 and 16). This situation reversed in both species as females began to outnumber males in the pool, as a result of male emigration and female immigration.

The size of the total (male and female) functional breeding population of *A. maculatum* peaked on March 16 with 24 animals (28.2% of total census), 18 males (27.7% of male census) and 6 females (30% of female), in the pool. The ratio of males to females at this time was 3:1, significantly different from 1:1 ( $P < 0.05$ ). The male functional breeding population was also at its peak size on March 16 and the size and sex ratio are the same. The size of the female functional breeding population peaked from March 18 to 19. On March 18, 15 *A. maculatum* (17.6% of total census), 4 males (6.2% of male census) and 11 females (55% of female census), were in the pool. The sex ratio (male:female) at this time was 1:2.75, significantly different from 1:1 ( $P < 0.05$ ). The functional breeding population on March 19 was 11 *A. maculatum* (12.9% of total census), 0 male (0% of male census) and 11 females (55% of female census). The ratio

of males to females at this time was 0:11 (no statistical test possible on values of zero).

The size of the total (male and female) functional breeding population of *A. jeffersonianum* peaked from March 3 to 15 at 7 animals (46.7% of total census), 6 males (66.7% of male census) and 1 female (16.7% of female census). The ratio of males to females at this time was 6:1, not significantly different from 1:1 ( $P > 0.05$ ). The size of the male functional breeding population was also at its peak and the size and sex ratio are the same. The size of the female functional breeding population peaked on March 18 with 2 animals (13.3% of total census), 0 male (0% of male census) and 2 females (13.3% of female census). The ratio of males to females was 0:2 (no statistical test possible).

The frequency distributions of snout-vent length, total length, and mass for each species by gender are given in Figures 17-22. The descriptive statistics and results of two sample t-tests comparing mean values of males and females are given in Table 10. Significant differences exist between the mean snout-vent length, total length, and mass of male and female *A. maculatum* (Figs. 17-19), with females larger in the three characters. A greater proportion of male *A. maculatum* occupy smaller size classes, skewing the frequency distributions toward smaller size classes in the three characters measured. No significant difference exists between the mean snout-vent length, total length, or mass of male and female *A. jeffersonianum* (Figs. 18-22). The lack of a statistically significant difference may be a result of the small sample size.

## **Orientation**

Orientation parameters of both species are given in Table 11 and the frequency histograms of distance between entry and exit points are shown in Figures 23-28. For *A. maculatum*, the mean number of fence sections between entry and exit points is significantly different ( $P < 0.05$ ) from the mean expected from random movement for males and females, when considered separately and pooled (male and female). The mean number of fence sections between entry

and exit points is not significantly different from the mean expected from random movement for any grouping of *A. jeffersonianum* (male, female, and pooled). The results here may be influenced by the small sample size of *A. jeffersonianum*. The orienteering ability of the sexes was compared by testing the null hypothesis that no difference exists between males and females in the observed mean number of fences sections between fence encounters using the two-sample t-test. For both species, no significant difference exists between the sexes, indicating similar orienteering ability.

## Discussion

### ***Reproductive Migration***

Dates of first arrival at breeding sites reported in the literature vary among locations and years. This is likely explained by variability in weather patterns among geographic locations, often as a result of latitudinal and altitudinal differences, (Landy, 1967) and through time (Downs, 1989). Green (1956) set common dates of breeding activity in West Virginia as late February to early March for *A. jeffersonianum* and from February 18 to the middle of March for *A. maculatum*. The date of first arrival for *A. maculatum* observed during the present study falls within the range given by Green (1956). *A. jeffersonianum* began breeding migration approximately one month prior to Green's start time. Any discrepancies are likely due to the unique qualities of each location, year, and breeding population.

Bishop (1941), Brodman (1995), Downs (1989), Landy (1967), and Williams (1973) reported *A. jeffersonianum* reaching breeding sites ahead of *A. maculatum*. Wacasey (1961) observed the simultaneous arrival of *A. jeffersonianum* and *A. maculatum*. Bishop (1941) suggested differences between the species in response to environmental cues, length of migratory route, and/or travel rate and continuity as possible reasons for the temporal staggering of arrivals. Phillips and Sexton (1989) suggested that differences in



orienting ability between two groups may cause one to move more directly, and quickly, to the breeding site. During the present study, *A. jeffersonianum* moved earlier than *A. maculatum* and during periods of lower temperatures. Also, stronger orientation ability was detected in *A. maculatum*, but this may be due to differences in sample size. Early arrival may be adaptive for *A. jeffersonianum* by allowing access to preferable oviposition sites and earlier hatching of larvae, allowing an advantage in procuring pond resources and earlier and larger body size at metamorphosis (Landy, 1967). The potential advantages of early arrival may come with an increased risk of freezing during early travel (Bishop, 1941). Staggered arrival of adults may benefit both species by decreasing interspecific larval competition, as different sized larvae may fill separate niches within the pond (Douglas and Monroe, 1981). For each species, it is likely that the timing of arrival is balanced between the potential benefits and risks of early migration.

During the present study, males of both species arrived first and constituted a majority of initial migratory waves. In *A. maculatum*, first arrival and predominance of males in initial migratory waves has been observed by Bishop (1941), Blanchard (1930), Downs (1989), Husting (1965), Landy (1967), Sexton et al. (1990), and Wacasey (1961). In *A. jeffersonianum*, the same phenomenon has been observed by Douglas (1979), Uzzell (1964), Williams (1973), and Wright and Allen (1909). Brodman (1995), Landy (1967), and Wilson (1976) found male and female *A. jeffersonianum* arriving on the same night, and Williams (1973) found male and female *A. maculatum* arriving on the same night. The reasons for early arrival of males may be similar to the reasons given by Bishop (1941) for the early arrival of *A. jeffersonianum* (differences in response to environmental cues, length of migratory route, and/or travel rate and continuity). Although not observed in the present study, Phillips and Sexton (1989) suggested that differences in orienting ability between the sexes may cause male *A. maculatum* to move more directly, and quickly, to the breeding site than females. Douglas (1979) found male *A. jeffersonianum* to have a lower temperature threshold for migration and to be more likely to continue migration during declining temperatures. In the present study, an ability of males to travel at lower temperatures than females was not observed in either species; cool

temperatures during periods of female movement were similar to those of initial male movements. Females may not be physiologically ready to migrate as early as males or may require a longer period of favorable conditions prior to first movement. Early arrival of males may be adaptive by increasing the likelihood of procuring a mate (Douglas, 1979). Conversely, hesitation by females may be adaptive by decreasing the risk of traveling early when the onset of cold weather can be sudden and fatal (Douglas, 1979). As with the arrival of each species, it is likely that the timing of arrival for each sex is balanced between the potential benefits and risks of early migration.

Movements of *A. jeffersonianum* early in the breeding season occurred during brief periods of warm, moist weather and were repeatedly interrupted by the onset of cold, dry weather. In comparison, *A. maculatum* immigrated later in the year during a period of extended warm, moist weather. The effect of changes in weather pattern during different periods of the breeding season on the synchrony of immigration is reflected by the longer period of immigration of *A. jeffersonianum*. Interruption of immigration of *A. jeffersonianum* by intermittent weather has been observed by Brodman (1995), Douglas (1979), and Downs (1989). Although not prevalent during this study, interruption of *A. maculatum* immigration by intermittent weather has been observed Husting (1965), King (1939), and Landy (1967). Variability in weather patterns among geographic locations and years create differences in the length and synchrony of immigration among ambystomatid salamander breeding populations. Also, other unique or unrecognized qualities of breeding populations and their habitats may add to this effect. For example, Husting (1965) observed a range of 9 to 29 days of immigration during a 5-year study of a single breeding population of *A. maculatum*.

In *A. maculatum* and *A. jeffersonianum*, male immigration occurred over a longer time period than that of females. Males of both species began immigration earlier than females and, therefore, were more affected by fluctuations in weather prominent during the beginning of the breeding season. Lengthier immigration periods in male *A. maculatum* were also observed by Landy (1967).

Downs (1989) speculated that the length of time *A. maculatum* spends in breeding pools is dependent on how quickly the sexes reproduce and the length of time until the return of weather suitable for emigratory movement. Given the similarity of the species, this may also be the case for *A. jeffersonianum*. In the present study, *A. jeffersonianum* spent more time in the pool than *A. maculatum*. A period of favorable weather beginning on March 16 allowed a mass exodus of both species from the pool. The longer stay in the pool may reflect the early and intermittent arrival of *A. jeffersonianum* and not a difference in the period of time the species require to complete reproduction. Intermittence of the breeding migration may have increased the length of time male *A. jeffersonianum* remained in the pool awaiting a sufficient female breeding population. Unfavorable weather conditions during or after mating may have retained *A. jeffersonianum* of both sexes in the pool after reproductive activity had ended. The total length of stay of *A. maculatum* of both sexes was considerably shorter than that of *A. jeffersonianum*. The period of favorable weather (March 16-20) initiating mass immigration of *A. maculatum* remained long enough to allow many individuals to both breed and emigrate before the return of unfavorable weather.

In the present study, males of both species remained in the pool a longer time than females. Similarly, Landy (1967) observed *A. maculatum* males staying longer in the pool than females, and Douglas (1979) and Williams (1973) observed male *A. jeffersonianum* staying longer in the pool than females. Given the synchrony of emigration of the sexes, the earlier arrival of males may explain their longer stay in the pool. Williams (1973) also observed a longer stay of male *A. maculatum* and *A. jeffersonianum* and posited that this may be explained by males lingering in the pool to mate multiple times whereas females, capable of only a single reproductive event per breeding season, may be more likely to leave the pond during the next favorable weather period following oviposition. The breeding activity within the pool was not monitored and it is possible that males of the species bred multiple times.

## ***Population size and structure***

The size of *A. maculatum* and *A. jeffersonianum* breeding populations differ widely from place to place. The largest estimated *A. maculatum* breeding population in a single season found in the literature is a Lincoln Index estimate of  $478 \pm 19.77$  males and  $515 \pm 35.93$  females (Wilson, 1976). The actual numbers captured at this site were 190 males and 100 females (Wilson, 1976). The largest number of *A. maculatum* captured in a single year and location found in the literature is 315 males and 144 females (Husting, 1965). The smallest *A. maculatum* breeding population found in the literature was composed of 1 male and 7 females (Wacasey, 1961). The population sizes commonly reported in the literature are in the range of 50 to 200 total (Paton et al., 2000; Peckham and Dineen, 1954; Wacasey, 1961; Williams, 1973; Wilson, 1976; Woodward, 1982). The largest estimated *A. jeffersonianum* breeding population in a single season found in the literature is a Lincoln Index estimate of 559 males and 448 females (Williams, 1973). This is also the largest number of captures in a single year, 499 males and 417 females (Williams, 1973).

At individual sites, population size varies considerably among years. During a 4-year study of a single breeding habitat, Wilson (1976) observed fluctuation in male captures from 70 to 190 males and 59 to 153 females. Williams (1973), over a 3-year study at a single breeding site, observed fluctuation in the number of *A. jeffersonianum* captured from 327 to 499 males and 182 to 417 females. The breeding population size of *A. maculatum* and *A. jeffersonianum* recorded during the present study likely fluctuates yearly as well. Husting (1965), in a 5-year study of a single *A. maculatum* breeding population, found that on average only 36% of the male and 32% of the female total breeding population migrate to the pool each year. Although a similar study of *A. jeffersonianum* has not been carried out, the observed breeding population in a single year probably does not represent the entire adult population. From the one year population size data obtained from this study, it is difficult to predict the true size of adult populations or the size of the breeding populations past or future. Variability in environmental conditions may affect the size of the yearly breeding population, with favorable years triggering more animals to immigrate to

the pool. Although it appears that the *A. maculatum* breeding population is larger and perhaps more secure than the *A. jeffersonianum* breeding population observed during the present study, on another year the population size differences may be lessened or reversed.

*A. maculatum* adult survival is relatively high. Husting (1965) estimated high annual survival of *A. maculatum* males (79 and 94%) and females (63 and 80%). *A. maculatum* are relatively long-lived. Pope (1937) reported an *A. maculatum* living in captivity to 25 years. Using skeletochronology, Flageole and Leclair (1992) set the age of an *A. maculatum* at 32 years. A long life span and low adult mortality may allow small adult populations to persist in spite of years of low juvenile recruitment. It appears that populations are controlled during the embryonic and larval stage. The volume and hydrologic cycle of ephemeral pools may affect within pool mortality via competition for resources, predation, or early pond-drying. During one year, Stenhouse (1985) estimated pre-metamorphic mortality of *A. maculatum* to be 99.89%. During favorable years, survival to metamorphosis may be significantly higher. Wilson (1976) reported survival to metamorphosis as 93.43% in *A. jeffersonianum*. It appears that embryo and larval survival fluctuates widely, with some years adding greatly to the adult population and others adding little.

The male-biased sex ratios of the composite breeding population, as observed in the present study, have been reported in many studies of *A. maculatum* and *A. jeffersonianum* (Bishop, 1941; Collins, 1965; Douglas, 1979; Flageole and Leclair, 1992; Hillis, 1977; Husting, 1965; Minton, 1954; Mohr, 1930; Paton et al., 2000; Phillips, 1989; Sexton et al., 1990; Stenhouse, 1985; Uzzell, 1964; Wacasey, 1961; Whitford and Vinegar, 1966; Williams, 1973; Wilson, 1976; Woodward, 1982). Exceptions found in the literature are populations of the *A. jeffersonianum*-complex in regions where the all-female polyploid is present (Bishop, 1941; Wacasey, 1961).

A number of explanations have been set forth to explain the male-biased sex ratios observed in *A. maculatum* breeding populations. In a study of *A. maculatum*, Wacasey (1961) found that males reached sexual maturity at a smaller size. Based on this, it was estimated that males reach reproductive age 1 year earlier than females. Using skeletochronology, Flageole and Leclair

(1992) determined that female *A. maculatum* commonly mature at 7 years, while males can mature in as little as 2 years. If males mature sooner, then a larger proportion of the total male population will be seen at the pool each spring. Also, reproductive females observed at the pool will sustain additional years of mortality previous to first reproduction, further reducing their population size (Wacasey, 1961). In the present study, earlier maturation of male *A. maculatum* is supported circumstantially by the frequency distribution of male and female size measurements. In all measurements, a skew toward smaller size classes is more evident in males than in females. This could be a result of small or non-representative samples, sampling error, or differences in growth rate between the sexes and not indicative of shorter time to maturation in males. However, if size is indicative of age, the skew toward smaller size classes tends to support the assertions made by Wacasey (1961) and Flageole and Leclair (1992). Husting (1965) found that females, possibly due to greater reproductive cost associated with ova production, are more likely to skip breeding seasons. As well, Husting (1965) found that average annual survival of *A. maculatum* was higher in males (0.94) than in females (0.80). As in breeding frequency, lower survival in females may be attributed to greater reproductive costs (Husting, 1965). Differences between sexes in maturation rate, breeding frequency, and annual survival may interact to produce the observed predominance of males in the study population. These factors and others may interact to produce the male-biased sex ratios often observed. Also, the effect of any process or the interaction of several may vary among populations to produce differences in sex ratios. Less work has been done to address the question in *A. jeffersonianum*, but given the similarity between the two species, the same explanations may hold true.

Sizes and sex ratios of the functional breeding populations found within the pool fluctuated during the present study as animals entered and exited. Periods of large functional breeding population sizes may coincide with increased reproductive activity. When females were present, periods with sex ratios highly skewed in favor of males may coincide with increased sexual selection and male competition for receptive females (Douglas, 1979).

## **Orientation**

The ability of *A. maculatum* to enter and exit breeding sites at or near the same point has been established by several others (Douglas and Monroe, 1981; Phillips, 1989; Shoop, 1965; Stenhouse, 1985; Williams, 1973). The results of the present study corroborate these earlier findings, showing an association between the entry and exit points of both male and female *A. maculatum*. Males and females did not differ significantly in their orienteering ability (two-sample t-test,  $P=0.850$ ). This is similar to the results of Phillips (1989) who found no significant difference between males and females.

Similarly, the ability of *A. jeffersonianum* to enter and exit breeding locations at or near the same point has been established previously (Douglas and Monroe, 1981; Williams, 1973). However, results of the present study did not indicate this relationship for *A. jeffersonianum* collectively or by sex. Sample sizes in the present study are relatively small (male,  $n = 5$ ; female,  $n = 4$ ). Given the strong indication of others that *A. jeffersonianum* exit points are not random in regards to entrance, it is possible that orienteering ability exists in the study population but was not discernible given the small sample size. In the frequency histogram of distance between *A. jeffersonianum* fence encounters, frequency decreases as the number of fence sections between entry and exit increase. If the mean and shape of the distribution is maintained but the sample size is doubled ( $n=18$ ), a significant difference is detected between observed and expected means ( $P=0.049$ ). This does not change the outcome of the original statistical test but instead points out the potential effects of sample size. No significant difference was observed between the orienteering ability of male and female *A. jeffersonianum* using the two-sample t-test ( $P=0.945$ ).

