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Natural History of the red-spotted newt, Notophthalmus viridescens viridescens (Rafinesque), in West Virginia

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Natural History of the red-spotted newt, *Notophthalmus viridescens viridescens* (Rafinesque), in West Virginia

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Two years ago, when I moved to Huntington, I didn't know a soul and probably wouldn't have recognized a salamander if it dropped out of the sky. Since then, I've had the time of my life and even learned a thing or two about amphibians. It's difficult to imagine that it's only been two years.

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And most of all, I want to thank my mom. She showed me by example important it is to follow your heart. I know how proud she is of me right now and that means more to me than any other accomplishment in my life.

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Abstract

Many studies have been conducted on *Notophthalmus viridescens viridescens* but none have occurred in West Virginia. There are variations in the life history of newts depending on location. In this study, I studied a population of newts in Wayne County, West Virginia from February 1996 to June 1997. I examined population structure, seasonal activity, and reproductive biology.

The population structure can be divided into four classes: egg, larvae, eft, and adult. Eggs at Shoals were deposited in mid-May and larvae were present from mid-June to early September. Larvae began to transform at an approximate total length of 32.8 mm. Red efts were not studied at Shoals but their sizes ranged from a total length of 28.3 mm to a minimum of 78.3 mm. Adult snout-vent length ranged from 41.7 - 64.0 mm and averaged 49.3 mm.

The sex ratio of adults varied weekly. I captured up to 27 males for every female (27:1) in funnel traps in February and March. In summer, however, females outnumbered males up to 2.5 times The overall sex ratio in funnel traps was 5.1:1. While dipnetting, however, the weekly sex ratios were much closer to even. Overall, from December to June, the sex ratio was 1:1.4. According to current literature, this is the first population of newts studied where females outnumber males.

Seasonal activity patterns of male and female adult newts differ. Sex ratios in funnel traps reflect activity ratios since the traps capture moving animals. Males are much more active than females in the late fall and early spring. While dipnetting, females were captured more often from vegetation. There are also more females in the water in the summer.

Most of the newts at Shoals emigrate from the ponds to terrestrial hibernacula in late April. This migration correlates with the increase in water temperature. Over the summer, newts were found under cover objects and debris. Their skin texture and color and tail height is more suitable for terrestrial living. Newts return to the aquatic environment in mid-November, when ponds refill and water temperature begins to drop in mid-November.

Reproductive biology is divided into the breeding migration, breeding season, and oviposition. There are two breeding migrations at Shoals, one in November and one in February and March. In other

studies, the smallest adults, metamorphing efts, migrate to ponds in the fall. At Shoals, the smallest adults migrated in the spring. Also, it appears that females do not reproduce their first year.

Current literature describes only a spring breeding season and occasionally a "false fall breeding season". At Shoals, breeding actually occurs at both seasons. This is determined by looking at sperm waves in males, which showed sperm throughout the entire reproductive tract from November to May, and by witnessing males drop spermataphores in December.

Oviposition was determined visually and by monitoring female egg volume throughout the year. Both of these methods coincided and showed that eggs are deposited in May and June.

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Chapter 1 Introduction

PURPOSE OF STUDY

The purpose of this study was to determine the natural history of the red-spotted newt, *Notophthalmus v. viridescens,* in West Virginia. Many studies on *Notophthalamus v. viridescens* suggest that the life history varies with location. Until now, West Virginia newts have not been the subject of research. This study shows the similarities and differences between newts in West Virginia and other parts of its range.

This study was conducted at Shoals, West Virginia, in Wayne county. Data were collected weekly from February 1996 to June 1997. Information was gathered on population structure, seasonal activity, and reproductive biology of newts.

DESCRIPTION OF SPECIES

The red-spotted newt has four distinct life stages: egg, larvae, juvenile, and adult.

Eggs are approximately 1.5 mm in diameter. They are laid singly on vegetation and hatch in about a month, depending on water temperature (Jordan 1893, Smith and Pfingsten 1989).

The larval stage is aquatic and has a duration of approximately three months. The appearance of larvae is yellowish-green with grey or brown pigmentation on the dorsum with a pale, unmarked belly (Fig. 1). Larvae range in total length from 21.0 to 47.8 mm (Chadwick 1944, Hurlbert 1970a, Harris et al. 1988).

As a juvenile, this salamander goes through a terrestrial period. During this stage, the newt is known as a red eft. It ranges in total length from 40 to 97 mm (Chadwick 1944). It has a bright-orange dorsum with black-rimmed spots and a yellow venter (Fig. 2). This aposomatic coloration warns predators of the toxic skin secretions produced by this species. However, even brown efts were found to have a low predation rate (Brandon et al. 1979). Red efts are adapted to terrestrial habitat by rough, spinous skin and a rounded tail. The number of years the eft spends in this stage depends on the location of the population. Hurlbert (1969) and Pough (1971) found short eft stages of 2-4 years. Healy (1974) and Shure et al. (1989) studied efts with a terrestrial period of 2-8 years. In a few arid areas, newts skip the eft stage completely (Noble 1926, Brandon and Bremer 1966, Healy 1973, Gibbons and Semlitsch 1991, Humphries pers. comm.). Neoteny may be the result of decreased eft survivorship that stems from a lack of cover in these sandy areas. In neotenous individuals, reproduction may occur by the age of 2 years (Healy 1974).

The adult stage of *Notophthalamus v. viridescens* is an aquatic salamander. Total length ranges from 57-146 mm. Adams (1940) found that the average total length of males was 1.6 mm longer than that of the females. The smallest adult in West Virginia was a gravid female from Hardy County with a TL of 58 mm and the largest was a male with a SVL of 146 mm, found at Green Bottom Swamp in Mason County (Pauley 1986). Adults have an olive-colored dorsum with black-rimmed red spots (Fig. 3). The venter is yellow with flecks of black. This species is separated from other salamanders by the presence of cranial crests and the absence of costal grooves.

During the breeding season, males and females are easily differentiated. Male newts are recognized by black pads, or excrescences, on the hind toes and inner thighs (Fig. 4). Pads are used to grasp the female during mating. Males also have more muscular hind legs and a higher tail fin than females. The female, at this time, will not have these characteristics, but will often be gravid (Fig. 5).

Outside the breeding season, the characteristics described above are not as apparent. However, the cloaca is a diffinitive characteristic in differentiating between the sexes at any time of year. In males, the cloaca is round and bulbous. The cloaca in females is elliptical and the vent is a slit. There will also be visable folds perpendicular to the vent (Fig. 6).

TAXONOMY AND DISTRIBUTION

The taxonomy of the red-spotted newt is reflective of its complicated and variable life cycle. The adult was originally named *Triturus viridescens* by Rafinesque in 1820. The proposed subgenus name was *Diemictylus* and was confused with the genus taxon, leading to the synonym *Diemictylus viridescens*. Other generic names were used in the mid- to late-1800s. These include *Notophthalma*, *Triton*, and *Malge*. *Triturus miniatus* was the nomenclature given to a population around Lake Champlain. In 1962, the International

Commission selected *Notophthalamus viridescens* as the official taxonomy (Mecham 1967).

There are four subspecies of *Notophthalmus viridescens, N. v. viridescens, N. v. dorsalis, N. v. piaropicola*, and *N. v. louisianensis.* The red-spotted newt, *N. v. viridescens*, has a range extending from southeastern Canada to North Carolina and west to Alabama (Fig. 7) (Mecham 1967). This species is common in West Virginia and is widely distributed throughout the state. *Notophthalmus viridescens dorsalis* is found in the coastal plain of North and South Carolina. *Notophthalmus viridescens piaropicola* inhabits only the South Florida penninsula. *Notophthalmus viridescens louisianensis* occupies the area from Michigan and Wisconsin south to Texas and Louisiana.

DESCRIPTION OF HABITAT

Adult *N. viridescens* inhabit a variety of aquatic environments. While they have a broad tolerance for environmental conditions, they prefer still, deep pools that are open to solar radiation (Gates and Thompson 1982). *Notophthalmus viridescens* is often found in the shallow zones of these deep ponds, in water less than 30 centimeters deep (Bellis 1968, Burton 1977 , Gates and Thompson 1982). However, George (1977) found *N. viridescens* in water up to 13 meters deep in Lake George, NY. Temperature selection is given as the reason newts are found in predominantly one locality (Bellis 1968, Gates and Thompson 1982). Burton (1977), however, reasoned that newts stay near the shore to use macrophytes as cover. George (1977) also found newts closely associated with aquatic plants of *Nitella* sp.

Terrestrial red efts are usually found in wooded habitats, among leaves and logs. They can be found at a considerable distance from water. Migrations may exceed 800 meters (Healy 1975). The eft stage could be a means to increase gene flow (Gill 1978).

DESCRIPTION OF SITES

The population of newts at Shoals was chosen initially because of a previous study conducted there. Dr. James Joy (Marshall University Department of Biological Sciences) collected newts from the permanent pond for a parasite study in 1995. He found 100% females during the summer. Throughout the entire year, the sex ratio was close to even, 1.3:1. Since all the literature describes an adult sex ratios in favor of the male, I chose to take a closer look at this population.

The two ponds are located in Shoals, Wayne county, West Virginia. It is a low elevation site, 200 meters above sea level. The study ponds are located approximately 100 meters from Plymale Branch Road. Twelve Pole Creek feeds these ponds from the west (Fig. 8).

There is a temporary pond upstream and a permanent pond downstream. Both ponds have a muddy substrate with a thick leaf cover and are swamp-like, with a large number of emergent woody plants (Fig. 9). The temporary pond has larger trees than the permanent pond. Most of the woody vegetation at the temporary pond is maple and elm whereas the vegetation at the permanent pond is mostly alder. The deep region of the permanent pond, however, is without emergent vegetation and open to sunlight.

Another noticable difference between the two ponds is the presence of the marble salamander, *Ambystoma opacum*. This species is present in great numbers in the temporary pond but absent from the permanent one.

Habitat surrounding the ponds and stream is mostly field. Although, there is a wet woodland west of the temporary pond and a steep incline with shrubs, vines, and small trees east of the permanent pond (Fig. 10).

MATERIALS AND METHODS

Each week environmental data were collected at three marked locations in each pond. These data included water temperature (°C), water depth, dissolved oxygen (mg/L), water pH, and general appearance of the habitat (eg. change in vegetation, cover, or water color).

Water temperature was taken 12.5 centimeters below the surface of the water with a LaMotte thermometer. Weekly temperatures at each pond were determined by averaging the highest and lowest temperature taken at the markers. Temperatures were used to determine the monthly average temperatures at each pond.

Water depth was measured by placing a meterstick into the water at each marker. Depth measurements were taken at the deepest and shallowest pond markers each week. Weekly average depths were used to calculate the monthly average depth at each pond.

Dissolved oxygen (DO) and water pH were recorded with a YSI Model 55 DO meter and an Oakton pH tester 3, respectively. These two environmental data sets were measured only from March 1996 to September 1996. It was apparent that these factors fluctuated with rainfall and were not useful variables in seasonal environmental conditions.

RESULTS AND DISCUSSION

DEPTH OF POND

The pond upstream was dry from late June to early November in 1996. This pond averaged a maximum depth of 32.8 centimeters (Fig. 11).

The permanent pond is approximately 100 meters downstream from the temporary pond. Average maximum depth was 1 meter.

From January to May, the two ponds maintained approximately equal depths (Fig. 11). In June, July, and August, the temporary pond began to dry out quickly. It dried completely in September and

October. By November, the temporary pond began to refill at a more rapid rate than the permanent one.

TEMPERATURE

Temperatures of the ponds were similar throughout the year. Therefore, these data were pooled (Fig. 12). Temperatures were as expected, rising to a maximum temperature of approximately 23.2°C in July. Then, the temperatures dropped off throughout the rest of the year. Lowest temperatures of the year were in January, approximately 1.0°C.

ENVIRONMENTAL OBSERVATIONS

Seasonal divisions were made based on general environmental observations (Table 1). Early spring was defined by fluctuating air temperatures and a growth of early vegetation. Late spring was associated with an increase in growth of pond vegetation. Also, there was an increase in rainfall and temperatures as well as an increase in turbidity in the water, making it appear darker. A period of hot weather and lack of rainfall was characteristic of summer. During fall, vegetation dropped leaves or died back. This resulted in an increase of organic material on the ground and in the water. Winter was defined by the increasing presence of ice on the pond surface.

Table 1. Seasonal divisions with approximate start and end dates.

SEASON	*START DATE*	*END DATE*
Early Spring	Mid-February	Early April
Late Spring	Mid-April	Early June
Summer	Mid-June	Mid-September
Fall	Late September	Mid-November
Winter	Late November	Early February

Chapter 2 Population Structure

INTRODUCTION

Population structure of *N. v. viridescens* can be divided into four general classes: egg, larvae, eft, and adult. Each of the later three classes can be examined further by sex or size.

Eggs are laid in the spring (Logier 1952, Hurlbert 1970a, Gill 1978, Gates and Thompson 1982, Green and Pauley 1987, Sever et al. 1996). They hatch in approximately one month, depending on water temperature (Jordan 1893, Smith and Pfingsten 1989).

Larvae grow throughout the summer and transform in the fall (Hurlbert 1970a, Gill 1978, Brophy 1980). When larvae hatch, the average total length is 21.0 mm. Later in the summer, as they metamorphose, larvae average 50.4 mm (Harris et al. 1988).

The total length of efts range from 40 to 97 mm (Chadwick 1944). In general, most studies of efts estimate the length of time in this stage as 2 to 4 years (Hurlbert 1969, Pough 1971). The eft stage can last up to eight years (Healy 1974, Shure et al. 1989).

While adult males outnumber females, the opposite occurs during the eft stage. Chadwick (1944) found a sex ratio of 1:1.9. Hurlbert (1969) found a similar ratio, 1:1.4, and he suggested that the female efts may be more active than males.

The fourth class, the adults, were the focus of this study. Adults range in total length from 57 to 146 mm. Age and sex ratio have been the focus of many studies involving newts.

Age of newts can be calculated by skeletochronology, snout-vent length (SVL), and the number of testicular lobes in males. The most accurate of these techniques is skeletochronology, the process of examining a cross section of bone to count the number of growth rings. This technique has been reported in a number of recent papers (Hagstrom 1977, Hagstrom 1980, Dolman 1982, Hutton 1986, Leclair and Castanet 1987, Castanet et al. 1988, Hemelaar 1988, Francillon-Vieillot et al. 1990, Forester and Lykens 1991, Smirna 1994, Chinsamy et al. 1995, Caetano and Leclair 1996).

Skeletochronology has allowed researchers to compare the actual age of the animal to its size. In other newts, *Triturus* sp., Hagstrom (1980) discussed how food, weather, genetics, and disease play important roles in the SVL of newts. In *N. v. viridescens*, there is a correlation between SVL and age (Humphrey 1926, Sever 1974). Therefore, size classes can be used in determining the age structure of a population. The difficulty in using size classes is that the class limits would vary depending on location.

Size classes have been used by other newt researchers for age class determination (Noble 1926, Hurlbert 1969). However, Gill (1978) found an overlap in size classes, so that they could not be used for age determination. Springer (1909) found that growth depends on the amount of food eaten and Hurlbert (1970a) related size proportionally to the temperature of the water.

Gill (1978) extensively studied a marked population of newts in the mountains of Virginia. He stated that adult newts have a low survival rate, 1.9 years for males and 1.3 years for females. Massey (1990) and Sever et al. (1996) have also noticed this high mortality in adults. Gill (1985) reassessed average life spans, declaring up to 15 years for males and 12 years for females. The newts simply were not breeding every year. Smirina (1994) and Caetano and Leclair (1996) determined the life span of newts as 3 to 13 years.

The number of testicular lobes has also been used to estimate age in male salamanders (Humphrey 1926, Adams 1940, Sever 1974) (Fig. 13). Dolmen (1982) described the growth of additional testicular lobes and corrolated each lobe to two years of age. The lobes may be added from residual spermatagonia (Humphrey 1926).

Chadwick (1944), Gill (1978), and Harris (1981) noted an uneven sex ratio in adults, 2:1 to 5:1. Bellis (1968) and Massey (1988, 1990) also found this type of sex ratio. Hurlbert (1969) found a ratio that was close to even, but it still favored the males by 55 percent.

Dr. James Joy (pers. comm.), while studying parasites in the newt population at Shoals, noticed a sex ratio opposite to those recorded in the literature. He found only females during the summer months.

MATERIALS AND METHODS

The newt population at Shoals was monitored weekly from 23 February 1996 to 6 February 1997. Four funnel traps were used in the temporary pond, 2 in the stream, and 6 in the permanent pond.

The presence and duration of the egg stage was checked with biweekly dipnetting from 14 December 1996 to 6 June 1997.

Vegetation was carefully examined for eggs. The decrease in number of gravid females was used to indirectly determine the period when eggs had been laid. Eggs were not counted since females carry 250-300 eggs (Gill 1978). The volume of eggs was measured by water displacement. Eggs were removed from the female and dropped into a 10 ml flask filled with water to a marked line. The amount of water displaced by the eggs was removed with a graduated syringe.

Five males were preserved biweekly to examine testicular lobes. Lobes from both testes were counted since, on occasion, one testis had more lobes than the other.

Since the main focus of this research was adults, data on larvae and efts are limited. Only general observations were made of these stages.

Larvae were monitored by recording their presence or absence from funnel traps in 1996. They were measured monthly in captivity until their metamorphosis.

Efts were not monitored directly. However, 4 sets of 9 boards (22 x 16 cm) were placed around the permanent pond and stream.

Logs, leaf litter, moss, and mud were also checked biweekly for the presence of post-larval efts, pre-adult efts, and terrestrial adults.

Up to 60 adults per week were brought to the lab from 23 February 1996 to 6 February 1997. Size, weight, sexual condition, and spot pattern were recorded. Sex ratios were determined in the field using all the captured newts from the funnel traps and from dipnetting. The SVL of each newt was measured with a Spi 6" Dial Caliper and weighed with a Ohous E120 scale. Sexual condition was determined in males by the presence of excressences. Females were given a positive sexual condition if they were gravid. An animal was "marked" by recording its dorsal spot pattern (Fig. 14). Each newt has a spot pattern that is unique to that individual and constant throughout its life (Gill 1978).

