LIFE HISTORY, ECOLOGY, AND CONSERVATION GENETICS OF THE STRIPED NEWT (*Notophthalmus perstriatus*)

By

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The striped newt (*Notophthalmus perstriatus*) is a salamander endemic to south Georgia and north-central Florida. The species has declined throughout its range because of habitat destruction and modification. Before my research, little was known about striped newt life history.

To learn more about striped newt ecology in order to make management and conservation recommendations, I studied several aspects of striped newt life history. I used a multidisciplinary approach that incorporated fieldwork, a laboratory experiment, and DNA sequencing. For 2 years I monitored drift fences at a north-Florida breeding pond and in the sandhill uplands around the pond. This method was used to determine basic parameters of the species' life history. In the laboratory experiment I reared individual larvae on different food regimes to test the influence of growth rate on life-history expression. A portion of the Cytochrome *b* gene was sequenced to determine genetic population structure.

Field-collected data showed that striped newts have a complex life-cycle, involving terrestrial and aquatic stages. An individual may move between a breeding pond and upland retreats multiple times during its life. Larval development occurs in the pond, but once metamorphosis is complete, individuals leave the pond and may disperse in excess of 500 m from the pond. Striped newts may express one of two life-history pathways. An individual may initiate metamorphosis and disperse from the pond before it matures (metamorph), or it may remain in the pond and mature while retaining larval characteristics (paedomorph). The metamorph vs. paedomorph "decision" is not controlled by growth rate per se, but is likely influenced by a suite of genes. Based on DNA sequence data, significant population genetic structure was found among ten locations sampled throughout most of the species' range, showing that gene flow is severely restricted among populations.

It appears that striped newts form metapopulations and that long-term survival of the species depends on preserving those metapopulations that persist. Conservation efforts should focus on protecting and managing upland and aquatic habitats. A landscape approach is most effective, and prescribed fire in the landscape is essential.

CHAPTER 1
INTRODUCTION TO THE STRIPED NEWT (*Notophthalmus perstriatus*)

The Striped Newt

The striped newt (*Notophthalmus perstriatus*) is a salamander endemic to southeastern Georgia and north-central Florida (Christman and Means, 1992; Conant and Collins, 1991; Dodd and LaClaire, 1995; Franz and Smith, 1999; Mecham, 1967). Individuals are restricted to xeric upland habitats (primarily sandhill and scrub communities) and breed exclusively in temporary wetlands that lack predaceous fishes (Campbell and Christman, 1982; Carr, 1940; Christman and Means, 1992; Dodd and LaClaire, 1995; Dodd et al., in press; Franz and Smith, 1999; Stout et al., 1988). These upland ecosystems are pyrogenic (Myers, 1990), and fire appears to be crucial for the persistence of striped newts. Besides having a complex life history involving aquatic and terrestrial stages (Christman and Means, 1992; Dodd, 1993), individuals commonly exhibit paedomorphosis, the retention of larval morphology in mature individuals (Bishop, 1941a, 1943; S. A. Johnson, pers. obs.).

Status of the Striped Newt

Decline of the longleaf pine/wiregrass ecosystem, fire suppression, and the natural patchy distribution of upland habitats required by striped newts have resulted in the fragmentation of striped newt populations. Striped newts have declined throughout their range (Dodd and LaClaire, 1995; Franz and Smith, 1999). A complex life history makes striped newts vulnerable to threats at breeding ponds (e.g., ditching, draining, and filling of temporary ponds) and within the surrounding uplands (e.g., fire suppression, various silviculture practices, and urban and agricultural development). Relative abundance of striped newts is extremely low at most areas where the species persists (S. A. Johnson, B. Means, K. Greenberg, and D. Stevenson, unpubl. data). Because of historical declines and low relative abundance at most locations, the striped newt is recognized as a rare species throughout its range (Christman and Means, 1992; Cox and Kautz, 2000; Jensen, 1999). Its biological status is under review by the U.S. Fish and Wildlife Service (L. LaClaire, pers. comm.).

Current Knowledge and Research Justification

Striped newts have been characterized as "uncommon and enigmatic" (Christman and Means, 1992) and "poorly known" (Dodd, 1993; Dodd and LaClaire, 1995) and until the last decade or so, little was known about their ecology. Most of the literature on striped newts is limited to the results of surveys (Dodd and LaClaire, 1995; Franz and Smith, 1999; Hipes and Jackson, 1996) and to species accounts (Ashton and Ashton, 1988; Bishop, 1941a, 1943; Carmichael and Williams, 1991; Carr, 1940; Christman and Means, 1992; Dodd et al., in press; Mecham, 1967; Petranka, 1998). Johnson and Franz (1999) documented the occurrence of albinism in the species. Dodd and Charest (1988) and Dodd (1992) mentioned striped newts as part of the herpetofaunal community of a north Florida sandhills pond. Dodd (1996) included striped newts in his survey of terrestrial habitat use by amphibians. Studies of striped newt feeding habits (Christman and Franz, 1973), natural history at a breeding pond (Dodd, 1993), and orientation into and away from a breeding pond (Dodd and Cade, 1998) represent the only published works focusing specifically on striped newt life history. Petranka (1998) provided a summary of the biology of striped newts based mainly on the work of Dodd and coauthors.

Taking into account the decline of *N. perstriatus* throughout its range, and that its biological status is under review by the U.S. Fish and Wildlife Service, it is essential that natural resource managers acquire knowledge of striped newt life history. Such information will be required in order to draft a recovery plan, which would be required by law if the species was federally listed. Knowledge of striped newt life history also will be of immediate use to natural resources managers and may help circumvent the need to federally protect the species.

Striped Newt Life History and Life-history Stage Terminology

To better understand the following chapters of this dissertation, it would help to have a basic understanding of striped newt life history and terminology describing the various life-history stages. The life history stages are complex, and no published source adequately defines these stages as they relate to *N. perstriatus*. Throughout the life of an individual, both aquatic and terrestrial stages occur ontogenetically, and an individual may move several times between aquatic and terrestrial habitats (Fig. 1-1).

Reproduction occurs primarily in isolated, temporary ponds that lack predaceous fishes because the ponds dry relatively often. Courtship and oviposition by adult newts occur in the ponds and females lay eggs one at a time over a protracted period of several months. Eggs are often attached to aquatic vegetation. Eggs hatch into immature larvae that feed and grow in the pond.

Larvae

A larva is an immature aquatic stage newt. Larvae have bushy external gills, a membranous tail fin, and a conspicuous lateral line, which is visible as a series of dorso-lateral dashes on each side of the animal. Larvae do not posses the namesake lateral stripe and they do not have swollen vents. After a period of growth, but before sexual maturation, a larva may metamorphose and leave the pond as an immature eft (i.e., metamorphic pathway; Fig. 1-1). On the other hand, a larva may remain in the pond, continue to grow, and mature while retaining the larval morphology (i.e., paedomorphic pathway; Fig. 1-1).

Efts

An eft is an immature terrestrial stage newt. Efts lack gills and do not have a tail fin or lateral line. However, at metamorphosis the namesake dorso-lateral stripe, which is reddish to orange, appears on each side of an eft. Because efts are immature they do not have swollen vents. After larvae metamorphose into efts, they disperse into the uplands surrounding the breeding pond (Fig. 1-1). Efts mature in the uplands, at which point they are referred to as terrestrial adults.

Paedomorphs

A paedomorph is a mature aquatic stage newt. Paedomorphs are larger than immature larvae, have bushy external gills, a membranous tail fin, and a conspicuous lateral line. Paedomorphs do not usually possess the namesake lateral stripe but they do have swollen vents. Paedomorphs reproduce in the breeding pond, then metamorphose and disperse into the surrounding uplands (Fig. 1-1). Once a paedomorph transforms and leaves the pond it is referred to as a terrestrial adult. On rare occasions, a paedomorph may transform directly into an aquatic adult (e.g., dashed line in Fig. 1-1).

Adults

An adult is a mature terrestrial or aquatic stage newt. Adults lack gills and do not have a visible lateral line. Adults possess the namesake dorso-lateral stripes and have swollen vents. They are sexually dimorphic, and males have a light-colored gland that is visible at the posterior end of the vent. Adults occur in the uplands around breeding ponds (i.e., terrestrial adults) as well as in the ponds (i.e., aquatic adults), and there is movement between these habitats during the life of an adult. Aquatic adults develop a membranous tail fin similar to the tail fin larvae and paedomorphs. They do not regrow external gills, however. Terrestrial adults lack a tail fin. They differ from efts in that the vent of a terrestrial adult is swollen, whereas the vent of an eft is not swollen.

In the chapters that follow, I refer to the various life-history stages of striped newts as outlined above. Readers may need to refer back to this section, as well as Fig. 1-1, until they are familiar with the striped newt life cycle and the different stages that comprise it.

Overview of Dissertation

Chapters 2 through 5 present the results of a multidisciplinary research project on striped newt life history; they include data based on a fieldwork component, a laboratory experiment, and a molecular genetics study. Each of these chapters plays an integral role in a unifying theme of striped newt life history and conservation. Chapters are written in manuscript format, each with its own introduction, materials and methods, results, and discussion, to facilitate publication in peer-reviewed journals.

Prior to my research, knowledge of striped newt life history was limited to results of studies at a single pond during a drought period. Because life history information is crucial for conservation and management planning, I conducted a 2-year field study of striped newt life history at a different pond during a relatively wet period. In addition to monitoring newts at the breeding pond, I trapped newts at various distances from the pond in the surrounding uplands. Results from captures at the pond, which are presented in Chapter 2, demonstrated that striped newts have a complex life history and are adapted to taking advantage of temporary breeding habitats that fluctuate within and among seasons. Directionality of newt movements into and away from the pond was nonrandom (Chapter 3), and results of upland captures, also presented in Chapter 3, showed that striped newts dispersed hundreds of meters from the pond.

One component of the striped newt's complex life history is the expression of alternative life-history pathways (i.e., metamorphic pathway vs. paedomorphic pathway). Field-collected data showed that within a single cohort some larvae metamorphosed and left the breeding pond before attaining sexual maturity (metamorphic pathway), whereas others remained in the pond, continued to grow, and matured in the larval morphology (paedomorphic pathway). In a laboratory experiment, I tested the hypothesis that expression of these alternative life-history pathways is influenced by larval growth rate. The experiment also allowed me to test the applicability of two popular models of amphibian metamorphosis as they pertain to *N. perstriatus*. As presented in Chapter 4, growth rate did not significantly affect life-history pathway expression, and neither of the two models of metamorphosis was totally consistent with the results of the experiment.

Inasmuch as the genetic structuring of populations has important evolutionary, biogeographical, management, and conservation implications, I conducted analyses of mitochondrial DNA of striped newts from throughout their range. Results showed that there has been considerable evolutionary differentiation among the locations sampled, probably because of genetic drift caused by natural habitat fragmentation. Genetic data supported data from mark-recapture studies, which suggest that striped newts form metapopulations. The results of this molecular genetic study are presented in Chapter 5, and the consequences of metapopulation structure and population fragmentation for the conservation of this imperiled species are discussed in the last chapter.

Chapter 6, the final chapter, contains a brief summary of striped newt life history as well as conservation and management recommendations based on the results of the preceding chapters. In this chapter, I also provide suggestions for additional research on *N. perstriatus*.

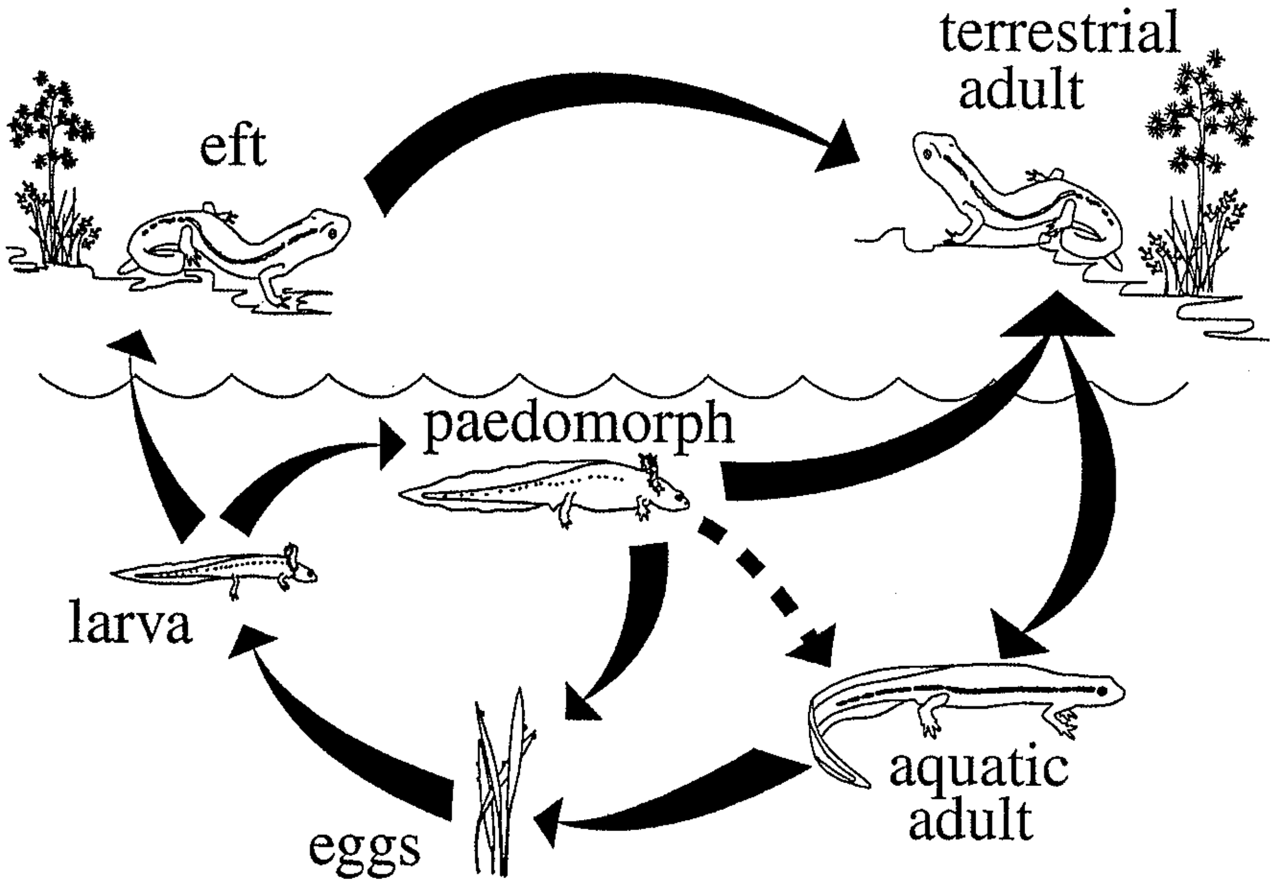


Fig. 1-1. Life-history schematic of the striped newt. Life-history stages include aquatic and terrestrial phases. During the life of an individual, it will move between aquatic and terrestrial habitats. Lines and arrows indicate direction of movement. The dashed line infers that this developmental path is possible, but uncommon.

CHAPTER 2
LIFE HISTORY OF THE STRIPED NEWT AT A NORTH-CENTRAL FLORIDA BREEDING POND

Introduction

Salamanders of the genus *Notophthalmus* occur exclusively in North America with three extant species: *N. viridescens* (eastern newt), *N. meridionalis* (black-spotted newt), and *N. perstriatus* (striped newt). *Notophthalmus viridescens* ranges throughout the eastern United States and into southeastern Canada, whereas *N. meridionalis* is confined to extreme southeast Texas and northeastern Mexico (Conant and Collins, 1991; Petranka, 1998). *Notophthalmus perstriatus* is limited to northern Florida and southern Georgia (Conant and Collins, 1991; Petranka, 1998). Each of the species exhibits a complex life cycle, involving aquatic and terrestrial phases. The ecology of *N. viridescens* has been well studied (Gill, 1978a, b; Harris, 1987; Harris et al., 1988; Healy, 1970, 1973, 1974a, b, 1975; Hurlbert, 1969; Pope, 1924). On the other hand, far less research has focused on *N. meridionalis* and *N. perstriatus* (Petranka, 1998).

Because of historical declines and current relative abundance, which is low throughout most of its range, *N. perstriatus* is recognized as a rare species in Florida and Georgia (Christman and Means, 1992; Cox and Kautz, 2000; Jensen, 1999). Its biological status is under review by the U.S. Fish and Wildlife Service (L. LaClaire, pers. comm.). Most of what has been reported about striped newts has been limited to the results of surveys (Dodd and LaClaire, 1995; Franz and Smith, 1999; Hipes and Jackson, 1996) and species accounts (Ashton and Ashton, 1988; Bishop, 1941a, 1943; Carmichael and Williams, 1991; Christman and Means, 1992; Carr, 1940; Dodd et al., in press; Mecham, 1967; Petranka, 1998). In the only study of *N. perstriatus* life history, Dodd (1993) monitored striped newt movements at a single breeding pond from 1985 through 1990. However, a severe drought impacted the pond throughout Dodd's study. Despite dry conditions, Dodd (1993) determined seasonal activity, population size structure, and sex ratio. Of necessity these data were limited primarily to the adult life stage. Very little information was available on metamorphic individuals because the breeding pond only held water for short periods. It was not clear if the patterns observed by Dodd were typical of striped newt life history.

To gain a better understanding of striped newt life history, I conducted a 2-year study at a breeding pond in north-central Florida. I used a drift fence (Gibbons and Semlitsch, 1981) to monitor striped newt immigration and emigration at the pond. My objectives were: 1) to determine the timing of immigration and emigration of newts, 2) to measure breeding success by monitoring emigration of metamorphic animals, 3) to estimate population size-structure and sex ratio, and 4) to evaluate the influence of hydroperiod and rainfall on striped newt movements and reproduction.

Materials and Methods

Study Site

The study was conducted at One Shot Pond (OSP), an isolated water body within a high pine community in north-central Florida, approximately 4 km west of Breezeway Pond, the site of Dodd's (1993) striped newt study. One Shot Pond is located in Putnam Co., FL, on the Katharine Ordway Preserve-Swisher Memorial Sanctuary (Fig. 2-1). Descriptions of the Preserve and its habitats are provided elsewhere (Dodd, 1996;

Eisenberg and Franz, 1995; LaClaire, 1995). One Shot Pond is a sinkhole-depression pond with a basin area of ca. 0.8 ha (LaClaire, 1995). The hydroperiod of the pond is variable (hydroperiod refers to the number of days a pond holds water between periods when it is dry) and it dries periodically. Because of this, OSP does not support fish, and many species of amphibians breed there (Johnson, 1999).

Drift Fence at One Shot Pond

Newt movements into (i.e., immigration) and away from (i.e., emigration) OSP were monitored with a continuous drift fence (Gibbons and Semlitsch, 1981) that encircled the pond. The galvanized metal fence was buried in the ground ca. 15 cm with ca. 35 cm extending above ground. The circumference of the fence was 190 m, with 38 pitfalls (19 pairs of 19 l plastic buckets) buried flush with the ground at intervals of ca. 10 m. For each pair of pitfalls, one was buried on the side of the fence toward the pond and one on the side away from the pond. To reduce mortality of trapped animals, foam sponges were placed in each trap and cover boards were leaned against the fence over each pitfall to provide shade. Each time traps were checked I removed invertebrates (e.g., spiders, predaceous beetles, and centipedes) and added water to keep the sponges moist. Traps were checked at least 3 times per week and daily during periods of warm weather and/or high rainfall. Because of relatively high rainfall during the winter of 1997/98, the water in OSP rose to a level at which three pairs of pitfalls became inundated. In March of 1998, the entire fence was moved ca. 12 m further up slope, requiring an additional 40 m of flashing. The fence was moved in one day, so there was no break in trapping. The number of pitfalls remained the same and each trap was reinstalled in the same relative position at the new fence location. The drift fence was monitored from 7 Oct-96 to 11 Sep-98. Pitfall traps were open for 705 consecutive days, for a total of 26,790 trap-nights (i.e., one trap-night = one pitfall trap open for 24 hours).

Newts Caught at Drift Fences

Most newts were marked with a unique toe clip so individuals could be identified (Donnelly et al., 1994), but recently metamorphosed efts captured after 11 Jul-98 were only marked with a "daily cohort" toe clip. Newts were weighed to the nearest 0.1 g using a Pesola® scale, and snout-vent length (SVL) was measured to the nearest 1 mm. The sex of each newt was recorded as male, female, or unknown. Sex was determined by examining the vent region; adult males have a light-colored gland visible at the posterior edge of the cloaca (Dodd, 1993). The condition of the cloaca was recorded as swollen, slightly swollen, or not swollen, indicative of mature, maturing, and immature individuals, respectively (Chapter 4). Animals were released on the opposite side of the fence from where they were captured.

Three distinct life-history stages of striped newts were examined: adults, efts (immature larvae that recently metamorphosed), and paedomorphs (mature larvae that recently metamorphosed, Table 2-1, Chapter 1). Recently metamorphosed newts retained vestiges of their gills (i.e., gill buds) for several days after they left the pond. Therefore, the presence of gill buds indicated that a newt had recently transformed and left the pond. Data for adults immigrating to the pond include recaptures. Many of the adults captured in pitfalls on the outside of the drift fence had been previously captured and marked in the uplands surrounding OSP (Chapter 3). Others were initially marked as they emigrated from the pond as immature efts. Data for emigrating adults also include recaptured individuals. These individuals had been initially marked as described above or when they were captured in pitfalls on the outside of the drift fence as they immigrated to breed. Data for recently transformed paedomorphs and efts only include initial captures. By excluding eft and paedomorph recaptures, I obtained a clearer pattern of striped newt movements.

Weather Data

To evaluate the influence of hydroperiod and rainfall on striped newt movements and reproduction, rainfall and pond depth were monitored at OSP. Rainfall (to the nearest mm) was measured with a rain gauge mounted in the open within the pond basin. Pond depth was measured with a permanent depth gauge placed in the center of the pond. I used binoculars to read the depth gauge.

Statistical Analyses

When assumptions of parametric tests were violated, nonparametric methods (Hollander and Wolfe, 1999) were used to test for differences between data sets. All statistical analyses, with the exception of χ^2 tests, were performed using SPSS ver. 10.0. I used χ^2 tests (Sokal and Rolf, 1995) to test for departure of 1:1 sex ratios for adults and paedomorphs. To calculate expected values, I divided the total number of males and females used in each analysis by two.

Results

Seasonal Activity

During the 2-year study, 10,290 striped newt captures were recorded at the drift-fence encircling OSP. At least one newt was captured during every week of the study, although four periods of activity accounted for the vast majority of captures (Fig. 2-2). Activity during these four peaks included newts moving into (immigration) and away from (emigration) the pond.

Immigration

Immigration was almost exclusively comprised of breeding migrations of adult striped newts, and there were four distinct adult immigrations during the study (Table 2-2, Fig. 2-3A). The largest and most prolonged immigration event was immigration Event E-3, which lasted for 6 months. Peak movement during this event occurred in Dec-97 (Fig. 2-3A). During this month, 1,567 adults were captured in outside pitfall traps. The other three immigration events were much smaller and occurred during 2-month or 3-month periods. Females and males immigrated during the same times of the year (Fig. 2-3A).

Although many juvenile newts were captured in pitfalls on the outside of the drift fence, these individuals had recently metamorphosed and were initially captured and marked on the inside of the fence after they left the pond. Rather than immediately dispersing into the uplands, some of these individuals headed back toward the pond and were caught in outside pitfalls. Nonetheless, captures of these animals were the result of very localized movements and not an indication of immigration by efts. When recaptures of recently transformed individuals are excluded, almost all (96%) newts captured in outside pitfalls had swollen vents, indicating that they were sexually mature. The remainder had slightly swollen vents, indicating that they were close to maturity.