The apparent association between the entry and exit route is thought to indicate fidelity to migratory corridors and an ability to home toward specific breeding and non-breeding habitats. Aside from drift fence studies, observational data and experiments of different designs have corroborated both species orienteering ability. Both species have been observed bypassing suitable breeding habitats without pause during migration, suggesting travel toward a specific target (Wilson, 1976). *A. maculatum* collected from one pool

placed within 10 meters of the border of another pool did not move to the new pool (Shoop, 1968). Williams (1973) tracked radioactively tagged specimens of each species and observed them entering the breeding habitat at the same point and returning to the same non-breeding, terrestrial retreat for two consecutive years. Madison (1997) radio-tracked *A. maculatum* and confirmed the correspondence between arrival and departure direction. Whitford and Vinegar (1966) and Shoop (1968) observed *A. maculatum* returning to breeding sites after being displaced 125 meters to 500 meters, respectively, indicating a sense of the location of the breeding site.

The fidelity to breeding and non-breeding habitats and tendency to enter and exit breeding sites at the same location indicate the use of similar migratory corridors among years. It is possible that *A. maculatum* and *A. jeffersonianum* migrate along known routes utilizing a series of imprinted cues, such as temperature, sun altitude, and star patterns, which they acquire as juveniles during initial emigration into the terrestrial habitat (Shoop, 1968). However, this may not explain the ability of animals to reach the pool after being displaced randomly into areas not along their normal route. This suggests an ability to locate the breeding site from afar and travel toward it. Mechanisms of orientation suggested include rheotaxis (Finneran, 1951) and olfaction (McGregor and Teska, 1989). Finneran (1951) observed *A. maculatum* traveling toward a breeding site along overflow brooks, possibly indicating rheotaxis (attraction to water). McGregor and Teska (1989) found that *A. maculatum* prefer substrate and water from home pools, indicating olfaction as a possible mechanism. Olfaction as a mechanism may be unlikely as heavy rains coincident with migration may wash away scent trails (Bishop, 1941). Also, animals have been observed migrating across fresh snow (Wilson, 1976) which may cover scent trails. However, precipitation would not affect olfactory cues originating from the breeding pool. *A. maculatum* has been observed migrating to areas where pools previously existed but are no longer present as a result of human disturbance (Shoop, 1968). This calls into question the idea that olfactory cues emanated by the pool are being followed. Currently, the orientation mechanisms being used are unknown. It is possible that *A. maculatum* and *A. jeffersonianum* utilize



rheotaxis and olfaction or other mechanisms, such as celestial cue, topographic cues, or magneto-reception.

Breeding site fidelity may be advantageous by insuring the continued utilization of a productive habitat (Stenhouse, 1985). However, breeding site fidelity may become a disadvantage if the quality of the breeding or surrounding non-breeding habitat is reduced and the animals are incapable of relocating (Bishop, 1941). In this case, an entire population may be lost. Accurate orientation may be adaptive by preventing excessive wandering and allowing animals to arrive synchronously and early in the season (Douglas and Monroe, 1981; Phillips, 1989). Prevention of wandering may decrease predation risk and energy expenditure during migration. Early arrival may be advantageous by insuring: the availability of suitable mates and oviposition sites (Douglas and Monroe, 1981); early hatch time and a competitive advantage for larvae in procuring pool resources and avoiding predation (Phillips, 1989); earlier metamorphosis in years of early pond-drying and larger size at metamorphosis, an advantage to juveniles (Bishop, 1941).

## Conclusions

The present study was the first that examines a breeding population of either *A. maculatum* or *A. jeffersonianum* in West Virginia by completely encircling an ephemeral pool with a drift fence. For the most part, results of the present study confirm the findings of the majority of previous studies of these species. In all cases of results differing from convention, small sample size is highly implicated as a potential cause. During the present study, *A. jeffersonianum* were observed to precede *A. maculatum* to the study site. This is in agreement with the findings of Bishop (1941), Brodman (1995), Downs (1989), Landy (1967), and Williams (1973). As well, males of both species preceded females. This in agreement with the findings of Bishop (1941), Blanchard (1930),

Douglas (1979), Downs (1989), Husting (1965), Landy (1967), Sexton et al. (1990), Uzzell (1964), Wacasey (1961), Williams (1973), and Wright and Allen (1909). During the present study, both species moved during rainy nights coincident with temperatures above freezing. Of the two species, *A. jeffersonianum* appeared to have a lower temperature threshold to migration, possibly explaining their earlier arrival. The population size of *A. maculatum* was larger than *A. jeffersonianum*. An extensive literature search showed no trend in *A. maculatum*-*A. jeffersonianum* breeding communities, with neither more likely to outnumber the other. In both species, sex ratios were skewed toward males. This is in agreement with the majority of studies of these animals (Bishop, 1941; Collins, 1965; Douglas, 1979; Flageole and Leclair, 1992; Hillis, 1977; Husting, 1965; Minton, 1954; Mohr, 1930; Paton et al., 2000; Phillips, 1989; Sexton et al., 1990; Stenhouse, 1985; Uzzell, 1964; Wacasey, 1961; Whitford and Vinegar, 1966; Williams, 1973; Wilson, 1976; Woodward, 1982). *A. maculatum* (male, female, and pooled) exhibited an association between entry and exit point of the study pool, indicating orienteering ability. The same was not observed in *A. jeffersonianum*, small sample size is suspected as a confounding factor. Orienteering ability in *A. maculatum* has been observed by Douglas and Monroe (1981), Phillips (1989), Shoop (1965), Stenhouse (1985), and Williams (1973). Orienteering ability has been observed in *A. jeffersonianum* by Douglas and Monroe (1989) and Williams (1973).

The present study indicates that the characteristics of the *A. maculatum* and *A. jeffersonianum* breeding populations of the present study do not differ radically from those studied in other areas. Similar conservation strategies may therefore be employed. The first and most important recommendation to be made for the conservation of these species in West Virginia is the compilation of a list of the known locations of ephemeral wetlands within the state. This could be accomplished by sending surveys to everyone likely to encounter these habitats, posting survey sheets on nature-related websites, utilizing on the ground searches, or using remotely sensed images (as is currently being done in the state of New Jersey). The sites on this list can later be checked to determine if they qualify as ephemeral wetlands and contain amphibian populations. Future scientific studies and conservation efforts would benefit greatly from such a list.

The status of *A. jeffersonianum* is not well understood in West Virginia. Trips to each of the pools on the list suggested in search of embryonic, larval, or adult *A. jeffersonianum* would greatly increase our knowledge of this animal in West Virginia. Also, efforts must be made to recognize ephemeral wetlands prior to land development. Too often, laws governing wetland conservation are ignored when ephemeral wetlands are destroyed due to non-recognition during the dry period of their hydrologic cycle. A buffer of suitable non-breeding habitat, or at the bare minimum a corridor to such an area, should be maintained adjacent to any ephemeral pool to be preserved. In other states, salamander tunnels have been installed beneath roads in areas where mass migrations to breeding sites occur in order to reduce road mortality. This may be especially important on roads frequented by *A. jeffersonianum*. Research aimed at successful creation of ephemeral wetlands is underway. Knowledge gained during these studies could be used to attempt creation of ephemeral wetlands in West Virginia. Water quality of ephemeral wetlands, especially in areas of highly acidic rainfall, must be considered. The drainage basin of any ephemeral wetland to be preserved must be free of disturbances releasing chemicals toxic to amphibians into the soil or ground water. Also, the drainage basin of an ephemeral wetland to be preserved must not be altered in such a way as to modify the hydrologic cycle of the wetland, making it uninhabitable by amphibians (either drying too frequently or infrequently).

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## **Appendix 1: Tables**



**Table 1.** Record of all periods of migratory movement of *A. maculatum* at the study pool (DC = day of capture; 1P = 1 day prior to capture; 2P = 2 days prior to capture; Ave = average of DC, 1P, and 2P)

Order, Size, and Direction of Migration	Date	Air Temperature (°C)												Soil Temperature (°C)				Precipitation (cm)			
		Maximum				Minimum				Average				Time of Observation				Total			
		DC	1P	2P	Ave	DC	1P	2P	Ave	DC	1P	2P	Ave	DC	1P	2P	Ave	DC	1P	2P	Ave
1st Movement	3-Mar	11	10	11	11	-6	4	-5	-2.3	3	7	3	4.3	2	4.5	0	2.2	0.05	1.04	0	0.363
1 ♂ IN																					
0 ♀ IN																					
1 ♂ OUT																					
0 ♀ OUT																					
2nd Movement	16-Mar	18	26	22	22	4	14	4	7.3	11	20	13	15	9	14	14	12	1.55	0.3	0	0.617
27 ♂ IN																					
6 ♀ IN																					
9 ♂ OUT																					
0 ♀ OUT																					
3rd Movement	17-Mar	10	18	26	18	4	4	14	7.3	7	11	20	13	9	9	14	11	1.8	1.55	0.3	1.217
7 ♂ IN																					
3 ♀ IN																					
20 ♂ OUT																					
1 ♀ OUT																					
4th Movement	18-Mar	15	10	18	14	9	4	4	5.7	12	7	11	10	10	9	9	9.3	0.61	1.8	1.55	1.32
19 ♂ IN																					
6 ♀ IN																					
20 ♂ OUT																					
3 ♀ OUT																					
5th Movement	19-Mar	11	15	10	12	8	9	4	7	9	12	7	9.3	9	10	9	9.3	3.63	0.61	1.8	2.013
0 ♂ IN																					
1 ♀ IN																					
15 ♂ OUT																					
1 ♀ OUT																					
6th Movement	20-Mar	12	11	15	13	8	8	9	8.3	10	9	12	10	10	9	10	9.7	8.28	3.63	0.61	4.173
4 ♂ IN																					
4 ♀ IN																					
6 ♂ OUT																					
5 ♀ OUT																					
7th Movement	21-Mar	14	12	11	12	-4	8	8	4	5	10	9	8	14	10	9	11	0.05	8.28	3.63	3.987
0 ♂ IN																					
0 ♀ IN																					
3 ♂ OUT																					
0 ♀ OUT																					

**Table 1 (continued).** Record of all periods of migratory movement of *A. maculatum* at the study pool (DC = day of capture; 1P = 1 day prior to capture; 2P = 2 days prior to capture; Ave = average of DC, 1P, and 2P)

Order, Size, and Direction of Migration	Date	Air Temperature (°C)												Soil Temperature (°C)				Precipitation (cm)			
		Maximum				Minimum				Average				Time of Observation				Total			
		DC	1P	2P	Ave	DC	1P	2P	Ave	DC	1P	2P	Ave	DC	1P	2P	Ave	DC	1P	2P	Ave
8th Movement	22-Mar	2	14	12	9.3	-8	-4	8	-1.3	-3	5	10	4	-	14	10	7.8	0	0.05	8.28	2.777
0 ♂ IN																					
0 ♀ IN																					
0 ♂ OUT																					
1 ♀ OUT																					
9th Movement	27-Mar	5	14	22	14	-1	1	5	1.7	2	8	13	7.7	4	8	12	7.8	0	1.8	0	0.6
0 ♂ IN																					
0 ♀ IN																					
0 ♂ OUT																					
2 ♀ OUT																					
10th Movement	30-Mar	16	26	14	19	6	8	-4	3.3	11	17	5	11	17	17	12	15	0	1.07	0	0.357
0 ♂ IN																					
0 ♀ IN																					
0 ♂ OUT																					
2 ♀ OUT																					
11th Movement	1-Apr	14	11	16	14	5	7	6	6	9	9	11	9.7	16	9.5	17	14	0	1.78	0	0.593
0 ♂ IN																					
0 ♀ IN																					
0 ♂ OUT																					
2 ♀ OUT																					
12th Movement	2-Apr	26	14	11	17	4	5	7	5.3	15	9	9	11	20	16	9.5	15	0	0	1.78	0.593
0 ♂ IN																					
0 ♀ IN																					
1 ♂ OUT																					
0 ♀ OUT																					
13th Movement	3-Apr	21	26	14	20	4	4	5	4.3	12	15	9	12	6	20	16	14	0.28	0	0	0.093
1 ♂ IN																					
0 ♀ IN																					
0 ♂ OUT																					
0 ♀ OUT																					
14th Movement	13-Apr	22	25	27	25	16	13	6	12	19	19	17	18	20	18	20	19	1.4	0.18	0	0.527
0 ♂ IN																					
0 ♀ IN																					
0 ♂ OUT																					
1 ♀ OUT																					

**Table 2.** Record of all periods of migratory movement of *A. jeffersonianum* at the study pool (DC = day of capture; 1P = 1 day prior to capture; 2P = 2 days prior to capture; Ave = average of DC, 1P, and 2P)

		Air Temperature (°C)												Soil Temperature (°C)				Precipitation (cm)			
		Maximum				Minimum				Average				Time of Observation				Total			
Order, Size, and Direction of Migration	Date	DC	1P	2P	Ave	DC	1P	2P	Ave	DC	1P	2P	Ave	DC	1P	2P	Ave	DC	1P	2P	Ave
1st Movement	24-Jan	16	16	11	14	3	6	-4	1.7	9	11	3	7.7	6				1.91	0.13	0.03	0.69
3 ♂ IN																					
0 ♀ IN																					
0 ♂ OUT																					
0 ♀ OUT																					
2nd Movement	25-Jan	8	16	16	13	-2	3	6	2.3	3	9	11	7.7	4	6			0	1.91	0.13	0.68
0 ♂ IN																					
0 ♀ IN																					
1 ♂ OUT																					
0 ♀ OUT																					
3rd Movement	1-Feb	22	21	19	21	1	6	9	5.3	11	10	14	12	6	11	16	11	0.43	0	0.53	0.32
1 ♂ IN																					
0 ♀ IN																					
1 ♂ OUT																					
0 ♀ OUT																					
4th Movement	7-Feb	9	2	2	4.3	-1	-6	-9	-5.3	4	-2	-3	-0.3	1	0	0	0.3	0	0.13	0	0.043
0 ♂ IN																					
0 ♀ in																					
0 ♂ OUT																					
1 ♀ OUT																					
5th Movement	11-Feb	6	17	19	14	-2	6	-4	0	2	12	8	7.3	4	10	0	4.7	0	0.71	0	0.237
2 ♂ IN																					
1 ♀ IN																					
0 ♂ OUT																					
0 ♀ OUT																					
6th Movement	3-Mar	11	10	11	11	-6	4	-5	-2.3	3	7	3	4.3	2	4.5	0	2.2	0.05	1.04	0	0.363
2 ♂ IN																					
1 ♀ IN																					
0 ♂ OUT																					
0 ♀ OUT																					

**Table 2 (continued).** Record of all periods of migratory movement of *A. jeffersonianum* at the study pool (DC = day of capture; 1P = 1 day prior to capture; 2P = 2 days prior to capture; Ave = average of DC, 1P, and 2P)

Order, Size, and Direction of Migration	Date	Air Temperature (°C)												Soil Temperature (°C)				Precipitation (cm)			
		Maximum				Minimum				Average				Time of Observation				Total			
		DC	1P	2P	Ave	DC	1P	2P	Ave	DC	1P	2P	Ave	DC	1P	2P	Ave	DC	1P	2P	Ave
7th Movement	16-Mar	18	26	22	22	4	14	4	7.3	11	20	13	15	9	14	14	12	1.55	0.3	0	0.617
1 ♂ IN																					
1 ♀ IN																					
5 ♂ OUT																					
1 ♀ OUT																					
8th Movement	17-Mar	10	18	26	18	4	4	14	7.3	7	11	20	13	9	9	14	11	1.8	1.55	0.3	1.217
0 ♂ IN																					
0 ♀ IN																					
1 ♂ OUT																					
0 ♀ OUT																					
9th Movement	18-Mar	15	10	18	14	9	4	4	5.7	12	7	11	10	10	9	9	9.3	0.61	1.8	1.55	1.32
0 ♂ IN																					
1 ♀ IN																					
2 ♂ OUT																					
0 ♀ OUT																					
10th Movement	19-Mar	11	15	10	12	8	9	4	7	9	12	7	9.3	9	10	9	9.3	3.63	0.61	1.8	2.013
0 ♂ IN																					
0 ♀ IN																					
0 ♂ OUT																					
1 ♀ OUT																					
11th Movement	20-Mar	12	11	15	13	8	8	9	8.3	10	9	12	10	10	9	10	9.7	8.28	3.63	0.61	4.173
0 ♂ IN																					
1 ♀ IN																					
0 ♂ OUT																					
1 ♀ OUT																					

**Table 3.** Description of *A. maculatum* and *A. jeffersonianum* reproductive migration

	<i>Ambystoma maculatum</i>			<i>Ambystoma jeffersonianum</i>	
	Male	Female		Male	Female
<b>Date of First Arrival</b>					
Range of Immigration Dates (# of days)	3-20 Mar (18)	16-20 Mar (5)		24 Jan-16 Mar (52)	11 Feb-20 Mar (38)
5 <sup>th</sup> - 95 <sup>th</sup> Percentile (# of days)	16-20 Mar (5)	16-20 Mar (5)		24 Jan-16 Mar (52)	11 Feb-16 Mar (34)
Median Day of First Arrival	16 Mar	18 Mar		11 Feb	3 Mar
Date of Modal Class	16 Mar	16&18 Mar		24 Jan	‡
% of ♂ or ♀ Census in Modal Class	42%	30%		33%	16.7%
# of Movement Periods (MP)	6	5		5	5
Median # of Days Between MP	2	1		11.5	7.5
<b>Date of Last Exit</b>					
Range of Emigration Dates (# of days)	16 Mar-2 Apr (18)	17 Mar-13 Apr (28)		25 Jan-18 Mar (53)	16-20 Mar (5)
5 <sup>th</sup> - 95 <sup>th</sup> Percentile	16 Mar-2 Apr (18)	17 Mar-27 Mar (11)		25 Jan-18 Mar (53)	16-20 Mar (5)
Median Day of Last Exit	19 Mar	18 Mar		16 Mar	19 Mar
Date of Modal Class	17&18 Mar	20 Mar		16 Mar	‡
% of ♂ or ♀ Census in Modal Class	31%	25%		56%	16.7%
# of Movement Periods (MP)	8	9		5	4
Median # of Days Between MP	1	2		4	3
<b>Number of Days in Pool</b>					
Min-Max Length of Stay	1-28	1-9		1-51	4-37
5 <sup>th</sup> - 95 <sup>th</sup> Percentile	1-14	1-9		1-51	4-37
Median Length of Stay	2	1		33	24
Modal Class	2	1		1	***
% of ♂ or ♀ Census in Modal Class	34%	63%		40%	***
<b>Number of Visits</b>					
Min-Max Number of Visits	1-3	1-3		1-2	1-2
5 <sup>th</sup> - 95 <sup>th</sup> Percentile	1-2	1-2		1-2	1-2
Median Number of Visits	1	1		1	1
Modal Class	1	1		1	1
% of ♂ or ♀ Census in Modal Class	72.7%	85%		88.9%	83.3%