The size of the population at Shoals was calculated using the Lincoln Index (Seber 1973):

$$N/M = n/m \qquad \text{S.E.} = \frac{\sqrt{M^2 n(n-m)}}{m^3}$$

Where: N = population number
M = number of animals marked and released
n = total number of animals caught
m = number of animals recaptured

RESULTS AND DISCUSSION

EGGS

Eggs of *N. v. viridescens* at Shoals were found while dipnetting in early May of 1997. This coincides with egg volume data from the 1996 season, when egg deposition was calculated to occur from late April to early June (Fig. 15). Highest egg volumes were at the beginning of January (0.36 cc) and at the beginning of April (0.34 cc). The drop in egg volume between these two peaks appears to be the result of an immigration of immature adults to the pond, lowering the average egg volume. The decrease in egg volume in late April was due to oviposition. Any egg volume below 0.1 cc appeared to be primordial follicles only. The drop below this point occured in early June. This decrease continued through early August to the volume of 0.0 cc. Dates of oviposition agree with other studies (Pope 1924, Chadwick 1944, Smith 1950, Logier 1952, Hurlbert 1970a, Gill 1978, Sever et al. 1996).

Since larvae were found by June, the egg stage at Shoals extends from late April and early May to early June.

There should be a large number of eggs deposited throughout the ponds, especially the permanent pond. A population estimate of 20,000 newts was made. If half the newts were female and they each carried 250-300 eggs, there should be over 2.5 million eggs. However, I could not find any eggs in 1996 and only a few in 1997.

There may be high predation rates, low reproductive success, or the females are laying the eggs elsewhere. Gill (1978) discovered that newts have a higher survival rate at young ponds. Chadwick (1950) found that newts cannibalize eggs.

LARVAE

Larvae were present in funnel traps from June to early September. These dates correlate with Gill (1978).

Larval lengths were measured in early August, at the end of the larval stage. These lengths (N=3) averaged 18.7 mm. By late August, these individuals were post-larval efts and averaged 32.8 mm. This average size is smaller than the reported sizes from other studies.

Number of larvae captured in the traps was not counted. However, the number of *N. v. viridescens* larvae was small compared to the number of *A. opacum* larvae which had been captured over the fall and winter in the temporary pond. Given the number of newts in these ponds and the number of eggs per female, this was unexpected.

This low number of larvae could be explained by many factors (eg. low survival of eggs, high levels of predation or parasitism, or low activity levels).

Predation on larvae could have occurred by any number of insects, invertebrates, fish, amphibians, reptiles, or birds using the pond. Also, since larvae have lower toxicity levels than efts and adults, they are more apt to be preyed upon. However, they may still be toxic enough to be avoided since larvae have been shown to be unpalatable to another salamander, *A. tigrinum* (Brophy 1980).

A low reproductive success was described by Gill (1978) in his metapopulation theory. According to him, the ponds are all part of a large population. Poor reproductive success at one pond is offset by higher reproductive success at another pond. Over time, different ponds become the feeder ponds for the metapopulation.

EFTS

Size range of efts was determined indirectly. Post-larval efts averaged 32.8 mm total length. The SVL of the smallest adult in this study was

41.7 mm (TL = 78.3 mm). Most efts probably grow larger.

Length of the eft stage at Shoals was not studied. The only adult newt whose age was determined by skeletochronology was 4 years old with a SVL of 51.0 mm. That female spent up to 3 years as an eft. Since she was gravid and females may require an extra year before becoming sexually active, she probably only spent 2 years in the eft stage.

Efts metamorphose in February and March. This was determined using various data. When looking at seasonal egg volume, seasonal tail ratio, and seasonal SVL, there is an obvious decrease during late February and March (Figs. 15, 16, 17). This is due to the influx of young, terrestrial newts entering the ponds and becoming aquatic adults.

ADULT

The range of adult SVL was from 41.7 to 64.0 mm; the average SVL was 49.3 mm. There was no significant difference in average SVLs of males and females (Table 2).

Table 2. Ranges and averages of male and female SVL

	Sample # (n)	*Range of SVLs*	*Average SVL*
Males	634	41.7 - 60.6	49.3
Females	176	42.8 - 64.0	50.0
All	812	41.7 - 64.0	49.3

There were no clear size groupings that could be divided into classes. Like Gill's study, size classing does not apply for this population.

When average SVL was examined over the course of a year, larger, and therefore older, individuals were found in the ponds throughout the summer (Fig. 17). This may indicate that older newts are less capable of undergoing necessary physiological changes to leave the pond. Healy (1974) and Harris et al. (1988) noticed that larger *N. v. viridescens* are not tolerant to drought, which may prevent them from leaving the pond.

Monthly average weights show similar results (Fig. 18). Lowest weights occur in October/November and in March. The highest were in August. Weights were more variable, probably because they are more dependant on the microhabitats and the stressors and availability of food.

In general, females had a higher SVL and their weights were slightly lower. This may indicate that females take longer to mature than males. Low weights in October may indicate that the adults are not eating as much in the terrestrial habitats, that the larger individuals are dying on land, or that there are younger newts arriving at the pond.

Sex ratios depend on the type of trapping. Funnel traps captured moving animals. This is an activity ratio, not a sex ratio. Males show a high amount of activity during the breeding season. There are two peaks, one in December and one in April. During some weeks in February and March, the activity ratio was as high as 27:1 (Fig. 19). This figure also shows the decline in the summer, as most newts leave the ponds for terrestrial hibernacula.

Sex ratios from dipnetting also show a high number of newts in the early spring (Fig. 20). However, the number of males versus females are close to even. In April and May, females outnumbered the males. Overall, the sex ratio is 1:1.4.

According to Humphrey (1926) and Dolmen (1982), each testis grows an additional lobe every other year. The number of testicular lobes, determined during dissection, was examined using the Newman-Keuls multiple comparisons test. There was no significant correlation with SVL at the 0.05 confidence level.

The highest number of total lobes was 7 and occurred in a newt with a SVL of 48.2 mm. This is one of the smallest newts captured. Based on these data, the number of lobes in male newts at Shoals do not correlate with size or indicate age.

The size of the newt population at Shoals was calculated at 21,796 $\pm$ 3840 individuals. However, the assumptions of population estimates were not met. This population was affected by mortality and recruitment throughout the year. Also, the funnel traps captured more males, making an unequal probability of individuals being counted.

High mortality of captured newts was seen in May and June. At the time, it was suspected that this was the result of low levels of oxygen in the increasing temperatures of the pond. However, the high mortality continued after styrofoam blocks were placed in the traps, allowing a portion of the trap to stay above water. I also noticed that these deceased individuals were usually large males. Since the larger, older individuals stay in the pond later in the season, it subjects them to increasing heat stress. Males may also be less tolerant to heat and parasites due to the higher activity exhibited during the breeding season.

Gill (1978) showed that parasitism by leeches affect the survival rates of newts. Joy (pers. comm.) described extensive parasitism, both in terms of diversity and numbers, to the newts of these ponds. This may affect the survival of this population.

CONCLUSION

There were few eggs and few larvae found in the ponds at Shoals which may indicate poor reproductive success. Larvae averaged a total length of 32.8mm at metamorphosis. Efts metamorphose into adults in February and March. The SVLs of adults range from 41.7 to 64.0mm and average 49.3mm. There were no clear size classes at these ponds, preventing the assignment of age classes. Number of testicular lobes, another aging technique, did not show significant correlation to size. Activity ratios, which indicate breeding activity, peak in December and April. Weekly funnel trapping yielded activity ratios up to 27:1 in December, February, and March. The sex ratio, determined by dipnetting, was 1:1.4.

Chapter 3 Seasonal Activity

INTRODUCTION

Activity patterns of newts vary depending on life stage, sex, habitat, season, and time of day.

Very few studies have been conducted on the activity patterns of larval newts. Chadwick (1950) described larvae as bottom-dwellers until metamorphosis, when they reside just below the surface.

The eft has a diurnal activity pattern although nocturnal post-larval migration has been described by Chadwick (1950), Hurlbert (1970a), and Massey (1990). This post-larval migration occurs in late summer, between July and September (Hurlbert 1970a, Gibbons and Semliech 1991). Rain also causes an increase in activities (Healy 1973, MacNamara 1977, Massey 1990). Hurlbert (1969) found a sex ratio in efts that favored females, possibly due to a higher activity level. Healy (1975) studied numerous aspects of eft activity. He estimated that home range increases throughout the eft stage, from 270 to 500 square meters. He also found that efts congregate near food sources and have a large overlap in home ranges. This indicates a lack of territoriality. Efts, in their transition from the terrestrial juvenials to aquatic adults, make a migration back to a pond of up to 0.4 km (Smith and Phingsten 1989). Healy (1975) state that this migration occurs from August to November.

Adult activity patterns differ between the sexes. Chadwick (1944) and Bellis (1968) suggested that females exhibit a lower activity level than males. This theory was offered as an explanation to the male-biased sex ratio seen in adult newts (Noble 1926, Gill 1978, Harris 1981, Massey 1988, 1990).

Adult newts also appear to have a habitat preference. They are usually found in water that is less than 30.5 cm deep, apparently using vegetation for cover, a source of food, and a substrate for egg deposition (Burton 1977, Bellis 1968, Gates and Thompson 1982).

It is generally accepted that adults remain active throughout the year and can even be seen swimming beneath ice in winter (Green and Pauley 1987, Conant and Collins 1991). According to Hurlbert (1970a), active newts in winter are females. Massey (1990), however, found males overwintering in the ponds.

Noble (1926), Morgan and Grierson (1932), Hurlbert (1969), and Ducey and Dulkiewicz (1994) found that the adult newts are terrestrial for part of the year. This terrestrialism occurs at different times depending on location. Often terrestrialism occurs in the summer (Brimley 1921, Hurlbert 1969). Gill (1978, 1985) described newts in ponds over summer, leaving in the fall, and overwintering on land. Gibbons and Semlitsch (1991) noted that newts leave ponds as they dry up in the fall.

Gill (1978) theorized that *N. v. viridescens* leave ponds because of high water temperatures. George (1977) and Bellis (1968) also found that newts are associated with deeper water in the summer and proposed that there is a thermal preference for cooler water. However, newts have a tolerance for high temperatures (Zweifel 1957). Gates and Thompson (1982) gave a thermal maximum of 36°C. In the red-bellied newt, *Taricha rivularis*, Licht and Brown (1967) found a thermal preference of less than 18-20°C and no avoidance of near-freezing temperatures.

Physiological changes that occur during the transition from aquatic to terrestrial environments are significant. These changes occur during a period of time when newts exhibit "wandering behavior" (Hurlbert 1969, Hasumi and Iwasama 1992). Most notably, the tail fin height decreases, the skin becomes more granular, and the skin color gets darker (Fig. 20). Adams (1940) found a low average tail height during July and August for males and during October for females. Females had a high average tail height from April to June. The characteristic of rough skin was described by Brimley (1921) in November.

Whether *N. v. viridescens* has a home range or homing ability is arguable. Bellis (1968) found that individual newts occupied a small home area and had homing ability. Tabachnick and Underhill (1972) also described a homing ability and a population so subdivided that inbreeding is a possibility. In another study, *N. v. viridescens* was found to have random movement, no homing ability, and no territoriality (Harris 1981). Hurlbert (1969) also determined that newts lack a homing instinct.

Food and predation also affect activity patterns. I did not conduct studies on either subject. Therefore, the only discussion on those subjects will be the following results from other studies.

Many diet studies have been conducted on larvae (Morgan and Grierson 1932, Brophy 1980), efts (MacNamara 1977), and adults

(Morgan and Grierson 1932, Wood and Goodwin 1954, Hurlbert 1970a, Burton 1977, Brophy 1980, Jiang and Claussen 1993). Overall, *N. v. v* is an opportunistic feeder. Stomach contents of aquatic stages include ostracods, zooplankton, fish and amphibian eggs, insects, snails, salamander larvae, and molted skin. Efts forage for a variety of invertebrates (MacNamara 1977). Food has been found in the stomachs of adults throughout the winter (Morgan and Grierson 1932, Jiang and Claussen 1993).

N. v. v. has toxic skin secretions, making it unpalatable to most predators. Gates and Thompson (1982) stated that newts are virtually free from predation. However, Hurlbert (1970a) noted that sunfish, minnows, pickerel, and trout all preyed upon *N. v. viridescens.* Shure et al. (1989) found that, in one area, half the eft population were eviscerated by an unidentified predator. Brodie (1968) and Hurlbert (1970b) observed bullfrogs (*Rana catesbiana*) eating newts without any obvious ill effects.

MATERIALS AND METHODS

Seasonal activity was monitored by capturing newts in funnel traps and by dipnetting. Each week, between 23 February 1996 and 6 February 1997, funnel traps were checked. Up to 60 newts were taken to the laboratory to record SVL, weight, sexual characteristics, and spot patterns. All newts from the traps were sexed to determine the weekly sex ratio.

Dipnetting was carried out every other week from 14 December 1996 to 6 June 1997. Numbers and ratios of newts captured while dipnetting were compared to the funnel trap data. This allowed for a comparison between the actual sex ratio and seasonal activity.

Every other week, up to 5 females and 5 males were killed in chlorotone, fixed in formalin, and preserved in alcohol. These specimens were used to determine reproductive condition and habitat.

Habitat can be indirectly monitored by measuring relative tail height (actual tail height divided into actual tail width). A value of 1 is a round tail. Higher values reflect a higher tail fin, indicating an aquatic environment.

Skin texture also appears as a useful tool in rating the terrestriality of newts. In this study, skin texture was a general observation only.

Terrestrial newts were monitored in the field by turning logs, rocks, and leaves, by dipnetting through mud, and by monitoring board sets (12- 22 x 16 cm boards placed in 3x4 arrangement). Two sets of drift fence/pit fall traps were originally set in late March of 1996. No newts were captured in approximately a month probably due to the small coverage area or poor locations. During a flood in mid-May, the fencing/traps were damaged. They were not replaced because of the poor capture record.

RESULTS AND DISCUSSION

Since larvae were not the main focus of this study, they were only monitored for presence or absence. However, it was observed that the number of larvae captured in funnel traps was only a small fraction of the number of *A. opacum* larvae captured earlier in the year. This may reflect a low number of larvae in the ponds or a low activity level. Larvae were present in funnel traps from mid June to late August. Since dipnetting occurred only through early June, larvae were not expected.

The timing of emergence and submergence is fairly noticable when examining the numbers of newts captured (Fig. 21). These numbers dropped sharply at the end of April and continued to decrease slowly until late July when no more than one or two newts were captured each week. This decrease in newt numbers coincides with high water temperatures (Fig. 21).

Water began to fill the ponds in the middle of November. At this time, there is a sharp increase in the number of newts at the ponds as well as a sharp decrease in water temperature (Fig. 21).

There was a decrease in the number of newts captured in January. This was due to cold temperatures that caused the ponds to freeze and probably slowed the newt activity levels. Both males and females were found in the ponds over winter.

An indirect method of determining the submergence or emigration of newts is the tail fin ratio. An aquatic newt has a tail fin that is up to 3 times as high as it is wide. It is used to propel the newt through water. On the other hand, the increase in surface area of a high tail fin on land actually deters the mobility of the newt by sticking to surfaces. For a terrestrial newt, the tail fin height-width ratio approaches one.

There is a decreasing tail fn ratio throughout the summer to the lowest ratios in October. This indicates that newts are not utilizing aquatic habitats at this time. The tail ratio increases from November to February, when there is another low tail fin ratio. At this point, there appears to be another wave of immigrants into the pond. These immigrants are probably transforming efts, since they have a smaller average SVL (Fig. 23). Their low tail fin ratios decrease the monthly average. As this group adapts to the aquatic environment, the tail ratio increases to the highest point in May (Fig. 22).

Skin texture was not given quantitative values. However, it was noticed that terrestrial newts had much grainier, coarser skin. When placed in water, the skin appeared silvery due to the small bubbles of air captured in the texture of the skin. This animal is not suited for aquatic habitat.

Over the summer, it was originally assumed that the newts were either becoming terrestrial or burrowing into the mud on the pond bottom. A number of microhabitats were checked, including under cover objects, at the base of trees, in the mud, and even in crayfish holes. In captivity, newts burrowed in the dirt even when water and cover objects were present. Finally, in mid-September, a terrestrial male and a post-larval eft were found at the base of a tree, under almost 5 cm of debris. This location was approximately 30 m from the nearest water source. Other newts were located during the following weeks under cover objects. Each week, the newts were found nearer to water.

A much higher number of newts were captured in the permanent pond as opposed to the temporary pond (Table 3).

Table 3. Comparisons of total numbers and sex ratios of newts at each pond.

Pond	*Total Number of Newts*	*Sex (Activity) Ratio*
Temporary Pond	176	3.6 : 1
Permanant Pond	1445	6.2 : 1

Either there were more males using the permanent pond or the breeding activity was higher.

The results of funnel trap captures can be compared to dipnetting captures. This allows for a comparison between activity levels and sex ratios.

The results of dipnetting shows two points. One is supportive of the arguement that newts at Shoals become terrestrial over the summer. Almost no newts were captured in June, July, August, and September of 1996. Also, there is an increase in the number of newts captured during December and February to May, the highest numbers were found during the spring breeding season (Fig. 24).

The second point is that the sex ratio is much closer to even. The total sex ratio for the year comparing the two trapping techniques also illustrates this point (Table 4).

Table 4. Comparison of the sex ratios for each trapping method.

Trapping method	*Sex ratio*
Funnel trap	5.1 :1
Dipnetting	1 : 1.4

As for habitat preference, only observations were made. Females seemed to prefer vegetation more than males. Males appeared to spend more time floating at the water surface during sunny days.

Newts in captivity spent more time out of water than in it. Even in the field, a large number of newts were observed resting on the alder branches just above the water level.

CONCLUSIONS

Few larvae, in comparison to the number of adult newts and to the number of other amphibian larvae, were captured in funnel traps in 1996. Larvae metamorphose into juveniles in August.

The majority of efts transform into adults in February and March when there is an influx of small adults to the ponds.