Emigration

Emigration events included individuals representing all three life-history stages: adults, efts, and recently metamorphosed paedomorphs (Table 2-2). Similar to immigration, there were four distinct periods of adult emigration (Table 2-2, Fig. 2-4). The largest of these (E-4) occurred toward the end of the study (Fig 2-4). This emigration event accounted for 88% of all emigrating adults with more adults captured leaving the pond in Jun-98 than any other month of the study. Female and male adults immigrated during the same times of the year (Fig. 2-3B).

Efts metamorphosed and emigrated during all months of the year except February, but there were four distinct periods of emigration (Table 2-2, Fig. 2-4). Most efts (81%) emigrated during the last 5 months of the study period (eft emigration Event E-4). Recently metamorphosed paedomorphs were captured during three emigration events (Table 2-2, Fig. 2-4). Most (94%) were captured from Mar-97 through Aug-97 (paedomorph emigration Event E-2).

Reproduction

Totals of 5,296 recently transformed larvae (i.e., efts) and 435 recently transformed paedomorphs were captured during the 2 years. These individuals likely represented successful reproduction of four distinct breeding bouts, as indicated by emigration of recently transformed newts throughout the study (Fig. 2-4). The first evidence of successful reproduction was provided by captures of emigrating efts (E-1, Table 2-2) and paedomorphs (E-1, Table 2-2) during the first few months of the study (Fig. 2-4). During this period, 776 efts and 25 recently transformed paedomorphs were captured dispersing from OSP (Fig. 2-4). The second period of eft and paedomorph production occurred in spring and early summer of 1997. During this time, 214 efts and 407 recently transformed paedomorphs were captured (E-2, Table 2-2, Fig. 2-4). Only 16 efts were produced during the third eft emigration event (E-3, Table 2-2), but no recently transformed paedomorphs were captured during this period (Fig. 2-4). By far, the most successful reproductive bout during the 2 years was indicated by eft emigration (E-4) that occurred during the last 5 months of the study. Efts were captured starting in late May-98, and immature larvae continued to transform and leave the pond until the end of the study (Fig. 2-4). I likely did not document the full extent of this emigration event since 98 efts were captured in inside pitfalls on the last day of the study. Only nine recently transformed paedomorphs were caught during this period.

After they transformed and emigrated from the breeding pond, efts migrated into the surrounding sandhill uplands (Chapter 3). While in the uplands, efts matured before they returned to the pond to breed as adults. The largest immigration of adults (Event I-3), which occurred from Oct-97 through Mar-98, consisted of many newts that were captured initially as they emigrated as efts during the first few months of the study (eft Event E-1). Although these newts were easily recognized as recaptures when they returned to the pond, I could not be sure of individual toe clips in some instances. Of 40 newts that I was confident of their toe clip, all of which had been marked as efts when they immigrated (i.e., vents not swollen), 39 had matured (i.e., vents swollen) by the time they were recaptured in outside pitfalls. Based on dissections and examination of gonads (Chapter 4), newts with swollen vents are always sexually mature. Therefore, at least 39 of the 40 recaptured efts had matured in the uplands, then migrated back to the pond to breed a year or more after they left the pond. These 40 newts had remained at large in the uplands around OSP for an average of 416 days (SD = 19.7; range = 359 to 456 days). The average number of days at large since metamorphosis was similar between the sexes. Males (n = 16) averaged 412 days at large (SD = 22.8; range = 359 to 440 days), whereas females (n = 24) averaged 419 days (SD = 17.4; range = 394 to 456 days). Net growth, measured as the difference in SVL between initial capture during emigration and recapture during immigration, was similar between females and males (Fig. 2-5).

Differences in growth rates (net growth (mm)/days at large) between the sexes (Table 2-3) were not significantly different (Wilcoxon rank sum test; $t_s = 0.815$, $P > 0.4$).

Population Size Structure

The size-structure of striped newts differed between immigrating and emigrating adults. Snout-vent length and mass differed significantly among immigrating and emigrating males and females (SVL: $F_{3,3136} = 776$, $P < 0.0001$; mass: $F_{3,3135} = 628$, $P < 0.0001$). Post hoc comparisons showed that immigrating adults of both sexes were significantly smaller than emigrating adults for SVL (Fig. 2-6) and mass (Fig. 2-7). On average, immigrating females were slightly larger (SVL and mass) than immigrating males, and this pattern was evident during immigration Events I-1, I-3, and I-4 (Table 2-4). During immigration Event I-2, adult males and females were almost the same size (Table 2-4). However, overall differences were not significant for SVL or mass (Figs. 2-6A, 2-7A). Adult females slightly exceeded males in SVL and mass for emigration Events E-3 and E-4, but males were slightly larger than females during the first two emigration events (Table 2-4). Overall, emigrating females were significantly larger in SVL (Fig. 2-6B) and mass (Fig. 2-7B) than emigrating males (Scheffé's tests, all $P < 0.0001$).

Recently metamorphosed efts ranged in SVL from 20 – 32 mm (n = 2605) and from 0.2 – 1.0 g in mass (n = 1886). Body size (SVL and mass) of efts differed among the four emigration events (Table 2-5). They were smallest during Event E-1 and largest during Event E-4. Snout-vent length and mass of efts differed significantly among three (E-1, E-2, E-4) of the four emigration events (SVL: $F_{2,2581} = 2114$, $P < 0.0001$; mass: $F_{2,1862} = 128$, $P < 0.0001$; Table 2-5). Post hoc comparisons showed that both measures of body size were significantly different for efts during Events E-1, E-2, and E-4

(Scheffé's tests, all $P < 0.0001$; Table 2-5). Event E-3 was excluded from the analyses because of small sample sizes.

Male and female paedomorphs were essentially the same size (SVL and mass) during all three emigration events. Overall, males were slightly longer than females but the average mass of males and females was the same (Table 2-5). There were no statistical differences in either measure of body size between the sexes (t-tests; SVL: $t = 1.42$, $P = 0.156$; mass: $t = -0.159$, $P = 0.874$; Table 2-5). Of the three paedomorph emigrations, Event E-2 had the largest number of individuals (Table 2-5). Because of small sample sizes for Events E-1 and E-3, I did not make statistical comparisons of body size among the three events.

Body sizes of the three different life-history stages differed (Table 2-5). Emigrating efts that had recently transformed had the smallest body size (SVL and mass), followed by recently transformed paedomorphs, then emigrating adult males. Emigrating adult females, on average, were the largest of all stages. These differences were statistically significant (ANOVA; SVL: $F_{3,4017} = 3789$, $P < 0.0001$; mass: $F_{3,3266} = 1578$, $P < 0.0001$) and post hoc tests showed that means differed among all four groups (efts, paedomorphs, males, and females; Scheffé's tests, all $P < 0.0001$).

Sex Ratios

Sex ratios were male biased during immigration Events I-1 and I-4 but female biased during Events I-2 and I-3 (Table 2-6). Because of the relatively large number of captures during immigration event I-3, when the sex ratio was 1:1.26 (m:f), the overall sex ratio of immigrating adults was 1:1.26. During emigration, the sex ratio of adults was female biased during all events except E-1 (Table 2-6). The relative contribution of sex ratio data provided by emigration Event E-4 (88% of all emigrating adults) had a large influence on the overall sex ratio of emigrating adults, which was 1:1.22 (Table 2-6). Overall adult sex ratio (emigrating and immigrating individuals) was female biased (Table 2-6; $\chi^2 = 43.9$, df = 1, $P < 0.001$).

The sex ratio of recently metamorphosed paedomorphs was highly female-biased during each of the three emigration events. Event E-2 was by far the largest of the three events, representing 92% of paedomorph captures. Therefore E2 had a large impact on the overall sex ratio of paedomorphs, which was significantly skewed toward females (m:f = 1:4.64; $\chi^2 = 161.8$, df = 1, $P < 0.001$).

Rainfall and Hydroperiod

Monthly rainfall at OSP varied ranged from 12 mm to 283 mm (Fig. 2-8). The driest periods were Nov-96 through Mar-97 and Mar-98 through Jul-98 (Fig. 2-8). The wettest period was from Jun-97 through Feb-98 because of an El Niño Southern Oscillation event. Rainfall exceeded 100 mm during 13 months of the study period, and beginning in Jun-97, there were 7 months consecutively in which rainfall exceeded 100 mm. Summer rainfall resulted from localized thunderstorms, whereas winter rain was associated with cold fronts.

Newts tended to move during wetter periods and newt captures were significantly correlated with rainfall ($P < 0.001$). Nonetheless, rainfall was a weak predictor of the magnitude of newt movements and only explained a small portion of variation in movements of newts at OSP ($r^2 = 0.06$).

One Shot Pond held water throughout the study period (Fig. 2-9). Pond depth was lowest (68 cm) in Oct-97, but the El Niño rains filled the pond to its greatest depth (275 cm) the following Apr. Analyses of the influence of pond drying and filling on striped newt reproduction are precluded because OSP always held water during the study.

Although pond depth exceeded 65 cm for the duration of the study, water depth may have influenced the survivorship of larvae, and therefore the number of emigrating efts. Of the four eft emigration events, Event E-3 was the smallest (Table 2-5), coinciding with the shallowest pond depth during the study (Fig. 2-9). The largest eft emigration (Event E-4, Table 2-5) began in May-98, when pond depth exceed 260 cm. Pond depth increased steeply during the months before May-98 (Fig. 2-9), when larvae that transformed during Event E-4 were growing in the pond. Although pond depth may have influenced the survivorship of striped newt larvae, conclusions are confounded by the fact that a variable number of females potentially contributed eggs that resulted in efts for each emigration event. Fewer than 70 females appear to have contributed to the production of larvae during eft emigration E-3, whereas ca. 1300 females potentially produced the larvae that transformed and emigrated during Event E-4.

Discussion

Seasonal Activity

Striped newts were active at OSP during all months of the year, but there were four periods of activity that accounted for most captures. In the only published study of striped newt life history, Dodd (1993) also found several periods of activity that accounted for the majority of his striped newt captures over a 5-year period. At OSP, two activity periods occurred during the fall/winter, whereas the other two took place during the spring/summer. At Breezeway Pond, striped newts were mainly active during the fall/winter portion of the year (Dodd, 1993).

Immigration

Adults moved into OSP to breed from Oct. through Mar. and from Apr. through Jul. At Breezeway Pond, 75% of adults immigrated from Jan. through Mar. (Dodd, 1993). Although data collected at OSP support the fact that striped newts tend to breed during the winter (Dodd, 1993; Petranka 1998), there were also two distinct migrations (presumably breeding migrations) during the spring/summer. Clearly, striped newts are plastic in the timing of breeding migrations. The only months adults were not documented moving into OSP were Aug. and Sep. Dodd (1993) suggested that the extended breeding period of striped newts allows them to take advantage of temporary breeding habitats that fluctuate within and among seasons. Such a plastic life history is likely an adaptation to living in an unpredictable environment.

Emigration

As with immigration, there were four distinct periods of emigration. These periods overlapped with the four immigration events. Adults migrated to the wetland, then courted and bred I assume, and then moved back into the surrounding uplands. This pattern persisted throughout the study even though OSP always held water. Therefore, emigration of adults was not simply because of pond drying, which appeared to be the case at Breezeway Pond (Dodd, 1993). Based on the interval adults spent in the pond, as well as laboratory observations of reproductive activity (Johnson, unpubl.), striped newts have protracted courtship and oviposition. Females, including paedomorphic individuals, lay eggs one at a time and do so over the course of several months. As a result, adults that immigrated into OSP during the winter of 1997/98 (Event I-3) for example, stayed in the pond until they had finished breeding and then emigrated during the summer of 1998 (Event E-4). This staggered pattern of immigration, later followed by emigration, applies to the two other immigration events as well. Therefore, adults immigrating during Events I-1 and I-2 left the pond several months later, during Events E-2 and E-3, respectively (Tables 2-4, 2-5, Fig. 2-3). A similar pattern is apparent in Dodd's (1993) data early in his study (Fig. 1 in Dodd, 1993), although the variable hydroperiod of Breezeway Pond and small number of captures confounds interpretation during the later years.

Reproduction

More than 5,500 recently transformed striped newts were captured as they emigrated from OSP. Production of very large numbers of metamorphic individuals is not uncommon for pond-breeding amphibians (Semlitsch et al., 1996). However, no previous studies have found so many metamorphic *N. perstriatus* (Dodd, 1993; B. Means, pers comm.; K. Greenberg, pers. comm.; D. Stevenson, pers. comm.). As a result of a drought, Dodd (1993) only captured 42 recently metamorphosed newts during the entire 5-year study at Breezeway Pond.

Recently transformed efts emigrated in all months except January, but there were periods of concentrated migration, three of which accounted for 99.6% of the captures (Fig. 2-4, Table 2-5). At Breezeway Pond, recently transformed striped newts were only captured from Jun. through Aug-97. The four eft emigration events at OSP presumably represent four bouts of reproduction. Eft emigration E-1 during the first two months of the study resulted from a reproductive event that likely occurred before the study began. The other three emigrations of efts probably represent reproduction of adults that immigrated during the study period. For example,` adult immigration Event I-1 produced larvae that metamorphosed and left the pond during eft emigration Event E-2. Adults that were captured immigrating during Events I-2 and I-3, probably produced most of the larvae that transformed and left OSP during eft emigration Events E-3 and E-4, respectively (Figs. 2-3A, 2-4). This staggered pattern of adult immigration, later followed by eft emigration, was because larvae apparently required approximately 6 months to reach metamorphosis. In the single successful reproductive bout recorded by Dodd at Breezeway Pond, larvae required a 139-day hydroperiod. Paedomorphs also likely contributed to production of larvae in OSP but the relative contributions of non-gilled adults and paedomorphs are unknown.

A successful reproductive event often appeared to produce a bimodal distribution of emigrating newts. This is because within a single cohort of larvae, both immature and mature larvae may result. Some immature larvae transformed and exited the pond as efts, whereas others remained in the pond, attained sexual maturation (i.e., paedomorphs), reproduced, then transformed and exited the pond. This resulted in a bimodal pattern of emigration of a cohort with immature efts showing up first, followed by transformed paedomorphs. For example, the recently transformed paedomorphs captured in the spring of 1997 (paedomorph Event E-2) were probably members of the same cohort that produced the efts that emigrated the previous fall (eft Event E-1; Fig. 2-4). The few paedomorphs that were caught in Jun. and Jul. of 1998 were likely members of the same cohort that produced the few efts that emigrated during eft Event E-3. Monthly samples taken in OSP with dip nets showed that the larvae that eventually matured as paedomorphs remained in the pond after their counterparts had transformed and emigrated as efts (S. A. Johnson, unpubl. data). Comparisons of size at metamorphosis and sex ratio for paedomorphs are precluded because no comparable data are available from other studies.

Population Size Structure

Sizes of recently transformed efts at OSP encompassed the range of sizes of this life-history stage at Breezeway Pond with the exception of the smallest individuals captured at Breezeway. Recently transformed juveniles that Dodd (1993) captured at Breezeway Pond ranged from 18 to 25 mm (n = 47) and 0.1 to 0.4 g (n = 44). Based on Dodd's (1993) data, a snout-vent length of 18 mm and a mass of 0.1 g. appear to be absolute minimum body sizes required for a striped newt to initiate metamorphosis. Although the average SVL of recently transformed efts at OSP was 25.8 mm, the average SVL during the four emigration events varied significantly across all events. Variation in zooplankton availability during each of the periods preceding the emigration events may have caused the differences.

The sizes of adult striped newts at OSP were similar to sizes of adults from Breezeway Pond. Snout-vent length of females at OSP ranged from 25 to 43 mm, whereas SVL of females at Breezeway Pond ranged from 26 to 43 mm. One Shot Pond females ranged from 0.3 to 1.6 g and Breezeway Pond females ranged from 0.3 to 2.0 g. Adult males at OSP were, on average, slightly smaller than females and ranged in SVL from 26 to 38 mm with mass ranging from 0.4 to 1.2 g. Dodd (1993) also found that male striped newts were smaller than females. Snout-vent length of males at Breezeway Pond was the same as that for OSP, whereas mass ranged from 0.2 – 1.6 g (Dodd, 1993).

Sex Ratios

Overall sex ratio of striped newts at OSP and Breezeway Pond were significantly female-biased. At OSP, there was one male for every 1.25 females, and at Breezeway Pond Dodd (1993) captured one male for every 1.46 females. The significance and cause(s) of the female bias in striped newts at the Katharine Ordway Preserve are unknown.

Hydroperiod and Rainfall

The hydroperiod of amphibian breeding ponds has a strong influence on reproduction (Pechmann et. al., 1989; Semlitsch, 2000; Semlitsch et al., 1996). If hydroperiod is too short, larvae do not have adequate time to initiate metamorphosis and will therefore perish as the pond dries. On the other end of the spectrum, permanent ponds usually support predacious fishes that can extirpate some aquatic-breeding amphibians (Semlitsch, 2000). Although OSP held water during the entire study, over the past 2 decades it has dried often enough to preclude predatory fishes (R. Franz, pers. comm.). The large number of efts emigrating from OSP during the 2-year study was probably because the pond held water continuously. In contrast, Dodd (1993) observed standing water in Breezeway Pond during only 14 months of the 5-year study period. Breezeway Pond held water in five distinct episodes (Fig. 1 in Dodd, 1993), and the longest of these episodes was a 139-day hydroperiod. This was the only time during the study when Dodd (1993) captured recently transformed juveniles. The shorter hydroperiods precluded larval maturation, and consequently, no recently transformed paedomorphs were captured at Breezeway Pond.

Long-term rainfall patterns likely have a significant impact on the striped newt population at the Katharine Ordway Preserve. Variability in hydroperiods of striped newt breeding ponds over relatively long time periods probably result in “boom or bust” scenarios for striped newt reproduction. Alternating relatively dry and wet intervals appear to result in highly variable striped newt reproductive success within and among ponds. Dodd (1993) captured very few metamorphic newts during his 5-year study and attributed an observed decline in striped newts at Breezeway Pond to persistent drought conditions. At OSP on the other hand, I observed an increase in the number of striped newts, mainly because of the large number of larvae that metamorphosed during the last several months of the study. The heavy rainfall during the winter of 1997/98 filled the pond to its greatest depth (275 cm) while these larvae were developing. Because of the relatively great depth of the pond, I suggest that there was more habitat and food (zooplankton) available to the larvae. This could have reduced intraspecific competition and contributed to the reproductive success and corresponding survivorship.

Comparisons with *Notophthalmus viridescens*

The life history of the red-spotted newt, *Notophthalmus viridescens*, has been studied in detail (Gill, 1978a, b; Harris et al., 1988; Healy, 1970, 1973, 1974a, b, 1975; Hurlbert, 1969; Pope, 1924). Dodd (1993) compared and contrasted the life history of *N. viridescens* with *N. perstriatus* at Breezeway Pond. Data for striped newts at OSP allow some additional comparisons that Dodd was unable to make because of the poor reproductive success at Breezeway Pond.

Striped newt larvae appear to be more variable than red-spotted newts with regard to the time of year when metamorphosis occurs. Recently transformed efts of *N. viridescens* have been found from Jun. through Nov. (Bishop, 1941b; Gill, 1978a; Hurlbert, 1970; Worthington, 1968). Recently transformed striped newt efts at OSP were found during these months, but they were also captured during Dec., Mar., Apr., and May. The variation in timing of adult immigration and breeding of striped newts at OSP, along with variability of the aquatic habitat quality (e.g., food and pond depth), is likely responsible for the extreme variation in timing of larval metamorphosis. Healy (1973) estimated that red-spotted newt larvae in Massachusetts had a larval period of approximately six months. The same was true for striped newt larvae (excluding paedomorphs) in OSP during my 2-year study. However, red-spotted newt larvae from other locations have shorter larval periods (Bishop, 1941b; Harris et al., 1988; Worthington, 1968). Red-spotted newt larvae transform into efts when they reach a SVL of 19 to 21 mm (Petranka, 1998). The minimum size for metamorphosis of immature striped newt larvae is similar (Dodd, 1993; this study)

The duration of the eft stage can be shorter for striped newts than red-spotted newts. At OSP, many efts matured and immigrated to breed after an eft stage of about 14 months. *Notophthalmus viridescens* efts may remain on land from 2-8 years before returning to breeding ponds (Bishop, 1941b; Healy, 1974a). Striped newts certainly have much greater variability in duration of the eft stage than I documented at OSP. Although many efts matured and returned to OSP after a period of about 14 months, this is likely a minimum time-frame. Some efts probably remained in the uplands around OSP and did not migrate to breed. Therefore, these individuals, once they matured and migrated to the pond to breed, would have an eft stage longer than 14 months. Moreover, if drought conditions had prevailed in the vicinity of OSP during the winter of 1997/98, the efts that did migrate to breed would not have had the opportunity to do so, thus increasing the estimate of duration of the eft stage. Annual variation in rainfall certainly has an impact on the duration of the terrestrial stage of striped newts.

Growth rates of *N. perstriatus* efts at OSP appear similar to growth rates of juvenile red-spotted newts. Healy (1973) calculated growth rates of marked efts in a Massachusetts's population of red-spotted newts for three consecutive years. Healy (1973) presented "mean growth increment" values (Table 2 in Healy, 1973), and I estimated daily growth rates by dividing his mean values by 365. The range of growth rates (mm SVL / day) for red-spotted newts varied from 0.0048 to 0.0159. Growth rates of striped newt efts (females: 0.0167 mm SVL / day; males: 0.0183 mm SVL / day) were similar to growth rates of red-spotted newts in Massachusetts (0.0159 mm SVL / day; Healy, 1973). Because of the short duration of my study, annual variation in growth rates of striped newt efts is unknown.

For striped newts and red-spotted newts, life-history pathway has a profound influence on age at first reproduction. In both species, individuals that omit the eft stage reach sexual maturity earlier than individuals that metamorphose when immature. For *N. perstriatus*, an individual that omits the eft stage matures as a paedomorph and reproduces at about 1 year old. For *N. viridescens*, an individual that omits the eft stage may remain in the pond and later mature as an aquatic adult, or mature as a paedomorph (Brandon and Bremer, 1966; Healy, 1970, 1974a; Petranka, 1998). According to Healy (1974a), immature red-spotted newts that remain in the pond and omit the eft stage reproduce earlier (at 2 years old) than newts that migrate into the uplands as efts. This life-history pathway has not been detected in stripe newts. Red-spotted newts that become paedomorphic may reach sexual maturity in as little as seven months (Petranka, 1998). Expression of the paedomorphic life-history pathway is common throughout the range of *N. perstriatus* (S. A. Johnson, unpubl. data; D. Stevenson, pers. comm.; D. B. Means, pers. comm.; J. Jensen pers. comm.). Paedomorphosis is most common in coastal populations of *N. viridescens* and in places where the terrestrial environment is perceived as exceptionally harsh (Bishop, 1941b; Brandon and Bremer, 1966; Healy, 1974a;

Petranka, 1998). In both species, genetic and environmental factors are believed to control the expression of life history pathway (Chapter 4; Harris, 1987).