‡ each movement period composed of only one individual and is considered a modal class; \*\*\*frequency of all classes is equal to 1

**Table 4.** Synchrony of the immigratory period of each species/sex group is ranked from 1 to 4 (most to least synchronous, ties are indicated by \*\*) based on 5 criteria: TLIMP (total length of immigratory period); 90% IM (length of 5th to 95th percentile range of immigratory period); # MP (number of movement periods); MNDMP (median number of days between movement periods); % MC (percentage contained in modal class); SUM (sum of the rankings for each group)

	TLIMP	90% IM	# MP	MNDMP	% MC	SUM
Male <i>A. maculatum</i>	<b>2</b>	<b>1**</b>	<b>2</b>	<b>2</b>	<b>3</b>	<b>10</b>
Female <i>A. maculatum</i>	<b>1</b>	<b>1**</b>	<b>1**</b>	<b>1</b>	<b>1</b>	<b>5</b>
Male <i>A. jeffersonianum</i>	<b>4</b>	<b>3</b>	<b>1**</b>	<b>4</b>	<b>2</b>	<b>14</b>
Female <i>A. jeffersonianum</i>	<b>3</b>	<b>2</b>	<b>1**</b>	<b>3</b>	<b>4</b>	<b>13</b>

**Table 5.** Synchrony of the emigratory period of each species/sex group is ranked from 1 to 4 (most to least synchronous, ties are indicated by \*\*) based on 5 criteria: TLIMP (total length of emigratory period); 90% IM (length of 5th to 95th percentile range of emigratory period); # MP (number of movement periods); MNDMP (median number of days between movement periods); % MC (percentage contained in modal class); SUM (sum of the rankings for each group)

	TLEMP	90% EM	# MP	MNDMP	% MC	SUM
Male <i>A. maculatum</i>	<b>2</b>	<b>3</b>	<b>3</b>	<b>1</b>	<b>3</b>	<b>12</b>
Female <i>A. maculatum</i>	<b>3</b>	<b>2</b>	<b>4</b>	<b>2</b>	<b>2</b>	<b>13</b>
Male <i>A. jeffersonianum</i>	<b>4</b>	<b>4</b>	<b>2</b>	<b>4</b>	<b>4</b>	<b>18</b>
Female <i>A. jeffersonianum</i>	<b>1</b>	<b>1</b>	<b>1</b>	<b>3</b>	<b>1</b>	<b>7</b>

**Table 6.** Mark-recapture history and calculation of trapping efficiency for *A. maculatum* and *A. jeffersonianum*

Species	# marked while entering	# marked recaptures	# unmarked recaptures	Trapping Efficiency
<i>Ambystoma maculatum</i>				
Males	55	46	10	0.836
Female	11	7	9	0.636
<i>Ambystoma jeffersonianum</i>				
Males	7	4	2	0.571
Female	5	4	1	0.8



**Table 7.** Composite breeding population size and sex ratio of *A. maculatum* and *A. jeffersonianum* by two methods

Method	<i>Ambystoma maculatum</i>				<i>Ambystoma jeffersonianum</i>			
	Male	Female	Total	Sex Ratio (M : F)	Male	Female	Total	Sex Ratio (M : F)
Raw Census	65	20	85	3.25 : 1	9	6	15	1.5 : 1
Population Estimate	67	25	92	2.68 : 1	11	6	17	1.83 : 1

**Table 8.** Composite sex ratio of *A. maculatum* and *A. jeffersonianum* by two methods and results of  $\chi^2$  goodness-of-fit test ( $P \leq 0.05$  indicates significant difference from 1:1 ratio)

Species	Raw Census Male : Female	$\chi^2$ goodness-of-fit, $P \leq 0.05$	Population Estimate Male : Female	$\chi^2$ goodness-of-fit, $P \leq 0.05$
<i>Ambystoma maculatum</i>	65 : 20	Yes	67 : 25	Yes
<i>Ambystoma jeffersonianum</i>	9 : 6	Yes	11 : 6	Yes

**Table 9.** Date, size, and composition at maximum size of total (male and female), male, and female functional (within pool) breeding populations and  $\chi^2$  goodness-of-fit test of sex ratios ( $P \leq 0.05$  indicates a significant difference from 1:1 ratio) for *A. maculatum* and *A. jeffersonianum*

	<i>Ambystoma maculatum</i>		<i>Ambystoma jeffersonianum</i>
<b>Maximum <u>Total</u> Functional Breeding Population</b>			
Date	16 March		3-15 March
# of Males (% of Male Census)	18 (27.7%)		6 (66.7%)
# of Females (% of Female Census)	6 (30%)		1 (16.7%)
Total (% of Total Population Census)	24 (28.2%)		7 (46.7%)
Sex Ratio (P-value, $\chi^2$ goodness-of-fit)	3 : 1 (P < 0.05)		6 : 1 (P > 0.05)
<b>Maximum <u>Male</u> Functional Breeding Population</b>			
Date	16 March		3-15 March
# of Males (% of Male Census)	18 (27.7%)		6 (66.7%)
# of Females (% of Female Census)	6 (30%)		1 (16.7%)
Total (% of Total Population Census)	24 (28.2%)		7 (46.7%)
Sex Ratio (P-value, $\chi^2$ goodness-of-fit)	3 : 1 (P < 0.05)		6 : 1 (P > 0.05)
<b>Maximum <u>Female</u> Functional Breeding Population</b>	1st Occurrence	2nd Occurrence	
Date	18 March	19 March	18 March
# of Males (% of Male Census)	4 (6.2%)	0	0 (0%)
# of Females (% of Female Census)	11 (55%)	11	2 (13.3%)
Total (% of Total Population Census)	15 (17.6%)	11	2 (13.3%)
Sex Ratio (P-value, $\chi^2$ goodness-of-fit)	1 : 2.75 (P < 0.05)	0 : 11 (not tested)	0 : 2 (not tested)

**Table 10.** Analyses of frequency distributions of snout-vent length, total length, and mass for *A. maculatum* and *A. jeffersonianum*; shown are sample size, mean with 95% confidence interval, and result of two-sample t-test comparing male and female means ( $P \leq 0.05$  indicates significant difference)

Species	n	Snout-Vent Length (mm)			Total Length (mm)			Mass (grams)		
	M/F	Male	Female	P	Male	Female	P	Male	Female	P
<i>Ambystoma maculatum</i>	67/20	91.9 $\pm$ 1.568	98.0 $\pm$ 2.976	< 0.001	182.4 $\pm$ 4.156	191.3 $\pm$ 6.605	0.036	18.3 $\pm$ 0.674	23.7 $\pm$ 1.736	< 0.001
<i>Ambystoma jeffersonianum</i>	9/7	82.5 $\pm$ 2.796	84.9 $\pm$ 3.623	0.236	163.8 $\pm$ 7.39	162.6 $\pm$ 5.836	0.747	10.6 $\pm$ 1.219	12.5 $\pm$ 2.062	0.064

**Table 11.** Analyses of frequency distributions of number of fence sections between fence encounters for *A. maculatum* and *A. jeffersonianum*; shown are sample size, observed mean, standard error, expected mean with random orientation, and result of one-sample t-test comparing observed and expected mean ( $P \leq 0.05$  indicates significant difference)

Species	Number of Fence Sections Between Entry and Exit Point				
	Sample size	Observed Mean	Standard Error	Expected Mean	P
<i>Ambystoma maculatum</i>					
Male	52	1.904	0.238	3.5	< 0.001
Female	12	1.917	0.452	3.5	0.005
Pooled	64	1.906	0.21	3.5	< 0.001
<i>Ambystoma jeffersonianum</i>					
Male	5	2.6	0.678	3.5	0.255
Female	4	2.5	1.323	3.5	0.505
Pooled	9	2.556	0.648	3.5	0.183