Adults leave the ponds for terrestrial hibernacula in April and return in November. The absence of newts in the ponds is correlated with high water temperatures.

Aquatic adult males have a higher activity level than females. During the breeding season, males may be up to 27 times as active as females. The sex ratio of the permanent pond, however, slightly favors females at 1:1.4. This is the first female-biased population of adult newts reported.

Chapter 4 Reproductive Biology

INTRODUCTION

Breeding migrations occur in the fall and/or spring. Hurlbert (1969) described two breeding migrations, April to May and August to October. He attributed this to whether the females had over-wintered in a pond or on land. He also saw that males migrate first in the spring and females migrate first in the fall. However, Gill (1978) saw only one migration to the ponds and no difference between the sexes. Adams (1940) found the smallest newts, metamorphing efts, migrate in October. It is important to note that this is a breeding migration, not a breeding season.

The breeding season, according to literature, is only in the early spring. Sever et al. (1996) gave the months of December to March in South Carolina. Further north, in the mountains of Virginia, newts breed from March to late June (Massey 1988). Gill (1985) estimated that newts breed an average of three seasons, though not necessarily in consecutive years.

The literature describes a "false" fall breeding season (Chadwick 1944, Hurlbert 1969, Gill 1978, Massey 1990). However, Pope (1924) describes an actual breeding season in November and December in Pennsylvania. Adams (1940) saw excressences on males from September to June but the breeding season only lasted from April to June.

Massey (1990) found that females can store sperm for 10 months or longer. However, Sever et al. (1996) stated that females can only store sperm from December to May, limiting them to one breeding season.

The behavior of sexual interactions has been described precisely in many papers. Wise et al. (1993) discussed recognition and social interactions between newts. Verrell (1982) explained courtship patterns and Massey (1988) illustrated interference tactics used by males.

Oviposition occurs in the spring (Hurlbert 1970a, Gates and Thompson 1982, Green and Pauley 1987). Hurlbert (1970a) and Sever et al. (1996) observed egg deposition in May, while Chadwick (1944) noticed eggs from April to July. Eggs are laid singley on the leaves of aquatic vegetation. Sometimes the leaf is folded around each egg, protecting it from predators.

MATERIALS AND METHODS

When checking funnel traps weekly, males and females were counted to determine the sex ratio. This sex ratio was actually an activity ratio since the numbers of captures depended on how much newts moved. Activity ratio is an indirect method of determining the breeding season, since males move more at that time.

Reproductive condition of up to 60 animals per week was visually examined and described as either positive or negative. For the males, a positive reproductive condition was the presence of black excressences on the hind limbs and toes, a high tail fin, and an enlarged cloaca. The female was rated as positive for reproductive condition if she was gravid.

Presence of eggs was determined during the biweekly dip netting. Numbers of eggs were not counted although a comparison could be made with the other species of amphibian eggs in the pond.

Every other week, up to 5 males and 5 females were collected and preserved. These specimens were used to monitor egg volume in females and to count the testicular lobes and conduct a spermatogenic wave analysis in males.

Egg volume was measured by filling a 10 ml flask to a marked line. Eggs from a female were transferred to this flask. The displaced water was then removed with a graduated syringe. The amount of water in the syringe equaled the volume of eggs and was recorded in cubic centimeters (cc).

The number of testicular lobe for each male was determined visually. The total number of lobes for each male was recorded since, on occasion, one testis had a different number of lobes than the other.

Spermatagenic wave progression was analyzed by dividing the right side of the male reproductive tract into four portions - the posterior testis, anterior testis, anterior vas deferens, and posterior vas deferens. Each portion was ground with the dull end of a probe onto a slide. This was diluted with a few drops of water and stained with a few drops of Wright's stain. These slides were examined under a light microscope at 40X magnification. Each portion of the reproductive tract that contained sperm was assigned one point (Fig. 25). The total number of points, up to 4, was recorded.

RESULTS AND DISCUSSION

Two major breeding migrations occured, one in the fall and one in the spring. During the fall breeding migration, the average snout-vent length (SVL) was 50.0 mm but in the spring it was 48.4 mm (Fig. 26). Not only were the adults smaller in the spring but the small females were not gravid (Fig. 27). In the funnel traps, there may have been an overestimation of gravid females due to my inexperience in telling the two phases apart during the spring of 1996. The percentage of gravid females collected from dipnetting is more accurate (Fig. 27). Small, non-gravid females were probably new immigrants to the pond and needed an extra year before reproduction. This supports results from Caetano and Leclair (1996).

Breeding season was determined by sperm wave analysis of the males. Males had a consistantly high rating from November through May (Fig. 28). They were seen dropping spermatophores in the laboratory in early December. The activity ratios also show this breeding activity in two peaks in the early winter and early spring (Fig. 29). The drop in activity between the two peaks seems to be from cold weather. Therefore, there may actually be only one breeding season, from November to April.

Egg volume was also monitored over the breeding season. There are high egg volumes from November to February and in April. The lower egg volume in March is due to the influx of new immigrants. Most of these females are not gravid, decreasing the total average for that month (Fig. 30). As discussed above, these adults are smaller and are probably newly transformed efts. Adult females may not be capable of breeding the first year. The average size for breeding and non-breeding adults shows no difference ($p=1.000$) for males but a significant difference for females (t-test; $p=<0.001$). Females must be larger and/or older before reproducing (Fig. 31). This has been seen in other amphibians as well (Hemelaar 1988, Bruce 1993).

The second decrease in seasonal egg volume, from May to August, is obviously due to oviposition (Fig. 29). Oviposition occurs in May and June while the decrease in egg volume for July and August is probably due to regression of the ovary and reabsorbtion of primary eggs. Eggs were found in the pond in mid-May.

One gravid female had originally been marked in November. She was recaptured in December, without eggs. This individual may have dropped her eggs accidentally or purposefully. An accidental egg drop by a female in captivity was described by Pope (1924). If she deliberately laid her eggs, they were not found while dip netting. Although, with such a small number of eggs dropped at a time of year with limited food, the eggs may have been eaten by predators.

CONCLUSIONS

The population of newts at Shoals exhibited two breeding migrations, in November and in February/March. There are also two breeding seasons in late fall (November/December) and early spring (February/March).

Members of the spring breeding migration average smaller SVLs, indicating new adults. Female newts in these ponds do not breed in their first year as an adult.

Oviposition occurs in May and June.

Figure 1

Larval characteristics of *N. v. viridescens*

photo by J. Piascik

Figure 2
Aposomatic coloration of the red eft stage
of *N. v. viridescens*

photo by T. Pauley

Figure 3
Physical appearance of adult *N. v. viridescens*
(terrestrial male)

photo by T. Pauley

Figure 4
Breeding male and female adult *N. v. viridescens*:
Presence of black excressences on male

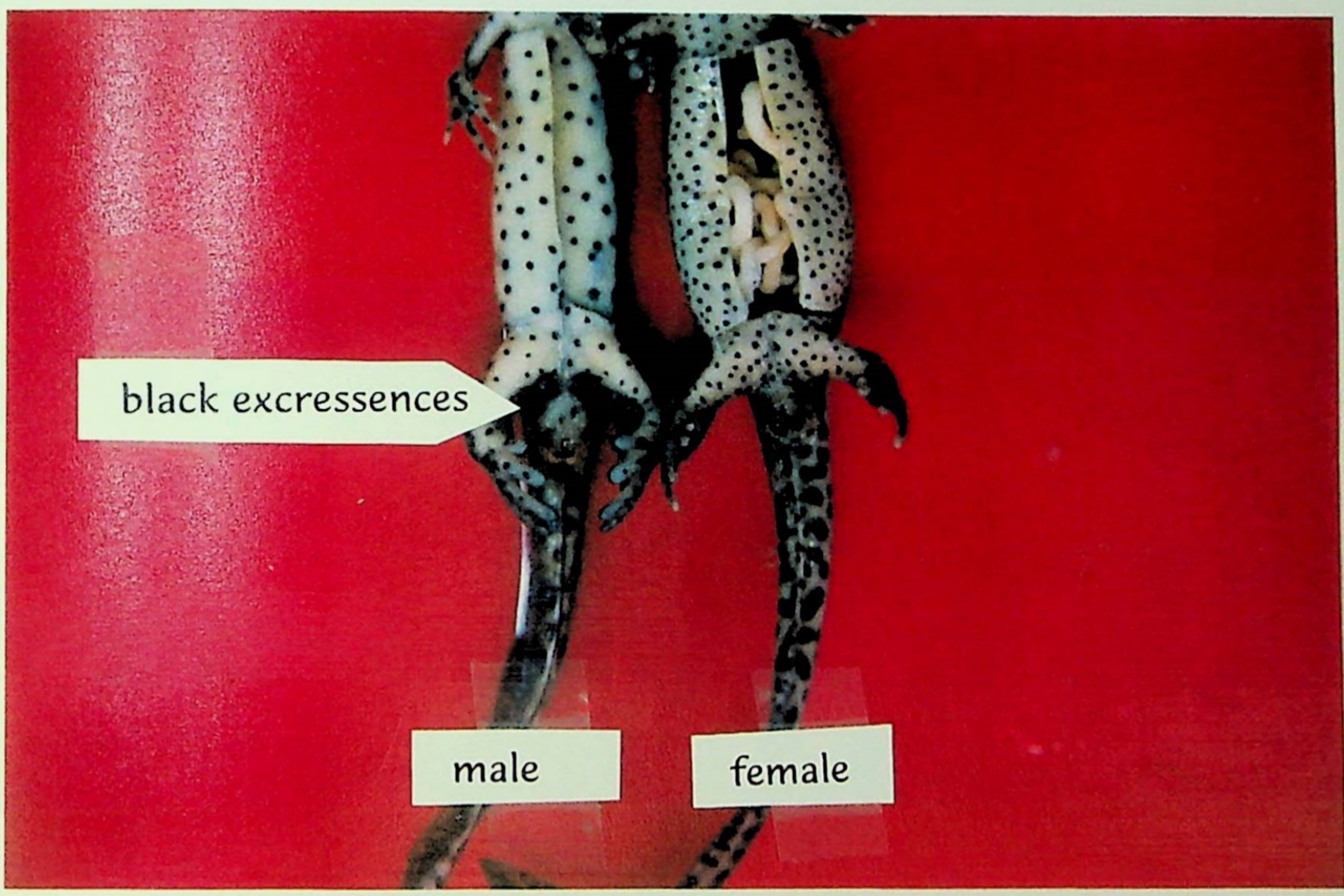


photo by J. Piascik

Figure 5
Comparison of gravid and non-gravid female adult
N. V. viridescens

photo by J. Piascik

Figure 6
Comparison of male and female adult
N. V. viridescens in non-breeding season

photo by J. Piascik

Figure 7
Range of *N. v. viridescens* according to Mecham (1967)

Range of *N. v. viridescens*

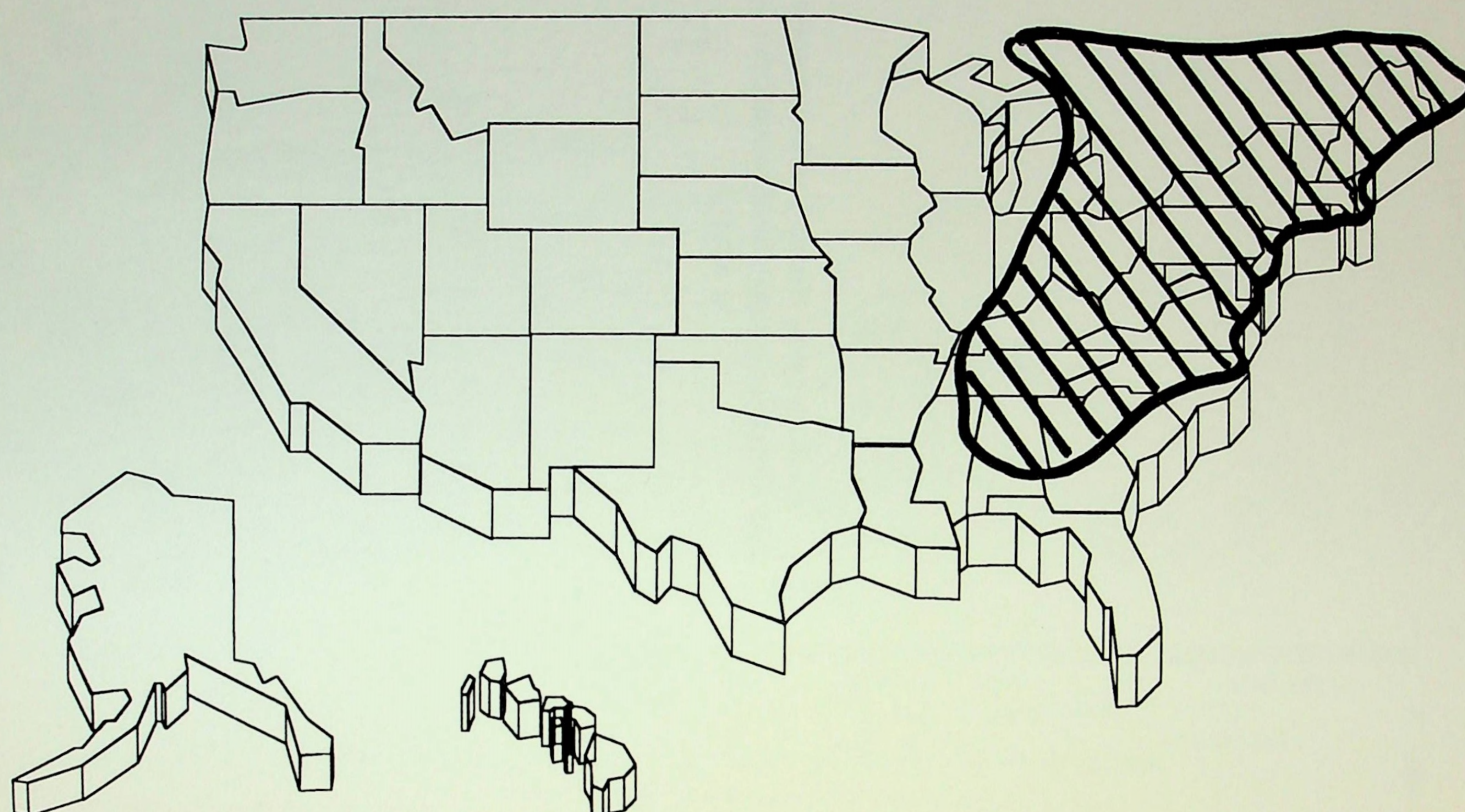
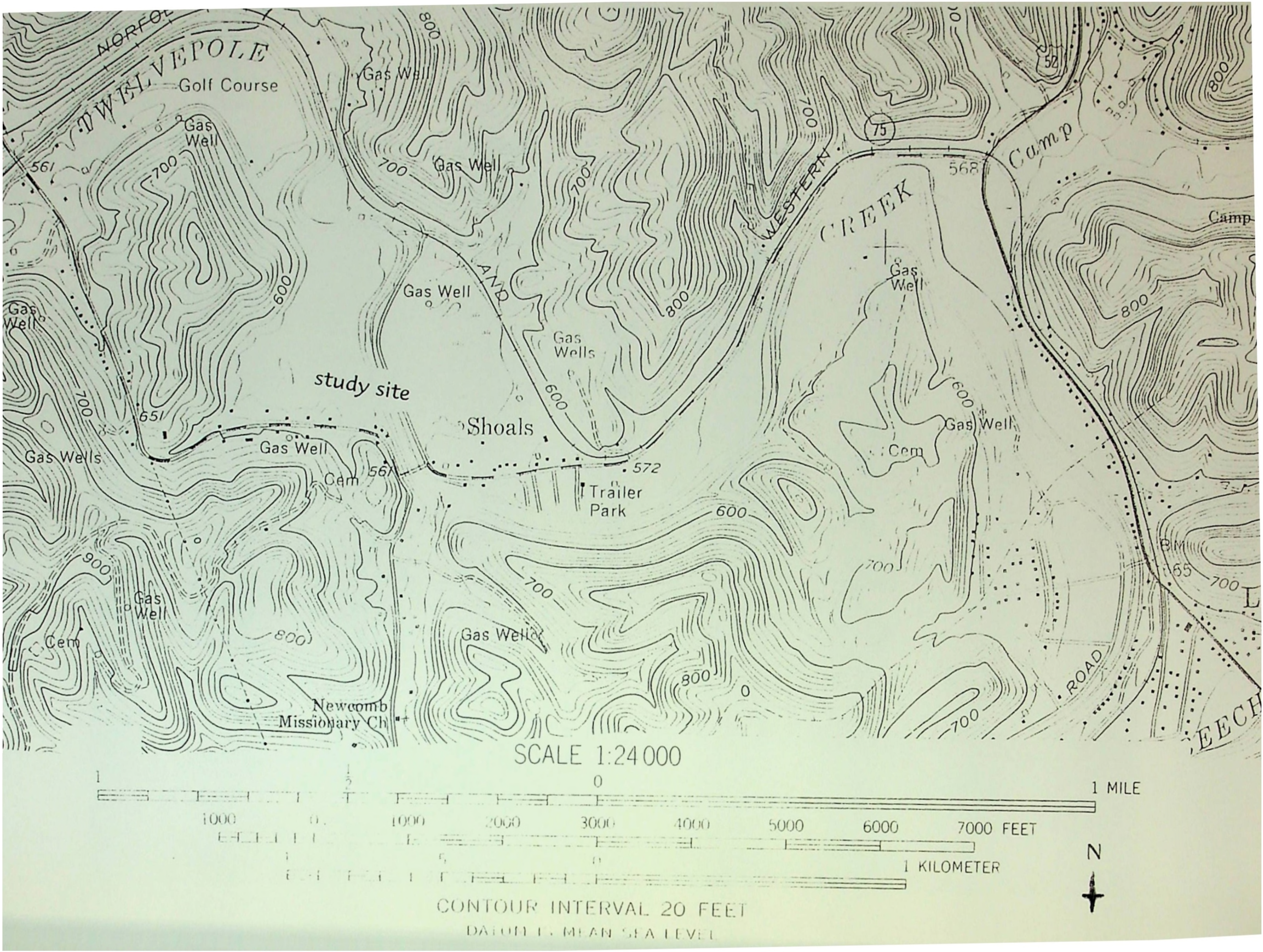