Implications for Striped Newt Status Surveys

Life history data for striped newts at OSP have implications for management of the species. Considering the imperiled status throughout its range (Cox and Kautz, 2000; Jensen, 1999), identifying undocumented breeding ponds and monitoring striped newts at known breeding ponds will help ensure the long-term persistence of the species. Probably the most efficient method to survey multiple sites is by sampling breeding ponds for striped newts. Obviously, such surveys must be conducted during non-drought periods when breeding ponds hold water. Dodd's (1993) work proved that during drought conditions, a suitable striped newt pond may only hold water for short periods. Furthermore, as drought conditions persist, newt abundance declines. Therefore, even when potential breeding ponds hold water, newts might be present in such low numbers as to elude detection. Use of drift fences around ponds will increase the likelihood of detection, but this method is very labor-intensive and is not practical for range-wide surveys when time and personnel are limited. Failure to detect newts during drought periods may result from low relative abundance caused by the drought, rather than local extirpation. On the other hand, during wet conditions, such as was the case at OSP following the winter of 1997/98, newt abundance can be relatively high. Wet periods increase the likelihood of detecting the species during aquatic sampling. Surveys conducted during relatively wet periods will prove fruitful for monitoring persistence and locating new breeding ponds. Additionally, as suggested by Dodd (1993), surveys for striped newts should include assessment of biotic and abiotic characteristics of known and potential breeding sites.

Striped newts of various life-history stages may be found in breeding ponds during all months of the year. However, I suggest that spring (Apr. through Jun.) is the best time of the year for conducting aquatic sampling for the species, assuming ponds hold water. At this time of year, OSP contained all three life-history stages. Adults and paedomorphs that had recently bred were still in the pond, as were developing larvae. Sampling for newts in breeding ponds during this time of the year should maximize the probability of capturing newts. However, considering the temporary nature of striped newt breeding ponds, individuals conducting striped newt sampling should conduct surveys whenever breeding ponds hold water.

Table 2-1. Descriptions of the three life-history stages of striped newts referred to in the Chapter 2.

Stage	Description
Adult	Mature newt as indicated by a swollen vent; no evidence of gills; males with a distinct, light-colored gland at posterior edge of cloaca
Eft	Immature newt as indicated by a vent that is not swollen; gill vestiges present--indicating recent metamorphosis of an immature branchiate; sex recorded as unknown
Paedomorph	Mature newt as indicated by a swollen vent, gill vestiges present--indicating recent metamorphosis of a mature branchiate; males with a distinct, light-colored gland at posterior edge of cloaca

Table 2-2. Timing of immigration (I) and emigration (E) events of the three life-history stages of striped newts captured at One Shot Pond, Putnam Co., FL.

Event	Life-history Stage		
	Adults	Efts	Paedomorphs
I-1	Oct.-96 through Dec.-96	not applicable	not applicable
I-2	Apr.-97 and May-97	not applicable	not applicable
I-3	Oct.-97 through Mar.-98	not applicable	not applicable
I-4	Jun.-98 and Jul.-98	not applicable	not applicable
E-1	Oct.-96 through Dec.-96	Oct.-96 through Dec.-96	Oct.-96 through Dec.-96
E-2	Apr.-97 through Aug.-97	Mar.-97 through Jun.-97	Mar.-97 through Aug.-97
E-3	Nov.-97 through Jan.-98	Aug.-97 through Dec.-97	Jun.-98 and Jul.-98
E-4	May.-98 through Aug.-98	May.-98 through Sep.-98	not applicable

Table 2-3. Growth of striped newt efts at One Shot Pond, Putnam Co., FL. Growth is expressed as mm/day from initial capture during emigration (shortly after metamorphosis) until recapture during immigration.

	Females	Males
n	24	16
Mean	0.0167	0.0183
Range	0.0068 - 0.0295	0.0129 - 0.0306
SD	0.0054	0.0043

Table 2-4. Snout-vent length (SVL) and live mass of adult striped newts caught at One Shot Pond, Putnam Co., FL during four immigration events.

		Females		Males	
Event		SVL (mm)	Mass (g)	SVL (mm)	Mass (g)
I-1	n	11	7	18	11
	Mean	36.27	0.80	33.80	0.62
	Range	26 - 40	0.6 - 1.0	27 - 39	0.3 - 1.0
	SD	4.34	0.13	3.80	0.20
I-2	n	58	56	22	22
	Mean	33.57	0.72	33.59	0.72
	Range	27 - 40	0.4 - 1.1	28 - 40	0.4 - 1.0
	SD	4.19	0.20	3.28	0.14
I-3	n	1148	1140	924	914
	Mean	30.90	0.61	30.77	0.61
	Range	26 - 41	0.4 - 1.2	26 - 39	0.3 - 1.0
	SD	1.87	0.11	1.66	0.11
I-4	n	10	9	8	6
	Mean	35.6	1.0	34.25	0.90
	Range	33 - 39	0.8 - 1.2	33 - 36	0.8 - 1.0
	SD	1.90	0.14	0.89	0.11
Total	n	1227	1212	972	953
	Mean	31.11	0.62	30.91	0.61
	Range	26 - 41	0.4 - 1.2	26 - 40	0.3 - 1.0
	SD	2.24	0.13	1.88	0.11

Table 2-5. Snout-vent length (SVL) and live mass of adult, recently transformed eft, and recently transformed paedomorph striped newts captured at One Shot Pond, Putnam Co., FL during four emigration events.

		Adults						Paedomorphs			
		Females		Males		Efts		Females		Males	
Event		SVL (mm)	Mass (g)	SVL (mm)	Mass (g)	SVL (mm)	Mass (g)	SVL (mm)	Mass (g)	SVL (mm)	Mass (g)
E-1	n	4	2	7	4	772	54	17	6	7	3
	Mean	29.00	0.65	30.57	0.73	23.02	0.31	26.47	0.42	27.00	0.48
	Range	25 - 38	0.4 - 0.9	26 - 38	0.6 - 0.9	20 - 29	0.2 - 0.5	24 - 30	0.4 - 0.5	24 - 29	0.4 - 0.5
	SD	6.06	0.35	4.24	0.15	1.34	0.07	1.55	0.04	1.63	0.06
E-2	n	70	66	18	18	209	213	334	320	72	70
	Mean	32.40	0.70	33.06	0.68	28.29	0.55	31.838323	0.73	32.57	0.73
	Range	26 - 41	0.3 -1.1	28 - 37	0.4 - 1.0	23 - 32	0.3 - 1.0	27 - 43	0.4 - 1.8	28 - 40	0.4 - 1.0
	SD	4.07	0.19	2.71	0.14	1.51	0.12	2.54	0.18	2.06	0.13
E-3	n	13	13	11	10	21	21	5	5	2	2
	Mean	30.54	0.58	29.82	0.54	24.43	0.33	37.40	1.04	35.00	1.05
	Range	28 - 33	0.4 - 0.8	26 - 33	0.5 - 0.6	21 - 32	0.2 - 0.8	35 - 41	0.5 - 1.6	33 - 37	0.9 - 1.2
	SD	1.45	0.14	1.99	0.05	2.84	0.15	2.51	0.40	2.83	0.21
E-4	n	469	460	414	406	1603	1598	not applicable	not applicable	not applicable	not applicable
	Mean	36.31	0.93	33.72	0.82	26.74	0.46				
	Range	30 - 43	0.5 - 1.6	31 - 38	0.4 - 1.2	22 - 31	0.2 - 1.0				
	SD	1.73	0.18	1.29	0.13	1.46	0.11				
Total	n	556	541	450	438	2605	1886	356	331	81	75
	Mean	35.63	0.88	33.55	0.80	25.75	0.47	31.66	0.73	32.15	0.73
	Range	25 - 43	0.3 - 1.6	26 - 38	0.4 - 1.2	20 - 32	0.2 - 1.0	24 - 43	0.4 - 1.8	24 - 40	0.4 - 1.2
	SD	2.73	0.21	1.63	0.14	2.33	0.12	2.83	0.19	2.60	0.15

Table 2-6. Sex ratios of adult and paedomorph striped newts captured at One Shot Pond, Putnam Co., FL. Overall and grand total values include several individuals not accounted for in the immigration (I) and emigration (E) events listed. Sex ratios are listed as the ratios of males:females, followed by the number males and females captured in parentheses.

Event	Adults	Paedomorph
I-1	1:0.57 (23:13)	not applicable
I-2	1:3.00 (22:66)	not applicable
I-3	1:1.26 (1038:1307)	not applicable
I-4	1:0.69 (32:22)	not applicable
Overall-I	1:1.26 (1119:1412)	not applicable
E-1	1:0.57 (7:4)	1:2.57 (7:18)
E-2	1:3.74 (19:71)	1:4.64 (72:334)
E-3	1:1.08 (12:13)	1:3.50 (2:7)
E-4	1:1.23 (431:484)	not applicable
Overall-E	1:1.22 (469:572)	1:4.43 (81:359)
Grand total	1:1.25 (1588:1984)	1:4.43 (81:359)

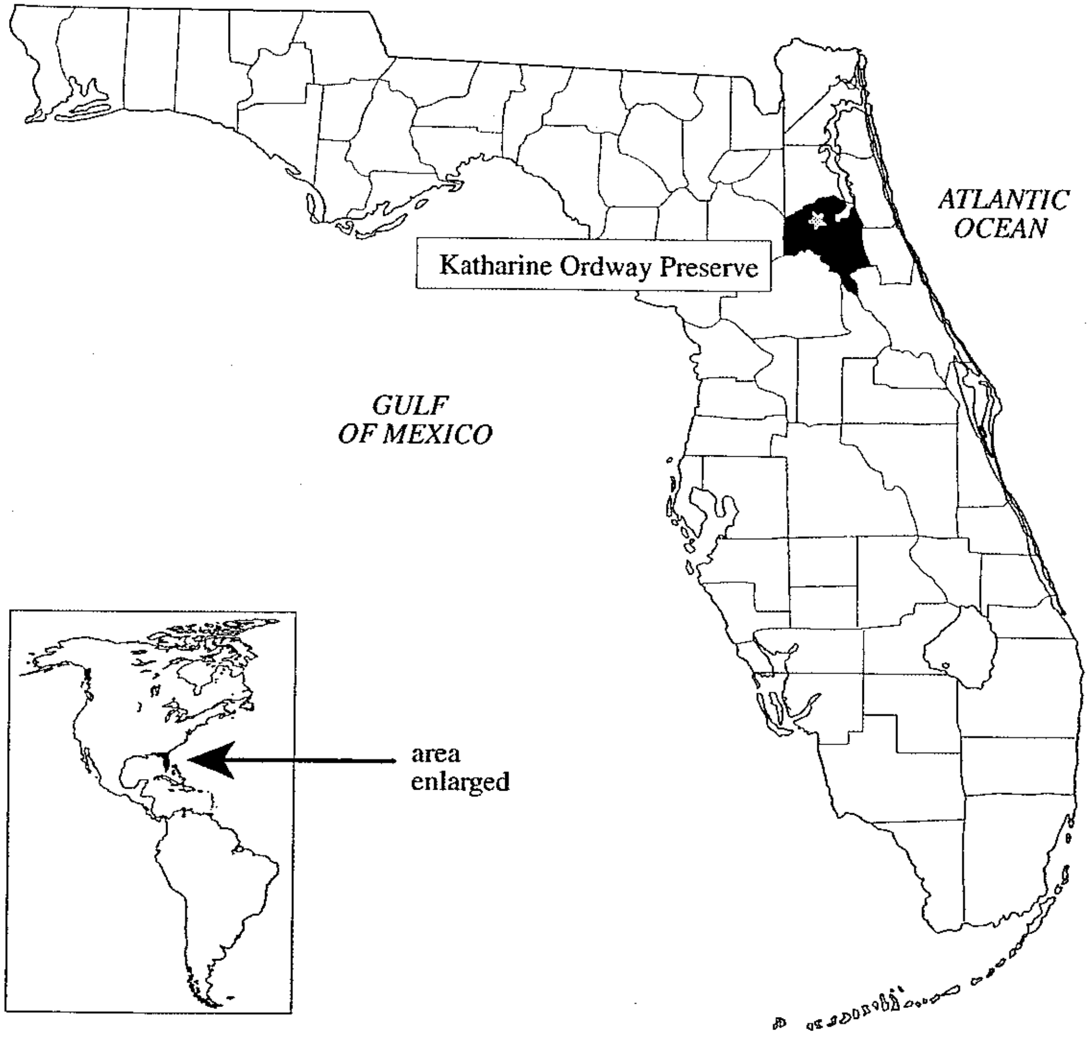


Fig. 2-1. Location of study area, Katharine Ordway Preserve, in Putnam Co., north-central Florida.

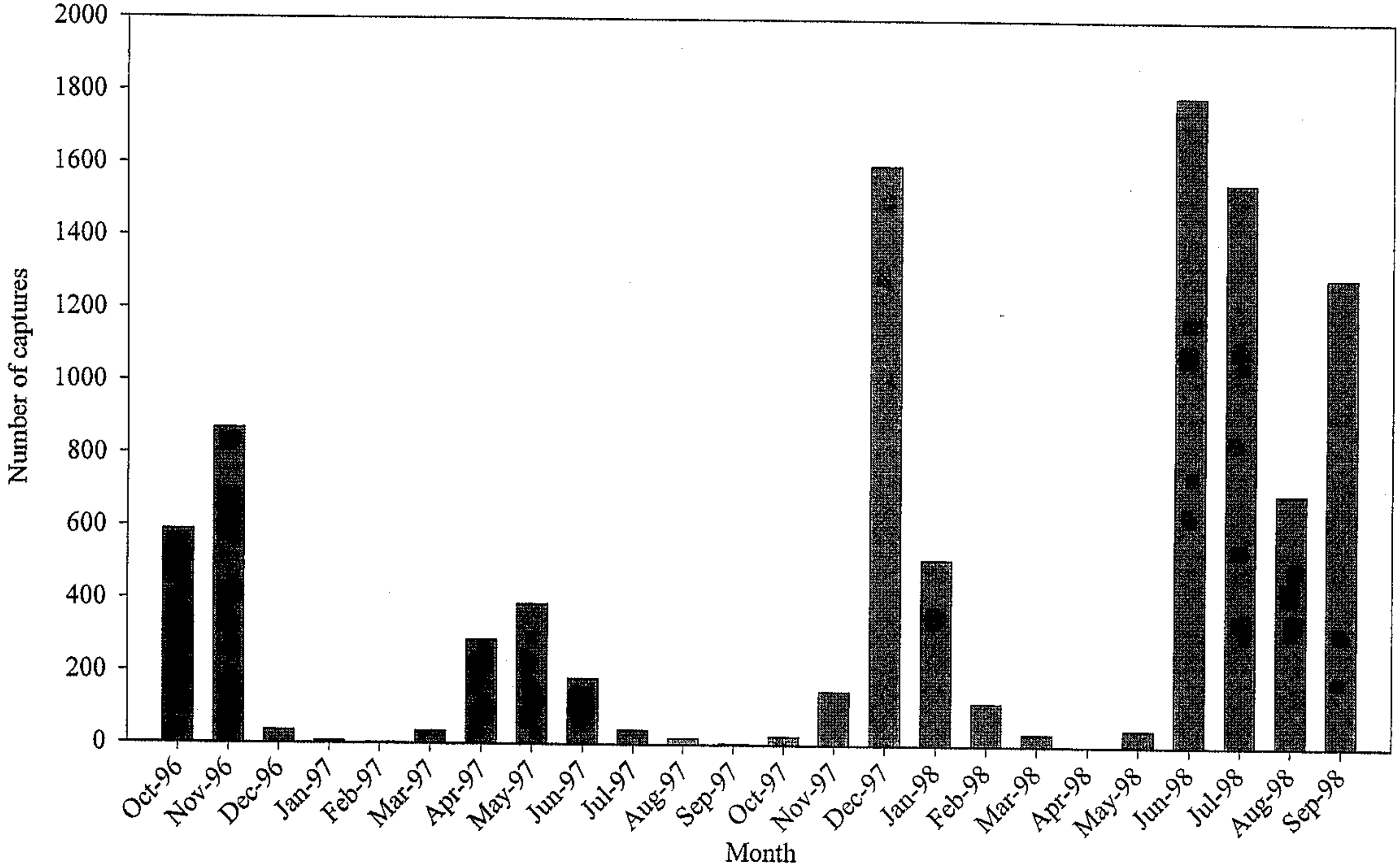


Fig. 2-2. Monthly activity patterns of all striped newt captures at One Shot Pond, Putnam Co., FL. Adult, recently tranformed efts, and recently transformed paedomorphs are included.

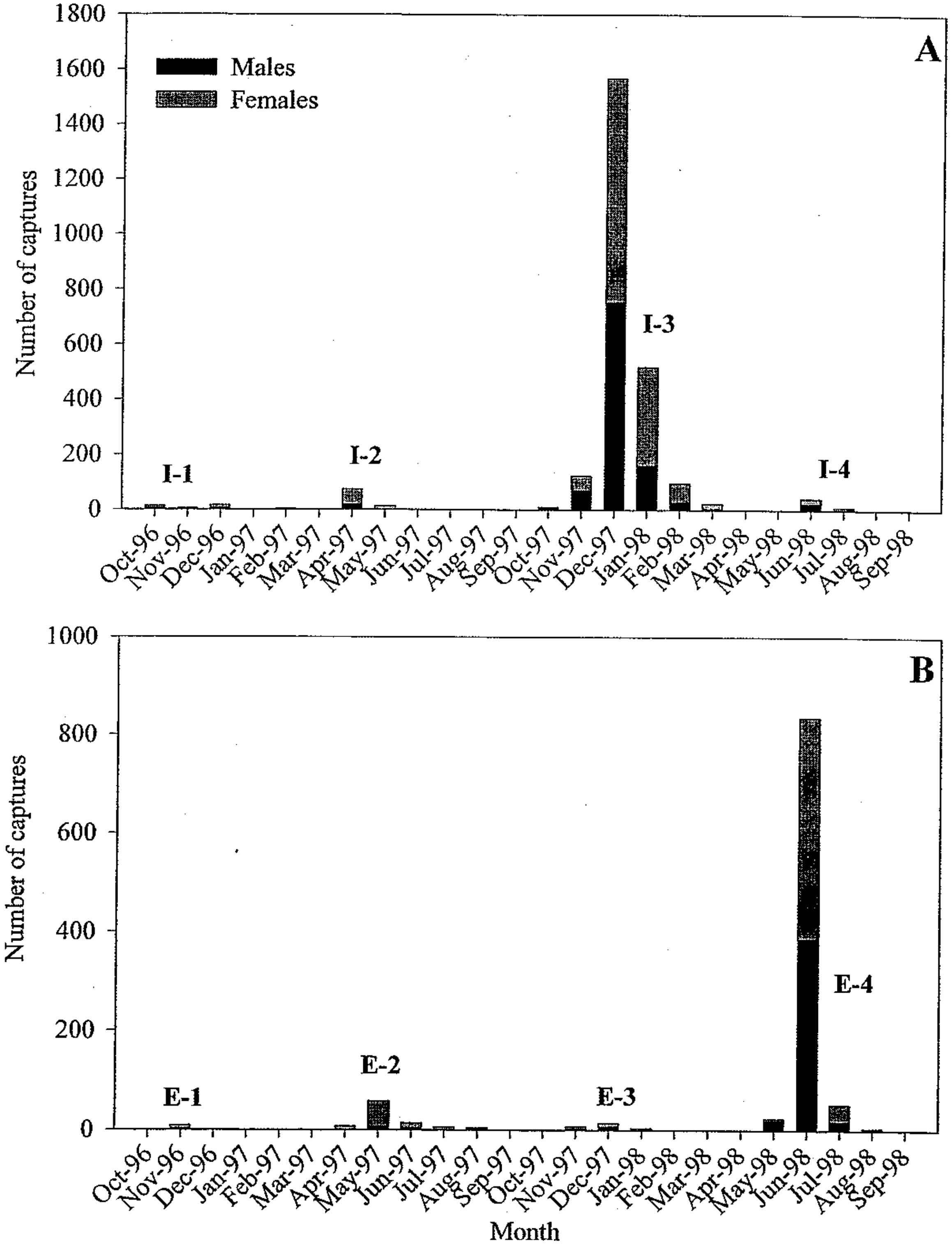


Fig. 2-3. Captures of adult female and male striped newts at One Shot Pond, Putnam Co., FL. A) Immigrating adults. B) Emigrating adults. Note differences in scales along the Y-axes. Four distinct periods of immigration (I) and emigration (E) are indicated.

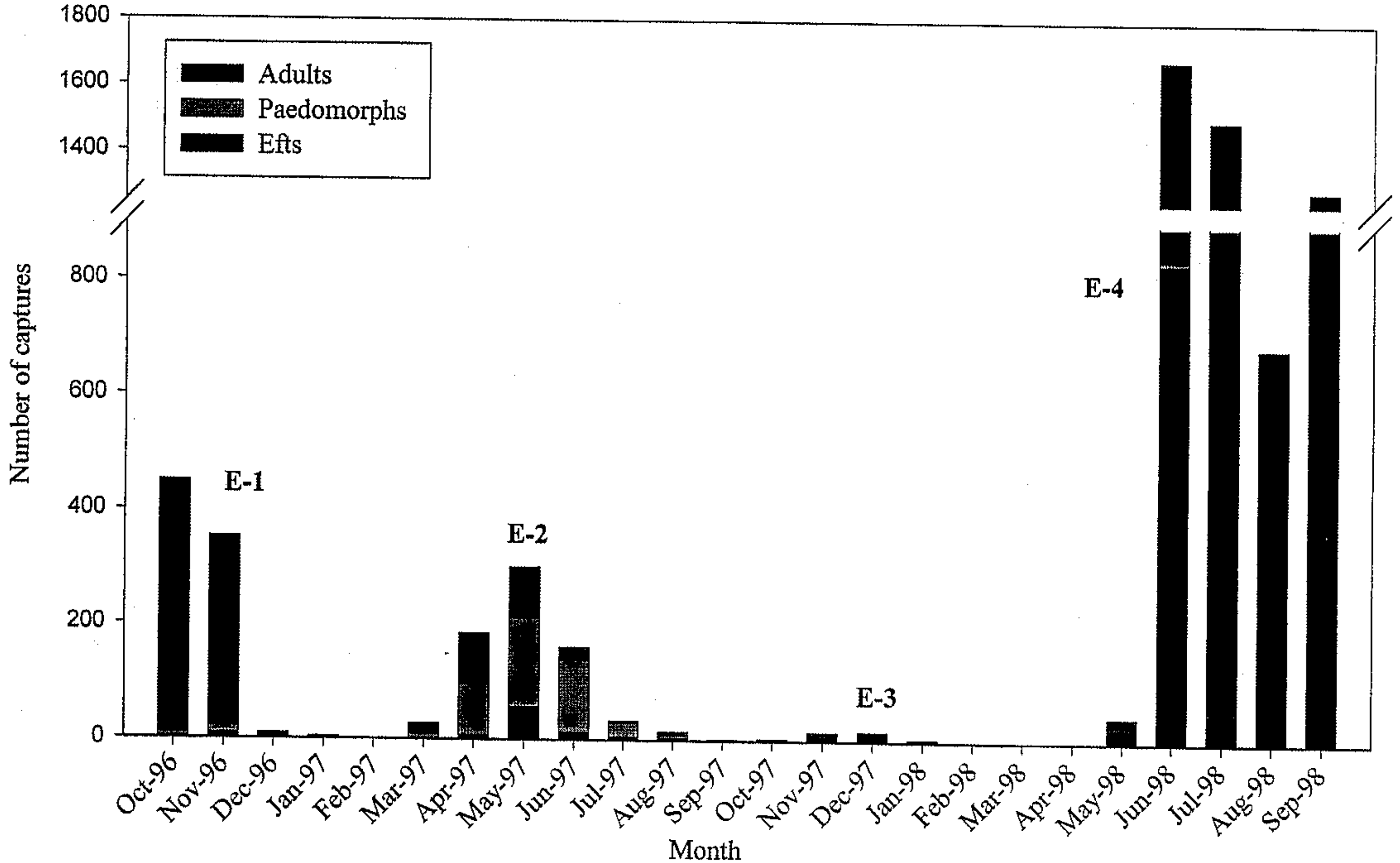


Fig. 2-4. Monthly captures of adults, recently transformed efts, and recently transformed paedomorphs emigrating from One Shot Pond, Putnam Co., FL. Four distinct periods of newt captures are indicated.