## **Appendix 2: Figures**

**Figure 1.** Spotted Salamander, *Ambystoma maculatum*, from study site at Beech Fork State Park, West Virginia

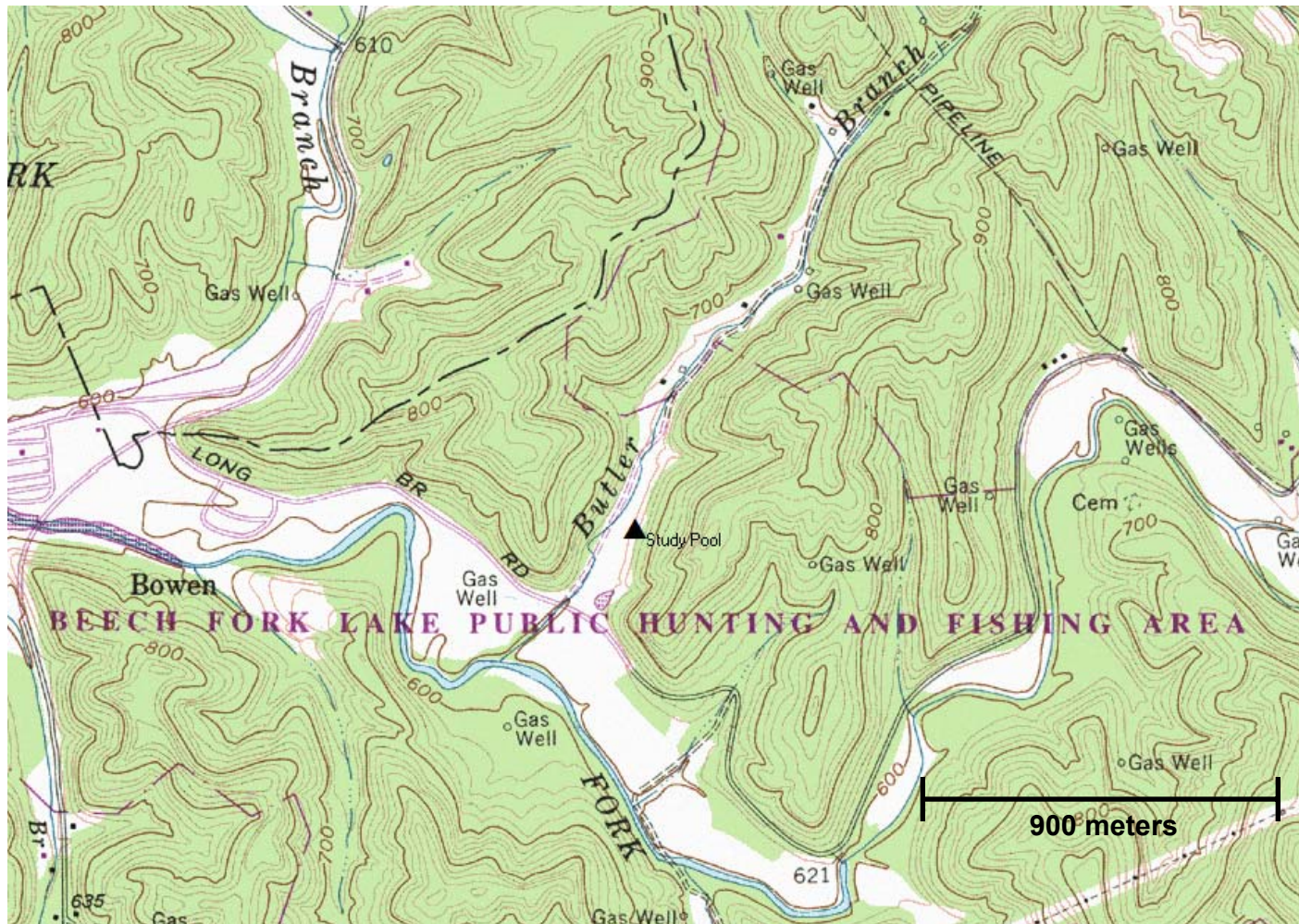




**Figure 2.** Jefferson Salamander, *Ambystoma jeffersonianum*, from study site at Beech Fork State Park, West Virginia



**Figure 3.** Topographic map showing location of study pool within Beech Fork State Park, West Virginia



**Figure 4.** Study pool prior to installation of drift fence array





**Figure 5.** Study pool after installation of drift fence array







**Figure 6.** Close-up of funnel traps adjacent to drift fence



**Figure 7.** Diagram of drift fence array with references to surrounding habitat

Mixed-Deciduous Woodland

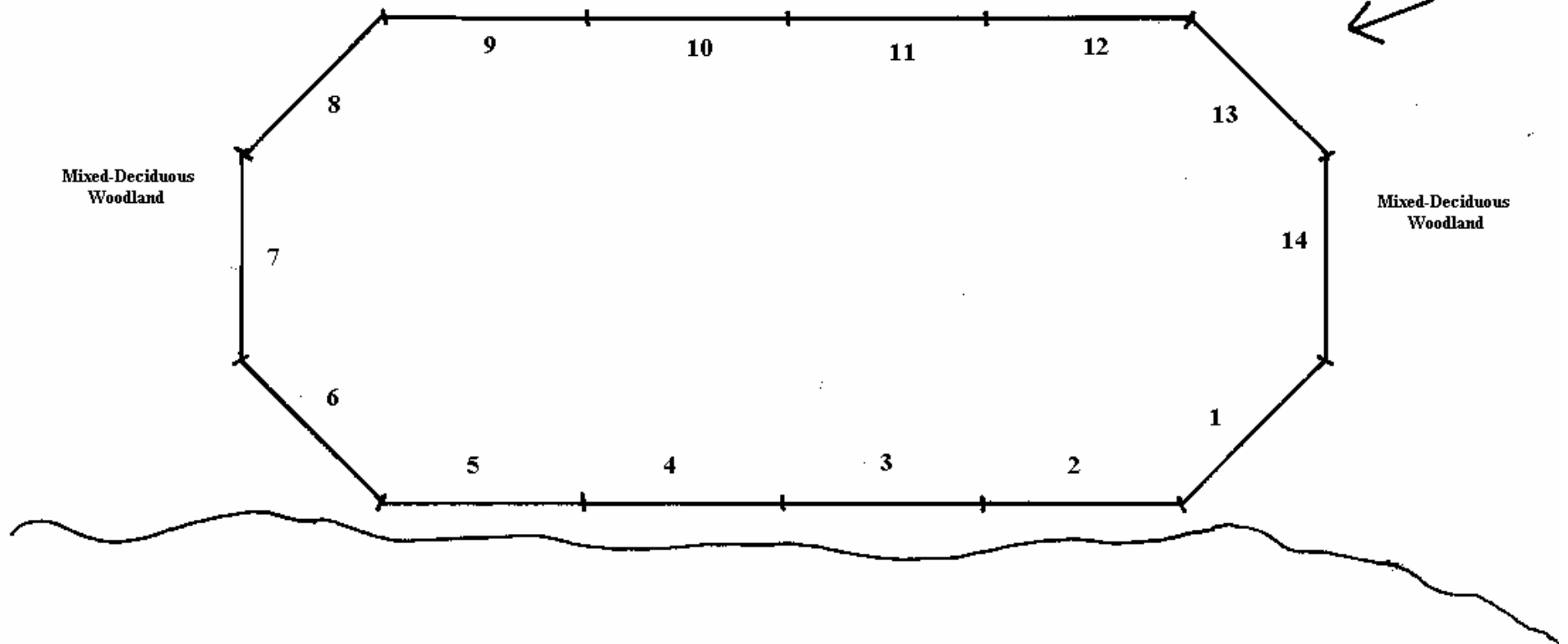
Mixed-Deciduous Woodland

Aspect = West  
↓

North  
↙

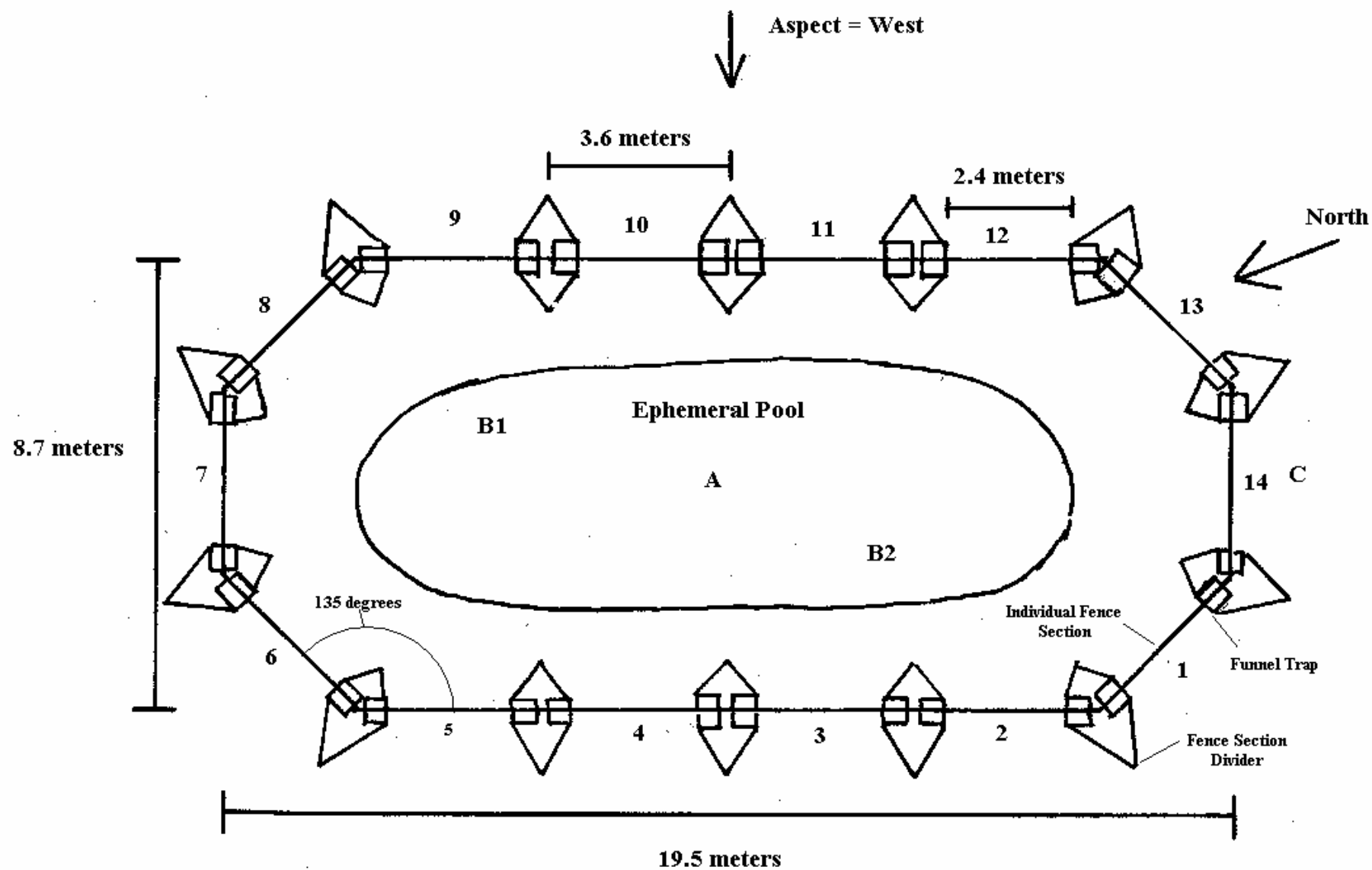
Mixed-Deciduous  
Woodland

Mixed-Deciduous  
Woodland

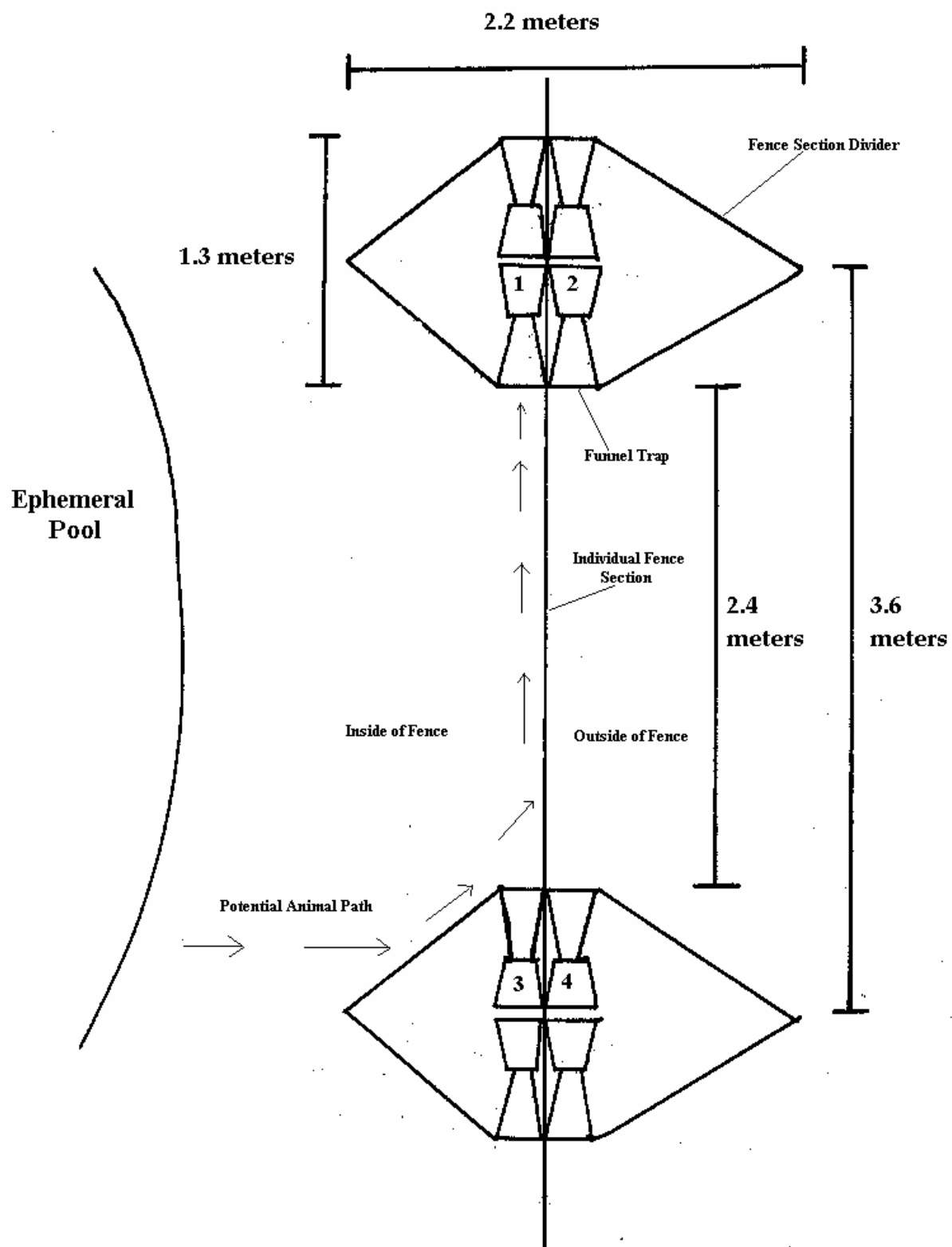


Clearcut Right-Of-Way

**Figure 8.** Diagram of drift fence array with dimensions

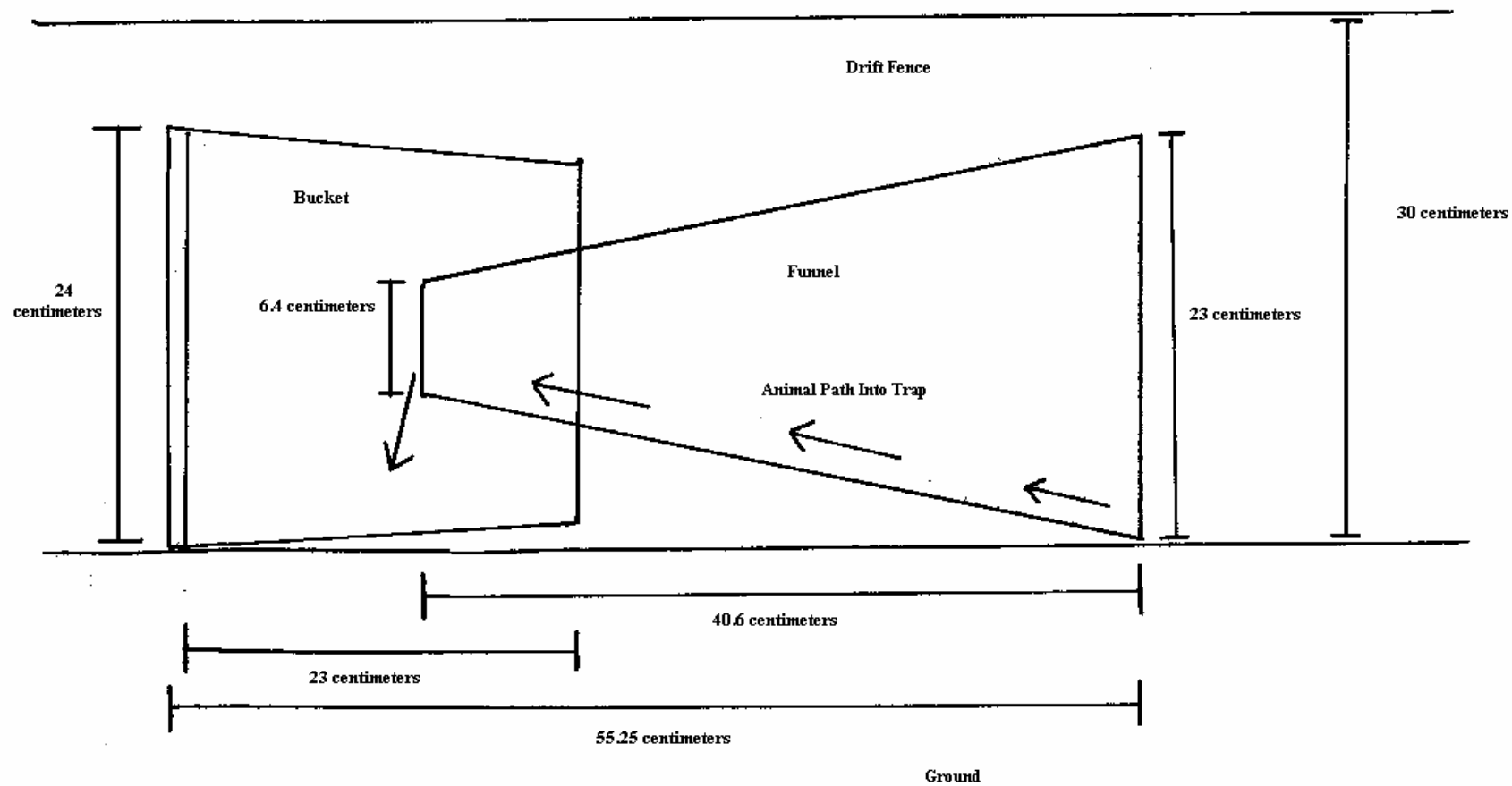


**Figure 9.** Diagram of fence section with associated funnel traps

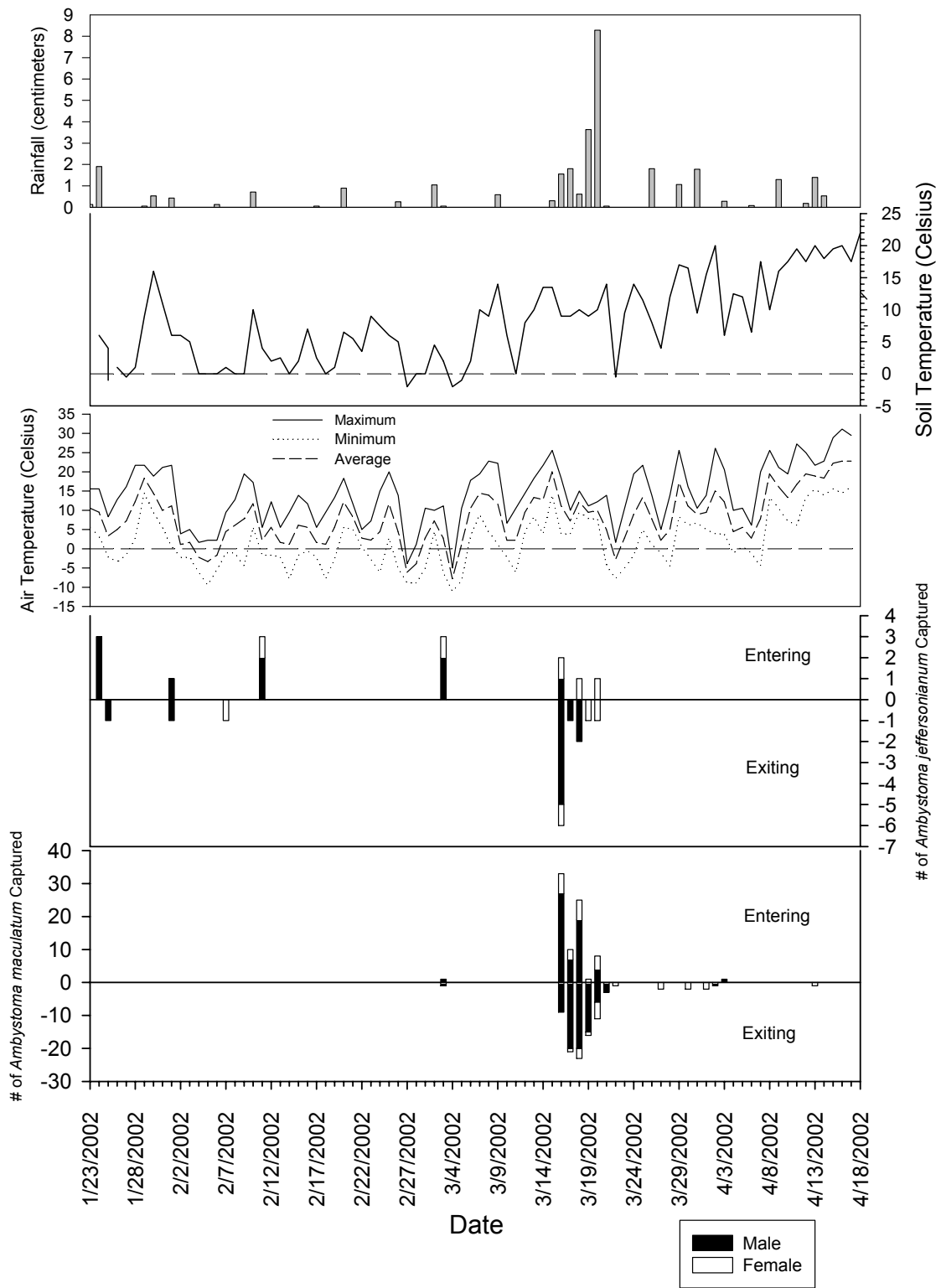




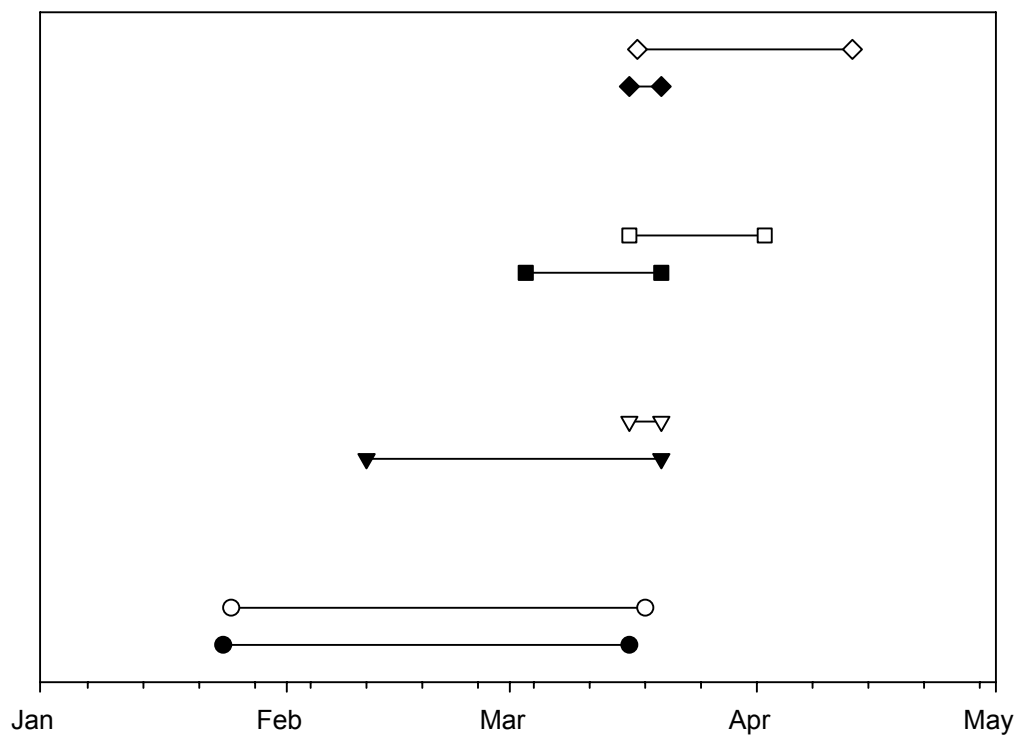
**Figure 10.** Diagram of funnel trap with dimensions



**Figure 11.** Movements of *A. maculatum* and *A. jeffersonianum* in and out of the study pool and weather data for each day