Figure 8
USGS topographic map (detail) of study site:
Shoals, Wayne County, West Virginia



NORFOLK
TWELVEPOLE
Golf Course
Gas Well
Gas Wells
Gas Well
study site
Shoals
AND
WESTERN
CREEK
Camp
Cem
Trailer
Park
Newcomb
Missionary Ch
ROAD
75
52
561
651
572
568
600
700
800
900
SCALE 1:24 000
1 MILE
1000
0
2000
3000
4000
5000
6000
7000 FEET
1 KILOMETER
N
CONTOUR INTERVAL 20 FEET

Figure 9
Characteristic habitat of study site

permanent pond

photos by J. Piascik

temporary pond

Figure 10
Schematic of study site

Schematic of Study Site

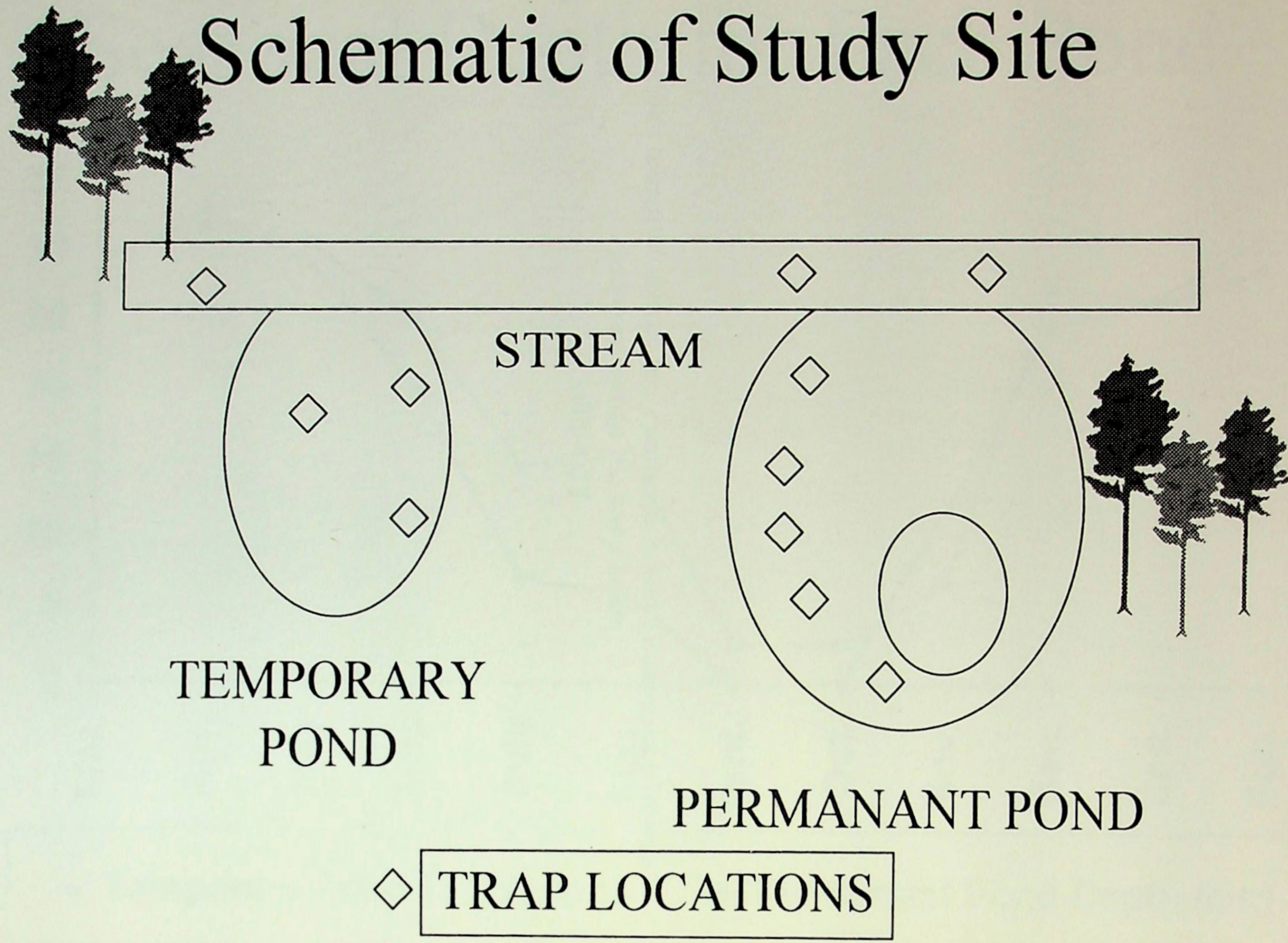


Figure 11
Seasonal depth for each pond:
average monthly depths for Temporary and Permanent ponds

Seasonal Depth for Each Pond

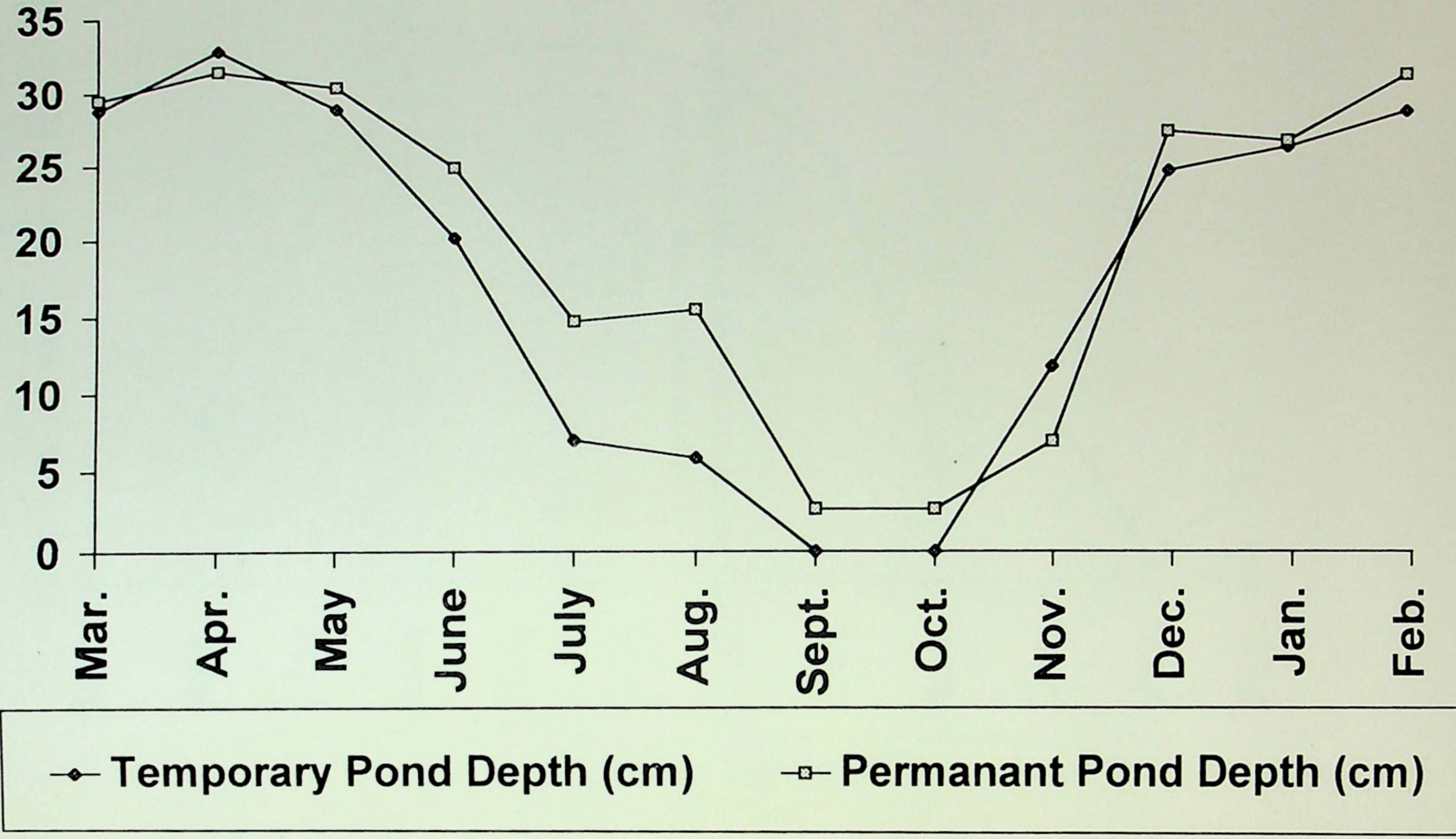


Figure 12
Seasonal water temperature:
average monthly temperatures for combined ponds

Seasonal Water Temperature

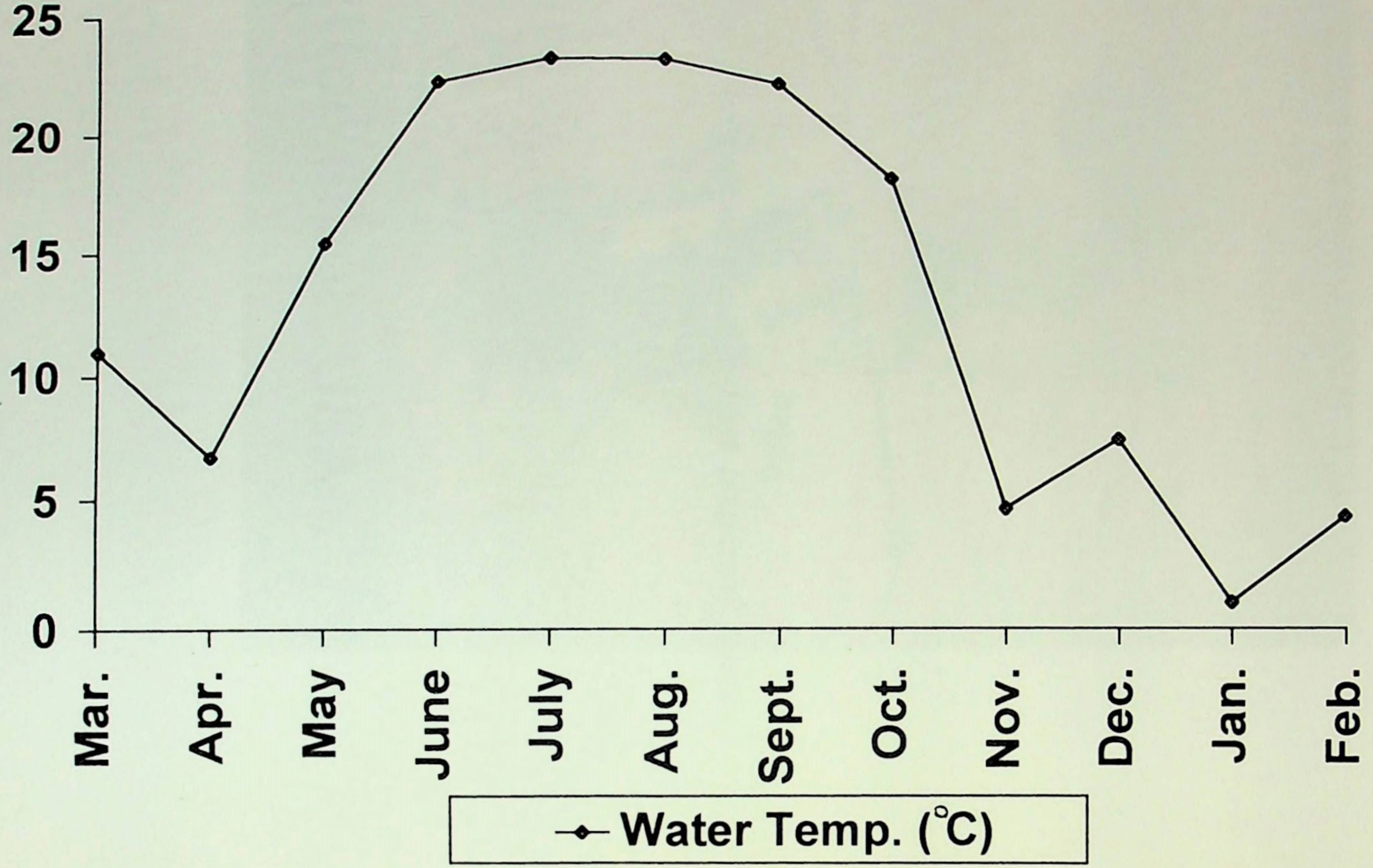
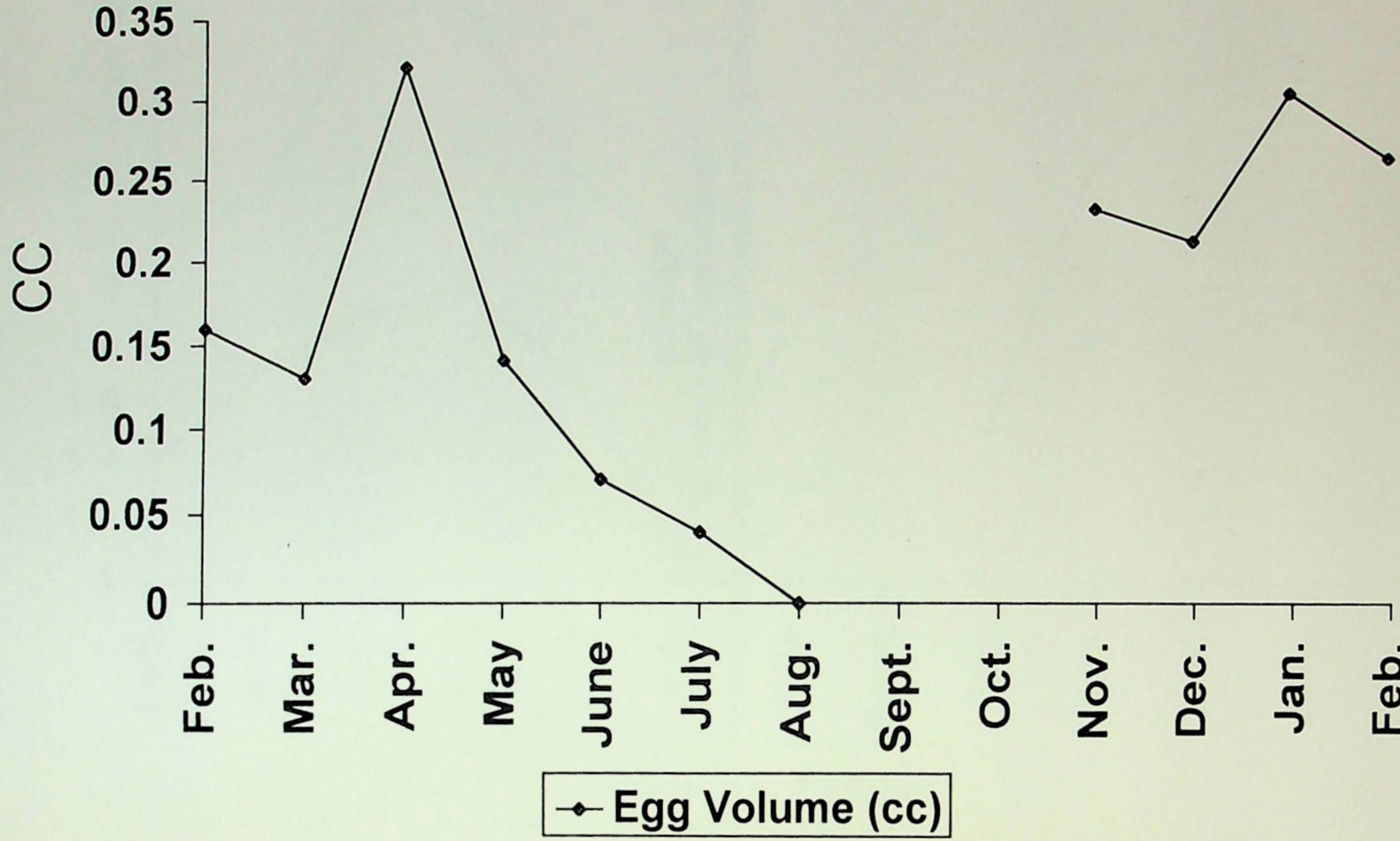


Figure 13
Male *N. v. viridescens* with multiple testicular lobes

photo by J. Joy

Figure 14
Seasonal egg volume:
average monthly egg volume (cc)