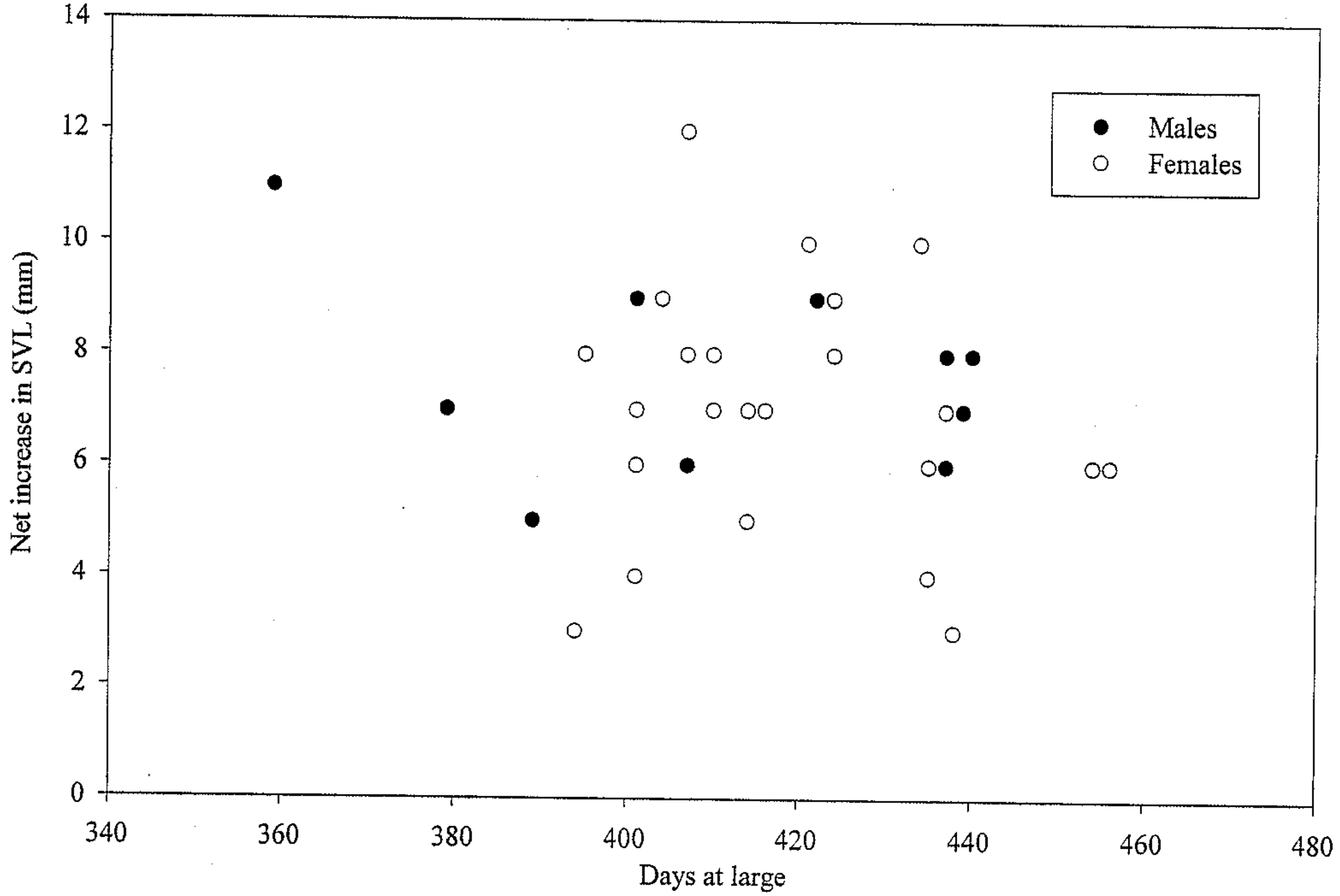


Fig. 2-5. Net increase in SVL of female (n = 24) and male (n = 16) efts since initial capture during emigration, shortly following metamorphosis, and recapture during immigration when they returned to breed. Note X-axis starts at 340 days and some symbols overlap.

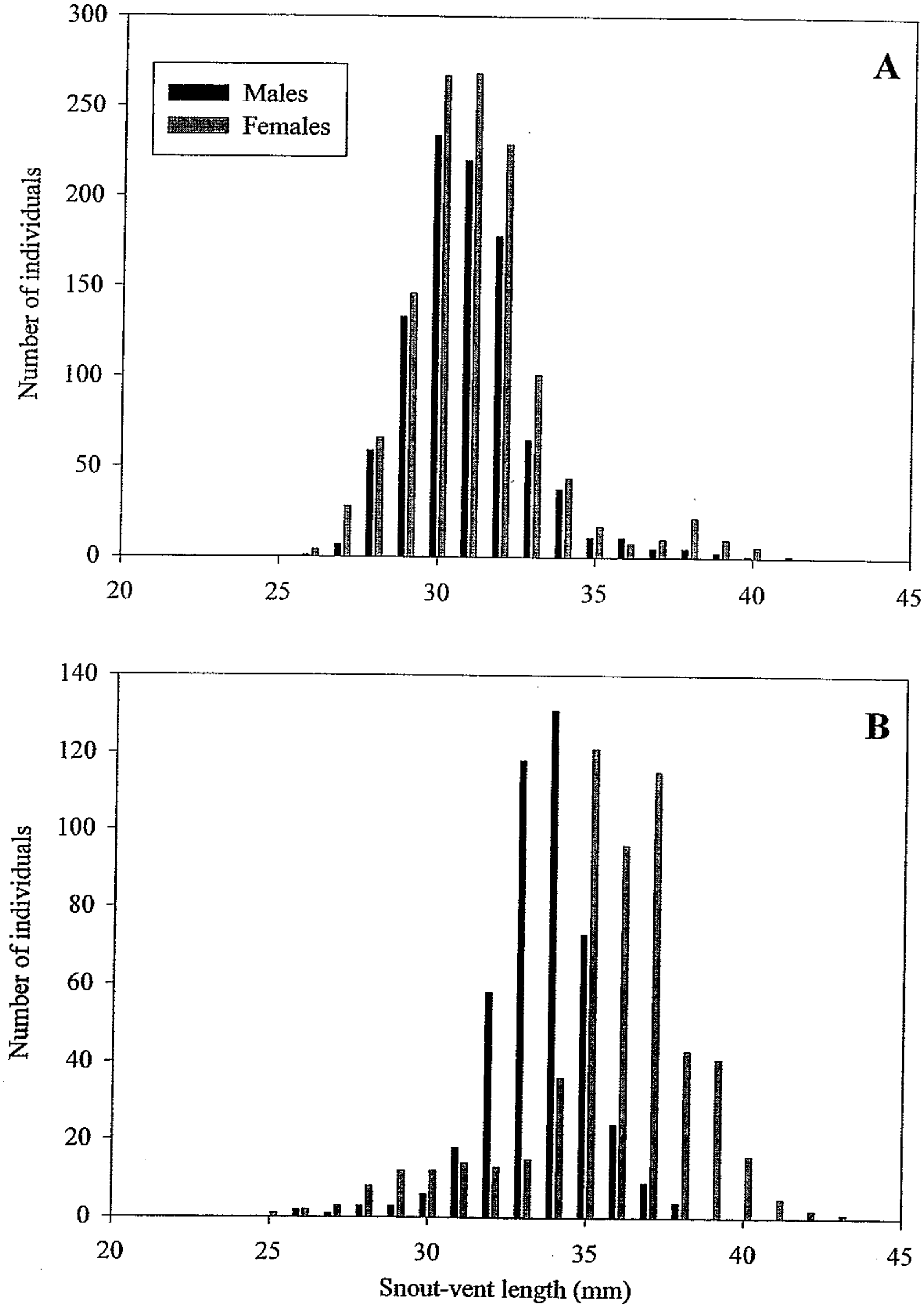


Fig. 2-6. Snout-vent lengths of adult female and male striped newts captured One Shot Pond, Putnam Co., FL. A) Immigrating adults. B) Emigrating adults.

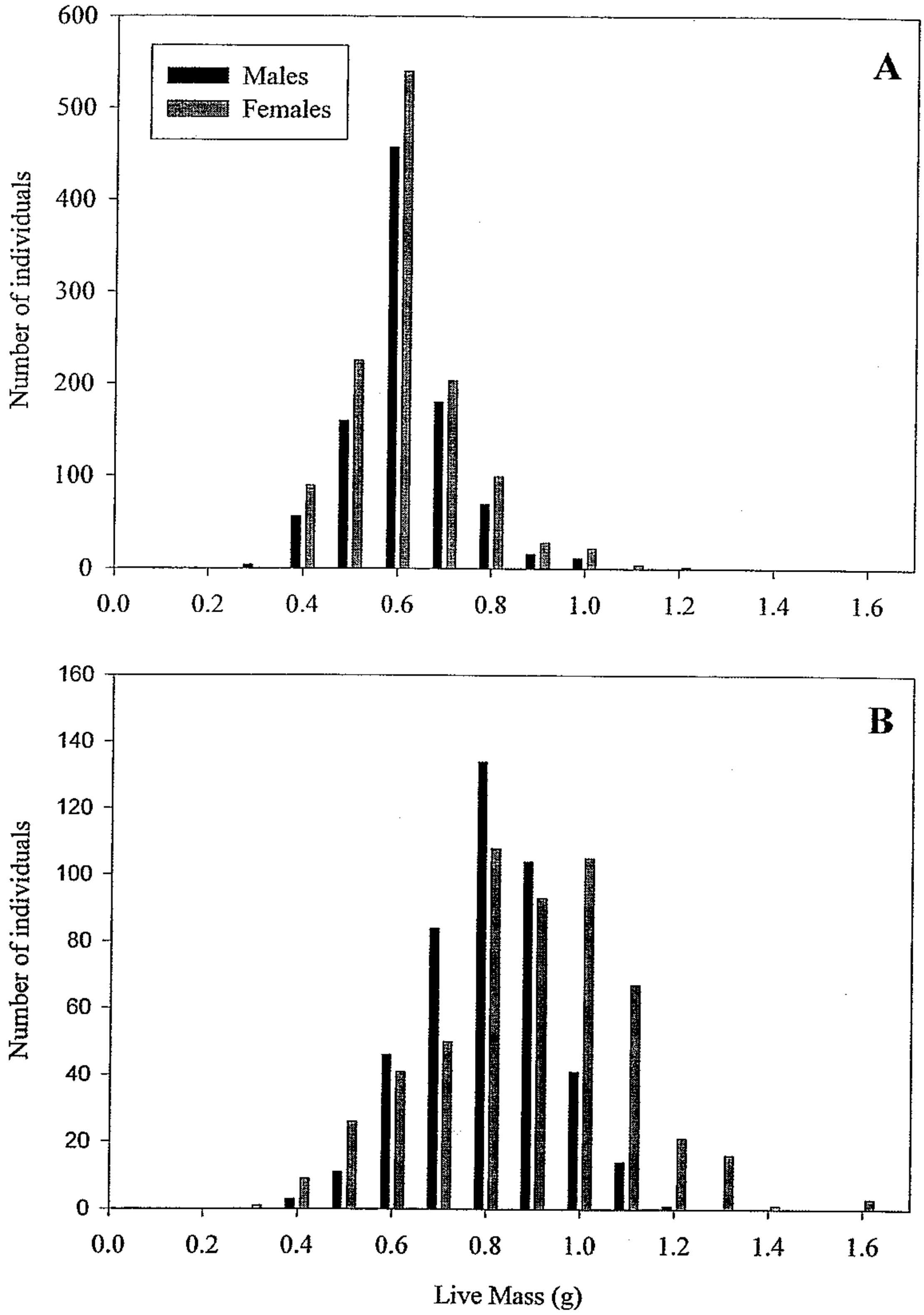


Fig. 2-7. Live mass of adult female and male striped newts captured at One Shot Pond, Putnam Co., FL. A) Immigrating adults. B) Emigrating adults.

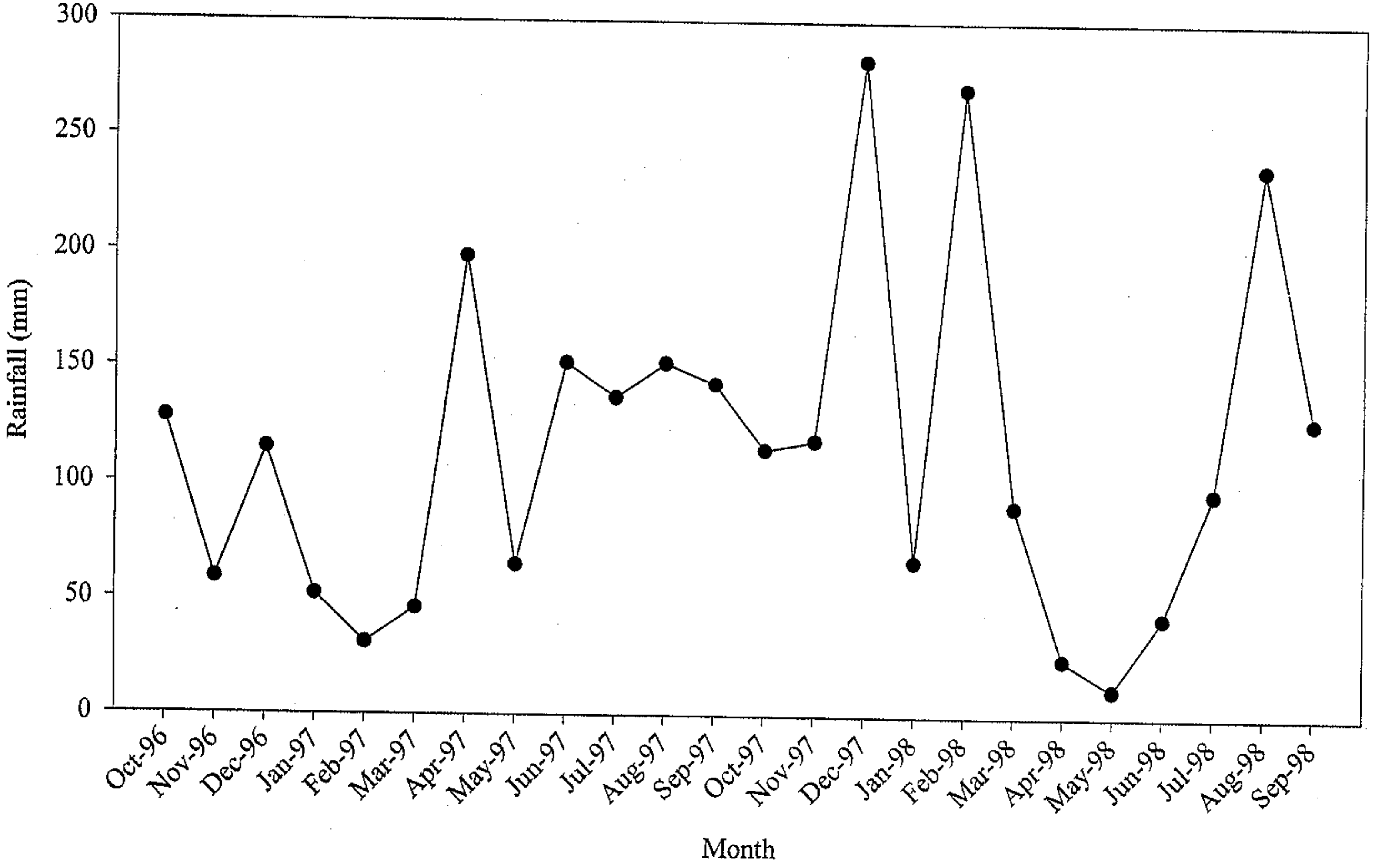


Fig. 2-8. Monthly rainfall recorded at One Shot Pond, Putnam Co., FL.

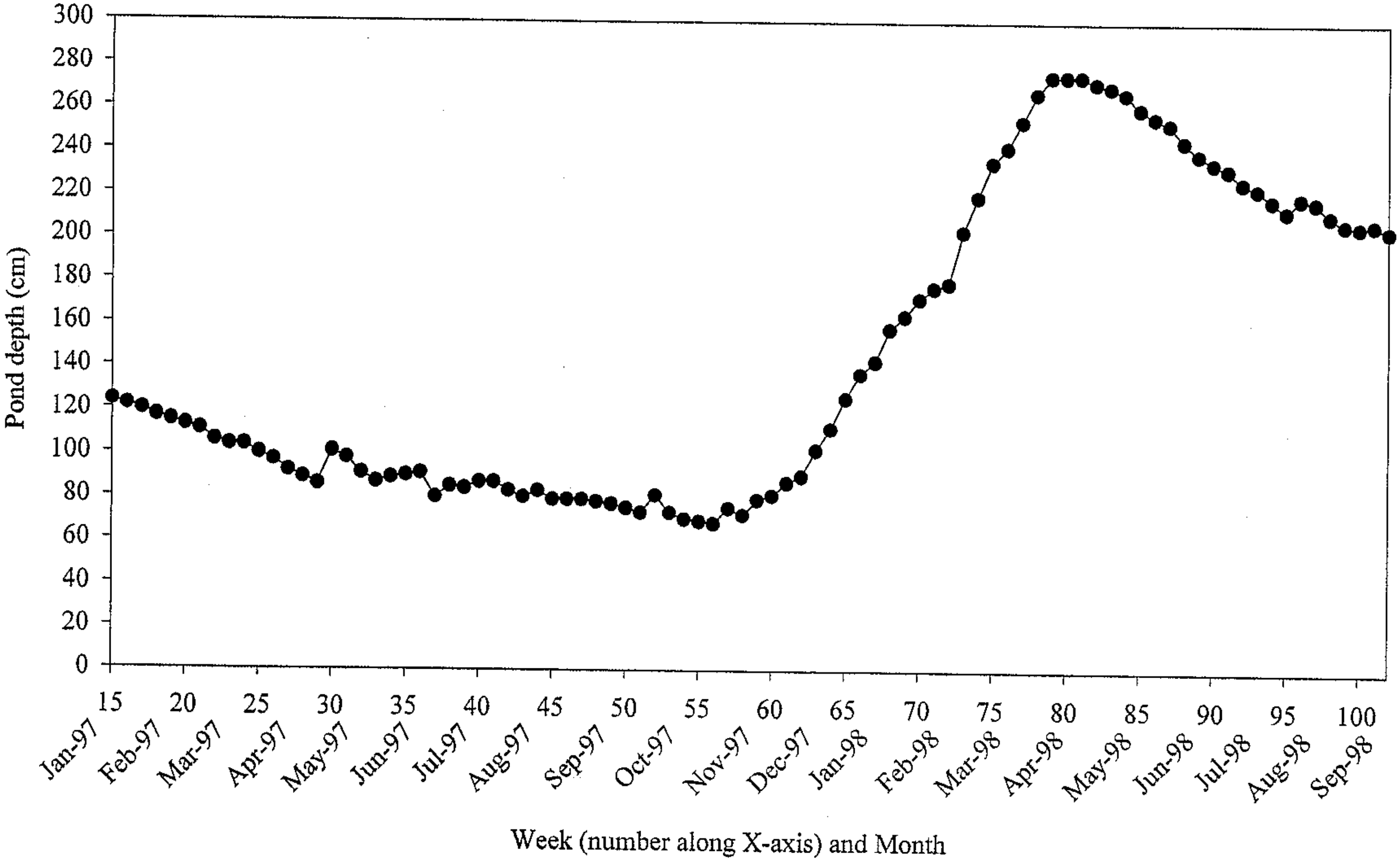


Fig. 2-9. Depth of One Shot Pond, Putnam Co., FL at the end of each week. Pond depth was not recored until week 15.

CHAPTER 3
ORIENTATION AND DISPERSAL DISTANCES OF STRIPED NEWTS AT A NORTH-CENTRAL FLORIDA BREEDING POND

Introduction

During the past two decades, amphibian declines have received considerable attention (Alford and Richards, 1999; Barinaga, 1990; Wake, 1991; Wake et al., 1991). Although pathogens have been implicated in several die-off events (Berger et al., 1998; Lips, 1998, 1999), there is a consensus among herpetologists that the global decline is a result of multiple factors (Alford and Richards, 1999). Habitat modification and destruction have been identified as significant factors contributing to the global decline (Alford and Richards, 1999; Dodd, 1997; Duellman, 1999; Semlitsch, 2000). Although they do not attract the media attention that mass mortality or deformed amphibians receive, habitat modification and loss are insidious processes that must be addressed if amphibians are to persist. The effects of habitat changes on amphibian populations are of particular concern in areas that are characterized by a high density of small, isolated wetlands (Alford and Richards, 1999; Babbitt and Tanner, 2000; Delis et al., 1996; Dodd, 1997; Greenberg, 2001; Hecnar and M'Closkey, 1996; Knutson et al., 1999; Knutson et al., 2000; Semlitsch, 2000; Snodgrass et al., 2000). In these areas (e.g., the Southeastern Coastal Plain of North America), amphibian diversity is high (Duellman and Sweet, 1999) and many species rely solely on small, isolated wetlands as breeding sites (Babbitt and Tanner, 2000; Dodd, 1997; Semlitsch and Bodie, 1998).

Despite their size (i.e., less than a few hectares), small, isolated wetlands are of tremendous biological importance, particularly for amphibians. In the Southeastern Coastal Plain, for example, these wetlands support a rich diversity of amphibian species, and several ponds that have been studied in detail were found to produce thousands of metamorphic individuals (Dodd, 1992; Gibbons and Semlitsch, 1981; K. Greenberg, pers. comm.; Hart and Newman, 1995; Johnson, 1999; R. Means, pers. comm.; Moler and Franz, 1988; Semlitsch et al., 1996; Semlitsch and Bodie, 1998). Small, isolated wetlands likely play a vital role in amphibian metapopulation dynamics, and therefore are essential in maintaining viable populations of amphibians at a landscape level (Semlitsch and Bodie, 1998; Semlitsch, 2000; Snodgrass et al., 2000). In addition to amphibians, numerous other vertebrates and a suite of invertebrate species depend on small, isolated wetlands (Brown et al., 1990; Burke and Gibbons, 1995; Hart and Newman, 1995; Moler and Franz, 1988; Semlitsch and Bodie, 1998).

Preserving a wetland alone may not result in protection of many of the organisms that depend upon the wetland. Many amphibians have complex life cycles in which they require ponds to breed but spend the majority of their lives in surrounding upland habitats (Dodd, 1997; Dodd and Cade, 1998; Semlitsch, 1998). If sufficient upland habitat surrounding isolated breeding-ponds is not preserved, amphibians with complex life cycles are not likely to persist at a local scale. Therefore, at some point the loss of uplands may lead to extirpation of some amphibian populations because of disruption of metapopulation dynamics (Semlitsch and Bodie, 1998; Semlitsch, 2000), even when the ponds themselves are preserved.

One strategy to curtail the loss of amphibians associated with habitat alteration around small, isolated wetlands is to preserve terrestrial "core zones" of upland habitat surrounding the ponds. These zones provide habitat for retreats and foraging for those species with complex life cycles, many of which are now considered common. Without preservation of appropriate upland habitat, even common species will decline.