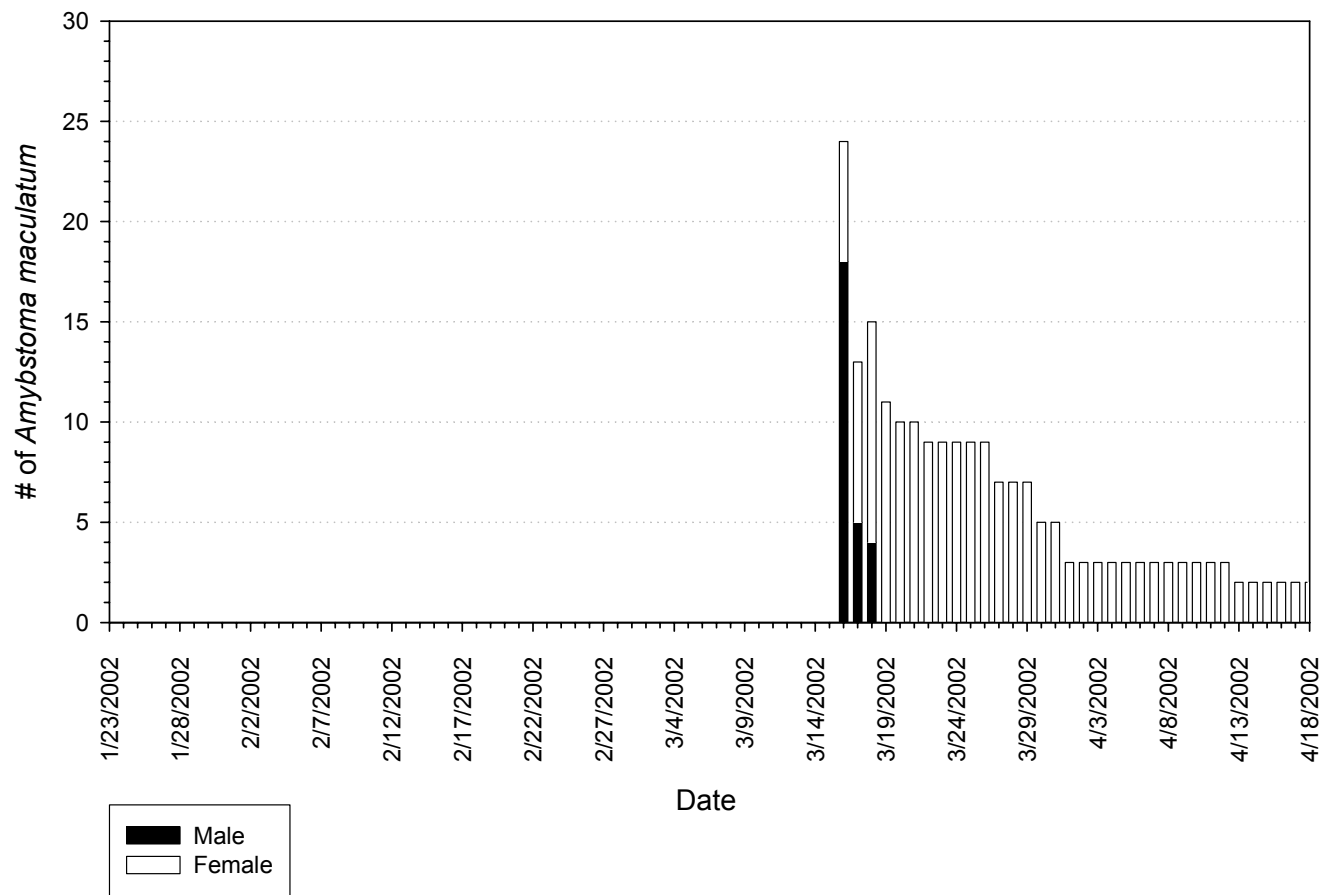


**Figure 12.** Onset and length of periods of immigration and emigration for each species by sex



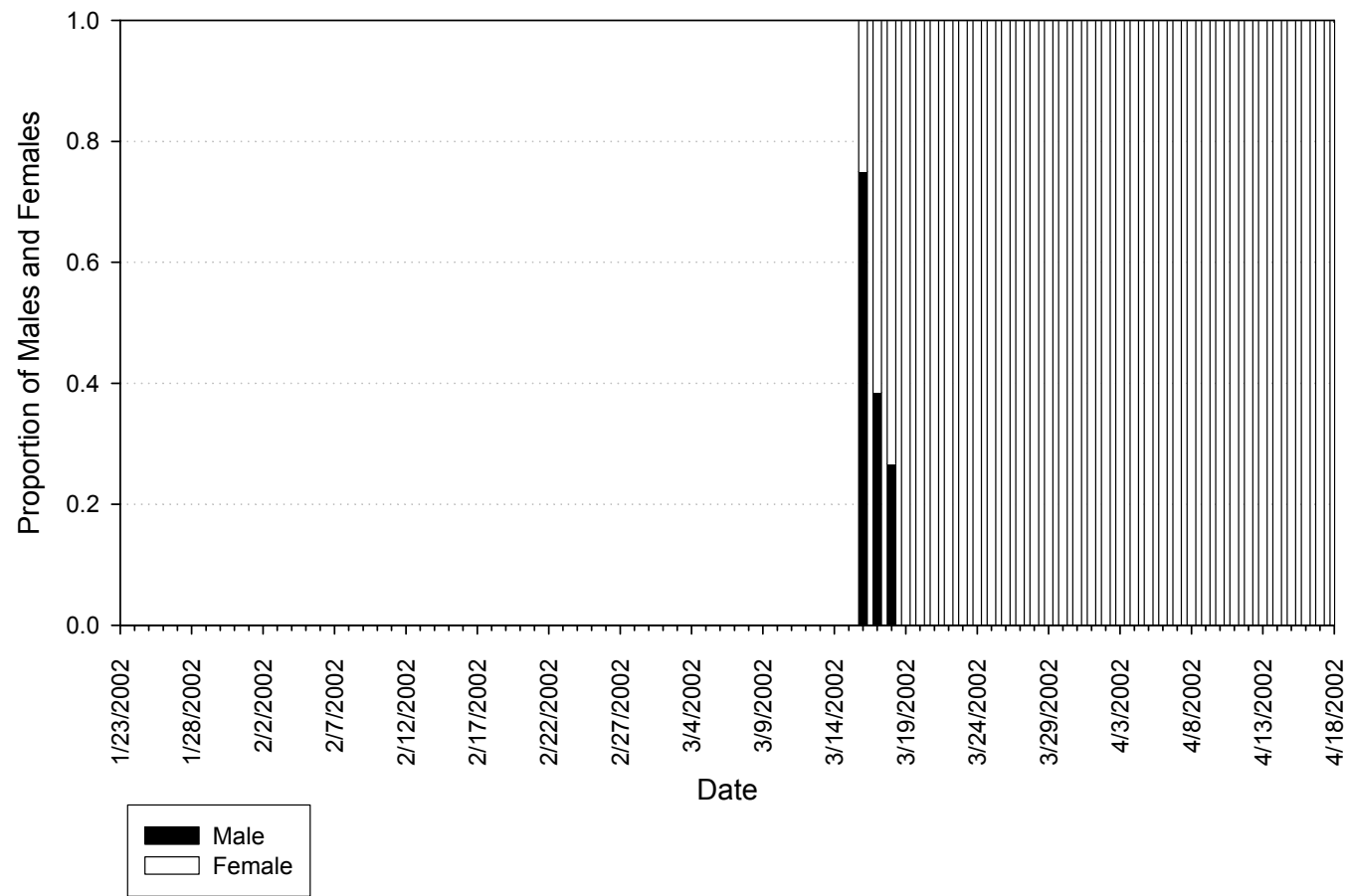
- Male *A. jeffersonianum* period of immigration
- Male *A. jeffersonianum* period of emigration
- ▼— Female *A. jeffersonianum* period of immigration
- ▽— Female *A. jeffersonianum* period of emigration
- Male *A. maculatum* period of immigration
- Male *A. maculatum* period of emigration
- ◆— Female *A. maculatum* period of immigration
- ◇— Female *A. maculatum* period of emigration

**Figure 13.** Size of *A. maculatum* functional (within pool) breeding population each day

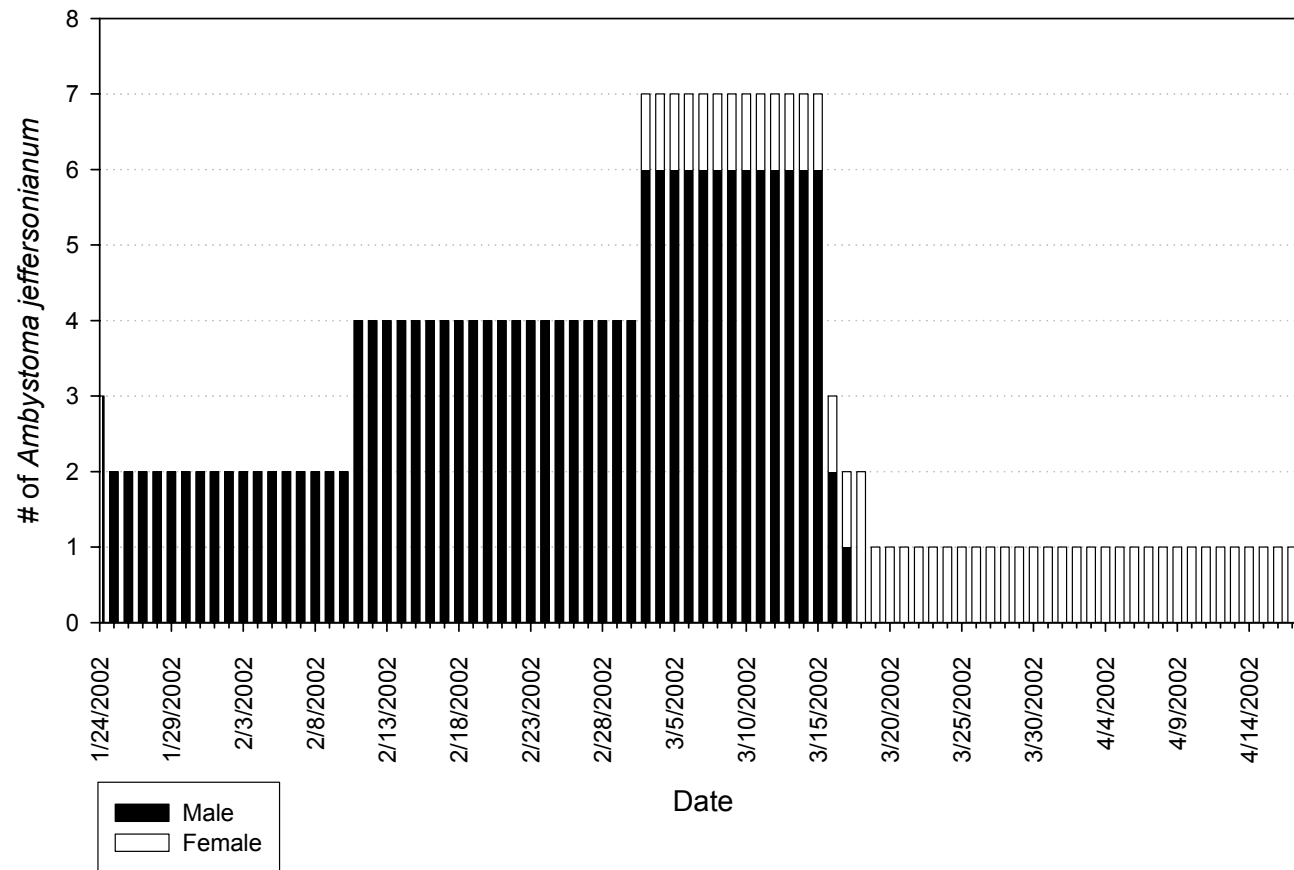




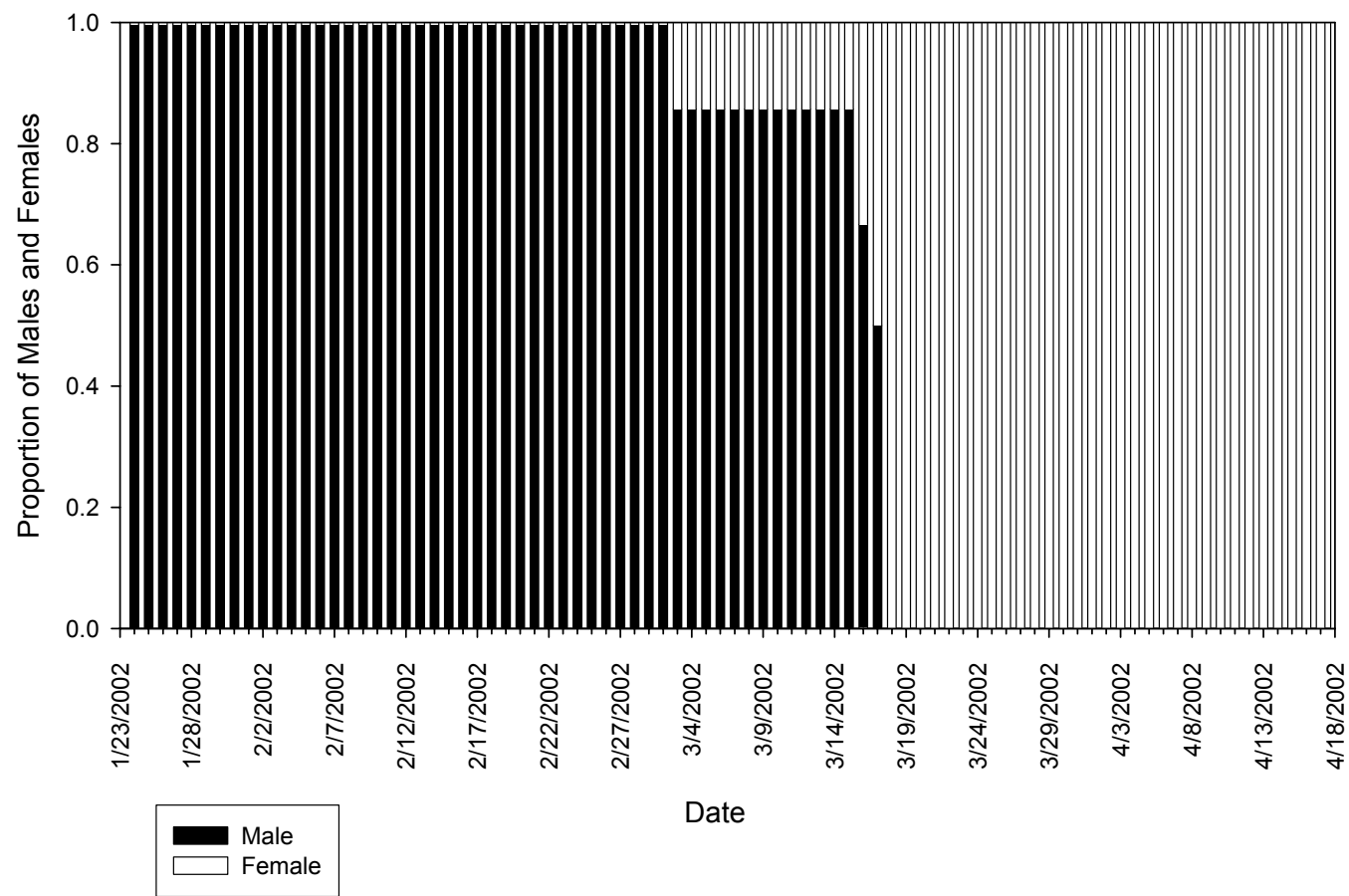
**Figure 14.** Proportion of male and female *A. maculam* in functional (within pool) breeding population each day