Seasonal Egg Volume



Seasonal Tail Ratio

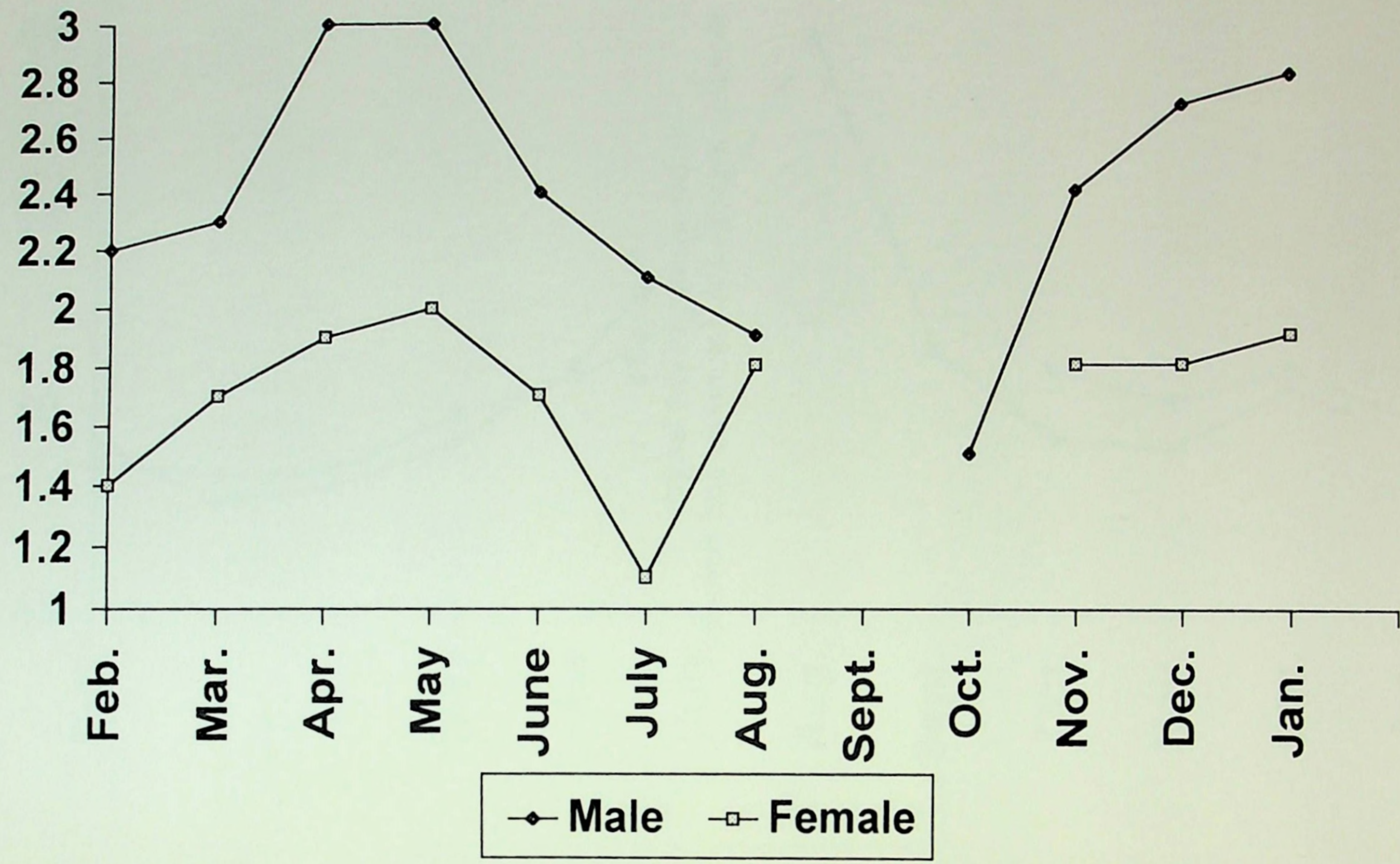


Figure 16
Seasonal snout-vent length:
monthly average SVL for males and females

Seasonal SVL

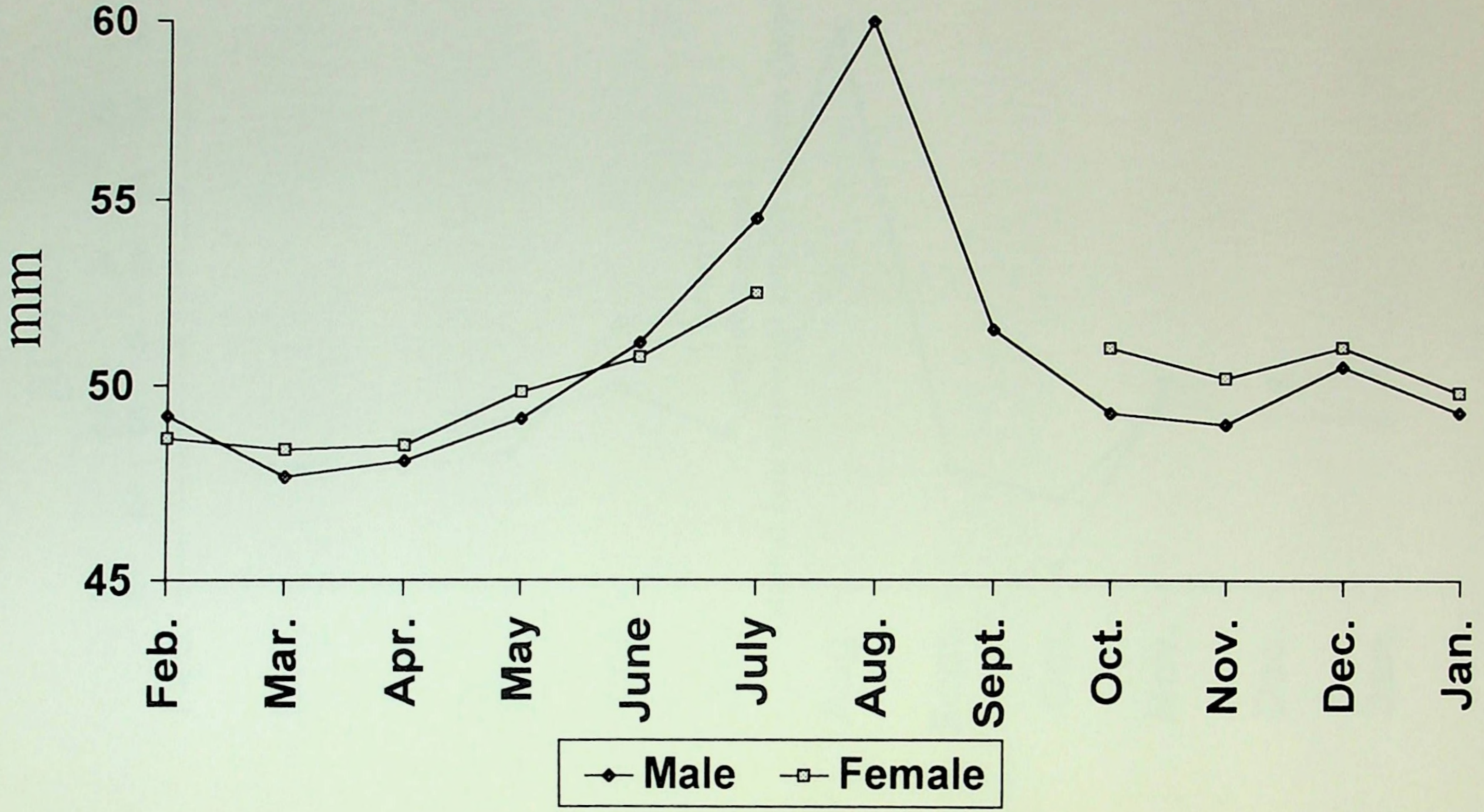


Figure 17
Seasonal weight:
monthly average weights for males and females

Seasonal Weight

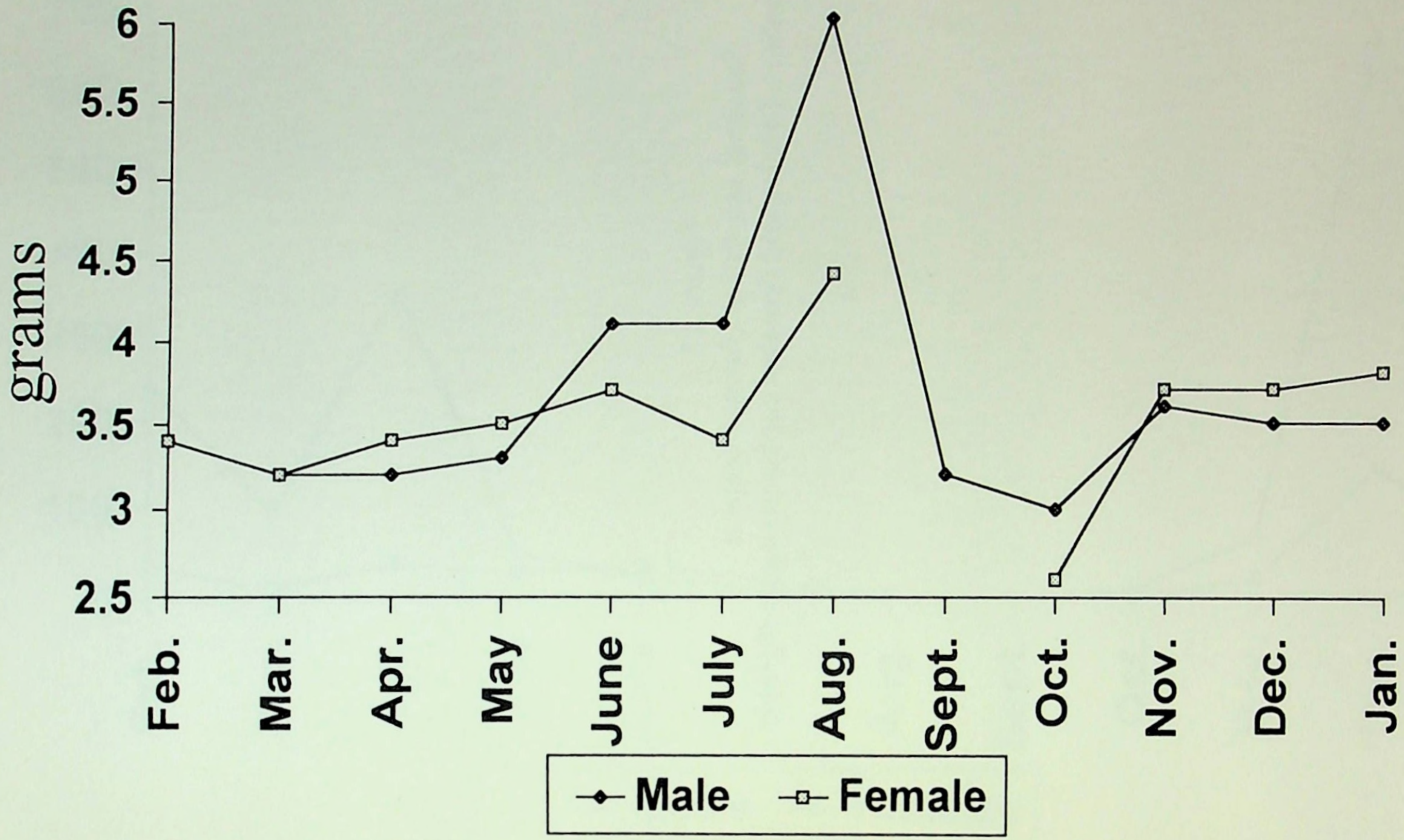


Figure 18
Seasonal sex ratios (funnel traps):
total number of males and females captured each month

Seasonal Sex Ratios (Funnel Traps)

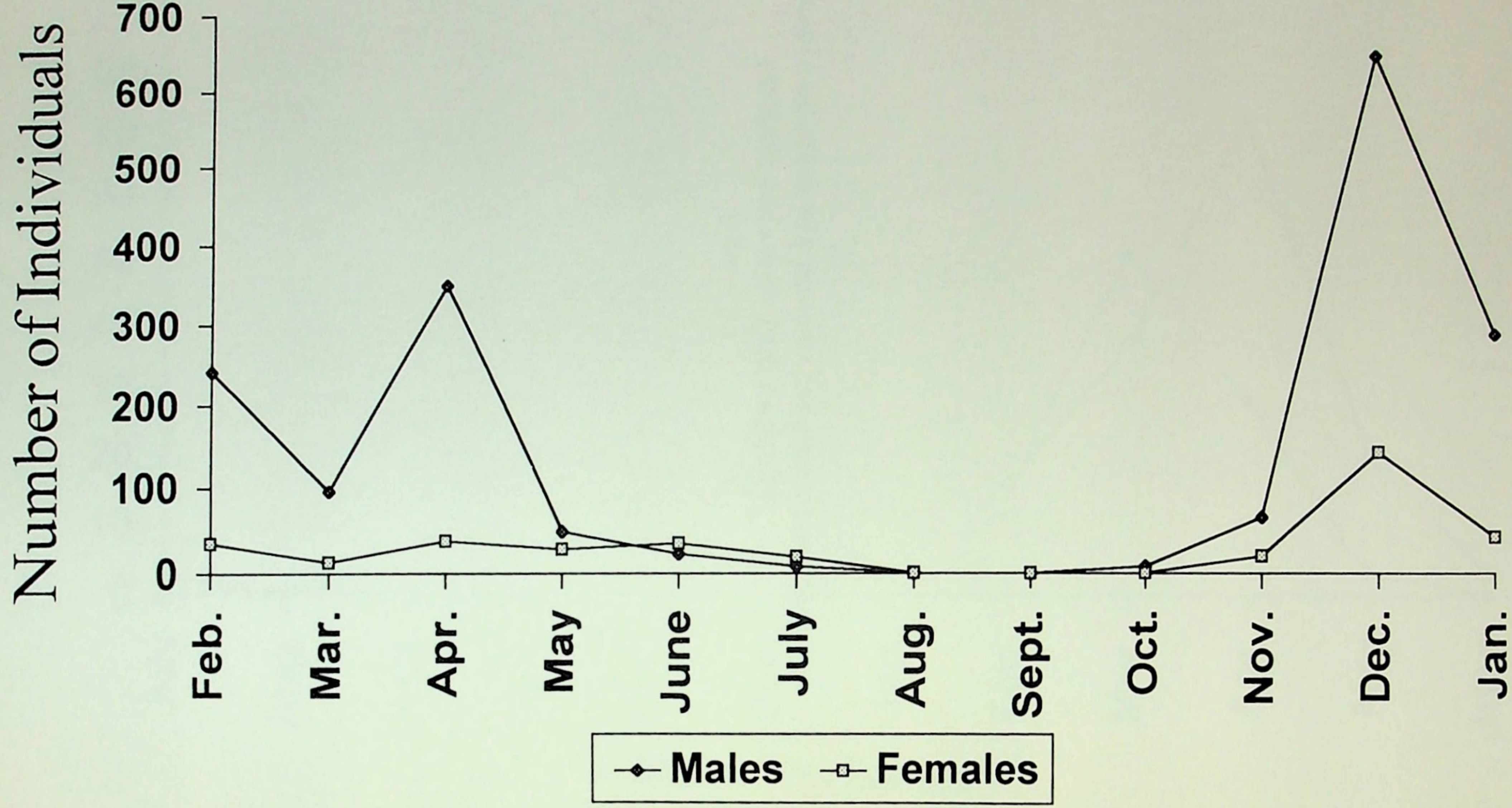
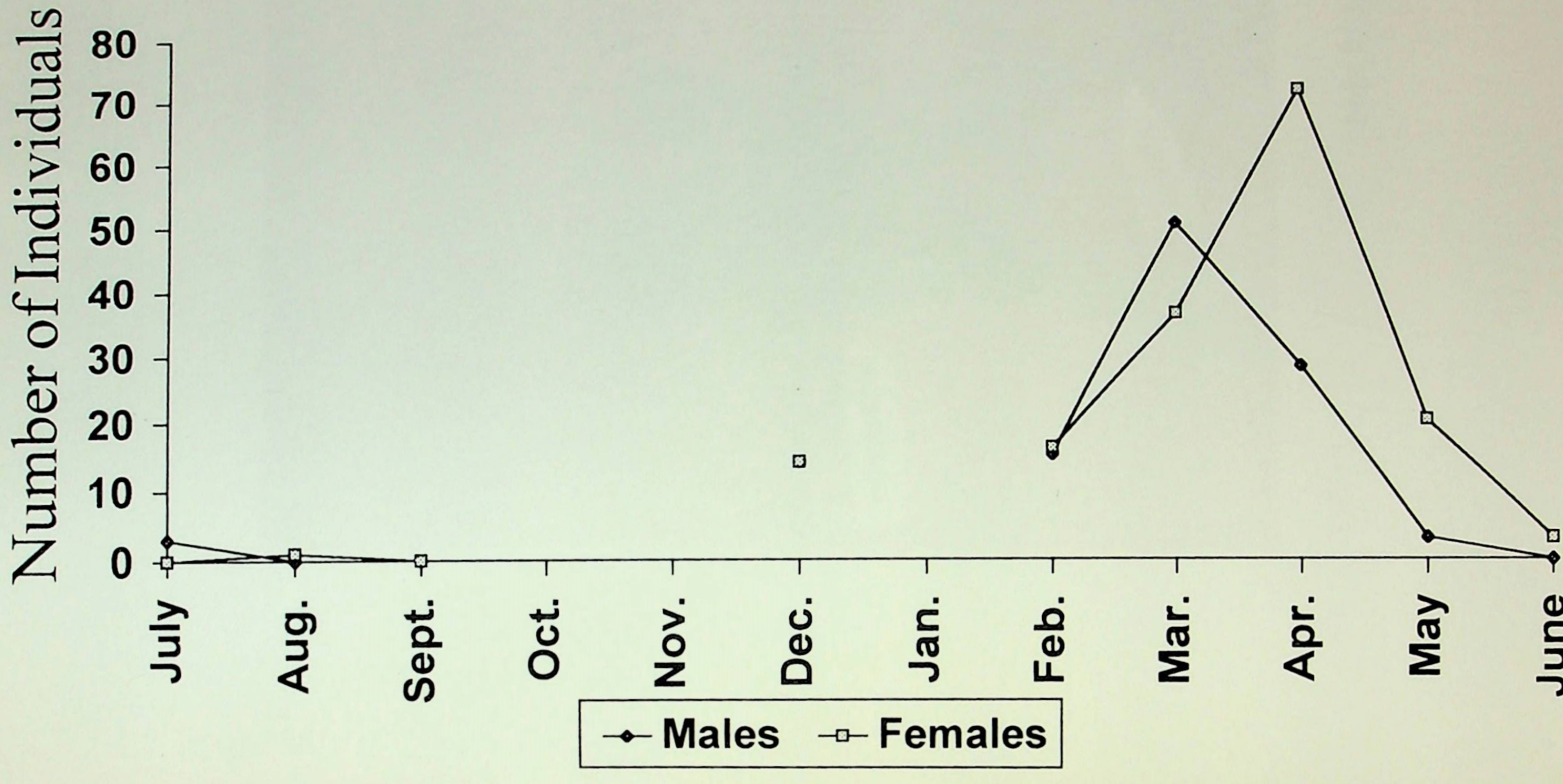


Figure 19
Seasonal sex ratios (dip netting):
total number of males and females captured each month

Seasonal Sex Ratio
(Dip Netting)



*Note: Change in x-axis

Figure 20
Examples of *N. v. viridescens* skin texture:
terrestrial and aquatic females

photo by J. Piascik

Figure 21
Seasonal activity versus seasonal temperatures:
monthly number of newts captured
compared to monthly average temperatures