Little is known, however, about the extent of upland "core areas" required by pond-breeding amphibians. Dodd (1996) summarized the literature on upland movements of amphibians in North America and found that this life stage is poorly known. From this summary and a review by Semlitsch (1998) on dispersal distances of ambystomatid salamanders, it is apparent that many amphibians disperse considerable distances from breeding ponds. Unfortunately, dispersal distances are only available for a few species and usually are based on a single or a few individuals. Clearly there is need for data on dispersal distances from breeding sites for most North American amphibians. These data are essential to justify establishing adequate "core areas" of upland habitat around amphibian breeding ponds.

I collected data on orientation and dispersal distances for striped newts (*Notopthalmus perstriatus*) at a breeding pond and in the surrounding uplands in north-central Florida. The striped newt breeds exclusively in small, isolated wetlands that lack fish. It has a complex life cycle and individuals spend much of their lives in uplands surrounding breeding ponds (Fig. 1-1; Carr, 1940; Christman and Means, 1992; Dodd and LaClaire, 1995; Dodd et al., in press; Franz and Smith, 1999; Chapter 2). Striped newts are restricted to xeric uplands (i.e., sandhill and scrub communities) in southern Georgia and northern Florida, U.S.A. (Fig. 3-1). The species has declined throughout its range (Dodd and LaClaire, 1995; Franz and Smith, 1999) and its biological status is under review by the U.S. Fish and Wildlife Service (L. LaClaire, pers. comm.). The objectives of my study were to 1) determine orientation patterns of striped newts into and away from a breeding pond and 2) determine dispersal distances of individuals into the surrounding upland habitat.

Methods

Study Site

The study was conducted on the Katharine Ordway Preserve-Swisher Memorial Sanctuary, Putnam Co., FL (29°41'N, 82°00'W; Fig. 2-1). Eisenberg and Franz (1995), LaClaire (1995), and Dodd (1996) provide descriptions of the Preserve and its habitats. Data were collected from 7 Oct-96 to 11 Sep-98 at One Shot Pond (OSP). One Shot Pond is a small, isolated pond with a variable hydroperiod (hydroperiod refers to the number of days a pond holds water between periods when it is dry) and is located in xeric sandhill uplands dominated by longleaf pine (*Pinus palustris*), turkey oak (*Quercus laevis*), and wiregrass (*Aristida beyrichiana*). A small pine plantation (*Pinus elliottii*) is located west of the pond basin (Fig. 3-2). Several water bodies are located near OSP (Fig. 3-2). These water bodies are isolated from one another and only receive water from rainfall and ground water seepage; their hydroperiods are dictated by fluctuations in the water table. Fox Pond held water from 26 Nov-97 until the end of the study, whereas OSP, Berry Pond, and the Anderson Cue Lakes held water throughout the entire study period. During the study, striped newts were only present in OSP and Fox Pond. However, only 32 newts (16 adults and 16 juveniles) were captured at Fox Pond (Johnson, 1999). The Anderson Cue lakes support predatory fishes, and striped newts do not breed there. No striped newts were captured during periodic sampling throughout the study period in Berry Pond. Because there were no other breeding ponds within several kilometers of OSP, I assumed that striped newts caught in upland fences around OSP originated from within OSP.

Orientation at One Shot Pond

I encircled OSP with a 190-m drift fence made of galvanized metal flashing that was buried ca. 15 cm below the ground, with ca. 35 cm extending above the ground. Thirty-eight pitfall traps (19 l plastic buckets) were buried flush with the ground. Pitfall traps were placed in pairs, one on each side of the fence, at intervals of about 10 m. I usually checked traps three to five days per week, depending on weather and movements of animals. I weighed and measured newts caught in pitfall traps at the pond and in the surrounding uplands (Chapter 2). Each newt was individually marked by toe clipping (Donnelly et al., 1994) and released on the opposite side of the fence. Sex of adults was determined by the presence of a conspicuous whitish gland visible at the posterior edge of the vent in mature males. Recently transformed newts were recognized by the presence of gill vestiges visible for several days after metamorphosis. Recently transformed newts with swollen vents were presumed to be mature (Chapter 4), and aquatic sampling in the pond showed that such individuals represent paedomorphic animals that recently bred.

I obtained a compass orientation for each pair of pitfall traps surrounding OSP. To do this, I stood in the center of the pond and took a bearing on each pair of traps at the drift fence. Following the methods of Dodd and Cade (1998), I used Rao's spacing test (Batchelet, 1981; Rao 1976) to determine if captures were distributed uniformly around the drift fence (i.e., random orientation). I analyzed orientation of newts into and away from the pond by sex and life history stage (paedomorph vs. metamorph; Table 2-1). I made comparisons between distinct migration events (Chapter 2) within the adult and eft life history stages. For comparisons between sexes, life history stages, and migration events, I ran the same multirepsonse permutation procedure (MRPP, Mielke et al., in press) used by Dodd and Cade (1998). Orientation analyses were performed with the statistical software package BLOSSOM, which was developed by the U.S. Geological Survey (Cade and Richards, 2000). BLOSSOM is available free at www.mesc.usgs.gov/blossom/blossom.html.

Upland Dispersal

Dispersal distances of newts in the sandhill uplands around OSP were determined through captures in pitfall traps associated with drift fences. Drift fences were oriented in such a manner as to capture newts during movements to and from the pond (Fig. 3-3). In year one, five fence sections were established at each of four distances from OSP (20 m, 40 m, 80 m, and 160 m). Fence sections at each distance totaled 20% of the circumference at that distance from the pond. Fence sections were distributed evenly at each distance, and they did not overlap with fence sections at the other distances (Fig. 3-3A). Fence sections at 20 m were 10.0 m long with 4 pitfalls (2 on each side of the fence); at 40 m, fence sections were 15.1 m with 6 pitfalls; at 80 m, sections were 25.1 m with 8 pitfalls; at 160 m, sections were 45.2 m with 10 pitfalls. Pitfall traps were installed on both sides of the upland fences (i.e., pond side and upland side; Fig 3-3A). This upland fence array was monitored from 7 Oct-96 to 5 Dec-97, and fences were constructed similarly to the fence at the pond.

Results from year one demonstrated that striped newts regularly dispersed more than 160 m. Therefore, a new upland fence array was installed in year two, with upland drift fences erected much farther away from OSP. On 5 Dec-97, the upland drift fences described above were replaced with a different array of fence sections (Fig. 3-3B) and the new fences were in place by 7 Dec-97. These fences were constructed of heavy-gauge silt-fence material buried ca. 15 cm into the ground; ca. 40 cm extended above ground. Two fence sections were installed at each of five distances (100 m, 200 m, 300 m, 400 m, and 500 m) from the pond. Fence sections at each distance totaled 13.4% of the circumference at that distance from the pond, and fence sections overlapped (Fig. 3-3B). The two fence sections at 100 m were each 42 m long with 6 pitfalls (3 on each side of the fence) installed evenly throughout each section; at 200 m, sections were 84 m with 10 pitfalls; at 300 m, sections were 126 m long with 14 pitfalls; at 400 m, sections were 168 m long with 18 pitfalls; at 500 m, sections were 210 m long with 22 pitfalls. Pitfall traps were oriented in the same manner as year one; pond-side traps were on the side of the fences toward OSP and upland-side traps were away from OSP (Fig. 3-3B). The upland fence array in year two was monitored until the study ended on 11 Sep-98.

In total, 280 pitfall traps were installed at upland fence sections and were monitored during the 2-year study, for a total of 98,140 trap-nights (i.e., one trap-night = one pitfall trap open for 24 hours). Upland traps were checked on the same schedule as those at the pond and newts were processed as described above.

I estimated the proportion of the newt population that dispersed different distances from the pond based on captures at upland fence sections and at the outside of the drift fence encircling OSP. Data used in the estimates were confined to 7 Dec-97 through 31 Mar-98. During this period, there was a mass migration of newts toward the pond and very little movement away from the pond (Chapter 2). Ninety-one percent of upland fence captures during year two occurred during this period. These captures, however, only represented newts that migrated through a subset of surrounding uplands. Because upland drift fences sampled only 13.4% of the uplands at each distance, I multiplied the number of captures in the outside pitfalls by 7.5. The product of this calculation is an estimate of the number of captures expected at each distance had the upland fence sections sampled 100% of the uplands at each distance. For each upland fence section, the estimate was divided by the number of total newt captures on the outside of the fence at OSP to approximate the proportion of individuals that had dispersed various distances (i.e., 100 m to 500 m, at 100 m intervals). I assumed that there was no strong nonrandom orientation of newts moving through the uplands. Nonetheless, movement of newts into and away from the pond was nonrandom, but there was no overwhelmingly strong directionality that would violate this assumption. However, estimates of the proportion of newts that had dispersed various distances from the pond are probably conservative.

I use the term "migration" to indicate seasonal movements of newts toward or away from the breeding pond. "Immigration" indicates a general pattern of migration toward the breeding pond, whereas "emigration" indicates migration away from the pond (Semlitsch and Ryan, 1999).

Results

Orientation at One Shot Pond

All patterns of adult immigration and emigration were significantly nonrandom (Fig. 3-4; Rao's Spacing Tests, all $P < 0.001$). Adult striped newts entered and exited the pond in all directions. They tended to enter the pond basin primarily from the east and west (Fig. 3-4). Adults emigrated in all directions but there was a single, distinct angle of emigration, as indicated by the relatively high number of captures in a pitfall trap located at a south-southeast direction (Fig. 3-4). Emigration of paedomorphs and efts also was nonrandom (Fig. 3-5; Rao's Spacing Tests, both $P < 0.001$). There was no obvious pattern to paedomorph emigration, but emigrating efts exited the pond basin most often in the southwest quadrant (Fig. 3-5).

Overall patterns of immigration differed significantly from emigration for females and males (Table 3-1). Although the directionality of immigrating adults appeared similar between the sexes (Fig. 3-4), patterns were significantly different (MRPP test, $P = 0.002$). There were three distinct immigration events of adults, but orientation patterns were significantly different between the sexes only during the third, and largest of these events (Table 3-2). Differences in emigration between males and females (Fig. 3-4) were not significant overall or when distinct emigration events were compared (Tables 3-1, 3-2).

There were two distinct emigration events of recently transformed striped newts comprising the 1996/97 cohort. The first emigration event took place from Oct. through Nov. 1996, and the second event from Apr. through Jun. 1997 (Chapter 2). Immature newts (i.e., efts) comprised the first event, whereas emigration later consisted mostly of recently transformed paedomorphs (Chapters 2 and 4). Patterns of emigration were significantly different between the eft and paedomorph life-history stages of the same cohort (Table 3-2). In addition to the eft emigration of 1996, a second emigration event of efts took place from Jun. through early Sep. 1998 (Chapter 2). Patterns of eft captures at OSP differed significantly between these two emigration events and, considering all efts and all adults, efts exited the pond basin in a different pattern from adults (Tables 3-1, 3-2).

Data for 44 uniquely-marked efts initially caught leaving the pond in the winter of 1996 and recaptured when they returned to breed in the winter of 1997 indicated that individuals tended to enter and exit the pond within the same quadrant. Sixty-four percent of these efts left and returned to OSP in the same quadrant (intervals 0 to 3 in Fig. 3-6) and four individuals (9%) were caught leaving and returning to the pond at the same pair of pitfall traps (interval 0 in Fig. 3-6). The vast majority of individuals (84%) entered the pond basin within the same half they had left from the previous year (intervals 0 to 6).

Dispersal Into Uplands

I captured 831 newts in the upland drift fences during year one (Fig. 3-3A, Table 3-3). Pond-side captures accounted for 73% of total captures, and migration in year one consisted primarily of recently transformed efts. I captured newts at all of the upland fence sections (Fig. 3-3A; Table 3-3), and in most (91.4%) of the pond-side pitfall traps. During each period of migration, the vast majority of newts were captured on the same sides of upland drift fences. However, for most movement events, a small percentage of newts were captured in pitfalls on the opposite side of fences from the majority of captures. I believe this is because there was a small degree of wandering by some newts in the uplands as they moved to or from OSP. Pond-side captures at upland fences in year one represented three distinct periods of newt migration, two emigration events and one immigration event (Table 3-4). Most newts captured on the pond-side of upland fences in year one (76% of pond-side captures) were caught during the first emigration event (i.e., E-1), which occurred from Oct-96 through Feb-97 (Table 3-4). Emigration during this period consisted almost exclusively of immature efts that had recently transformed. I captured far fewer newts (15% of pond-side captures) during emigration event two (E-2), which occurred from Apr. through Jul. of 1997 (Table 3-4). This emigration event was comprised of recently transformed paedomorphic newts (54% of the migrating newts), as well as recently transformed efts and several adults that likely had finished breeding and were moving back into the uplands. The third period of migration, indicated by pond-side fence captures in year one, was the result of an immigration event (i.e., I-3) that began in Oct-97 (Table 3-4). There was a major breeding migration of adults to the pond that began in Oct-97 and pond-side captures at this time probably resulted from adults that were moving toward the pond but happened to be captured on the pond-side of the upland drift fences (Table 3-4).

Upland-side captures of striped newts accounted for 27% of captures in year one. I captured newts at each of the five fence sections (Fig. 3-3A) at each distance from OSP (Table 3-3), and in most (81.4%) of the pitfall traps on the upland-side of the fences in year one. Upland-side captures occurred during three distinct periods of newt migration, all of which were immigration events. These migration events (I-1, I-2, and I-3; Table 3-4) occurred during the same time periods as describe above for pond-side captures (Table 3-4). Immigration event I-3 accounted for the largest proportion (54%) of upland-side captures in year one, followed by event I-1 (29%) and I-2 (17%). All of these migration events consisted of adult newts moving toward OSP to breed (Table 3-4).

I captured 495 newts in the upland drift fences during year two (Fig. 3-3B, Table 3-3). In contrast to year one, migration consisted primarily of immigrating adults. Pond-side captures accounted for only 9% of total captures. I captured newts at each of the two fence sections (Fig. 3-3B) at each distance from OSP (Table 3-3), but captures were recorded in less than half of the pitfall traps (42.8%) on the pond-side of the upland fences in year two. Pond-side captures at upland fences in year two represented two distinct periods of newt migration, one immigration event (i.e., I-3) and one emigration event (i.e., E-3). I captured few newts during both of these events; 16 during I-3, and 25 newts during E-3 (Table 3-4). Captures during migration event I-3 were adults that were moving to the pond to breed but were captured in pond-side traps as they wandered toward the pond. Captures during E-3 were recently transformed newts that were dispersing from OSP.

In year two, I captured far more newts (91% of total upland captures) on the upland-side of drift fences than on the pond-side (Table 3-3). I captured newts at all sections of drift fence and in almost all of the upland-side pitfalls (88.6%). Captures occurred only during a single immigration event (I-3; Table 3-4) and were exclusively of adults. The number of captures declined as the distance from the pond increased (Table 3-3). Based on estimated values, at least 360 newts (16% of the breeding migration) dispersed more than 500 m from OSP (Fig. 3-7). I estimated that 645 newts (29% of the breeding migration) dispersed at least 400 m. The estimate was the same for 300 m (645 newts). I estimated that 810 (36% of the breeding migration) and 908 (41% of the breeding migration) of newts dispersed from the pond at least 200 and 100 m, respectively (Fig. 3-7). Based on these estimates, it appears that roughly 60% of the striped newts emigrated less than 100 m. However, as indicated by captures at the 500 m fences, a substantial percentage of individuals comprising the 1997/98 breeding migration immigrated to OSP from farther than 500 m. In fact one newt that was marked leaving OSP as an eft on 18 Nov-96, was recaptured on 4 Feb-98 as it colonized Fox Pond, a dispersal distance of ca. 685 m.

Discussion

Orientation

Striped newts of all life history stages (i.e., adults, recently transformed paedomorphs and efts) emigrated and immigrated in a significantly nonrandom fashion, although individuals were captured at all pairs of pitfall traps encircling the pond. Directionality of emigration and immigration differed significantly between and within sexes, with the exception of emigration patterns between females and males. Directionality of emigration also differed significantly among life history stages. Although the percentage of newts dispersing into the uplands decreased as distance from the pond increased, I estimated that at least 16% of the breeding population dispersed more than 500 m.

The distribution of habitats surrounding a breeding pond should have a fundamental influence on patterns of immigration revealed by captures of salamanders at the pond. Habitat preferences among species and/or differential survivorship in various habitat types might be apparent as individuals arrive at the breeding pond. For example, imagine an amphibian breeding pond in which one half of the uplands surrounding the pond were pine plantation while the other half remained native uplands. The pattern of captures at the pond would be expected to reflect the distribution of upland habitats. One would predict significantly fewer captures along the half of the pond adjacent to the pine plantation as compared to the native upland half. This is because pond-breeding salamanders have the ability to select appropriate upland habitats and accurately navigate through uplands during migration, often using specific habitats (deMaynadier and Hunter, 1999; Hurlbert, 1969; Madison, 1997; Madison and Farrand, 1998; Semlitsch, 1981; Stenhouse, 1985; Shoop, 1968).

In this study, although newts entered and exited the pond basin from all directions, migration was nonrandom. Some directions were preferred over others, but there were no obvious upland habitat features that could explain the newts' orientation behavior. However, I did not measure habitat variables in the uplands and individuals could have used micro-topographic features as cues to navigate toward the pond. In a similar study, Dodd and Cade (1998) concluded that movements of striped newts and narrowmouth toads were a reflection of the distribution of favorable upland habitats around the pond. Although the uplands at OSP were primarily sandhill habitat, a small plantation of slash pine (with intact groundcover) was well within the dispersal capabilities of migrating newts (Fig. 3-2). In year one I often caught newts at a section of drift fence in the pine plantation. Newts could have resided within the plantation or have traveled through it en route to native sandhill. Nevertheless, this plantation represented only a small portion of the uplands and had no detectable effect on striped newt movements.

Although upland-habitat preferences and microenvironmental features I did not measure could have influenced the nonrandom pattern of immigration observed at OSP, if measured over several seasons, orientation may in fact be random. It is possible that striped newts are roughly evenly distributed in the uplands around OSP but that only a portion of the population migrates to the pond during any particular breeding event. If the portion of individuals moving was not indicative of the whole population, then what truly should be random orientation would appear as nonrandom because data were collected for a relatively short time.

Patterns of newt emigration were also nonrandom, and newts exited the pond basin in all directions. Efts emigrated predominantly in the southwest quadrant of the pond. The slope of the pond basin was shallowest in this quadrant, and water depth during metamorphic events could have influenced the behavior of recently transformed efts as they left the pond. Adults on the other hand, emigrated most often in the south-southeast portion of the basin. Differences in aquatic habitat preference (e.g., depth) between adult and immature newts might explain the varying emigration patterns, although habitat preferences of both life history stages are unknown.

Upland Dispersal

Using upland drift fence arrays in year two, I was able to estimate the percentage of the striped newt breeding population that migrated different distances (in increments of 100 m) from the pond. Captures at drift fences in the sandhill uplands surrounding OSP indicated that many striped newts (16%) dispersed more than 500 m from the pond. This is a conservative estimate because many individual captured in traps closer to the pond may have dispersed further than indicated by the traps. Captures at the drift fence surrounding the pond and at upland drift fences at the end of year one showed that a breeding migration of newts into OSP had begun before the installation of fences for year two (Chapter 2). Although the proportion of individuals caught at the pond before the new upland fence array was established was small (7% of the total), some newts already had moved toward the pond before the upland array was in place. Moreover, immigrating adults did not arrive at the pond in a random fashion during this breeding migration. The upland fence arrays in year two were located north and southeast of OSP and newts were caught at the pond with lowest frequency toward the north. Therefore, the proportions of the breeding population caught at each distance from the pond in year two is likely an underestimate of the actual proportion moving to that particular distance.

Many pond-breeding amphibians have complex life-cycles and spend much of their adult lives in terrestrial habitats away from breeding sites. Distances that individuals disperse from breeding ponds have been reported for some species (Dodd, 1996; Semlitsch, 1998 and references therein). It is clear that individuals disperse hundreds of meters from breeding sites into upland habitats, some even thousands of meters. With few exceptions, however, distance values usually have been presented for less than 10 individuals per species. The results from my study are the first estimates of dispersal distances for a breeding population of North American amphibians based on a substantial sample size.

Conservation Implications

Central to a successful amphibian conservation strategy is the protection of sufficient breeding and nonbreeding habitat. Studies of amphibian dispersal can provide the scientific basis for determining directional and distance components that can be used to establish protected areas around breeding ponds. Brown et al. (1990) used spatial requirements (i.e., distance dispersed from a wetland), among other data, to recommend width of "buffer zones" for wildlife protection at wetlands in Florida. Nevertheless, lack of data for amphibians forced them to use rough estimates for most of the species considered. Further utility of dispersal distance data can be found in regulations to protect the flatwoods salamander (*Ambystoma cingulatum*) which, as a result of severe population decline (Means et al., 1996), was federally listed as threatened (U.S. Fish and Wildlife Service, 1999). The U.S. Fish and Wildlife Service restricts specific silvicultural practices within 450 m of flatwoods salamander ponds. Additionally, only selective timber harvest at specific times is allowed within a primary radius of 164 m around breeding ponds (U.S. Fish and Wildlife Service, 1999). The width of the primary zone was derived from a review of dispersal distances for pond-breeding salamanders of the genus *Ambystoma* (Semlitsch, 1998), despite the fact that no data for A. *cingulatum* were available. This example underscores the need to determine dispersal distances for all pond-breeding amphibians. Semlitsch (1998) acknowledged that the core zone recommended for *Ambystoma* species may apply to some species of pond-breeding amphibians, but certainly not all. My data show that recommendations for protecting terrestrial habitat for ambystomatid salamanders are inadequate for *Notophthalmus perstriatus*. Therefore, it is not defensible to extrapolate data across taxa. Clearly, a 164 m protected zone would not protect all of the striped newts breeding at OSP. Based on extrapolation of dispersal distances revealed by upland drift fences, a protected core zone extending ca. 1000 m from OSP would likely be needed to encompass all of the newts that breed there.

Although they have great value as wildlife habitat, small, isolated wetlands in the United States are afforded little protection from development. Overall, more than 50% of wetlands have been destroyed by development in the United States (Dahl, 1990), and much of this loss has been small wetlands. In Florida, a state with an extremely large number and diversity of wetlands, isolated wetlands less than 0.2 ha receive no protection from development. This size threshold was adopted by the state's water management districts "based on a consensus of scientific and regulatory opinion rather than on biological and hydrological evidence" (Hart and Newman, 1995). Small wetlands are just as vulnerable at the national level as they are in Florida.

There is strong evidence that protection of core areas of terrestrial habitat surrounding breeding sites is crucial for persistence of amphibian populations and species. Data from OSP demonstrate that small, isolated wetlands can support breeding populations of salamanders that extend hundreds of meters into the surrounding uplands. Similar studies at other ponds and in different upland types are necessary because data on upland habitat requirements (quality and quantity) of most amphibian species are lacking. Without this information, designating terrestrial core habitat to conserve aquatic-breeding amphibians will largely remain guesswork, with generalizations made from data on relatively few individuals of a few species. However, unless more protection is afforded to small, isolated wetlands, arguments to preserve uplands surrounding the wetlands are irrelevant.

Table 3-1. Overall comparisons of directional orientation patterns for striped newts entering (immigrating) and leaving (emigrating) One Shot Pond, Putnam Co., FL.