**Figure 15.** Size of *A. jeffersonianum* functional (within pool) breeding population each day

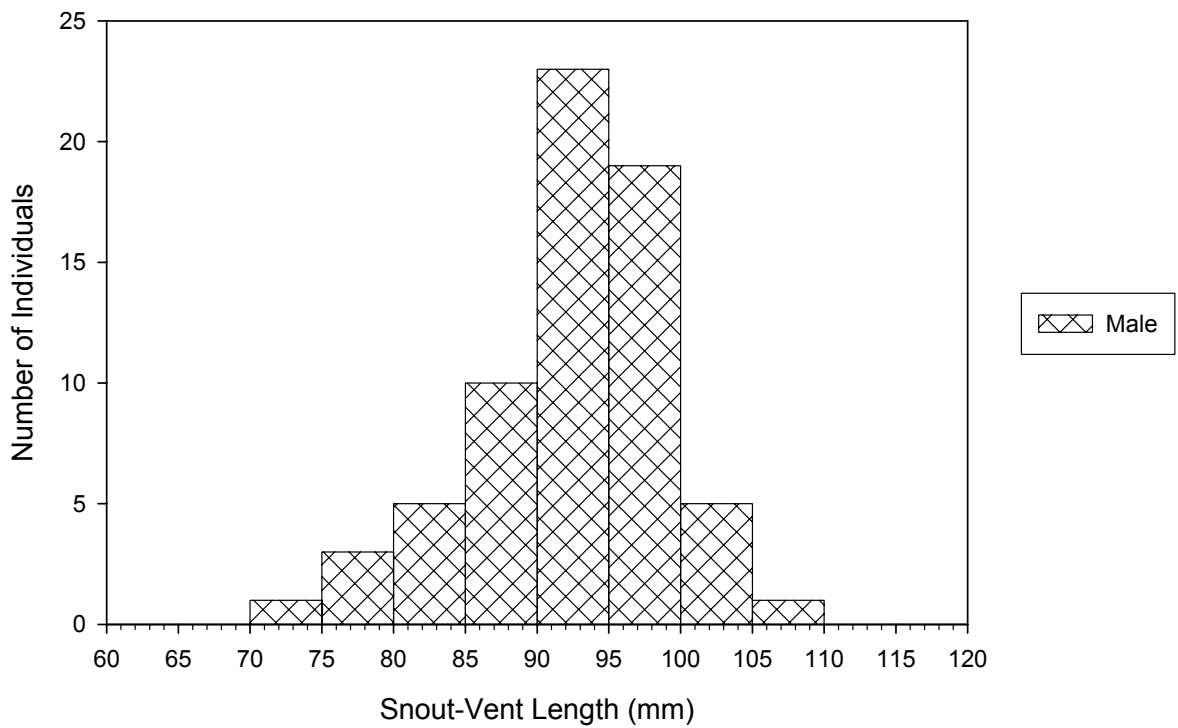
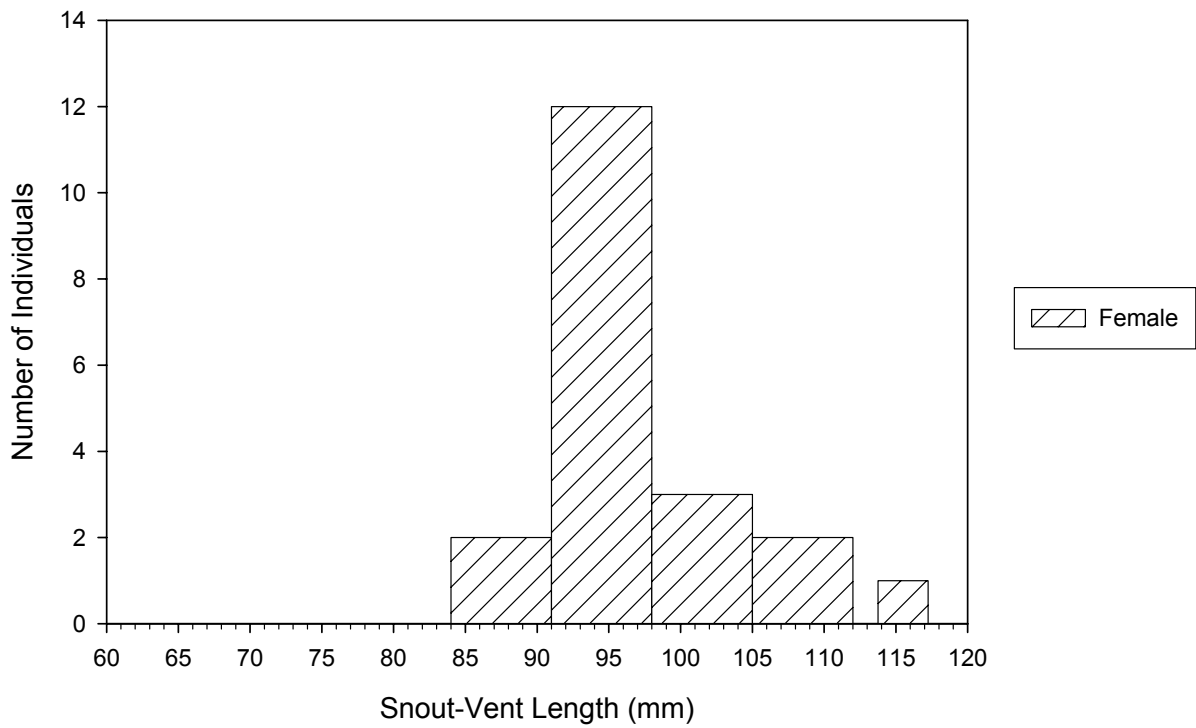


**Figure 16.** Proportion of male and female *A. jeffersonianum* in functional (within pool) breeding population each day



**Figure 17.** Snout-vent length frequency histograms of male (n = 67) and female (n= 20) *A. maculatum*; means are significantly different ( $P < 0.001$ ); refer to Table 8 for statistical analysis

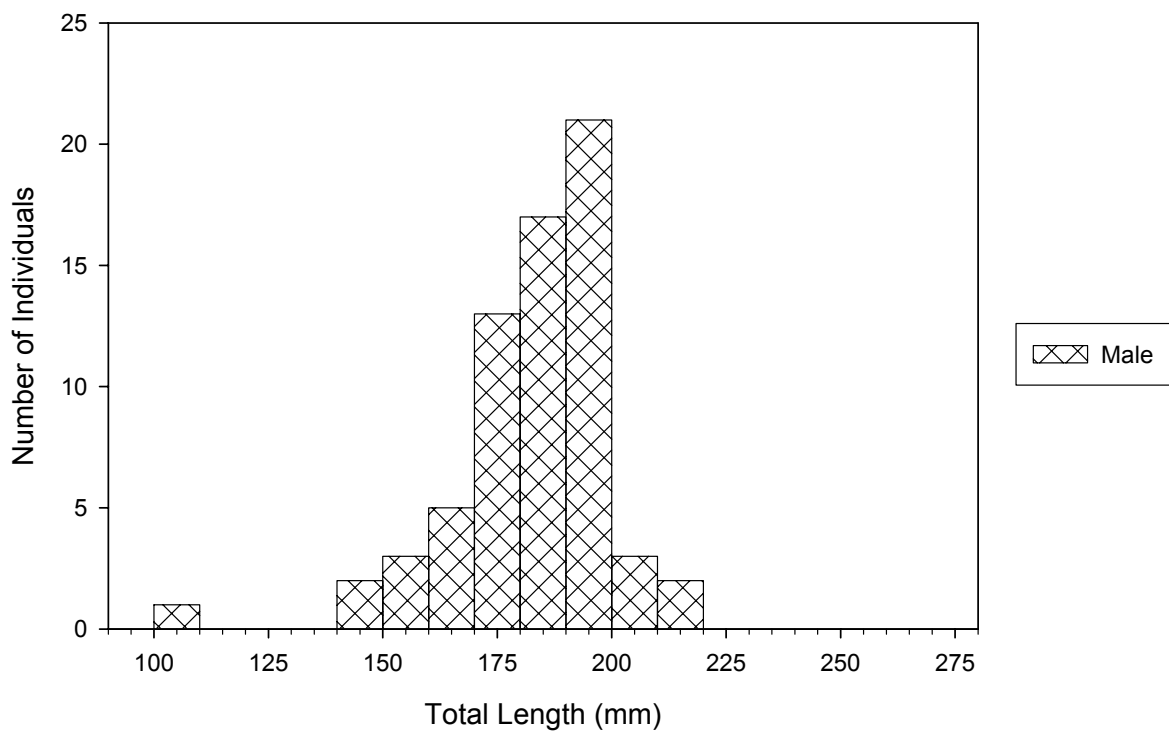
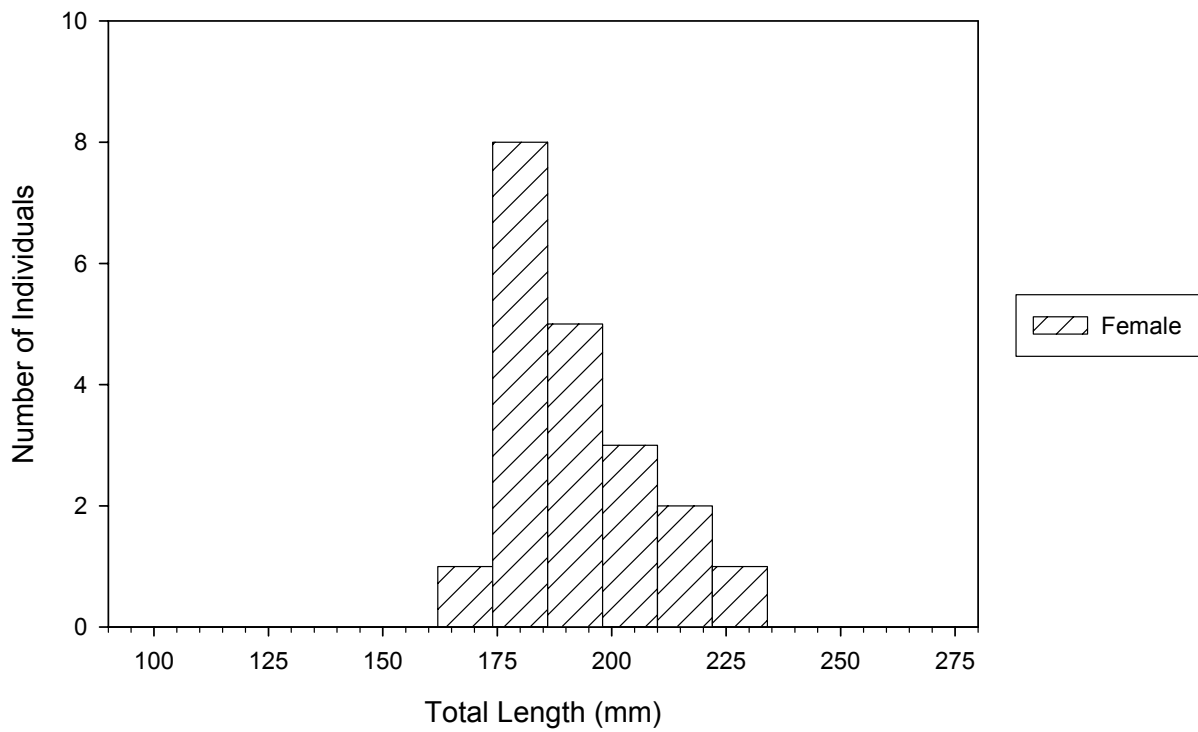
*Ambystoma maculatum* (male, n = 67; female, n = 20)





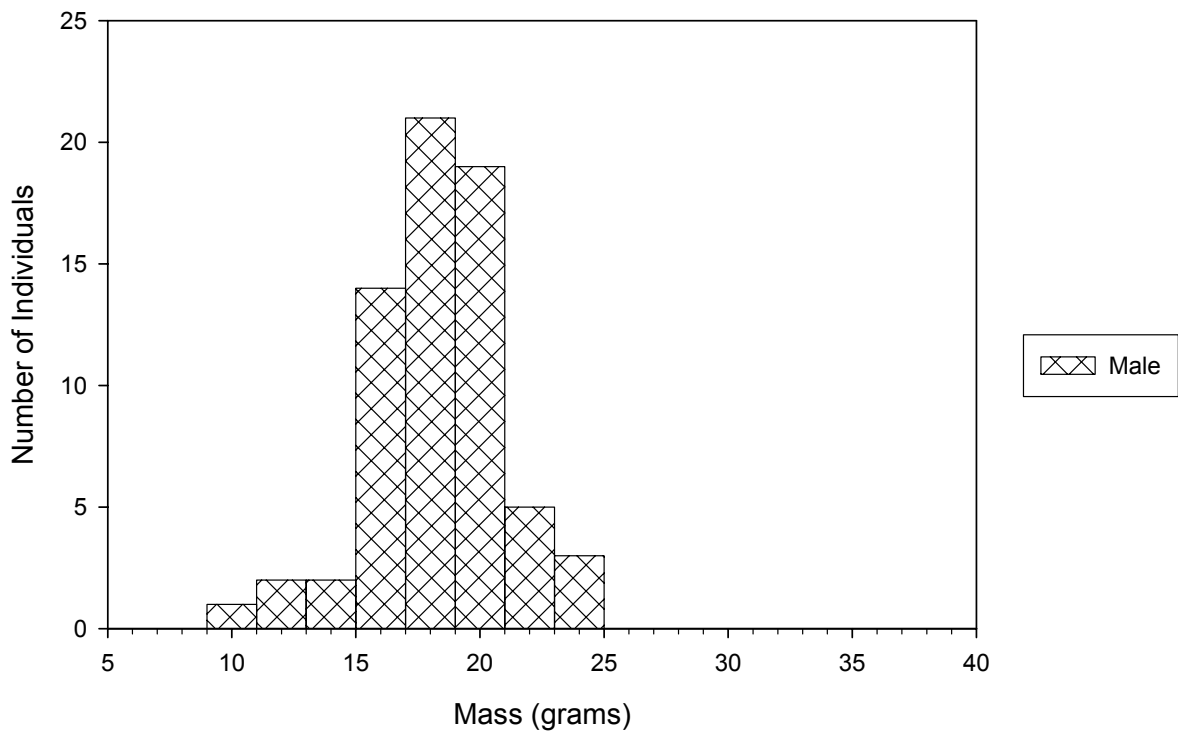
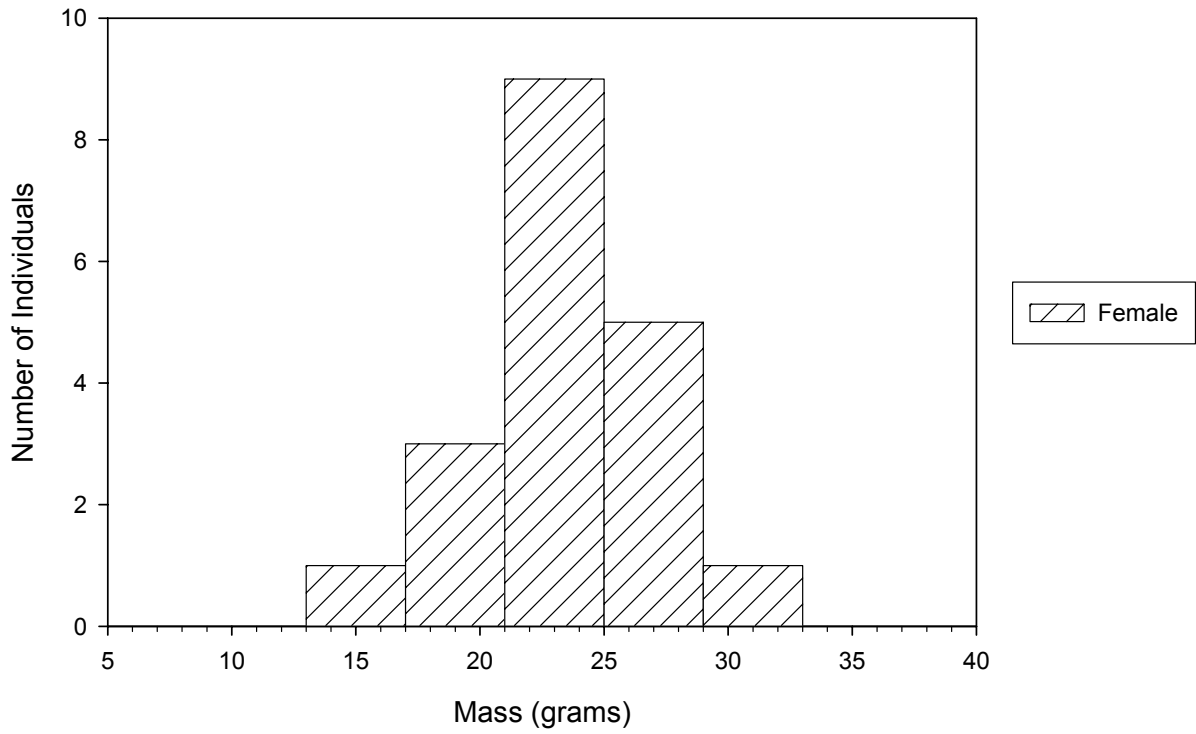
**Figure 18.** Total length frequency histograms of male (n = 67) and female (n = 20) *A. maculatum*; means are significantly different (P = 0.036); refer to Table 8 for statistical analysis

Adult *Ambystoma maculatum* (males, n = 67; females, n = 20)