Seasonal Activity

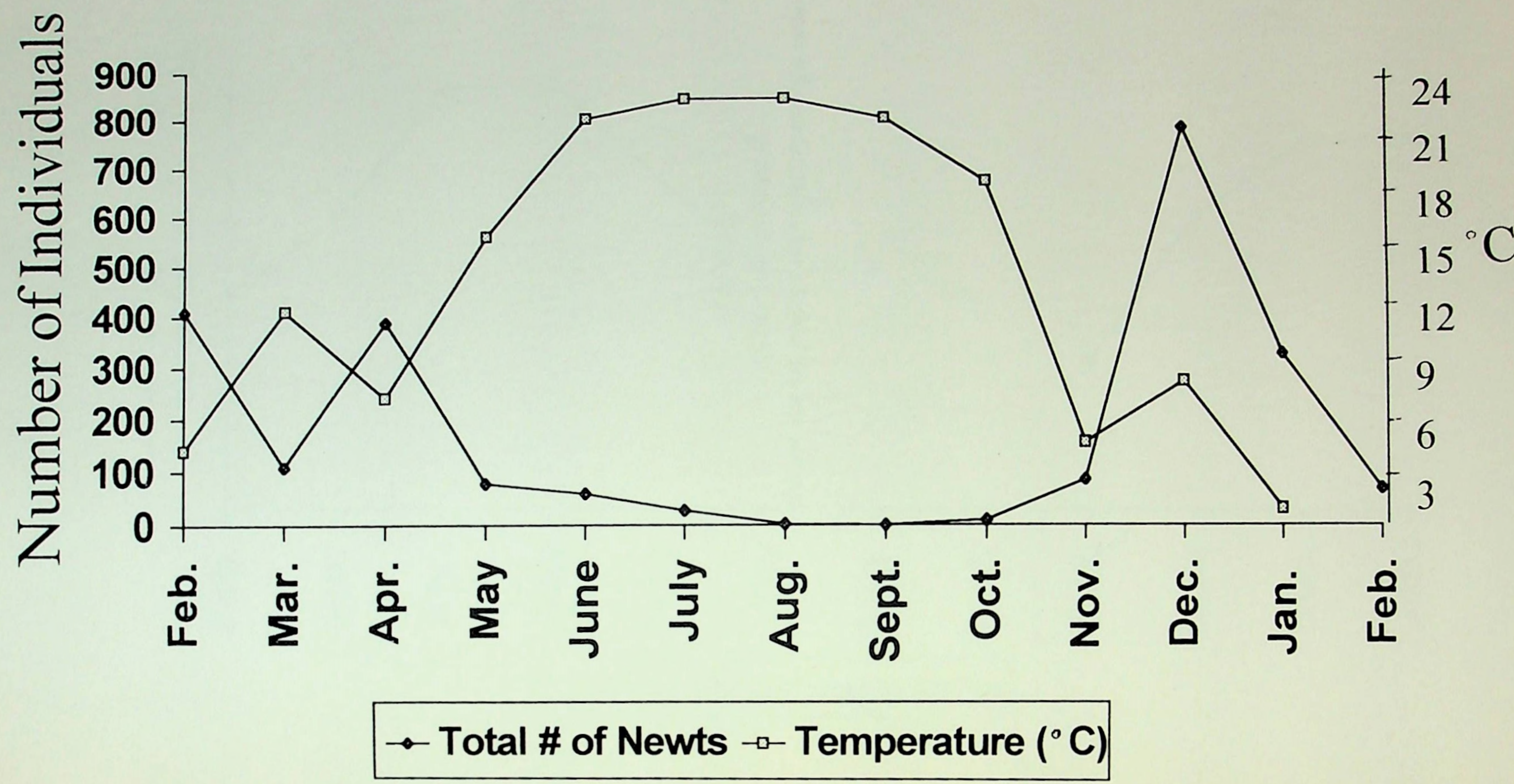


Figure 22
Seasonal tail ratio:
average monthly tail ratios of all newts

Seasonal Tail Ratio

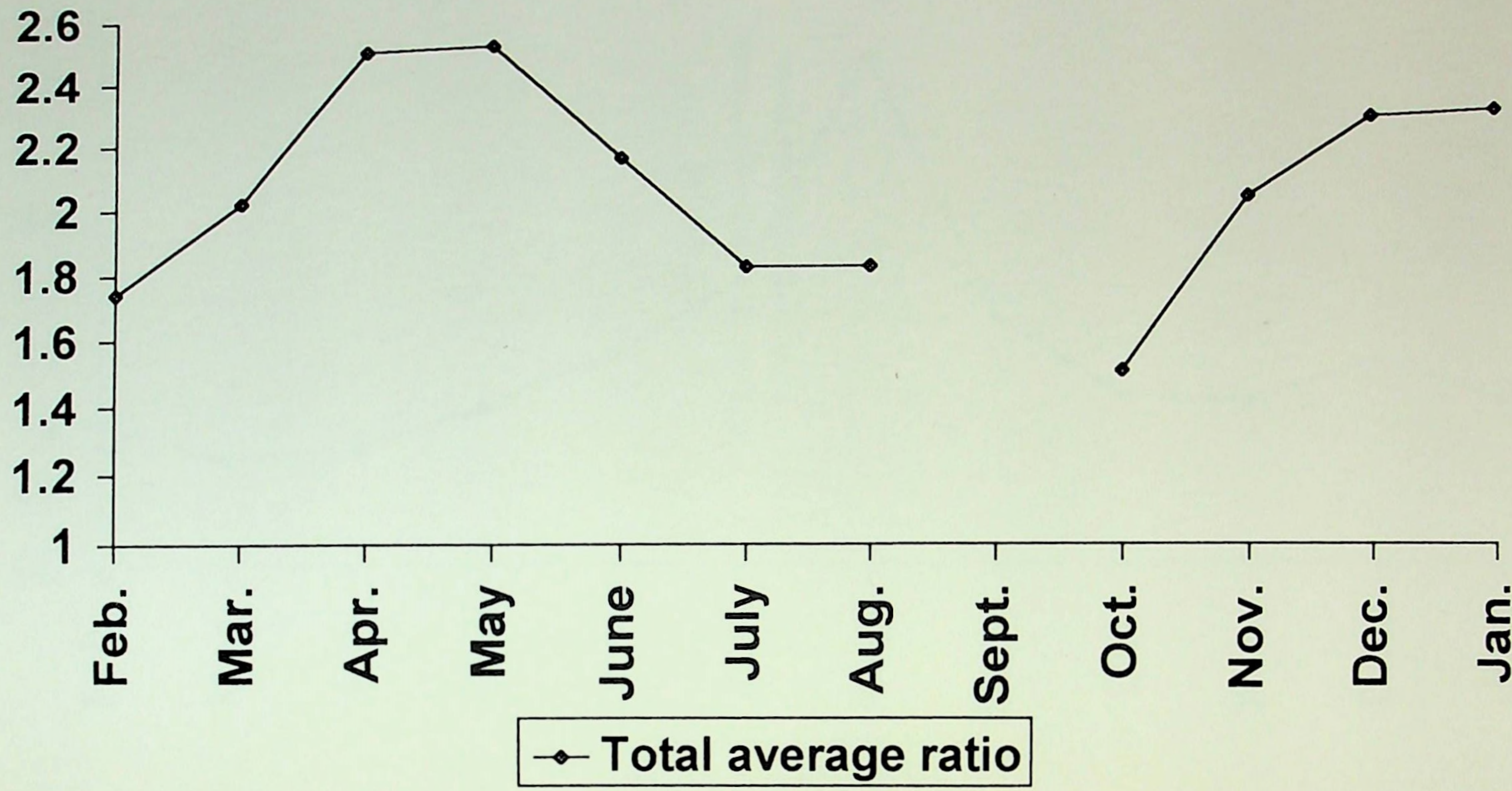


Figure 23
Seasonal snout-vent length:
average monthly SVLs

Seasonal SVL

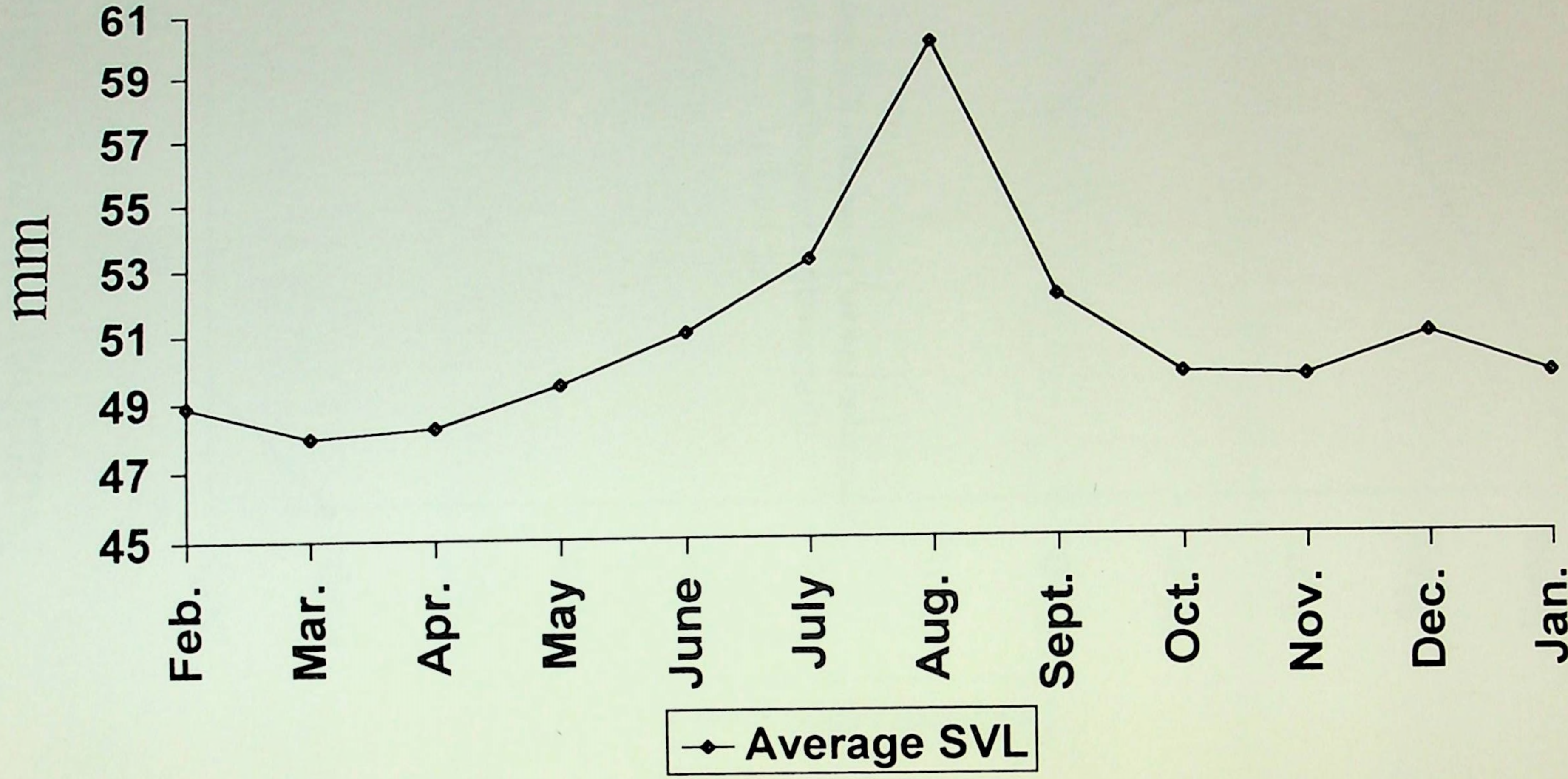


Figure 24
Seasonal activity (dipnetting):
total monthly number of newts captured

Seasonal Activity (Dipnetting)