Comparison	n	Standardized test statistic	*P*
Immigrating vs. emigrating males	1159, 486	-13.317	< 0.001
Immigrating vs. emigrating females	1489, 645	-3.798	0.008
Immigrating males vs. females	1159, 1489	-5.524	0.002
Emmigrating males vs. females	486, 645	-0.437	0.2
Emigrating efts vs. emigrating adults	5008, 1131	-67.639	< 0.001
Emigrating efts vs. emigrating	[redacted]	[redacted]	[redacted]
paedomorphs of the same cohort	745, 407	-9.506	< 0.001

Table 3-2. Comparisons of directional orientation patterns for striped newts entering (immigrating) and leaving (emigrating) One Shot Pond, Putnam Co., FL.

Comparison	n	Standardized test statistic	*P*
Immigrating males vs. immigrating females			
Immigration Event 1	23, 13	0.697	0.7
Immigration Event 2	22, 66	-0.130	0.3
Immigration Event 3	1049, 1290	-4.008	0.006
Emigrating males vs. emigrating females			
Emigration Event 2	15, 68	0.686	0.7
Emigration Event 3	430, 484	-0.005	0.3
Emigrating efts during metamorphic Event 1 vs. emigrating efts during metamorphic Event 3	745, 4237	-3.599	0.01

Table 3-3. Numbers of striped newts captured in pitfall traps at drift fence arrays in the sandhill uplands surrounding One Shot Pond, Putnam, Co., FL. Drift fences were located at various distances from the pond. See Fig. 3-3 for a depiction of the arrays.

	Year 1				Year 2				
	20 m	40 m	80 m	160 m	100 m	200 m	300 m	400 m	500 m
Pond-side	140	126	169	172	11	6	10	12	7
Upland-side	79	39	64	42	121	108	86	86	48
Total	219	165	233	214	132	114	96	98	55

Table 3-4. Captures of striped newts in upland fences around One Shot Pond, Putnam Co., FL during distinct periods of movement.

Side of fences of captures	Migration event	Predominant direction of newt movement	Time period of event	No. inds captured	Description
Year 1					
Pond-side	E-1	away from pond	Oct.-96 through Feb.-97	461	Emigrating efts
Pond-side	E-2	away from pond	Apr.-97 through Jul.-97	91	Primarily emigrating paedomorphs and efts
Pond-side	I-3	toward pond	Oct.-97 through Dec.-97*	55	Immigrating adults
Upland-side	I-1	toward pond	Oct.-96 through Jan.-97	65	Immigrating adults, some emigrating efts
Upland-side	I-2	toward pond	Apr.-97 through Jul.-97	36	Immigrating adults
Upland-side	I-3	toward pond	Nov.-97 through Dec.-97*	123	Immigrating adults
Year 2					
Pond-side	I-3	toward pond	Dec.-97* through Mar.-98	16	Immigrating adults
Pond-side	E-3	away from pond	Jun.-98 through Sep.-98	25	Emigrating efts
Upland-side	I-3	toward pond	Dec.-97* through Mar.-98	449	Immigrating adults

*Fence arrays modified in early Dec.-97

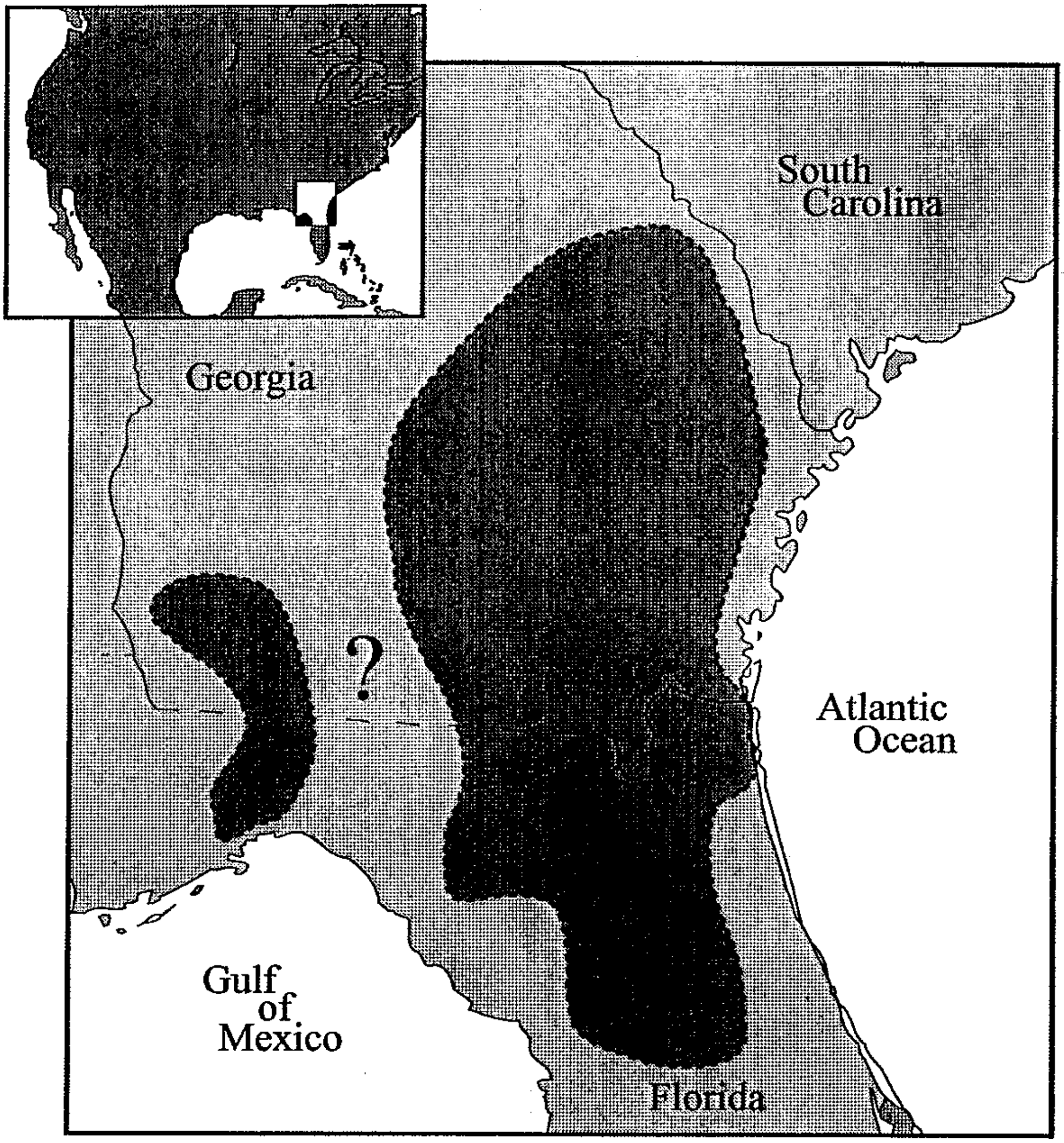


Fig. 3-1. Present range of the striped newt. Note the hiatus (?) between the western and eastern portions of the range. This area may represent a true gap in the species distribution, rather than an artifact of inadequate survey effort.

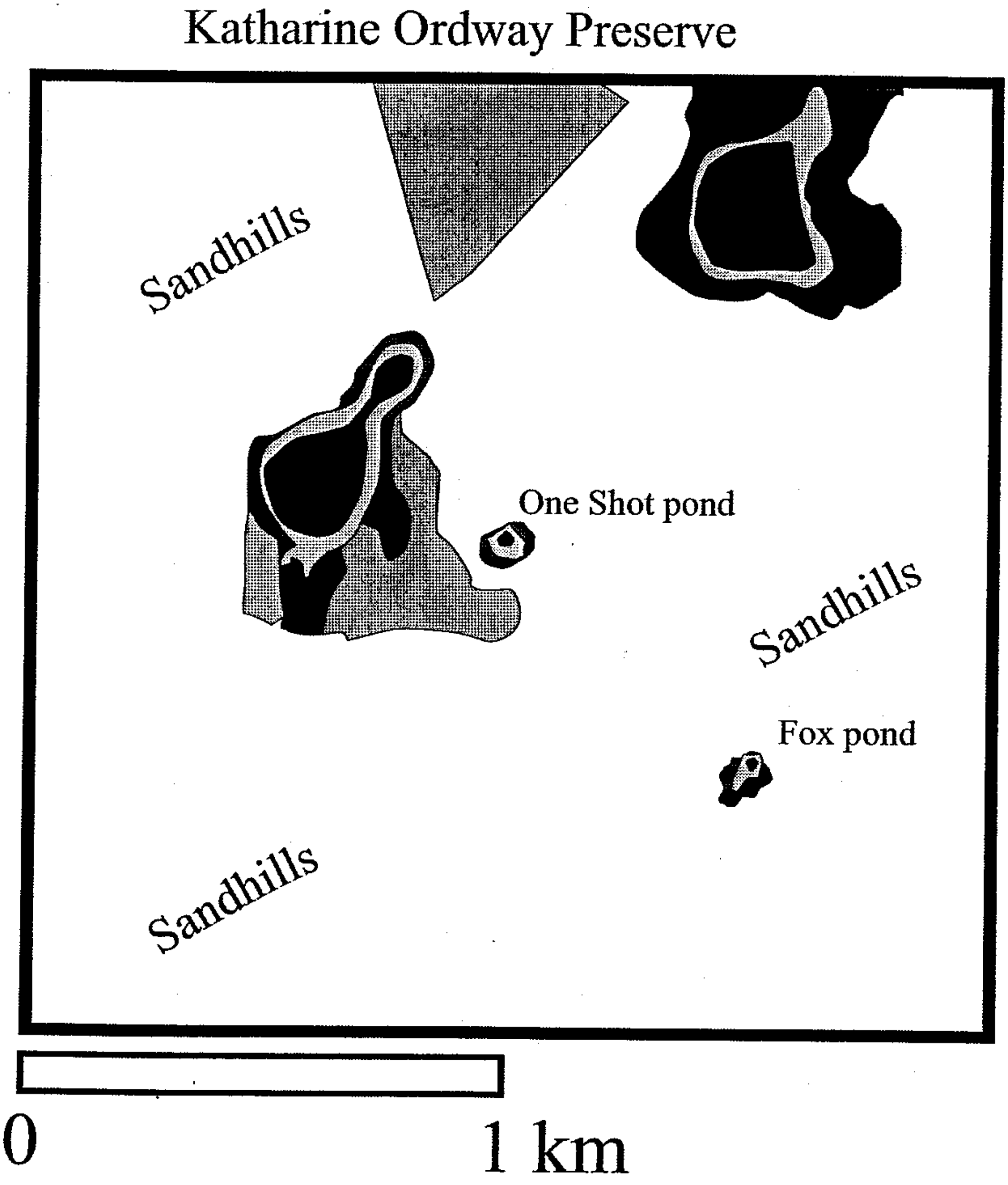


Fig. 3-2. The location of One Shot Pond within the Katharine Ordway Preserve, Putnam Co., FL. The pond is surrounded primarily by sandhill uplands but a small pine plantation (medium gray) is located to the west of pond. Ponds and lakes are indicated in black and north is at the top of the figure.

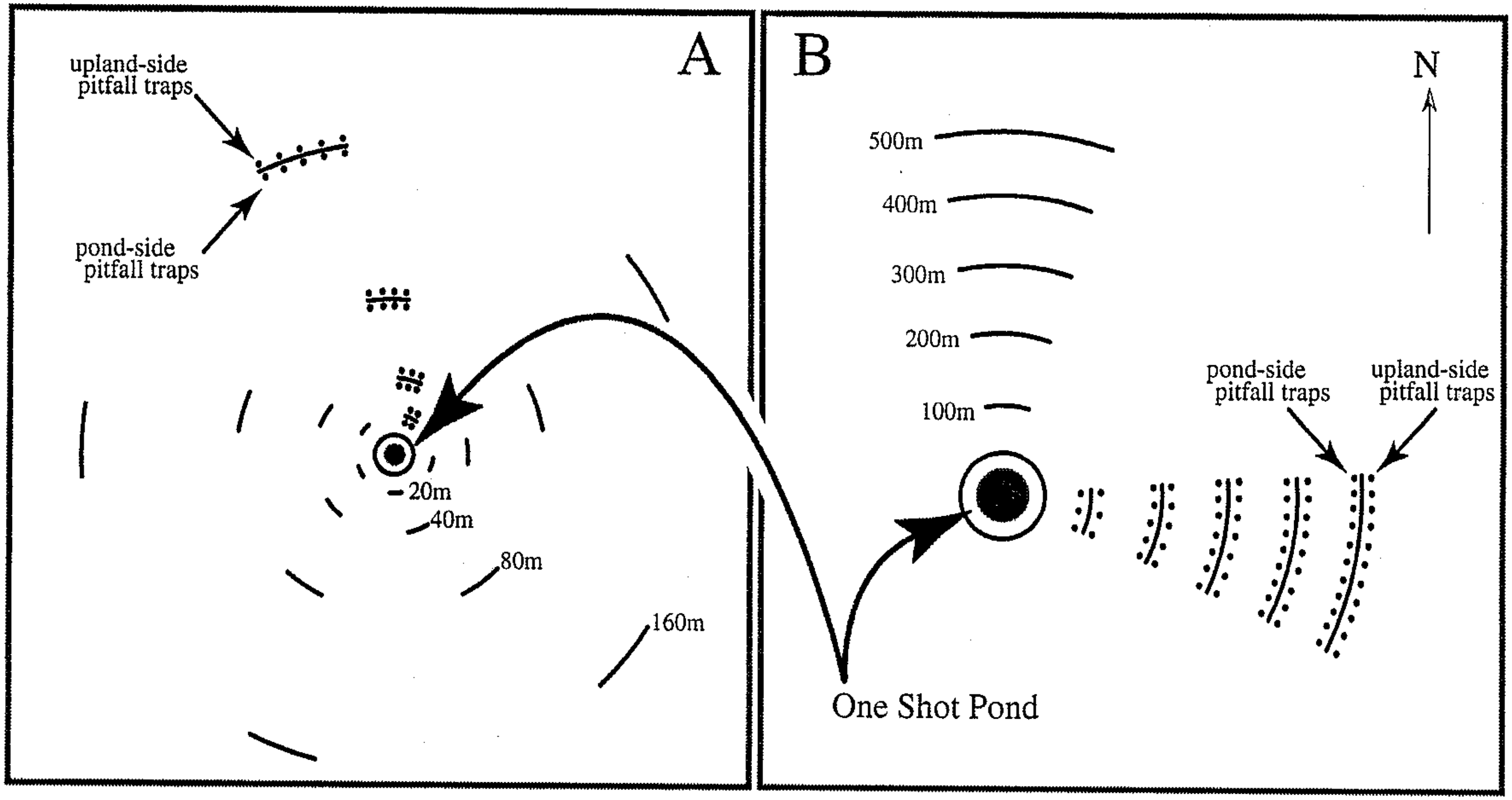
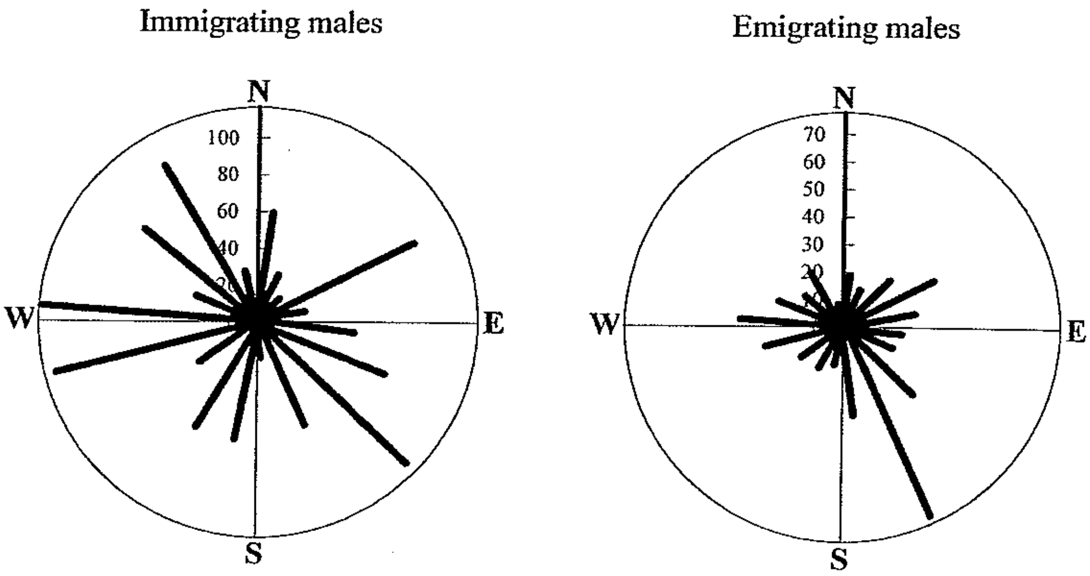


Fig. 3-3. Upland drift fence arrays around One Shot Pond, Putnam Co., FL. A) Array design in year 1. B) Array design in year 2. One Shot Pond is depicted as a solid gray circle, and the black circle around it represents the drift fence at the pond.



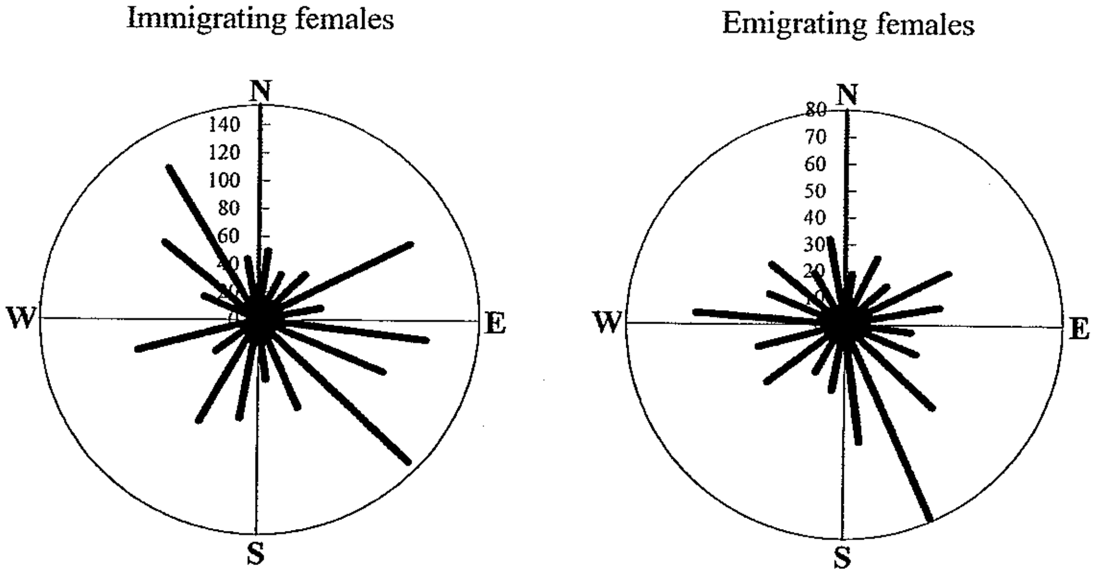
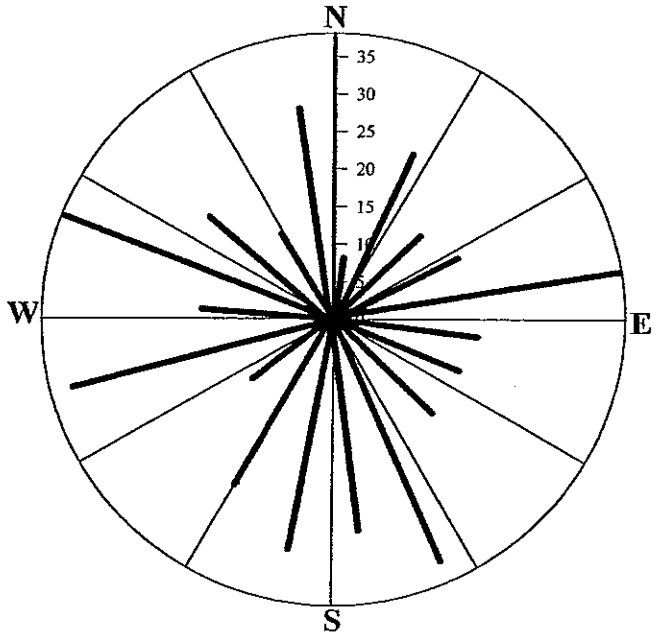


Fig. 3-4. Orientation patterns of immigrating and emigrating striped newt adults captured in pitfall traps at a drift fence encircling One Shot Pond, Putnam, Co., FL. Orientation was significantly different from random for all four patterns. The length of the lines indicate the number of newts entering and exiting the pond basin at each pitfall trap.

Emigrating paedomorphs



Emigrating efts

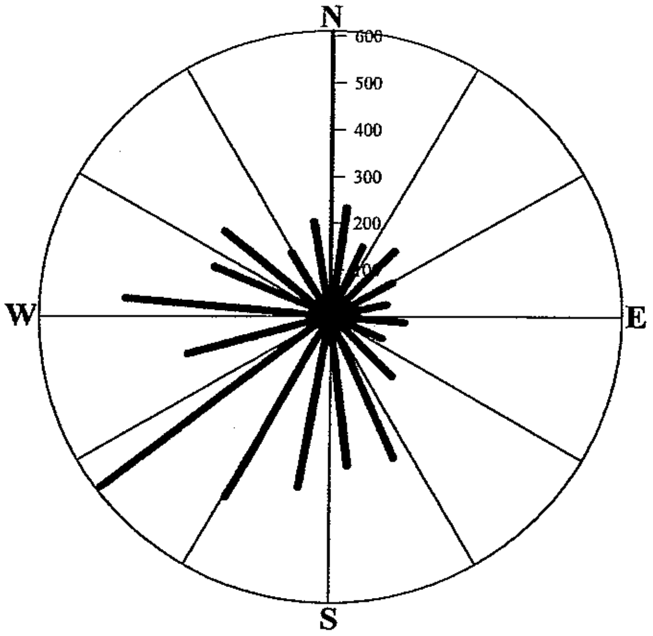


Fig. 3-5. Orientation patterns of emigrating striped newt paedomorphs and efts captured in pitfall traps at a drift fence encircling One Shot Pond, Putnam, Co., FL. Orientation was significantly different from random for both patterns. The length of the lines indicate the number of newts exiting the pond basin at each pitfall trap.