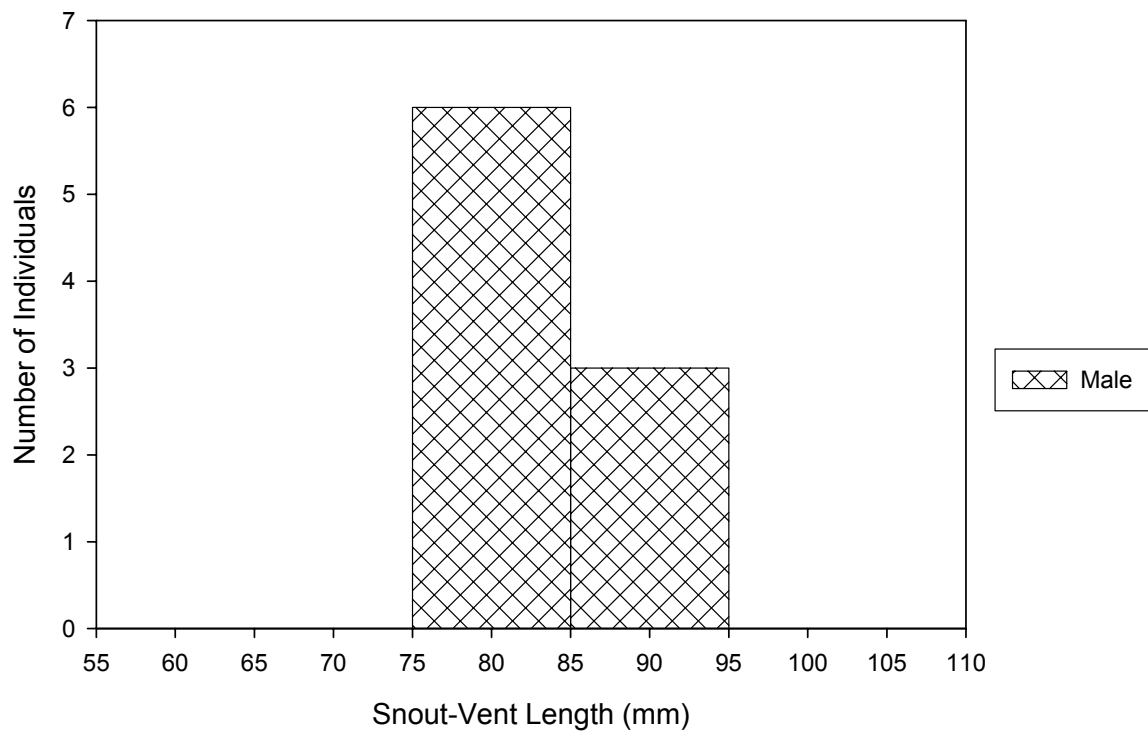
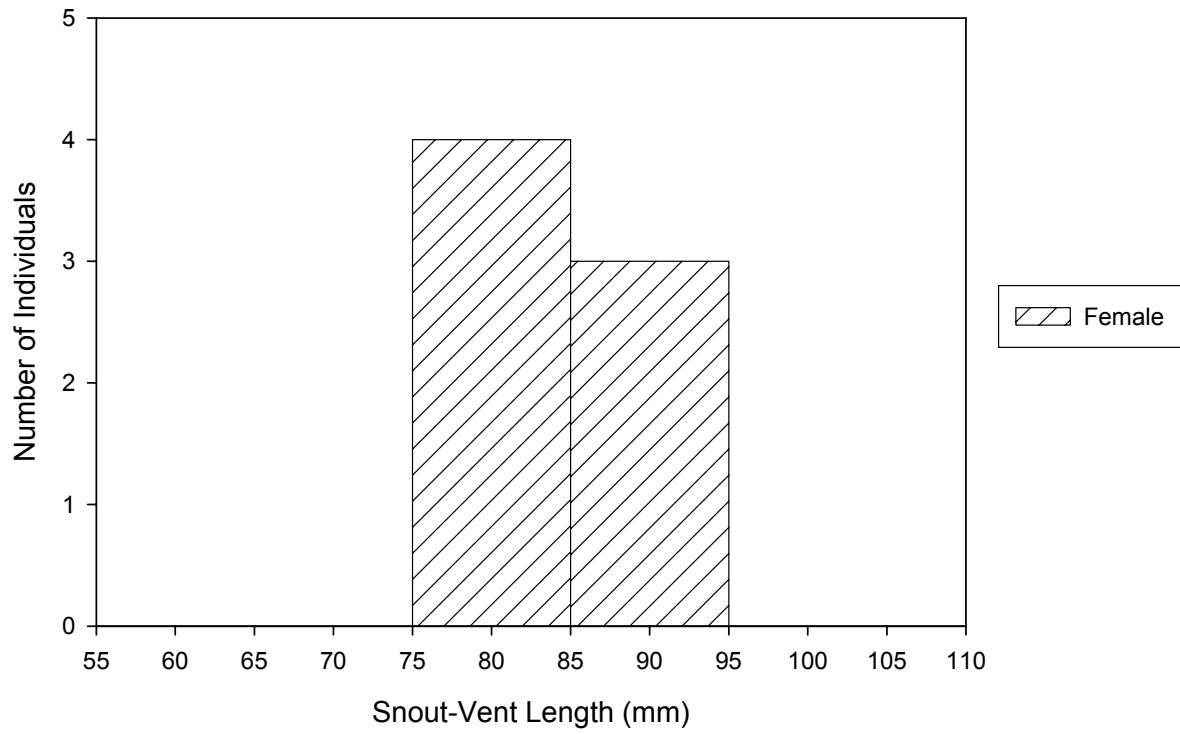
**Figure 19.** Mass frequency histograms of male (n = 67) and female (n = 20) *A. maculatum*; means are significantly different ( $P < 0.001$ ); refer to Table 8 for statistical analysis

Adult *Ambystoma maculatum* (males, n = 67; females, n = 20)



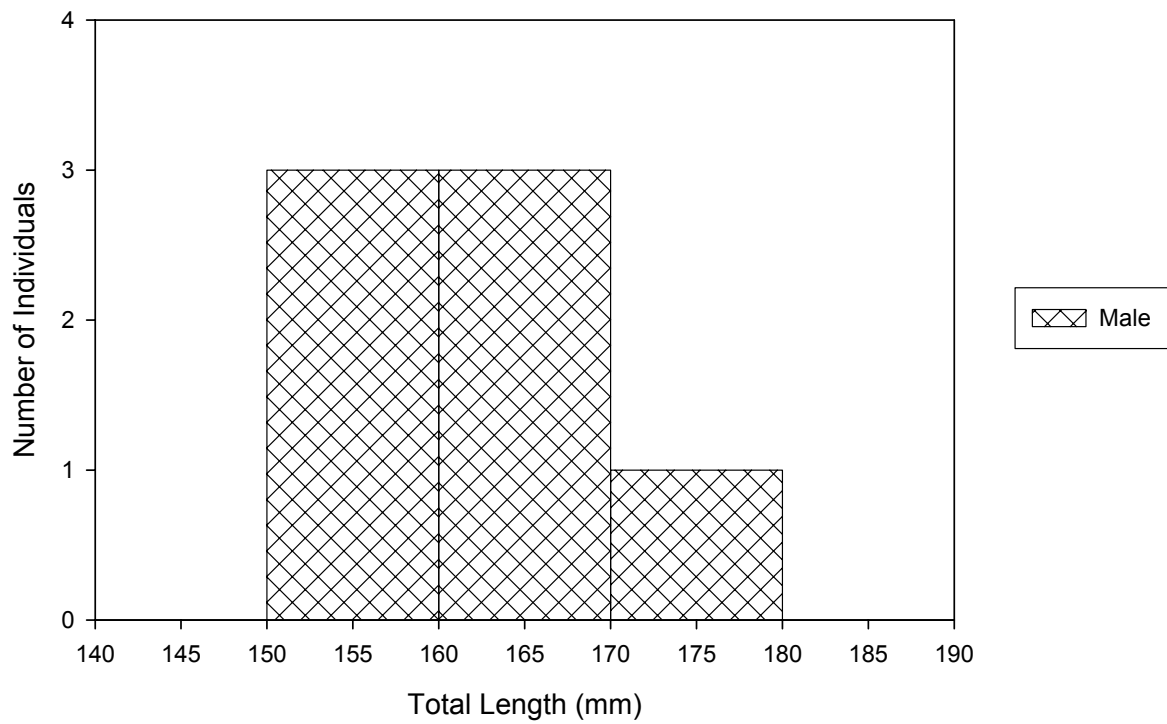
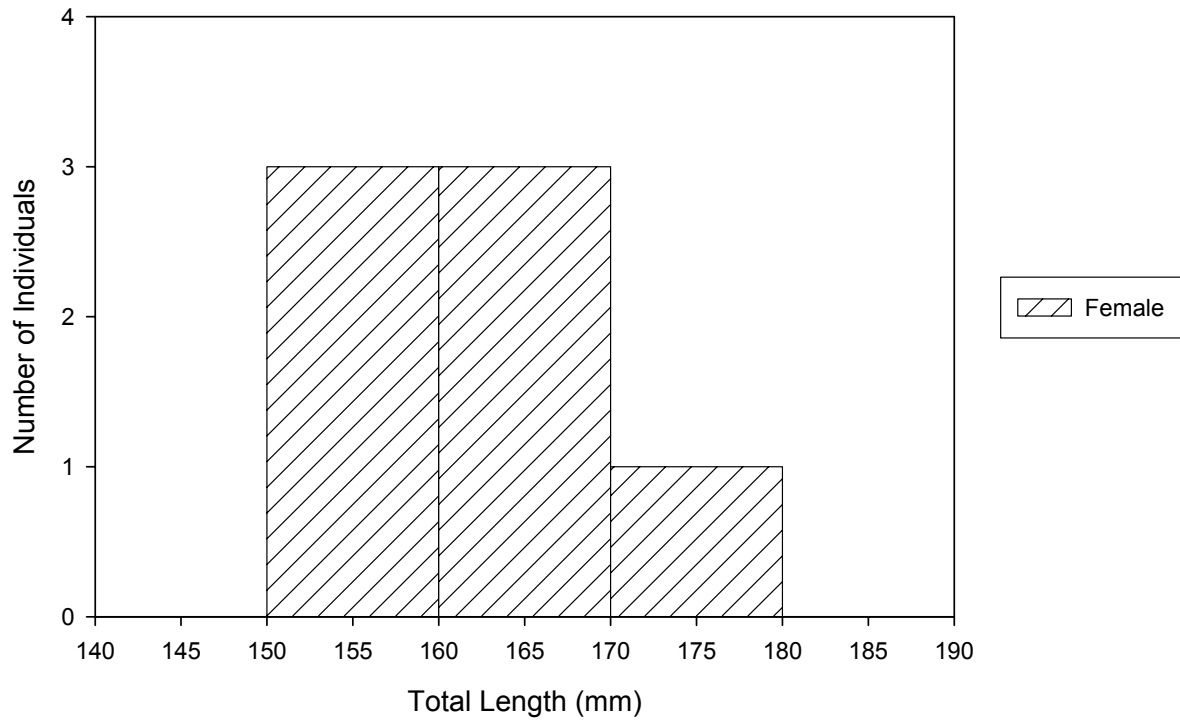
**Figure 20.** Snout-vent length frequency histograms of male (n = 9) and female (n = 7) *A. jeffersonianum*; means are not significantly different ( $P = 0.236$ ); refer to Table 8 for statistical analysis

*Ambystoma jeffersonianum* (males, n = 9; females, n = 7)



**Figure 21.** Total length frequency histograms of male (n = 7) and female (n = 7) *A. jeffersonianum*; means are significantly different (P = 0.036); refer to Table 8 for statistical analysis

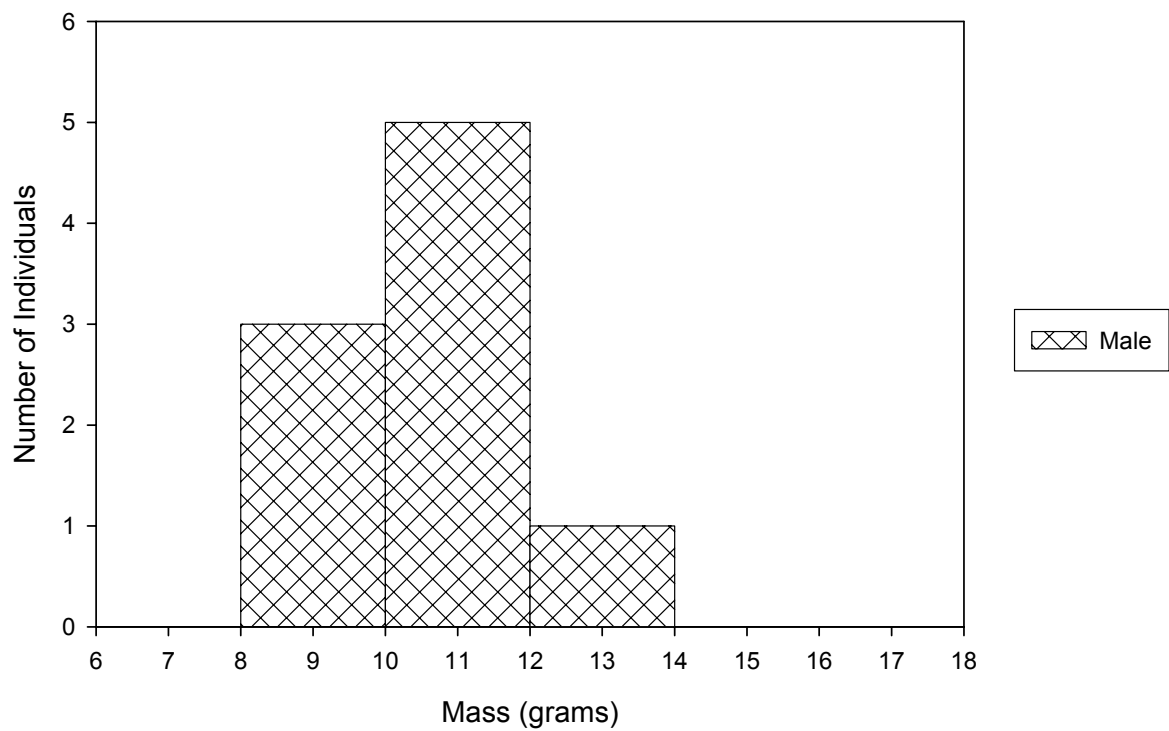
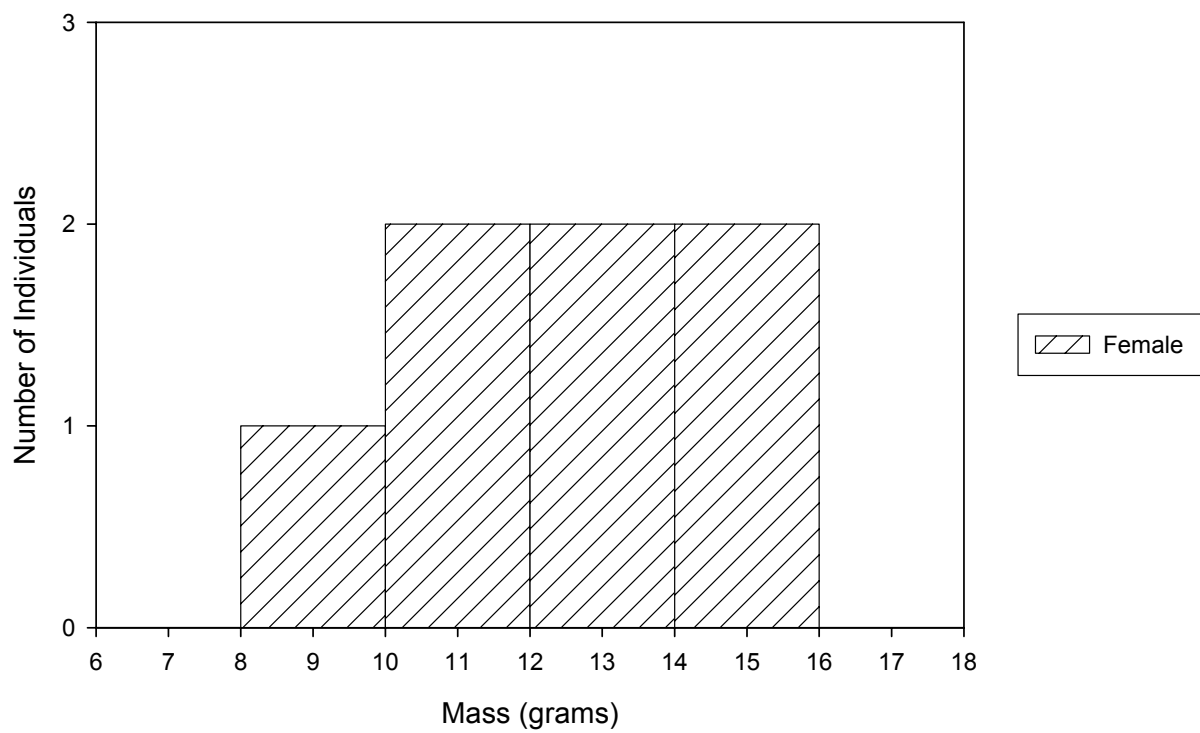
*Ambystoma jeffersonianum* (males, n = 7; females, n = 7)





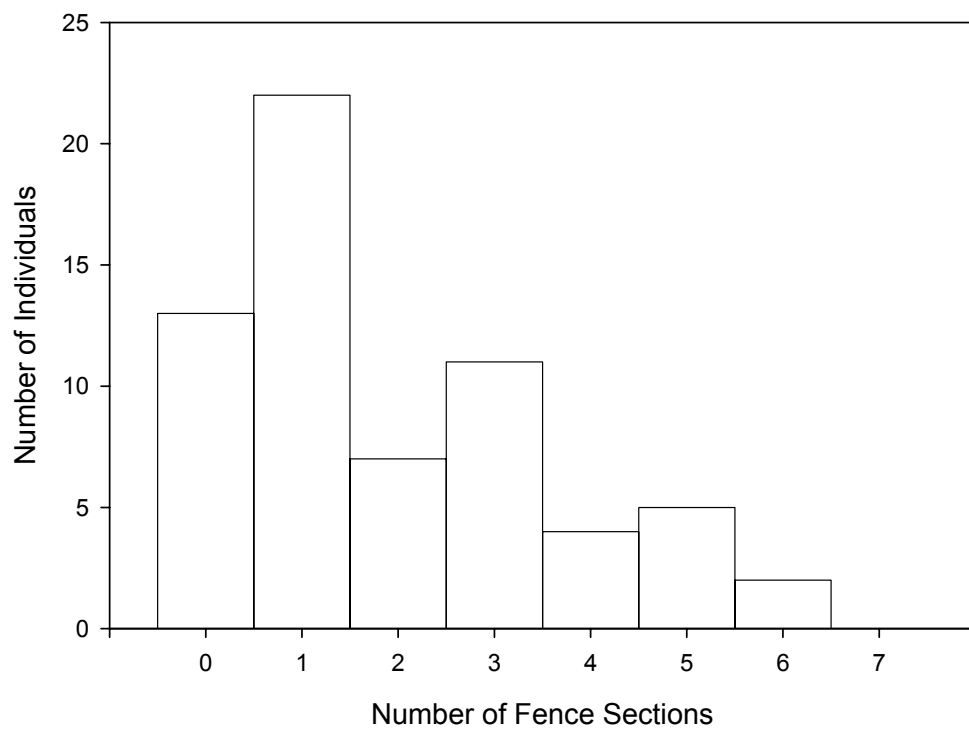
**Figure 22.** Mass frequency histograms of male (n = 9) and female (n = 7) *A. jeffersonianum*; means are not significantly different (P = 0.064); refer to Table 8 for statistical analysis