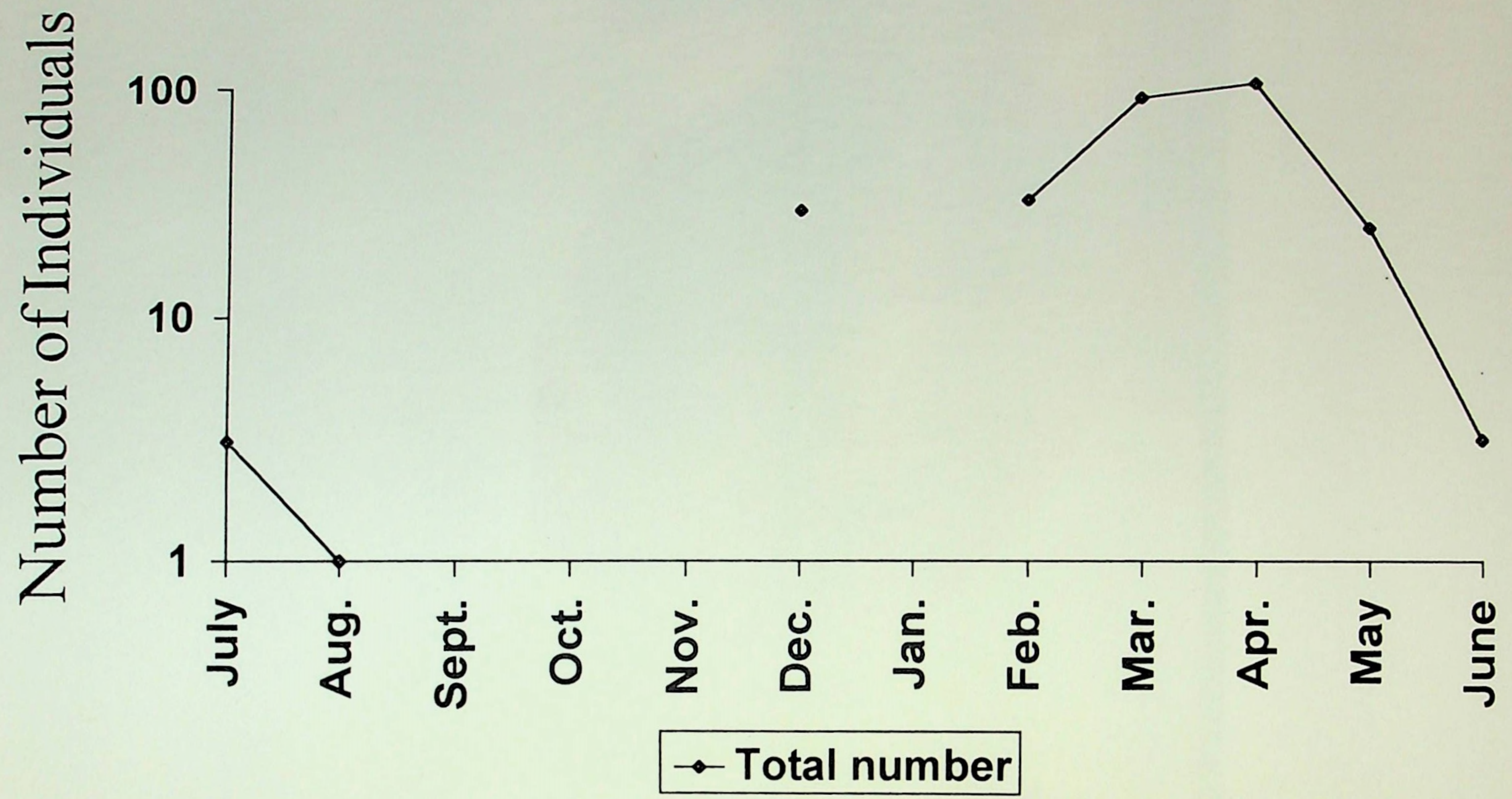


Figure 25
Example of sperm present in testis

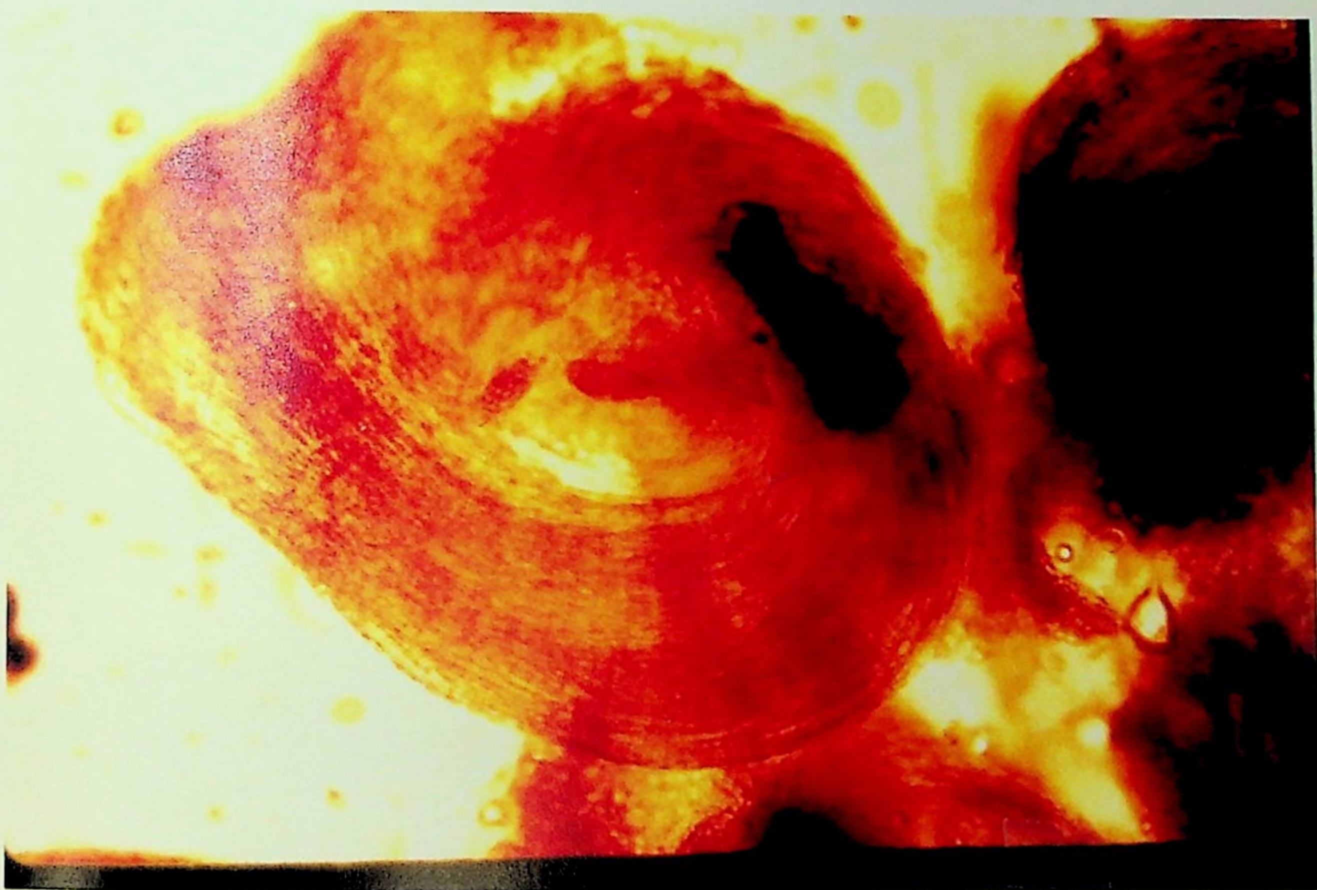


photo by J. Joy and J. Piascik

Figure 26
Seasonal snout-vent length:
monthly average SVL

Seasonal SVL

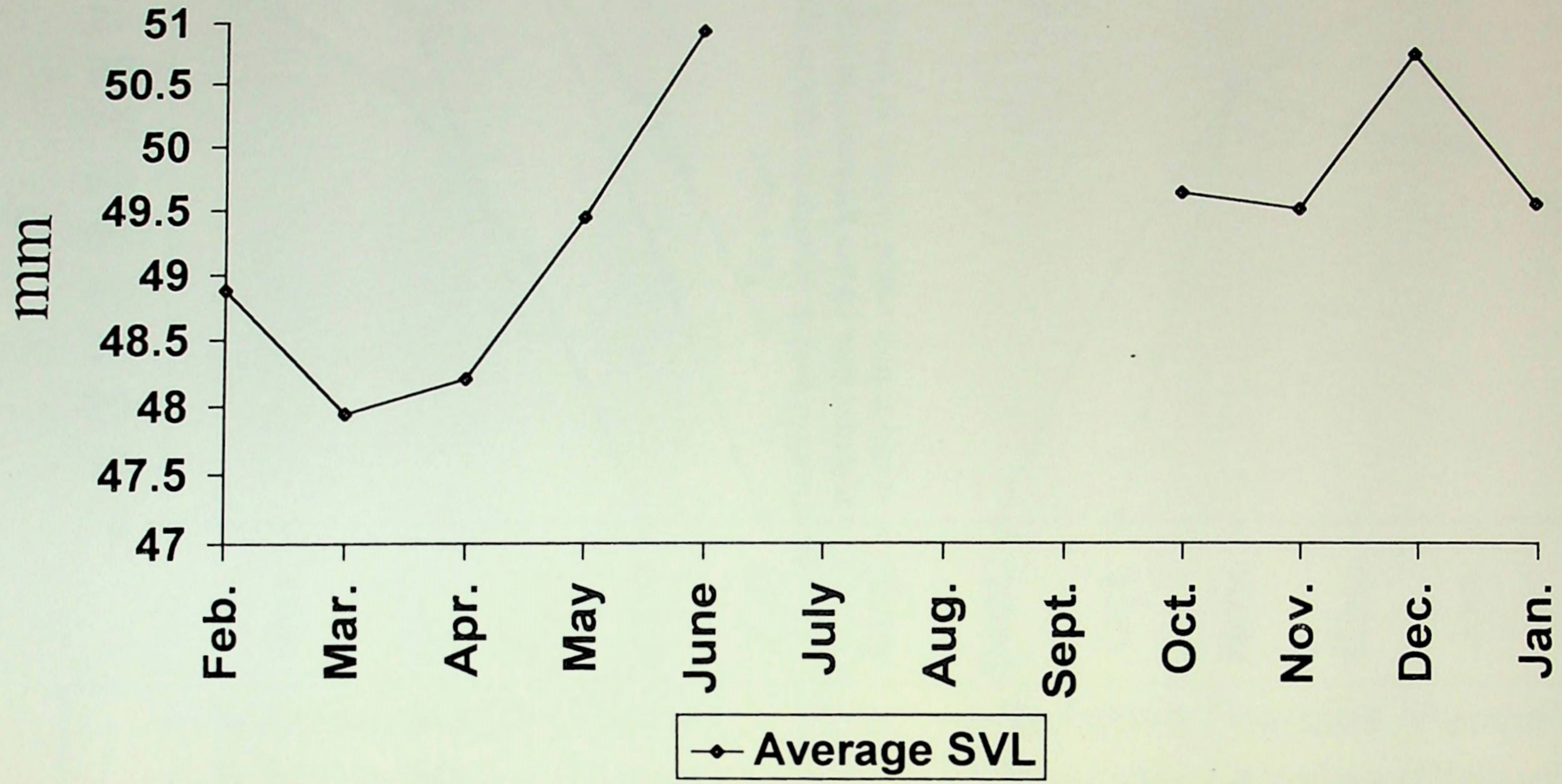


Figure 27
Percentage of reproductively active individuals: percent of breeding males and females captured by funnel traps and dipnet

Percentage of Reproductively Active Individuals

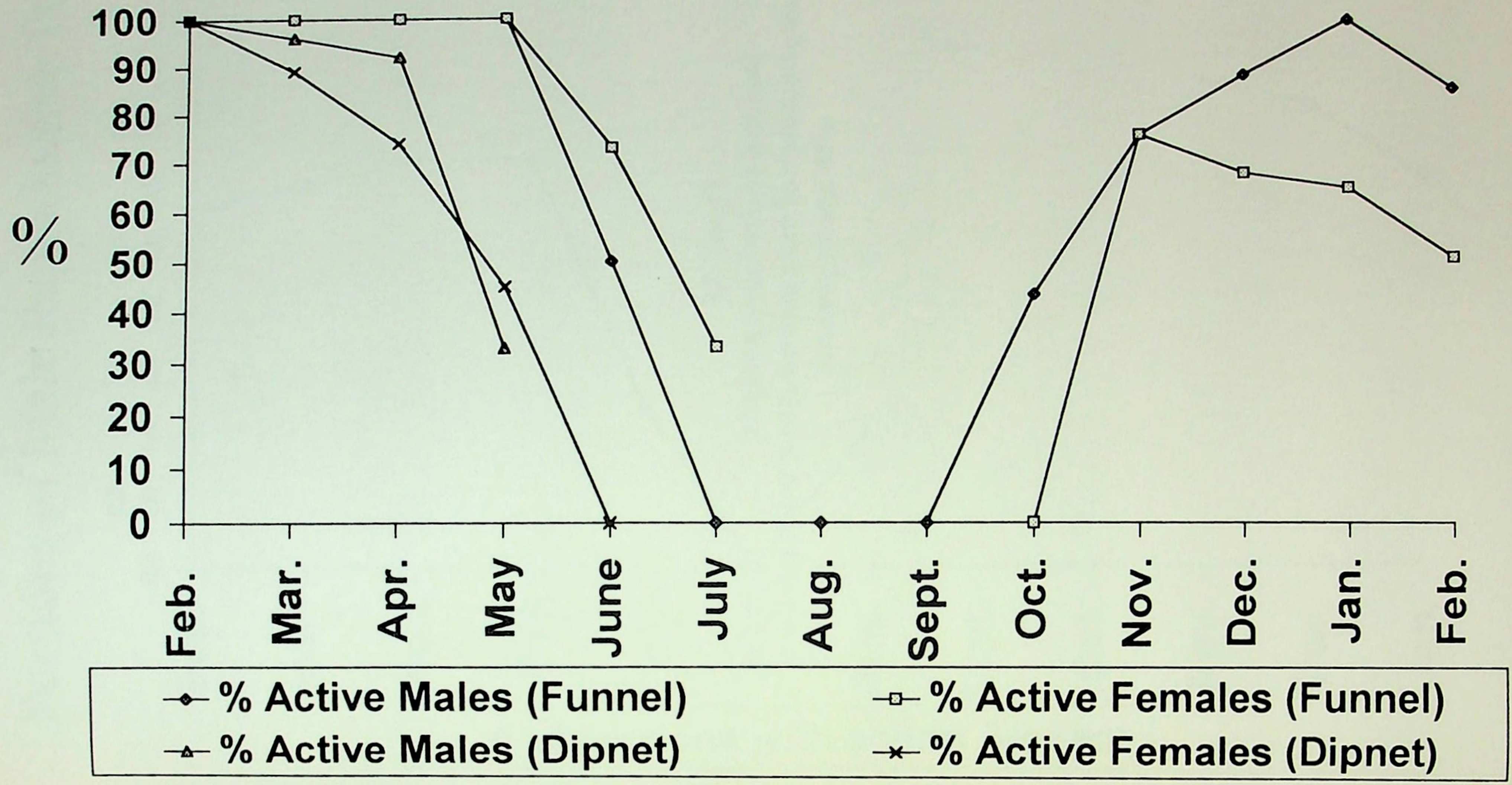


Figure 28
Seasonal sperm wave analysis:
monthly average number of male reproductive tract portions
with sperm present

Seasonal Sperm Wave Analysis

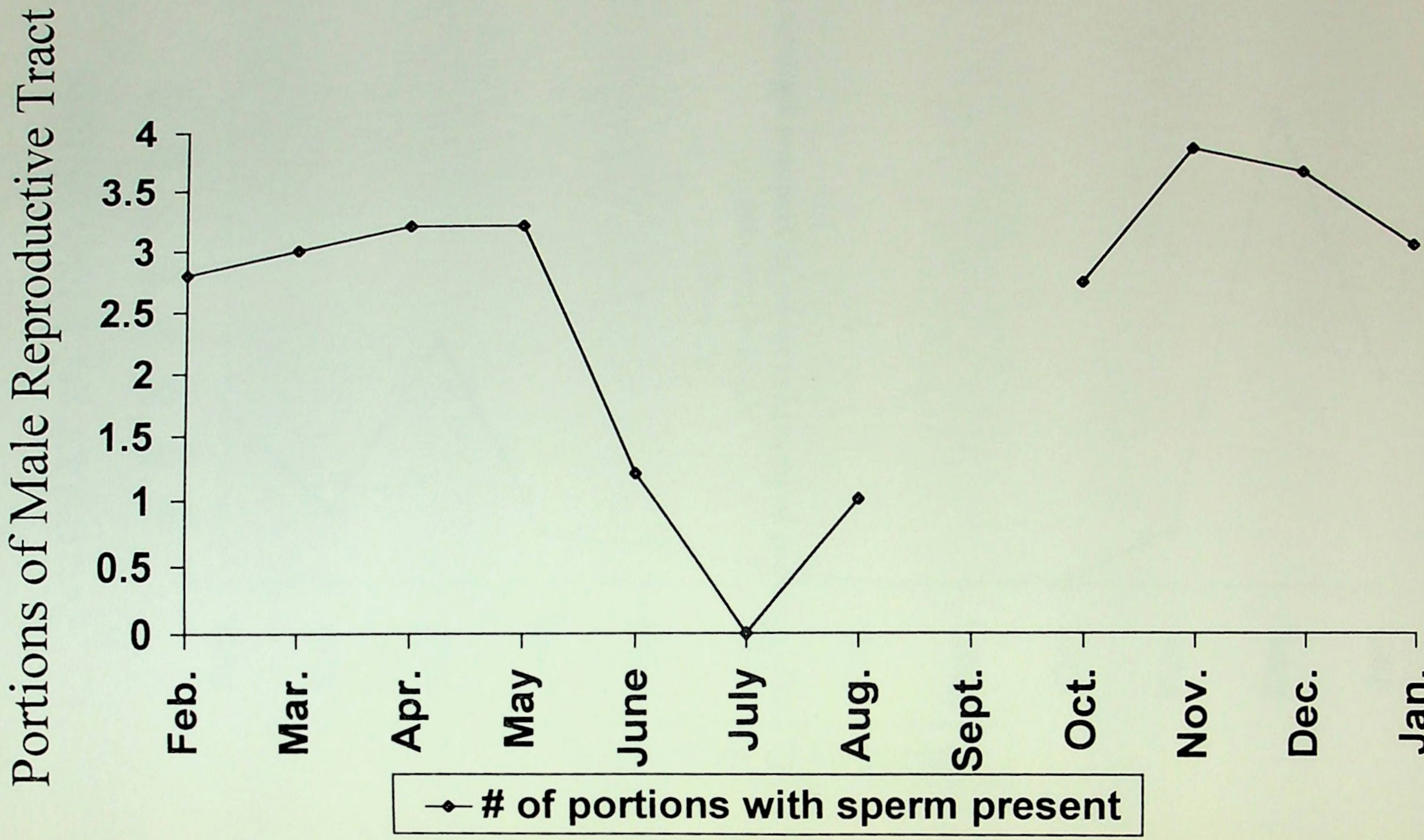


Figure 29
Seasonal activity:
total monthly numbers of newts captured in funnel traps

Seasonal Activity

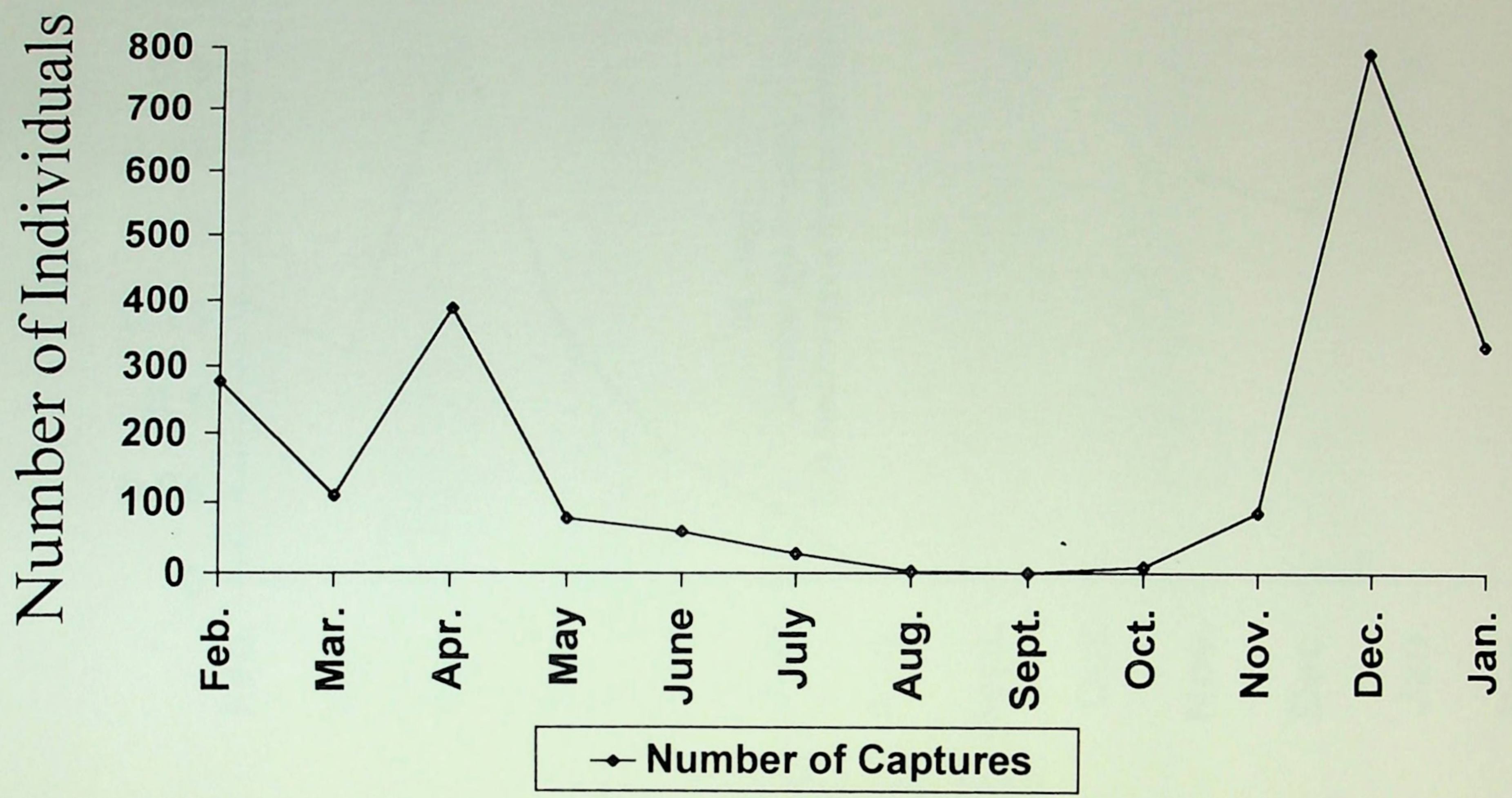


Figure 30
Seasonal egg volume:
average monthly egg volume (cc)