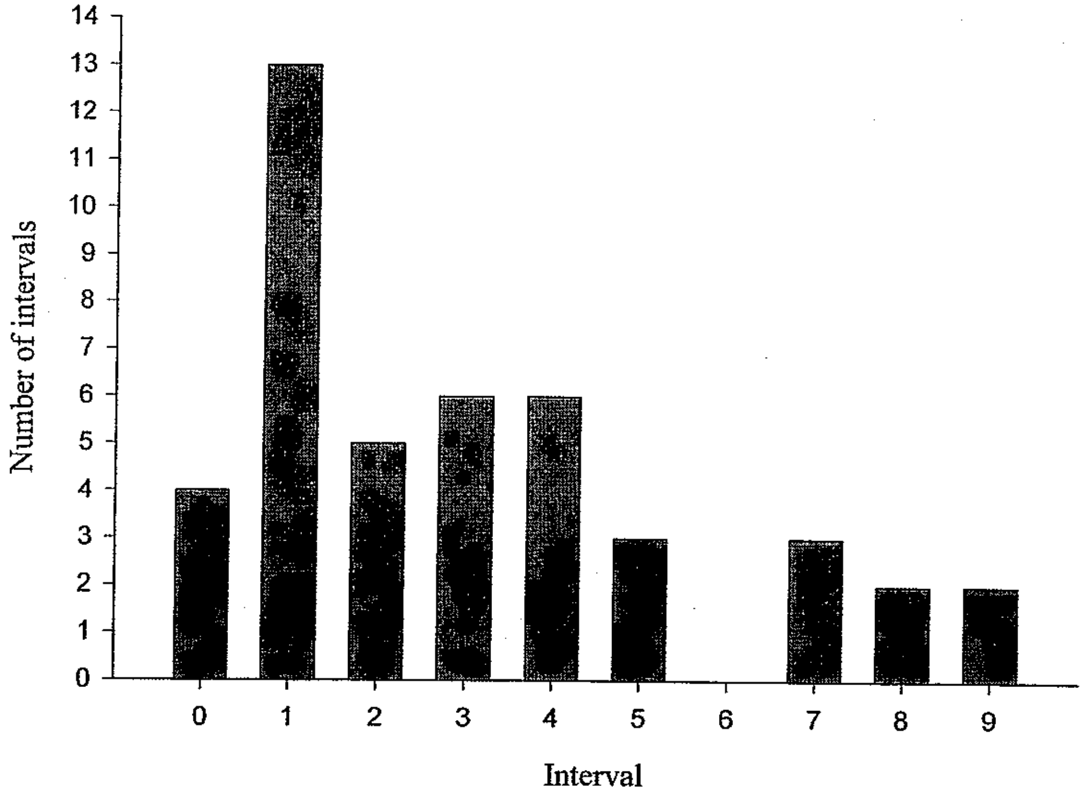


Fig. 3-6. Distance intervals between locations of initial capture during immigration and recapture during emigration for individualy marked striped newts at One Shot Pond, Putnam Co., FL. Locations were determined by established pairs of pitfall traps at a drift fence encircling the pond. Distances between trap pairs (i.e., distance interval) was approximately 10 m.

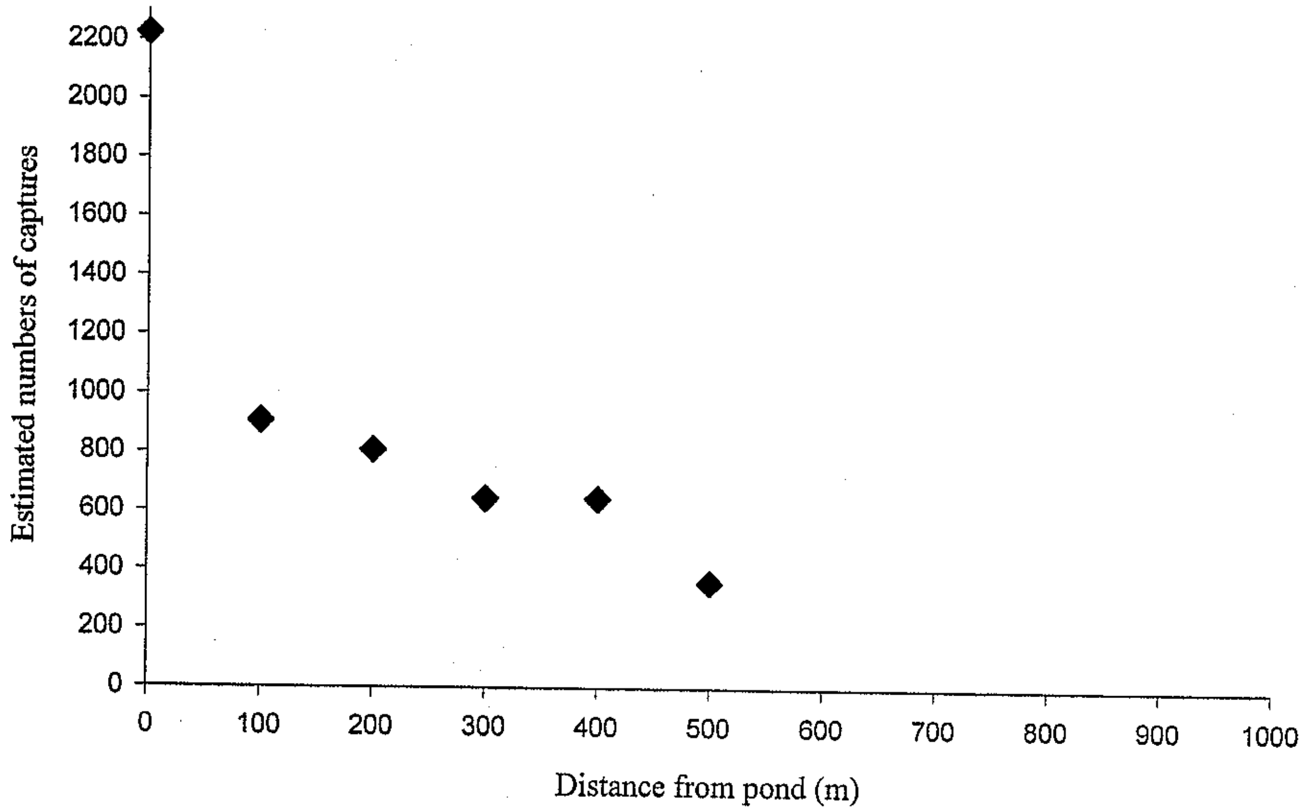


Fig. 3-7. Estimated numbers of striped newt captures in pitfall traps at drift fences in the sandhill uplands around One Shot Pond, Putnam Co., FL. Drift fences were located at 100 m intervals up to 500 m from the pond. The zero point represents captures at a drift fence encircling the pond. See "Methods" for an explanation of how the "estimated" numbers were calculated.

CHAPTER 4
INFLUENCE OF GROWTH RATE ON LIFE-HISTORY EXPRESSION OF STRIPED NEWTS

Introduction

The expression of alternative phenotypes as a function of the environment has been documented for many species of plants and animals (Moran, 1992; Scheiner, 1993; Stearns, 1989; Whiteman 1994; Whiteman et al., 1996). Although the environment can have a profound influence, an individual's genotype may exert a strong effect on phenotypic plasticity as well (Scheiner, 1993; Stearns, 1989).

Species that exhibit complex life cycles (Wilbur, 1980), such as many amphibians, are excellent models for studying expression of phenotypic plasticity (Newman, 1992). In these species there is a distinct ontogenetic change in an individual's morphology, physiology, and often its habitat, that occurs at metamorphosis. The larval stage is usually dedicated to feeding and growth, whereas the adult stage disperses and reproduces (Wilbur, 1980). In anurans, the size of an individual at metamorphosis and duration of larval period have proven to be extremely variable. A diversity of environmental factors affect these characters (Alford, 1989; Denver, 1997; Denver et al., 1998; Kupferberg, 1997; Morin, 1986; Skelly and Werner, 1990; Werner, 1986).

Some salamanders also exhibit complex life cycles, although morphological changes associated with metamorphosis are not as extreme as in anurans (Wassersug, 1974; Werner, 1986). In addition to those species in which individuals always transform from an aquatic larval stage into a terrestrial or semiterrestrial stage (i.e., obligate metamorphosis), there are species in which individuals reproduce while the larval or branchiate morphology persists. This paedomorphic habit (Gould, 1977) is fixed in those species that have evolved a simple life cycle. However, in other species, namely some mole salamanders and newts, paedomorphosis is facultative (Duellman and Trueb, 1986). In facultatively paedomorphic species (referred to as "paedotypic" by Reilly et al., 1997), individuals may follow one of two developmental trajectories. Once an individual reaches a threshold size it may transform into a terrestrial form (i.e., metamorphic phenotype). Alternatively, it may remain in the aquatic environment and mature while retaining larval characteristics (i.e., paedomorphic phenotype; Whiteman, 1994). In facultative species, paedomorphic and metamorphic individuals may be found in the same pond; furthermore, both phenotypes may result from the same cohort (Chapter 2; Semlitsch et al., 1990; Winne and Ryan, 2001). The expression of alternative phenotypes is believed to be environmentally induced and to depend on an interaction between an individual's genotype and the aquatic environment in which it develops (Whiteman, 1994, 1997).

Experiments, almost exclusively with species of *Ambystoma*, have identified a variety of biotic and abiotic factors that influence expression of the two alternative phenotypes. These include density of individuals in experimental tanks (Licht, 1992; Ryan and Semlitsch, 1998; Semlitsch, 1987), presence of fish predators (Jackson and Semlitsch, 1993), drying regime (i.e., hydroperiod) of tanks (Semlitsch and Gibbons, 1985; Semlitsch, 1987; Semlitsch et al., 1990), and potentially, nongenetic maternal effects (Licht, 1992; Semlitsch et al., 1990). Because growth rate is implicated as an important determinant of life history expression by several ecological models (Werner, 1986; Whiteman, 1994; Wilbur and Collins, 1973), the effect of food availability has been the focus of numerous studies. Results of these studies have varied, depending on the species of *Ambystoma* studied and type of food regime (Licht, 1992; Ryan and Semlitsch, in review; Semlitsch, 1987; Whiteman et al., 1996). Furthermore, studies with *Ambystoma* have suggested that the expression of facultative paedomorphosis has a genetic basis (Harris et al., 1990; Licht, 1992; Semlitsch and Gibbons, 1985; Semlitsch and Wilbur, 1989; Semlitsch et al., 1990).

Less attention has been given to factors affecting the expression of alternative life-history pathways in other groups of facultatively paedomorphic salamanders. A better understanding of the proximate and ultimate causes of this phenomenon can only be achieved through studies of other species and across populations within species (Whiteman, 1994). This is especially important considering that paedomorphosis (facultative and obligate) has evolved numerous times (Duellman and Trueb, 1986; Griffiths, 1996; Ryan and Bruce, 2000; Shaffer et al., 1991; Shaffer, 1993; Shaffer and Voss, 1996).

Species in the family Salamandridae (newts) provide an excellent opportunity to study the evolution and maintenance of facultative paedomorphosis. Newts exhibit a diversity of reproductive strategies, and facultative paedomorphosis occurs in several genera (Griffiths, 1996; Halliday, 1990; Petranka, 1998). Within North American newts (*Taricha* and *Notophthalmus*), facultative paedomorphosis is known to occur in *Taricha granulosa* (Marangio, 1978), *Notophthalmus viridescens* (Brandon and Bremer, 1966; Harris, 1987; Healy, 1970, 1974a), *Notophthalmus perstriatus* (Dodd et al., in press;

Chapter 2), and possibly in *Notophthalmus meridionalis* (Mecham, 1968). Nevertheless, the expression of facultative paedomorphosis has only been experimentally explored in a single study of *Notophthalmus viridescens dorsalis* (Harris 1987). Harris (1987) found that density, which influenced growth rate, had a significant affect on expression of paedomorphosis. Based on the literature and my research with *Notophthalmus perstriatus*, it appears that hypotheses invoked to explain the expression and maintenance of paedomorphosis may differ between *Ambystoma* and *Notophthalmus* species. In fact, several different hypotheses may explain the maintenance of facultative paedomorphosis (Whiteman, 1994, 1997). Therefore, results of experiments with *Ambystoma* may not be entirely applicable to newts or other salamander species.

Field research I conducted at several breeding ponds in north Florida revealed that the striped newt (*N. perstriatus*) has a complex life history (Fig. 1-1). Within a single breeding season, I found that some larvae transformed before maturing and left the pond (metamorphs), whereas others remained in the pond and matured while retaining their larval morphology (paedomorphs). This same pattern appeared to have occurred during three consecutive breeding seasons. The proximate cause(s) of the expression of the paedomorphic phenotype in some individuals but not others is unknown. A growth advantage for some individuals over others could explain the dichotomy in expression of the paedomorphic versus metamorphic life-history. Faster growing larvae of other newt species (*N. v. dorsalis*, Harris, 1987; *Triturus carnifex*, Kalezic et al. 1994) were more likely to become paedomorphic than slower growing larvae.

Some models of amphibian metamorphosis take into account the potential influence of growth rate on the expression of paedomorphosis in salamanders (Werner, 1986; Wilbur and Collins, 1973; Whiteman, 1994). In the Wilbur and Collins (1973) model, "physiological processes that initiate metamorphosis are related to recent growth history of the individual." Larvae with a growth advantage are predicted to remain in the aquatic environment and continue to grow, eventually expressing the paedomorphic life-history pathway. Slow growing larvae are predicted to metamorphose once they have reached some population-specific or species-specific threshold. Slow growing larvae thereby escape the potential density-dependent influence of competition with paedomorphs and larger larvae (Whiteman, 1994; Wilbur and Collins, 1973). Werner's (1986) model of amphibian metamorphosis also has been extended to paedomorphosis. In this model, the "decision" of an individual to remain in the aquatic environment or metamorphose and move into the terrestrial habitat is a result of growth potential in each habitat weighed against the habitat-specific risk of mortality. All else being equal, larvae with a growth advantage (i.e., relatively fast growing larvae) should be more likely to become paedomorphic as compared to slower growing larvae.

In addition to life-history expression, the Wilbur-Collins (1973) model predicts size and age at metamorphosis. This model can be viewed as a flexible-rate or optimal-growth rate model because mass-specific growth rates throughout much of the larval period dictate when metamorphosis should occur and at what body size. An alternative model, initially proposed by Smith-Gill and Berven (1979), and later extended by Travis (1984) and Leips and Travis (1994), differs from the Wilbur-Collins model in that rate of differentiation (i.e., development) of larvae, as opposed to growth *per se*, dictates larval period. Therefore, this alternative is referred to as a fixed differentiation-rate model. In this model, larval period is determined or fixed at some specific point in development.

Differences in growth rate after this stage of development are only predicted to influence body size at metamorphosis, not larval period. Travis (1984) suggested that this fixation period occurs early in development. Size at metamorphosis is still predicted to be a result of larval growth rate however, and because of this, both models account for the extreme plasticity in metamorphic body size of amphibians. Unlike the optimal growth-rate model of Wilbur and Collins, the fixed-rate model does not apply to paedomorphosis, however.

I tested the hypothesis that growth rate influences the expression of paedomorphosis in striped newts. I used varying food levels to generate different growth trajectories of larvae raised individually in the lab. The treatments included high and low levels of food, as well as switches in food levels. The objectives of the experiment were: 1) to determine the influence of growth rate on the expression of alternative life histories (i.e., metamorph vs. paedomorph), 2) to test the ability of the Wilbur and Collins model to predict the life-history expression, 3) to determine the influence of growth rate on larval period and size at metamorphosis, and 4) to simultaneously test the applicability of two types of models (optimal rate vs. fixed rate) for predicting metamorphosis in *Notophthalmus perstriatus*.

Methods

Experimental Design

I used different food treatments (constant High = HH, constant Low = LL, switch from Low to High = LH, and switch from High to Low = HL) to generate growth trajectories among four experimental groups of striped newt larvae. I used a randomized block design, with the two shelves treated as blocks. Ten individuals were randomly assigned to each of the four treatments. Newts were reared individually in plastic containers which were randomly assigned a position on one of two shelves. The experiment was designed to standardize all variables with the exception of food availability.

Procedures

Newts were housed in Sterilite® ClearView® storage boxes (43 cm X 28 cm X 16 cm). These were filled with 9 liters of aged water, which was changed every 5-7 days. During water changes, each container was cleaned with a scrub brush and antibacterial soap, then rinsed with tap water. Light was supplied by florescent bulbs mounted above the containers. Automatic timers controlled the lights and were adjusted several times during the experiment so that the light/dark regime approximated the natural light cycle. Newts were housed indoors, although the temperature fluctuated daily and seasonally, tracking the temperature variation for Gainesville, FL during the study period. I weighed and measured each newt twice a month (every 17 days on average). I weighed and measured newts singly by first removing an animal from its container and placing it in a plastic sandwich bag. I measured body length to nearest millimeter with a clear plastic ruler while the newt was in the bag. Because it was difficult to see the posterior edge of the vent on small larvae, I measured from the tip of the snout to the anterior edge of the rear legs where they meet the body (i.e., body length), rather than measure standard snout-vent length (SVL). Body length is highly correlated with SVL (Spearman Correlation test: $r = 0.988$, $P < 0.0001$, derived from measurements of 30 preserved striped newt larvae). Each newt was weighed to the nearest 0.1 g by transferring it to a small plastic cup filled with aged tap water that had already been tared on a Ohaus brand digital balance. I also recorded the degree of swelling of the vent (not swollen, slightly swollen, and swollen), condition of the gills and tail fin (full vs. regressing), and other external characteristics (e.g., presence of secondary sexual characters). These external characters can be used as indicators of maturation (i.e., vent swelling) and metamorphosis (i.e., gills and tail fin regress). In addition to using secondary sexual characters, I dissected each newt and examined its gonads under a dissecting scope to determine if it was sexually mature.

Newts were derived from eggs laid by paedomorphic adults that I collected on 3 Jan-99 from a breeding pond (Blue Pond) located on the Katharine Ordway Preserve, Putnam Co., FL. Striped newts are winter-breeders and these individuals were already in reproductive condition. Forty-eight paedomorphs were housed in 12 glass aquaria (2 females and 2 males per aquarium) and fed black worms every 2-3 days. Each aquarium contained an air stone, a constant water source, a standpipe, and vegetation on which to lay eggs. I collected eggs every 7-10 days and transferred them to shallow tubs containing dechlorinated water. Striped newt females lay eggs one at a time and have a prolonged breeding season of several months (Chapters 1 and 2). Hatchlings were transferred to another tub and raised on a diet of zooplankton until they were large enough to consume whole black worms. Water in the hatchling tubs was changed every 5-7 days. I waited until the larvae were large enough to eat black worms because this food source was easy to quantify and prior experience had shown that newts thrive on black worms. Although small larvae would readily eat *Artemia*, they always died within 2-3 days; they thrived however on native zooplankton. I grew zooplankton in large (1.2 m diameter) plastic (high-density polyethylene) tubs and harvested them with a fine-mesh net. The tubs were manufactured by the Lerio Co., Kissimmee, FL. The tubs contained ca. 700 liters of well water, soil collected from a dried pond basin at the Ordway Preserve, leaf litter, and aquatic vegetation. I also inoculated the tubs several times with zooplankton collected from local ephemeral ponds. Once enough larvae were reared to a size capable of consuming black worms, I began the experiment.

The experiment was initiated on 16 Jun-99 and continued until 27 Dec-99, for a total of 206 days. An individual was removed from its container when it showed obvious evidence of metamorphosis. This included the appearance of a bold stripe along the dorso-lateral portions of the body, and regression of the gills and membranous tail fin. A newt nearing metamorphosis also reduced its food intake and often floated at the surface of its container. At this point, the newt was transferred to a new container and placed on a damp paper towel to allow gill regression to continue. Once the gills had been completely resorbed, usually 2-3 days after removal from the plastic container, the newt was anesthetized in a chlorotone solution, weighed and measured. Each newt was tagged with a unique label and preserved in 10% formalin for dissection later. Newts that did not metamorphose remained in the experiment until its termination on Dec. 27. At this point, they were anesthetized, weighed, measured, and preserved.

Food Treatments

High food-treatment animals were fed black worms (*Lumbriculus*) *ad libitum*; the Low food-treatment was calculated as ¼ of the average number of worms consumed by the High food-treatment animals during the preceding feeding interval. Low food-treatment animals were fed every 3-5 days. Therefore, although the number of worms consumed by individuals in each food treatment increased as the newts grew (i.e., approximating mass-specific food levels), the animals on Low food always received ¼ of that of the High food animals. The LH and the HL treatment animals experienced a shift in available food during the experiment. On 17 Jul-99, I initiated the switch in food levels. The LH animals, which previously had received ¼ of the amount of food as the High food level animals, now received food *ad libitum*. The HL animals were now only fed ¼ of the average number of *Lumbriculus* consumed by High-treatment animals. High-food newts always had *Lumbriculus* available in their tanks; Low-food newts consumed all of their *Lumbriculus* within a few hours of feeding. The switch was initiated when mean mass of the HH and HL animals was at least 0.7 g and their body length was at least 22 mm. These body sizes are greater than the minima required for an individual striped newt to initiate metamorphosis but below the minima required for maturation in paedomorphic individuals (Chapter 2). Therefore, the switch in food levels occurred near the body size where metamorphosis can be initiated in nature but before maturation occurs. I chose this point to make the food-level switch because it should be a critical time in development. Once the minimum size for metamorphosis is reached, an individual may express the metamorphic life-history pathway or postpone metamorphosis and continue to grow, possibly expressing the paedomorphic pathway later.

Dissections

Internal and external characteristics were used to determine sex and reproductive condition. External secondary sexual characteristics that indicate maturity in salamandrids include: swelling of the vent, development of genial glands on the side of the head of males, and presence of nuptial excrescences on the rear limbs and toe tips of males (Duellman and Trueb, 1986). Mature striped newts are sexually dimorphic and in addition to the characters above, the shape of the cloacal lips differ between males and females. A conspicuous cloacal gland, which is whitish in color, is visible at the posterior edge of the cloaca in mature and some immature males (Dodd, 1993). I dissected all newts and examined their urogenital systems under a dissecting scope to determine reproductive condition. Dissection also allowed me to confirm the sex of newts that exhibited secondary sexual characteristics, and determine the sex of immature animals. Maturity of females was indicated by the presence of enlarged ovarian follicles and enlarged, convoluted oviducts. Maturity in males was indicated by the presence of enlarged, convoluted, and pigmented Wolffian ducts (Ryan and Semlitsch, in review; Semlitsch, 1985)

Data Analysis

Response variables used in statistical analyses were body length, body mass, larval period (number of days from initiation of the experiment to metamorphosis), and morph type (metamorph or paedomorph). Prior to analysis, each data set was tested for normality and heteroscedasticity. When assumptions of parametric tests were violated, nonparametric methods (Hollander and Wolfe, 1999) were used to test for treatment effects. All statistical analyses, with the exception of goodness-of-fit tests, were performed using SAS version 6.12 (SAS Institute Inc., 1990).

I used a two-part analysis to test for differences in growth rates among the four treatment groups. First, a MANOVA (on body length and mass) was used to test for differences among treatments the day before the switch in food level was initiated. Second, I tested for differences among growth rates during the remainder of the experiment. For each individual that remained in the experiment (i.e., had not yet metamorphosed), I subtracted the size (for BL and mass independently) of the individual on the most recent day it had been measured (before metamorphosis or at the end of the experiment for paedomorphs) from its size on the day before the food switch. This value was then divided by the number of days from the switch until the date a newt had been most recently measured to give a growth rate (unit of growth/day). Growth rates among treatments (excluding HL) were then tested with a Kruskal-Wallace test (Hollander and Wolfe, 1999). Growth rates of HL animals were excluded because all individuals had metamorphosed before the first scheduled date for measuring individuals following the food switch.