*Ambystoma jeffersonianum* (males, n = 9; females, n = 7)



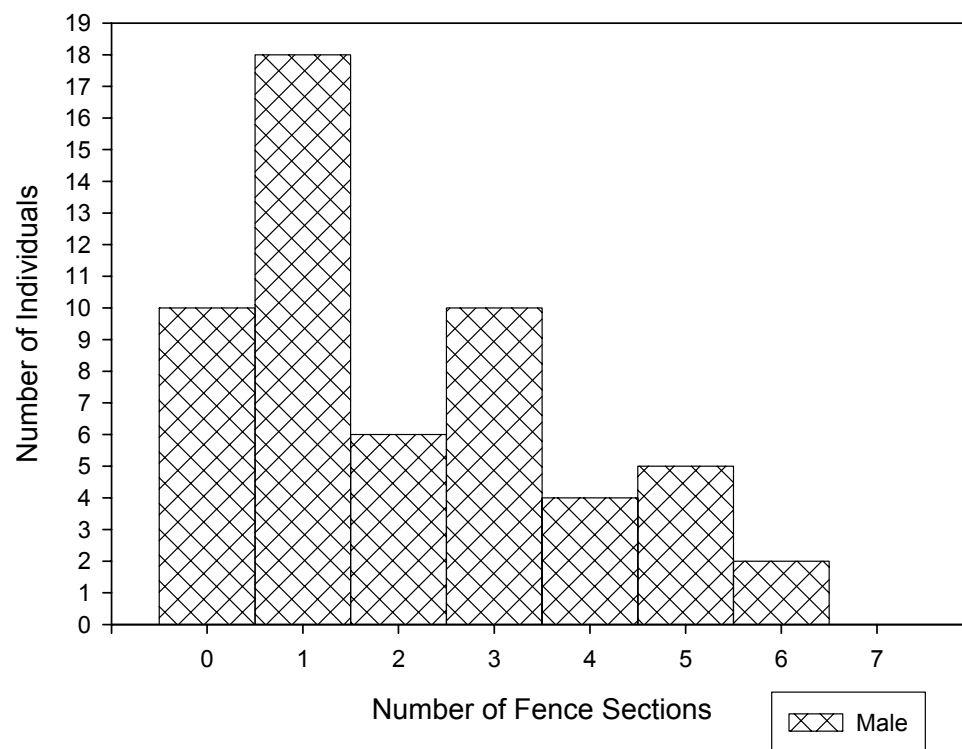
**Figure 23.** Frequency histogram of number of fence sections between entry and exit point for *A. maculatum* (n = 64); significant difference exists between observed and expected mean ( $P < 0.001$ ); refer to Table 9 for statistical analysis

*Ambystoma maculatum* (n = 64)



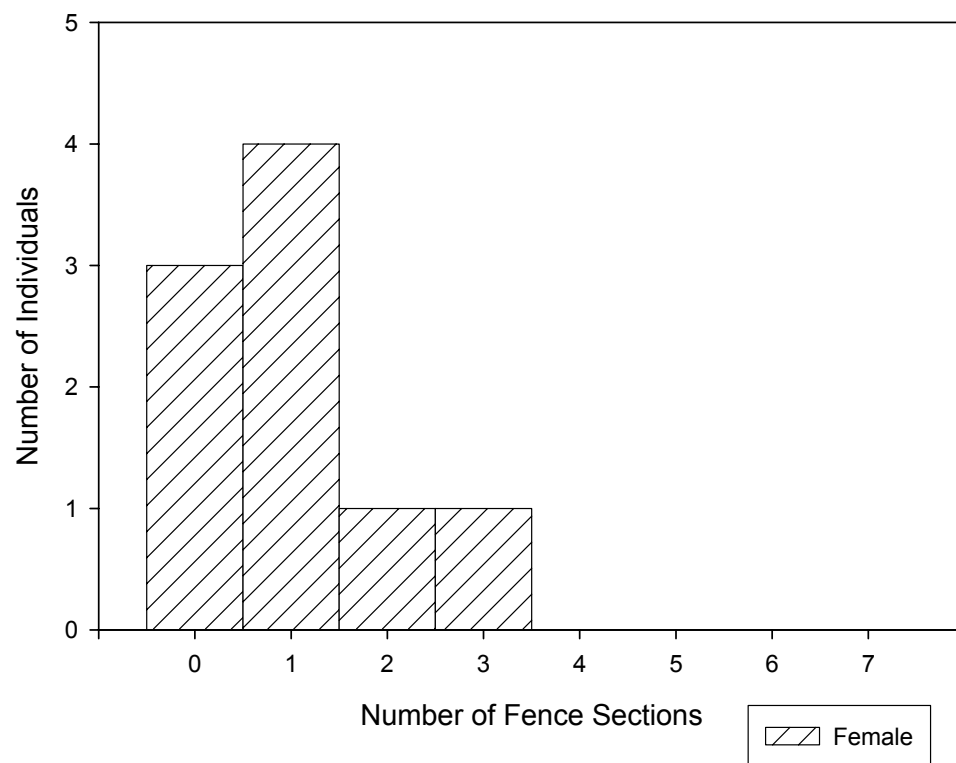
**Figure 24.** Frequency histogram of number of fence sections between entry and exit point for male *A. maculatum* (n = 55); significant difference exists between observed and expected mean ( $P < 0.001$ ); refer to Table 9 for statistical analysis

Male *Ambystoma maculatum* (n = 55)



**Figure 25.** Frequency histogram of number of fence sections between entry and exit point for female *A. maculatum* (n = 9); significant difference exists between observed and expected mean (P = 0.005); refer to Table 9 for statistical analysis

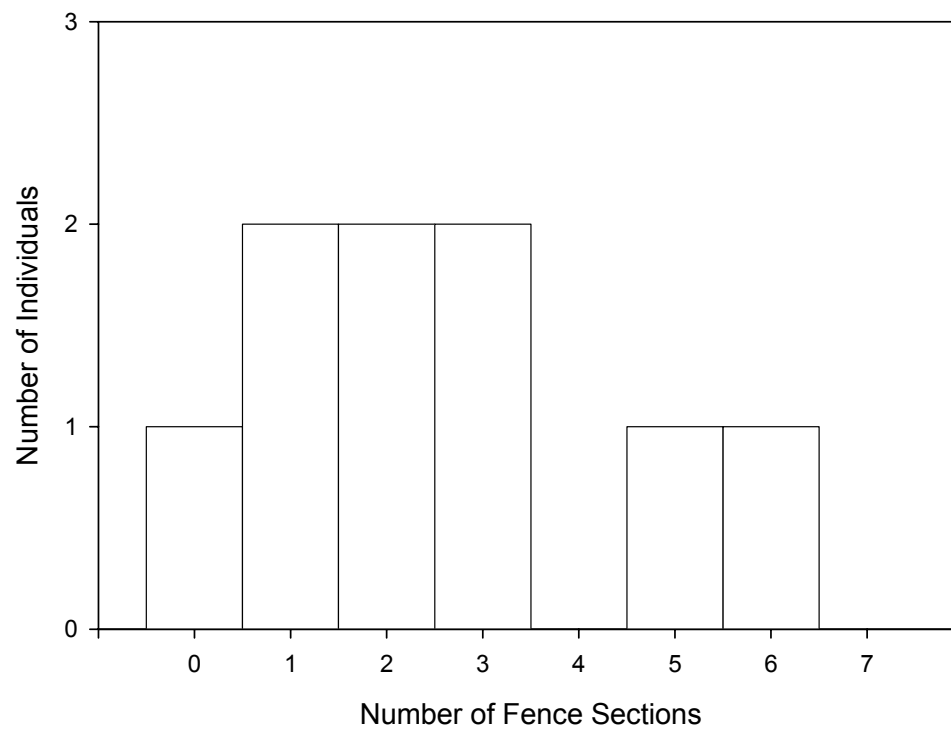
Female *Ambystoma maculatum* (n = 9)





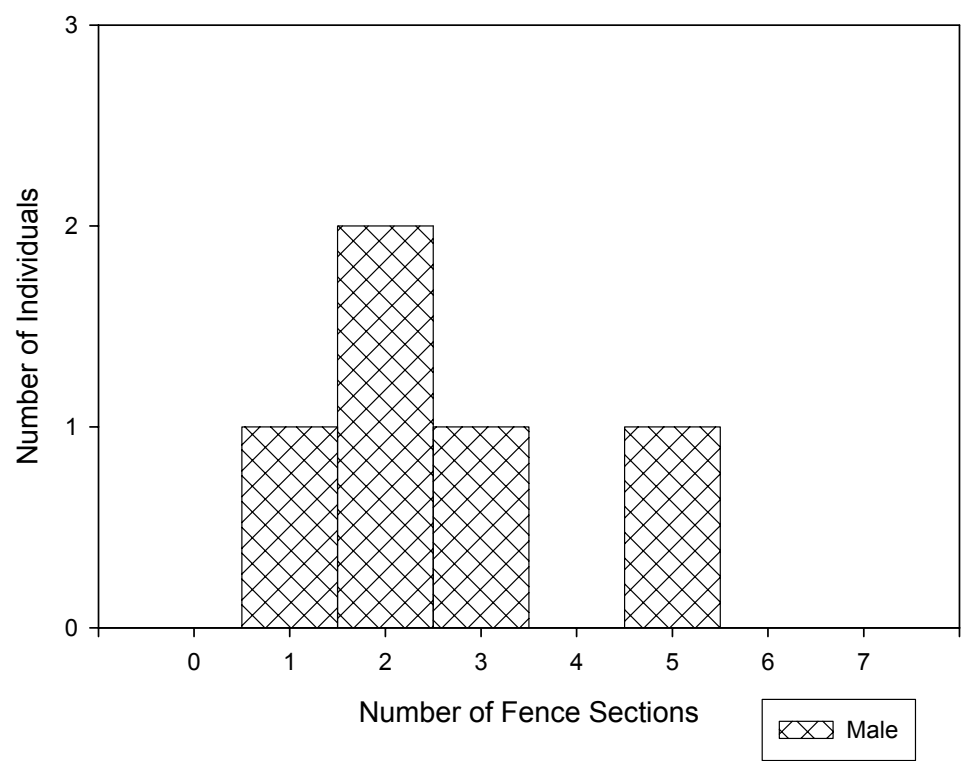
**Figure 26.** Frequency histogram of number of fence sections between entry and exit point for *A. jeffersonianum* (n = 9); no significant difference exists between observed and expected mean (P = 0.183); refer to Table 9 for statistical analysis

*Ambystoma jeffersonianum* (n = 9)



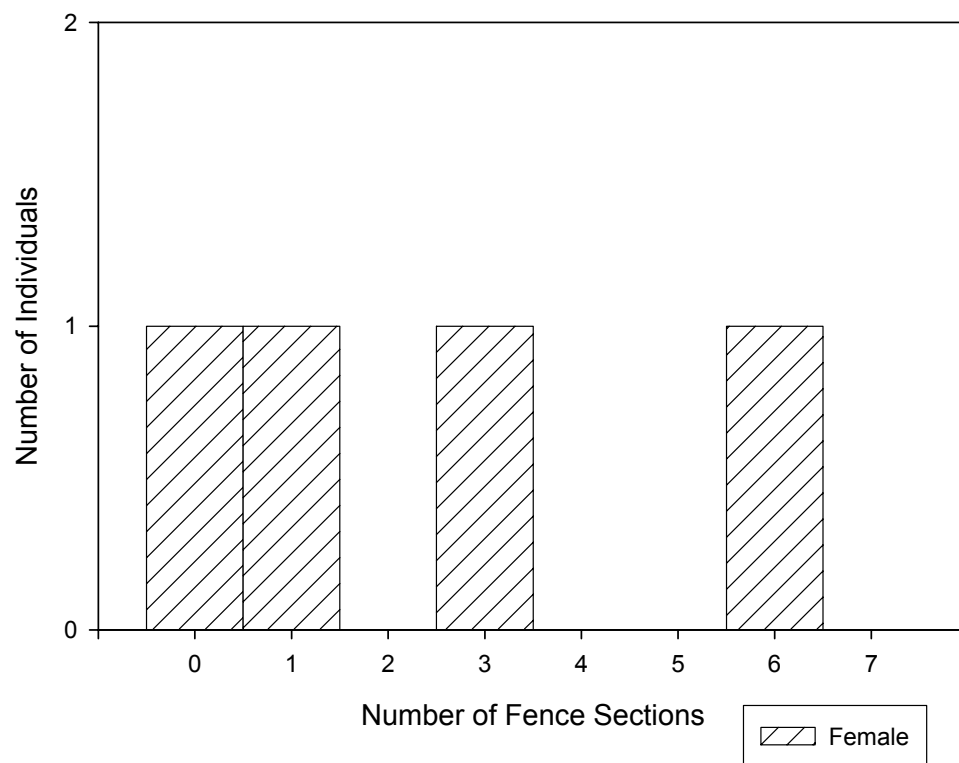
**Figure 27.** Frequency histogram of number of fence sections between entry and exit point for male *A. jeffersonianum* (n = 5); no significant difference exists between observed and expected mean ( $P = 0.255$ ); refer to Table 9 for statistical analysis

Male *Ambystoma jeffersonianum* (n = 5)



**Figure 28.** Frequency histogram of number of fence sections between entry and exit point for female *A. jeffersonianum* ( $n = 4$ ); no significant difference exists between observed and expected mean ( $P = 0.505$ ); refer to Table 9 for statistical analysis

Female *Ambystoma jeffersonianum* (n = 4)



# Curriculum Vitae

Seth Myers

## **EDUCATION**

### **M.S., Biology**, May 2003

Department of Biological Science  
Marshall University, Huntington, WV  
Concentrations: Herpetology, Conservation Biology  
Advisor: Dr. Thomas K. Pauley

### **B.S., Biology**, May 2000

Department of Biology  
Fairmont State College, Fairmont, WV  
Minor: Chemistry

## **RESEARCH AND PROFESSIONAL EXPERIENCE**

**Research Assistant**, funded by Dr. Thomas K. Pauley, Marshall University,  
August 2001-May 2003

- Supervised the N. Bayard Green Museum of Natural History as graduate curator (funded by WV Division of Natural Resources)
- Coordinated the North American Amphibian Monitoring Program within West Virginia
- Studied stream ecosystems to determine the potential effects of habitat disturbance on stream salamanders (funded by U.S. Geological Survey and U.S. EPA)
- Inventoried amphibians and reptiles in the Gauley River National Recreation Area, WV (funded by U.S. Dept. of Interior/National Park Service)
- Inventoried amphibians and reptiles in Harper's Ferry National Historic Park, WV (Funded by National Park Service)
- Inventoried amphibians and reptile along the Mud River, Cabell County, WV (funded by U.S. Army Corp of Engineers)
- Inventoried turtles in West Virginia (funded by WV Division of Natural Resources)
- Monitored the effects of gypsy moth treatment on forest salamanders in the George Washington National Forest and the Monongahela National Forest, WV as part of a long-term study(funded by U.S. Dept. of Agriculture/Forest Service)

**Thesis Research**, Marshall University, An Ecological Study of the Spotted Salamander, *Ambystoma maculatum*, and Jefferson Salamander, *A. jeffersonianum*, in West Virginia, 2002-2003

**Independent Research**, Fairmont State College, The effects of highway run-off on the water quality of an artificial wetland in north-central West Virginia, 2000

**Independent Research**, Fairmont State College, The effects of ethidium bromide and UV radiation on a SP20 cell line, 2000

### **GRANTS RECEIVED**

West Virginia Division of Natural Resources Wildlife Diversity Program Grant, Distribution and Habitat Selection of the Jefferson Salamander, *Ambystoma jeffersonianum*, in southwest West Virginia, Awarded March 2002

### **POSTERS PRESENTED**

Myers, Seth J. and Thomas K. Pauley, Breeding migration and population structure of the Spotted Salamander in West Virginia, Annual meeting of the Association of Southeastern Biologists, 2003

Pauley, Thomas K., Ariana N. Breisch, and Seth J. Myers, The status of the West Virginia reptile and amphibian collection, Annual meeting of the Association of Southeastern Biologists, 2002

Pauley, Thomas K., Seth J. Myers, Cody R. Lockhart, Adam M. Mann, Melissa R. Obermeyer, and Mark B. Watson, Influence of UV-b radiation, dissolved aluminum, and pH on amphibians in high elevation fens in West Virginia, Annual meeting of the Association of Southeastern Biologists, 2002

Myers, Seth J. and Donald Trisel, The effects of highway run-off on the water quality of an artificial wetland in north-central West Virginia, Annual meeting of the West Virginia Academy of Sciences, 2000

### **AWARDS**

**Summer Research Fellowship**, Marshall University, 2002

**First place award and cash prize for research**, 75th Annual Meeting of the West Virginia Academy of Sciences, 2000

**Full academic scholarship**, Fairmont State College, 1994-1998