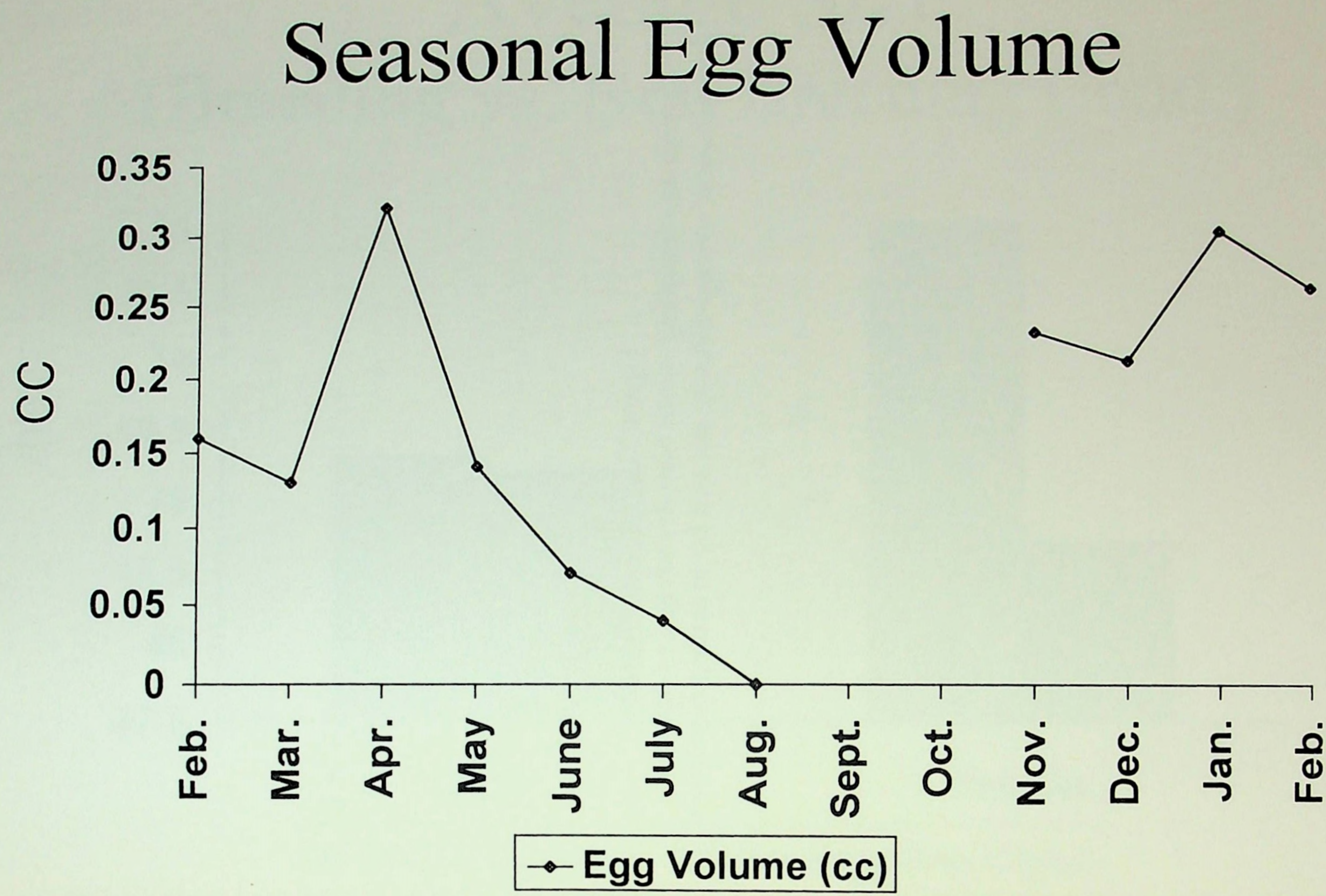
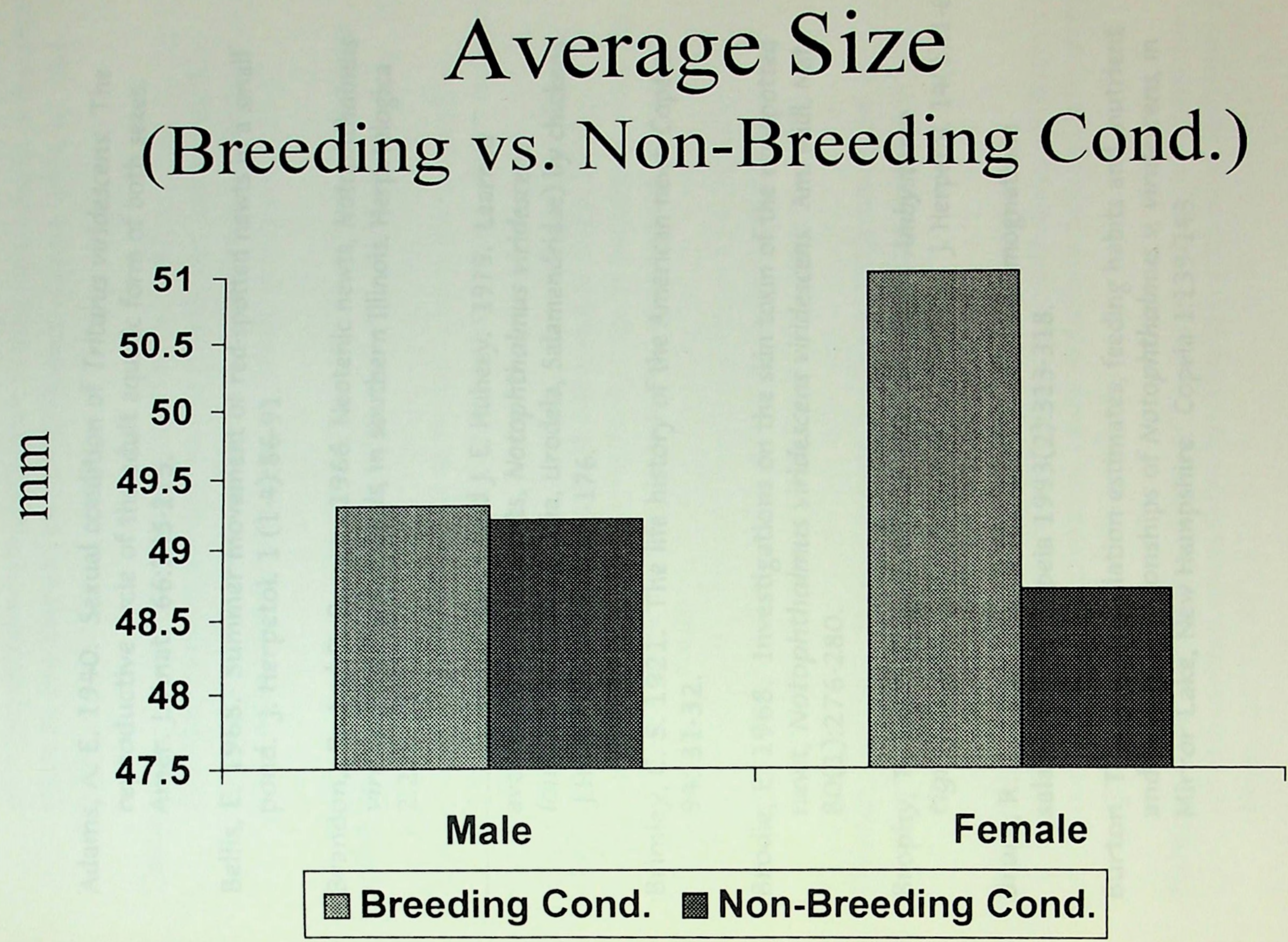

Seasonal Egg Volume
CC
0.35
0.3
0.25
0.2
0.15
0.1
0.05
0
Feb.
Mar.
Apr.
May
June
July
Aug.
Sept.
Oct.
Nov.
Dec.
Jan.
Feb.
Egg Volume (cc)

Figure 31

Average size (Breeding versus Non-Breeding Condition): Comparison of average SVLs by sex and by breeding condition


Average Size
(Breeding vs. Non-Breeding Cond.)
mm
51
50.5
50
49.5
49
48.5
48
47.5
Male
Female
Breeding Cond.
Non-Breeding Cond.

Literature Cited

Adams, A. E. 1940. Sexual condition of *Triturus viridescens*: The reproductive cycle of the adult aquatic form of both sexes. Amer. J. Anat. 66:235-275.

Bellis, E. 1968. Summer movement of red-spotted newts in a small pond. J. Herpetol. 1 (1-4):86-91.

Brandon, R. And D. Bremer. 1966. Neotenic newts, *Notophthalmus viridescens louisianensis*, in southern Illinois. Herpetologica 2:213-217.

___________., G. M. Labanick, and J. E. Huheey. 1979. Learned avoidance of brown efts, *Notophthalmus viridescens louisianensis* (Amphibia, Urodela, Salamandridae) by chickens. J.Herpetol. 13(2): 171-176.

Brimley, C. S. 1921. The life history of the American newt. Copeia 94: 31-32.

Brodie, E. 1968. Investigations on the skin toxin of the red-spotted newt, *Notophthalmus viridescens viridescens*. Am. Midl. Nat. 80(1):276-280.

Brophy, T. 1980. Food habits of sympatric larval *Ambystoma tigrinum* and *Notophthalmus viridescens*. J. Herpetol. 14(1):1-6.

Bruce, R. C. 1993. Sexual size dimorphism in desmognathine salamanders. Copeia 1993(2):313-318.

Burton, T. 1977. Population estimates, feeding habits and nutrient and energy relationships of *Notophthalmus v. viridescens*, in Mirror Lake, New Hampshire. Copeia 1:139-143.

Caetano, M. H. and R. Leclair. 1996. Growth and population structure of red-spotted newts (*Notophthalmus viridescens*) in permanent lakes of the Laurentian Shield, Quebec. Copeia 1996(4): 866-874.

Castanet, J., D. . Newman, and H. SaintGirons. 1988. Skeletochronological data on the growth, age, and population structure of the tuatara, *Sphenodon punctatus*, on Stephens and Lady Alice Islands, New Zealand. Herpetologica 44(1):25-37.

Chadwick, C. S. 1944. Observations on the life cycle of the common newt in western North Carolina. Am. Midl. Nat. 32:491-494.

__________. 1950. Observations of the behavior of the larvae of the common American newt during metamorphosis. Amer. Midl. Nat. 43(2): 392-398.

Chinsamy, A., S. A. Hanrahan, R. M. Neto, and M. Seely. 1995. Skeletochronological assessment of age in *Angolosaurus skoogi*, a cordylid lizard living in an aseasonal environment. J.Herpetol. 29(3): 457-460.

Conant, R. and J. Collins. 1991. A Field Guide to Reptiles and Amphibians. Boston : Houghton Mifflin Company. 450pp.

Dolmen, D. 1982. Skeletal growth marks and testis lobulation as criteria for age in *Triturus* spp. (Amphibia) in central Norway. Acta Zool. 63(2):73-80.

Ducey, P. and J. Dulkiewicz. 1994. Ontogenetic variation in antipredator behavior of the newt *Notophthalmus viridescens* : comparisons of terrestrial adults and efts in field and laboratory tests. J. Herpetol. 28(4):530-533.

Forester, D. C. and D. V. Lykens. 1991. Age structure in a population of red-spotted newts from the Allegheny plateau of Maryland. J. Herp. 25(3): 373-376.

Francillon-Vieillot, H., J. W. Arntzen, and J. Geraudie. 1990. Age, growth and longevity of sympatric *Triturus cristatus, T. marmoratus* and their hybrids (Amphibia, Urodela): a skeletochronological comparison. J. Herp. 24(1):13-2.

Gates, J. and E. Thompson. 1982. Small pool habitat selection by red-spotted newts in western Maryland. J. Herp. 16(1)7-15.

George, C. 1977. The presence of the red-spotted newt, *Notophthalmus viridescens* Rafinesque (Amphibia, Urodela, Salamandridae), in waters exceeding 12 meters in Lake George, New York. J. Herp. 11 (1):87-90.

Gibbons, J. W. and R. D. Semlitsch. 1991. Guide to the Reptiles and Amphibians of the Savannah River Site. University of Georgia Press, Athens. 131pp.

Gill, D. E. 1978. The metapopulation ecology of the red-spotted newt, *Notophthalmus viridescens* (Rafinesque). Ecol. Monogr. 48:145-166.

__________. 1985. Interpreting breeding patterns form census data: a solution to the Husting dilemma. Ecology 66(2): 344-354.

Green, N. and T. Pauley. 1987. Amphibians and Reptiles of West Virginia. Pittsburgh : University of Pittsburgh Press. 241pp.

Hagstrom, T. 1977. Growth studies and ageing methods for adult *Triturus vulgaris* L. and *T. cristatus* Laurenti (Urodela, Salamandridae). Zool. Scripta 6:61-68.

Hagstrom, T. 1980. Growth of newts (*Triturus cristatus* and *Triturus vulgaris*) at various ages. Salamandra 16(4):248-251.

Harris, R. 1981. Intrapond homing behavior in *Notophthalmus viridescens*. J. Herpetol. 15(3):355-356.

__________., R. A Alford, and H. M. Wilbur. 1988. Density and phenology of *Notophthalmus viridescens dorsalis* in a natural pond. Herpetologica 44(2): 234-242.

Hasumi, M. and H. Iwasawa. 1992. Wandering behavior and cutaneous changes in winter-dormant male salamanders (*Hynobius nigrescens*). Herpetologica 48(3):279-287.

Healy, W. 1973. Life history variation and the growth of juvenile *Notophthalmus viridescens* from Massachusetts. Copeia 4:641-647.

__________. 1974. Population consequences of alternative life histories in *Notophthalmus v. viridescens.* Copeia 1:221-229.

__________. 1975. Terrestrial activity and home range in efts of *Notophthalmus viridescens.* Am. Midl. Nat. 93(1):131-138.

Hemelaar, A. 1988. Age, growth and other population characteristics of *Bufo bufo* from different latitudes and altitudes. J. Herpetol. 22(4):369-388.

Humphrey, R. R. 1926. The multiple testis in *Diemyctylus.* J. Morph. Phys. 41(2): 283-309.

Hurlbert, S. 1969. The breeding migrations and interhabitat wandering of the vermilion-spotted newt *Notophthalmus viridescens* (Rafinesque). Ecol. Monogr. 39(4):465-488.

__________. 1970a. The post-larval migration of the red-spotted newt *Notophthalmus viridescens* (Rafinesque). Copeia 3:515- 528.

__________. 1970b. Predator responses to the vermilion-spotted newt (*Notophthalmus viridescens*). J. Herpetol. 4(1-2):47-55.

Hutton, J. M. 1986. Age determination of living nile crocodiles from the cortical stratification of bone. Copeia 1986(2):332-341.

Jordan, E. O. 1893. Habits and development of the newt (*Diemyctylus viridescens*). J. Morph. 8(2): 269-366.

Jiang, S. and D. Claussen. 1993. The effects of temperature on food passage time through the digestive tract in *Notophthalmus viridescens*. J. Herpetol. 27(4):414-419.

Leclair, R. and J. Castanet. 1987. A skeletochronological assessment of age and growth in the frog *Rana pipiens* Schreber (amphibia, Anura) from Southwestern Quebec. Copeia 1987(2):361-369.

Licht, P. and A. G. Brown. 1967. Behavioral thermoregulation and its role in the ecology of the red-bellied newt, *Taricha rivularis*. Ecology 48:598-611.

Logier, E. B. S. 1952. The Frogs, Toads, and Salamanders of Eastern Canada. Clark, Irwin, and Company, Ltd. Canada. 127pp.

MacNamara, M. 1977. Food habits of terrestrial adult migrants and immature red efts of the red-spotted newt *Notophthalmus viridescens*. Herpetologica 33:127-132.

Massey, A. 1988. Sexual interactions in red-spotted newt populations. Anim. Behav. 36:205-210.

__________. 1990. Notes on the reproductive ecology of red-spotted newts (*Notophthalmus viridescens*). J. Herptol. 24(1):106-107.

Mecham, J. S. 1967. *Notophthalmus viridescens*. Cat. Amer. Amphib. Rept. 53.1-53.4.

Morgan, A. and M. Grierson. 1932. Winter habits and yearly food consumption of adult spotted newts, *Triturus viridescens*. Ecology 13(1):54-62.

Noble, G. K. 1926. The Long Island newt: a contribution to the life history of *Triturus viridescens*. Amer. Mus. Nov. 228: 1-11.

Pauley, T. K. 1986. Herpetology field notes: two record size salamanders. Proc. W. Va. Acad. Sci. 58: 59.

Pope, P. H. 1924. The life-history of the common water-newt (*Notophthalmus viridescens*) together with observations on the sense of smell. Ann. Carn. Mus. 15: 305-369.

Pough, F. 1971. Leach-repellent properties of the eastern red-spotted newt, *Notophthalmus viridescens*. Science 174:1144-1146.

Rafinesque, C. S. 1820. Annals of nature or annual synopsis of new genera and species of animals, plants, etc., discovered in North America. Thomas Smith, Lexington. 16p.

Seber, G. A. F. 1973. The estimation of animal abundance and related parameters. Hafner Press, New York. 506pp.

Sever, D. M. 1974. The occurrence of multiple testes in the genus *Eurycea* (Amphibia: Plethodontidae). Herpetologica 30(2) 187-193.

__________., L. C. Rania, and J. D. Krenz. 1996. Annual cycle of sperm storage in spermathecae of the red-spotted newt, *Notophthalmus viridescens* (Amphibia: Salamandridae). J. Morph. 227:155-170.

Shure, D. J., L. A. Wilson, and C. Hochwender. 1989. Predation on aposematic efts of *Notophthalmus viridescens*. J. Herpetol. 23(4):437-439.

Smirina, E. M. 1994. Age determination and longevity in amphibians. Gerontology 40:133-146.

Smith, H. M. 1950. Handbook of Amphibians and Reptiles of Kansas. University of Kansas Publ., Mus. Nat. Hist., Kansas. 336pp.

Smith, C. J. and R. A. Pfingsten. 1989. *Notophthalmus viridescens* (Rafinesque) eastern newt. In R. A. Pfingsten and F. L. Downs (eds): Salamanders of Ohio. Columbus: College of Biol. Sci., Ohio State Univ., pp. 79-87.

Springer, A. 1909. A study of growth in the salamander *Diemyctylus viridescens.* J. Exp. Zool. 6:1-68.

Tabachnick, W. and D. Underhill. 1972. Serum transferrin and serum albumin polymorphism in two populations of the red spotted newt *Notophthalmus viridescens viridescens.* Copeia 3:525-528.

Verrell, P. 1982. The sexual behavior of the red-spotted newt *Notophthalmus viridescens* (Amphibia: Urodela: Salamandridae). Anim. Behav. 30:1224-1236.

Wise, S. E., K. S. Siex, K. M. Brown, and R. G. Jaeger. 1993. Recognition influences social interactions in red-spotted newts. J. Herpetol. 27(2): 149-154.

Wood, J. T., and O. K. Goodwin. 1954. Observations on the abundance, food, and feeding behavior of the newt, *Notophthamus viridescens viridescens* (Rafinesque), in Virginia. J. Eli. Mitch. Sci. Soc. 70(1): 27-30.

Zweifel, R. G. 1957. Studies on the critical thermal maxima of salamanders. Ecology 38(1): 64-69.