I used a MANOVA to test for differences among treatments on body length, mass, and larval period for those individuals that metamorphosed before the end of the experiment. Following significant univariate tests in MANOVA tests, a Student-Newman-Keuls (SNK) test was used to compare treatment means. For each MANOVA, if Wilks' λ was significant, alpha was adjusted for univariate tests with the Bonferroni method (Sokal and Rolf, 1995). I used a goodness-of-fit test (Sokal and Rolf, 1995) to analyze the different frequencies of metamorphs and paedomorphs across treatments and between sexes. For influence of treatment on morph type, I calculated the number expected for each morph in each treatment (expected metamorph:paedomorph = 7.75:2.25) by dividing the total number of metamorphs and paedomorphs by four. For influence of sex, I partitioned the observed numbers of each morph between the sexes to calculate expected numbers (expected metamorph:paedomorph = 14:4.5). Goodness-of-fit was used also to determine if sexes of the newts were distributed equally among the treatments. Expected values were derived by dividing the total number of males and females by four (expected male:female = 5.75:3.5)

Results

Larval Growth

On day one of the experiment there were no significant differences in mass (Kruskal-Wallace test: $H = 2.864$, df = 3, $P = 0.4131$) or body length (ANOVA: $F_{3,36} = 0.54$, $P = 0.6605$) of newts across all four food treatments (i.e., HH, HL, LL, LH). On the day before the switch in food levels (day 31), MANOVA indicated significant differences in size of newts among treatments even when alpha was adjusted with the Bonferroni method (Wilks' $\lambda = 0.219$, $F_{6,66} = 12.53$, $P < 0.0001$). Univariate tests were significant for both mass ($F_{3,35} = 39.41$, $P < 0.0001$) and body length ($F_{3,35} = 24.61$, $P < 0.0001$); block was not significant. SNK tests showed that for both body length and mass, the HH and HL treatment animals did not differ nor did the LL and LH animals. However, HH and HL newts had significantly greater mass and body length than the LL and LH newts. Therefore, before the switch in food levels, individuals receiving the H food treatment had grown faster than individuals fed at the L level (Fig. 4-1).

The switch in food levels was initiated on day 32 (17 Jul-99) of the experiment. By this point, newts in the HH and HL treatment groups had slightly surpassed the minimum size required for metamorphosis of *N. perstriatus* in nature (Chapter 2), whereas the LL and LH newts remained smaller than this minimum size. Analysis of growth rates following the switch day does not include any HL individuals because all of them metamorphosed before day 48 of the experiment, the first day after the switch when mass and body length were next measured. After the food switch, the growth rates of HL newts promptly increased and soon their rate paralleled those of the HH newts, whereas the LL newts continued to grow slower than individuals receiving the H food level (Fig. 4-1). After the switch in food levels, growth rates, measured both as differences in mass and body length, differed among remaining branchiates in the HH, LL, and LH treatments (Kruskal-Wallace test for mass: $H = 15.694$, df = 2, $P = 0.0005$; for body length: $H = 15.094$, df = 2, $P = 0.0004$; Fig. 4-1). Overall growth rates in mass and body length were greatest for LH newts, followed by HH then LL treatment animals (Fig. 4-2).

Size at Metamorphosis and Larval Period

Univariate tests from a MANOVA on mass, BL, and larval period (Wilks' $\lambda = 0.119$, $F_{9,66} = 7.57$, $P < 0.0001$) were not significant for either mass at metamorphosis ($F_{3,22} = 2.71$, $P = 0.0696$) or body length ($F_{3,22} = 0.27$, $P = 0.8496$; Table 4-1); block was not significant in any of the univariate tests. Larval period on the other hand, was significantly different among the food treatments ($F_{3,22} = 19.63$, $P < 0.0001$; Table 4-1). A SNK test showed that the larval period did not differ between the HH and HL groups but both of these differed from the LL and LH groups, which differed from each other. The relationships between mass and body length at metamorphosis and larval period is presented in Fig. 4-3.

Life-history Pathway Expression

At the termination of the experiment, 22.5% of the individuals were mature branchiates and the rest had metamorphosed earlier in the experiment before attaining maturity. All newts considered paedomorphs were mature based on external and internal characters. Paedomorphic females each had many enlarged, pigmented follicles in their ovaries, as well as enlarged and convoluted oviducts. All paedomorphic females also had swollen vents. The Wolffian ducts (i.e., vas deferens) of all paedomorphic males were enlarged, pigmented, and convoluted. Externally, paedomorphic males had very swollen vents, relatively enlarged rear limbs with cornifications on their toe tips, and well-developed hedonic pits on each side of their head. A light colored gland was obvious at the posterior end of their vents. None of the metamorphic newts had near the degree of cloacal swelling exhibited by the paedomorphs. The rear limbs of metamorphic males were not enlarged and their toe tips were not cornified; hedonic pits were barely visible in only a few immature males. Internally, neither the Wolffian ducts nor the oviducts were enlarged or convoluted in metamorphic newts. Follicles in the ovaries of metamorphic females were small and undeveloped. External gills were present in all paedomorphic newts at the end of the experiment, and the namesake stripe was well developed. External gills of experimental paedomorphs were not as large and filamentous as gills of paedomorphic striped newts observed in natural ponds (S. A. Johnson, pers. obs.).

Distribution of paedomorphs and metamorphs was not even across treatments, and no paedomorphs were produced in the HL treatment (Fig. 4-4). Nevertheless, a goodness-of-fit test did not detect significant differences in life history expression across the food treatments ($G = 6.968$, df = 3, $P = 0.062$). However, as compared to the overall sex ratio of metamorphs and paedomorphs in the experiment (both morphs, M:F = 1:0.6), significantly more females became paedomorphic (females, paedomorph:metamorph = 1:1.34) than males (males, p:m = 1:6.7; $G = 6.333$, df = 2, $P = 0.042$). Males and females were distributed equally among treatments ($G = 1.664$, df = 3, $P = 0.680$).

By the end of the experiment, all paedomorphs were longer than the metamorphs and all but one had greater mass than the metamorphs (Fig. 4-5). The body size of paedomorphs at the end of the experiment differed among the three treatments in which paedomorphs were produced. Mean mass and body length were greatest in paedomorphs produced by the HH food treatment, followed by paedomorphs in the LH then the LL treatments (Table 4-2).

Discussion

Differences in food levels resulted in differences in growth rates among treatments before and after the food-level switch (Figs. 4-1 and 4-2). Despite these differences, mass and body length were not significantly different at metamorphosis for those newts expressing this life-history pathway (Fig. 4-3, Table 4-1). However, treatment had a significant effect on duration of larval period. Mean larval period of HH newts did not differ significantly from that of HL newts, but both of these were significantly different from the LL and LH treatment individuals (Fig. 4-3, Table 4-1), which were significantly different from each other. The paedomorphic life-history pathway was expressed by newts in all treatment groups except the HL group (Fig. 4-4). Nonetheless, the proportion of paedomorphs and metamorphs resulting from each treatment did not differ significantly. Therefore, growth trajectories generated by the four different food regimes did not affect life-history pathway expression. There were however, significant differences in the expression of life-history pathway among the sexes. Proportionately more females became paedomorphic than expected considering the overall sex ratio of animals in the experiment.

Expression of Alternative Life-history Pathways

Optimal growth-rate models, primarily the Wilbur-Collins (1973) and the Werner (1986) models, make predictions about the expression of life-history pathways in salamanders. Growth rate is also central to Whiteman's (1994) three alternative hypotheses to explain the maintenance of facultative paedomorphosis. Each of these models essentially makes the same predictions with regard to life-history pathway expression that should have resulted from treatments in the experiment. High-High and LH newts should have expressed the paedomorphic phenotype, whereas LL and HL newts should have transformed before maturing. However, the results for life-history pathway expression clearly did not fit these predictions.

I found no significant influence of treatment, and thus growth trajectory, on life-history pathway expression. As predicted by the Wilbur-Collins model, HL newts transformed shortly after they were switched from a High to Low food ration and none became paedomorphic. However, all but two of the HH newts also transformed shortly after the switch, and there was not a significant difference in larval period between newts in the two treatments. No paedomorphs were predicted to result from the LL treatment. Nevertheless there were more paedomorphs in this treatment than any of the other three (Fig. 4-4). The LH treatment was predicted to produce only paedomorphs but seven larvae in this treatment transformed. To reiterate, food level did not influence an individual's expression of life-history pathway.

The role of food level on life-history expression has been tested in mole salamanders. Constant food levels did not significantly influence the expression of paedomorphosis in *A. gracile* or *A. talpoideum* (Licht, 1992; Semlitsch, 1987). Additional experiments with *A. talpoideum* revealed a significant effect of food level for individuals that received relatively low food rations late in development (Ryan and Semlitsch, in review), counter to predictions of the Wilbur-Collins model.

Life-history expression of striped newts depended on sex in my experiment. Females had a significantly greater propensity to become paedomorphic than males. The sex ratio of paedomorphs was female biased (m:f = 1:2), whereas the sex ratio of metamorphs was male biased (m:f = 5:2). Female-biased sex ratios in paedomorphs have been reported for several species of mole salamanders and newts and may play a role in maintenance of paedomorphosis in facultative species (Whiteman, 1997).

Even though food level, and therefore growth rate, did significantly impact the expression of life-history pathways in striped newts, other ecological conditions certainly have at least some effect on this process. My fieldwork indicates that hydroperiod is an important determinant of life-history expression. If pond hydroperiod is too short, paedomorphosis is not possible. Larval newts in a pond with a short hydroperiod will not have enough time to mature and will metamorphose before the pond dries, assuming they have reached the minimum threshold size. If hydroperiod has been long enough for some larvae to mature but the pond dries before the reproduction is complete, paedomorphic newts will initiate metamorphosis to escape the drying pond. Pond hydroperiod influences life history in mole salamanders as well (Semlitsch and Gibbons, 1985; Semlitsch, 1987; Semlitsch et al., 1990).

Along with ecological factors, the genetic component of life-history expression in salamanders has been an arena of active research contributing significantly toward an understanding of paedomorphosis (Harris et al., 1990; Ryan and Semlitsch, in review; Shaffer and Voss, 1996; Semlitsch and Gibbons, 1985; Semlitsch and Wilbur, 1989; Semlitsch et al., 1990; Tompkins, 1978; Voss, 1995; Voss and Shaffer, 1997, 2000). Tompkins (1978) initially reported that paedomorphosis in the axolotl (*Ambystoma mexicanum*, an obligate paedomorphic species) was caused by homozygosity of a single recessive gene. The work of Voss (1995) later disproved this idea and additional experiments supported the idea that paedomorphosis is controlled in the axolotl primarily via a major gene effect, "with smaller affect loci presumably influencing trait expression under certain environmental conditions" (Voss and Shaffer, 1997).

Several studies have revealed genetic variation in life-history expression among local populations of the mole salamander, a facultatively paedomorphic species (Harris et al., 1990; Semlitsch and Gibbons, 1985; Semlitsch and Wilbur, 1989; Semlitsch et al., 1990). This variation suggests that facultative paedomorphosis also has a genetic basis. The variation is assumed to have arisen through differential selective pressure on each morph resulting from varying hydroperiods among ponds. Salamanders from ponds with long hydroperiods had a greater propensity to become paedomorphic than those from sites that were more ephemeral (Semlitsch and Gibbons, 1985; Semlitsch and Wilbur, 1989).

Although the specific genetic architecture controlling expression of alternative phenotypes in facultatively paedomorphic salamanders is still unknown, it is clear that the genetic system is complex. Variability exists in the system among species and among populations within species (Shaffer and Voss, 1996). Experiments with *Ambystoma* sp. and *Notophthalmus viridescens* have provided evidence that facultative paedomorphosis is likely controlled by a polygenic system (Licht, 1992; Harris, 1987; Semlitsch et al., 1990; Voss 1995; Voss and Shaffer 1997). Such a system could involve a major gene effect with loci of smaller effect being influenced by environmental factors, or the system could be comprised of multiple loci, each with a relatively small effect (Ryan and Semlitsch, in review; Voss, 1995; Voss and Shaffer, 1997). Although my experiment was not designed to reveal the genetic component of paedomorphosis in *N. perstriatus*, the results rule out the possibility of a simple, single-locus, recessive-allele explanation.

If a single recessive allele controlled paedomorphosis in striped newts, all larvae in the experiment would have become paedomorphic. This is because each experimental animal would have been homozygous for paedomorphosis since the parent generation consisted entirely of paedomorphs. Based on the evidence currently available, life-history expression in striped newts may be controlled by a polygenic system.

Metamorphosis and Model Applicability

Optimal growth-rate and fixed differentiation-rate models types make the same predictions regarding body size at metamorphosis for striped newts in the experiment, but they differ in their predictions of larval period duration. Food treatments in the experiment were predicted to generate growth trajectories similar to those shown in Fig. 4-6. Both models predicted that body size at metamorphosis (i.e., mass and body length) should follow the pattern of (HH = LH) > HL > LL (Fig. 4-6). For the fixed differentiation-rate model I assumed that the fixation period should have occurred early in larval development (i.e., before the food switch), as Travis (1984) proposed. The difference between the two model predictions should be manifest in duration of larval period. The optimal rate model (Fig. 4-6A) predicts a pattern of HL < HH < LH < LL for time to metamorphosis. If I assume that the fixed-rate model applies to *N. perstriatus* and that fixation occurred before the switch in food levels, then duration of larval period is predicted to be (HH = HL) < (LH = LL) (Fig. 4-6B).

Size at metamorphosis was not significantly different among the four treatments for either mass or body length for those newts expressing the metamorphic life-history pathway. Furthermore, mean body length across treatments did not fit the pattern predicted by both models. Mean body length of the newts in the HH and HL treatments was predicted to be the same, and the mean body length of animals in these two treatments should have exceeded those of the HL treatment, followed by the LL animals. Mean body length of HH metamorphs was closest to that of the LL metamorphs, followed by newts in the LH treatment; HL newts exhibited the smallest mean body length at transformation (Table 4-1). Although not significantly different, mean mass at metamorphosis followed the pattern predicted by both models. Both the HH and LH newts had the same mean mass at metamorphosis followed by the HL newts and then the LL animals (Table 4-1).

Duration of larval period differed among the four food treatments. Mean larval periods for the HL newts and the HH newts were not significantly different. However, larval period for individuals in both of these treatments was significantly shorter than the LH animals, which in turn were shorter than the LL newts (Table 4-1). Despite the lack of statistical significance between HL and HH newts, larval duration across the four treatments matched the prediction of the Wilbur-Collins model for metamorphic animals. The data were not consistent with the pattern predicted by the fixed differentiation-rate model.

The majority of experiments to test the applicability of both types of models have been conducted with anuran larvae. Results have been variable, with some experiments providing support for the optimal growth-rate model (Alford and Harris, 1988; Wilbur and Collins, 1973) and the fixed differentiation-rate model (Beck, 1997; Smith-Gill and Berven, 1979). Nonetheless, other experiments have shown that neither model fit the data well (Hensley, 1993; Leips and Travis, 1994; Pandian and Marian, 1985; Travis 1984). Crump (1981) even suggested that, in addition to rates of growth and differentiation, accumulation of energy may also be key to predicting amphibian metamorphosis.

Few studies have tested the applicability of the two models in salamanders and discussions have usually focused on the predictions of the optimal growth-rate model. The results of Beachy's (1995) experiment with *Desmognathus ochrophaeus* "strongly suggest that the Wilbur-Collins model is inappropriate for this stream-dwelling salamander." However, because his food treatments only consisted of constant levels of food, Beachy (1995) admitted that his findings do not allow for a complete assessment of the applicability of the model. In a similar experiment with *Ambystoma gracile* (Licht, 1992), there were no differences in body mass at metamorphosis for salamanders receiving constant low or high food rations. However, the high food salamanders metamorphosed significantly sooner than the low food animals (Licht, 1992), consistent with both models as portrayed in Fig 4-6. Nevertheless, since the food treatments did not vary during the larval period, the ability of this experiment to serve as a fair test of the Wilbur-Collins model is arguable. Although the experimental design of Ryan and Semlitsch (in review) is appropriate for testing predictions of metamorphosis for *Ambystoma talpoideum* made by the Wilbur-Collins model, the emphasis of their experiment was on expression of phenotypes (i.e., metamorph vs. paedomorph). Unfortunately, they did not present data for treatment effects on size at metamorphosis and larval duration of metamorphs in their experiment. Therefore, it appears as if this experiment with *Notophthalmus perstriatus* is the first to evaluate predictions of the optimal growth-rate and fixed differentiation-rate models for a salamander.

As noted above, differences in mass and body length did not vary significantly across the four treatments, although the distribution of means for body mass were consistent with both models. The distribution of mean body length across the treatments did not fit the predictions of either model. Had I measured energy accumulation, as suggested by Crump (1981), rather than body length and mass, I may have found stronger support for one of the models. Response variables measured in experimental tests of both models have usually been body mass and/or body length. Use of these parameters, rather than some metric of general body condition, may in part be responsible for the variation in model applicability found by ecologists. In fact, Wilbur and Collins (1973) stated that "a more complete understanding of metamorphosis may suggest that some aspect of body quality rather than quantity is the critical factor in the initiation of metamorphosis." Differentiation rate, at least in some species, appears to be one measure of body quality that is important for predicting larval period. Larval periods of striped newts were not consistent with predictions of the fixed differentiation-rate model, regardless of when in development one assumes that differentiation is fixed. Duration of larval periods were consistent with the optimal growth-rate model, although larval period did not differ significantly between the HL and HH newts.

Neither of the two classic models of amphibian metamorphosis (i.e., optimal growth-rate model or fixed-differentiation rate model) accurately predicted body length or mass at metamorphosis for striped newt larvae. The discrepancies between model predictions and results of this study, as well as experiments cited earlier, show that neither model is applicable for all situations. Such discrepancies may be caused in part by genetic differences among taxa and/or populations. Additionally, as suggested by

Crump (1981), standard measures of body size (e.g., body mass and body length) might not be the appropriate response variables to consider when testing predictions of ecological models.

Experimental and field-collected data for *N. perstriatus* provide qualified support for Whiteman's (1994) "paedomorph advantage" hypothesis. This hypothesis, largely based on the Wilbur-Collins model, predicts that larvae with relatively high growth rates should become paedomorphic, whereas slow growing larvae should metamorphose. Growth rate did not have a significant influence on life-history pathway expression for striped newts in my experiment, counter to predictions of the the hypothesis. Nonetheless, other life history parameters provide support for Whiteman's (1994) "paedomorph advantage" hypothesis. For example, paedomorphs reproduce at a younger age than metamorphs of the same cohort (Chapter 2). Additionally, as predicted by the "paedomorph advantage" hypothesis, the minimum body size for metamorphosis in striped newts is smaller than the minimum size for paedomorphosis (Chapter 2).

Although ecological factors affect the expression of paedomorphosis in the striped newt, results of my experiment and field data support an important role for a genetic component in life-history pathway expression in this salamander. My experiment precludes a single recessive allele as the genetic basis for life-history expression in *N. perstriatus*. A polygenic system seems most parsimonious with current data. Additionally, striped newts have a distinct reproductive strategy in which most, if not all, paedomorphic individuals apparently transform after breeding, which occurs at ca. 1 year of age. Therefore, strict ecologically-based models of facultative paedomorphosis need to be extended to account for these phenomena.

Table 4-1. Body length (BL), mass, and larval period for metamorphic striped newts across the four food treatments. Body length and mass did not differ significantly among the four treatments. Larval period of HH and HL newts did not differ significantly. Larval period of HH and HL newts differed significantly from the LL and LH animals, which were significantly different from each other.

	BL (mm)			Mass (g)		Larval Period (days)		
Treatment	n	mean	SE	mean	SE	n	mean	SE
HH	7	28.0	0.23	0.6	0.04	8	42.4	1.73
HL	9	27.1	0.7	0.5	0.03	10	38.4	1.68
LL	5	27.6	0.76	0.4	0.04	6	101.7	15.39
LH	6	27.3	0.78	0.6	0.08	7	63.1	4.38

Table 4-2. Body length (BL) and mass for paedomorphs in each treatment. There were no paedomorphs produced in the HL treatment group.

	BL (mm)			Mass (g)	
Treatment	n	mean	SE	mean	SE
HH	2	36.5	0.50	2.5	0.14
LL	4	27.8	0.50	0.9	0.05
LH	3	33.3	0.87	2.0	0.23

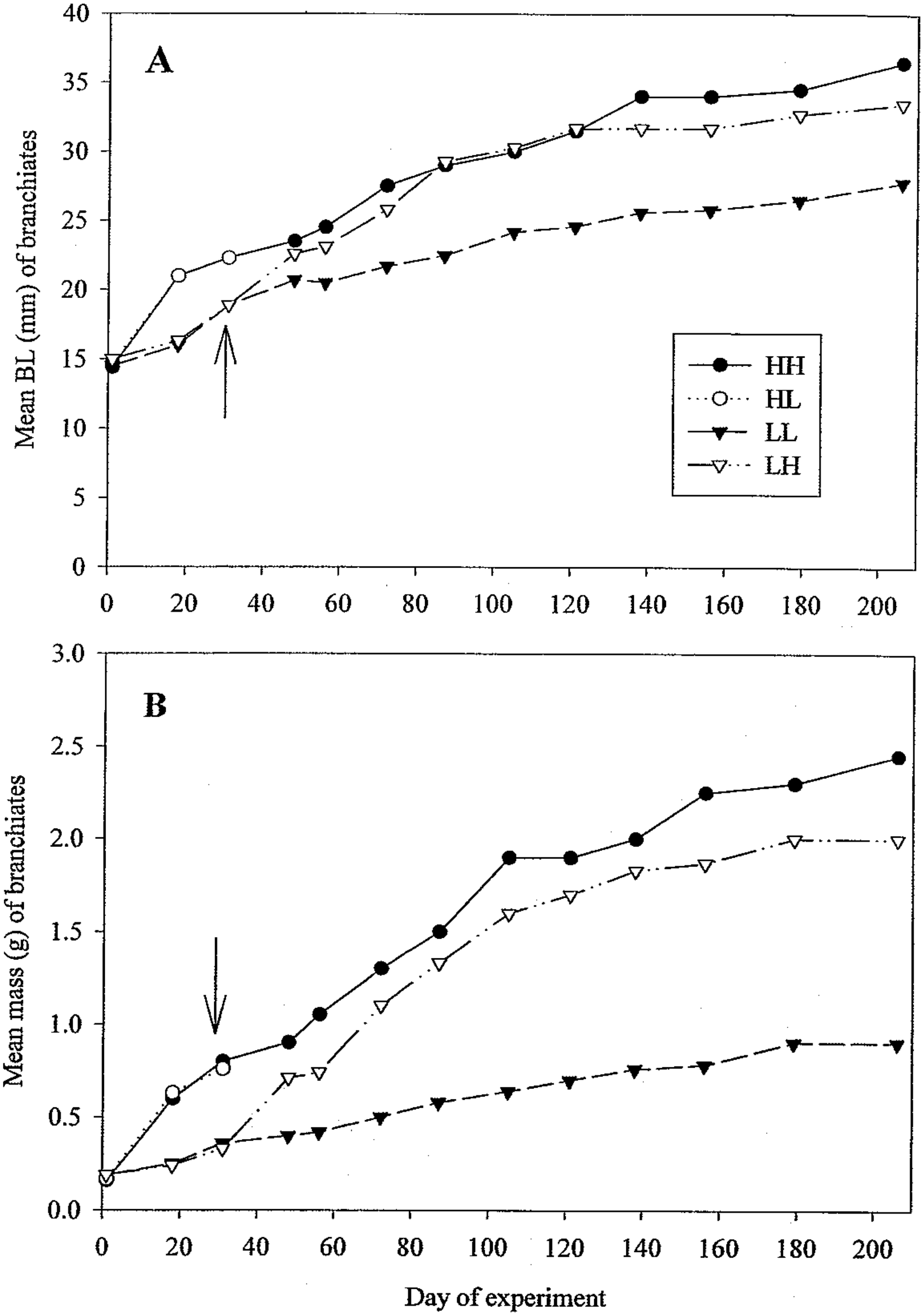


Fig. 4-1. Growth trajectories of larvae in the four different food treatments. A) Means of body length. B) Means of mass. All of the HL treatment larvae transformed shortly after the food level switch. Arrows indicate day of food level switch. Only means for untransformed individuals are plotted, and error bars have been omitted for clarity.

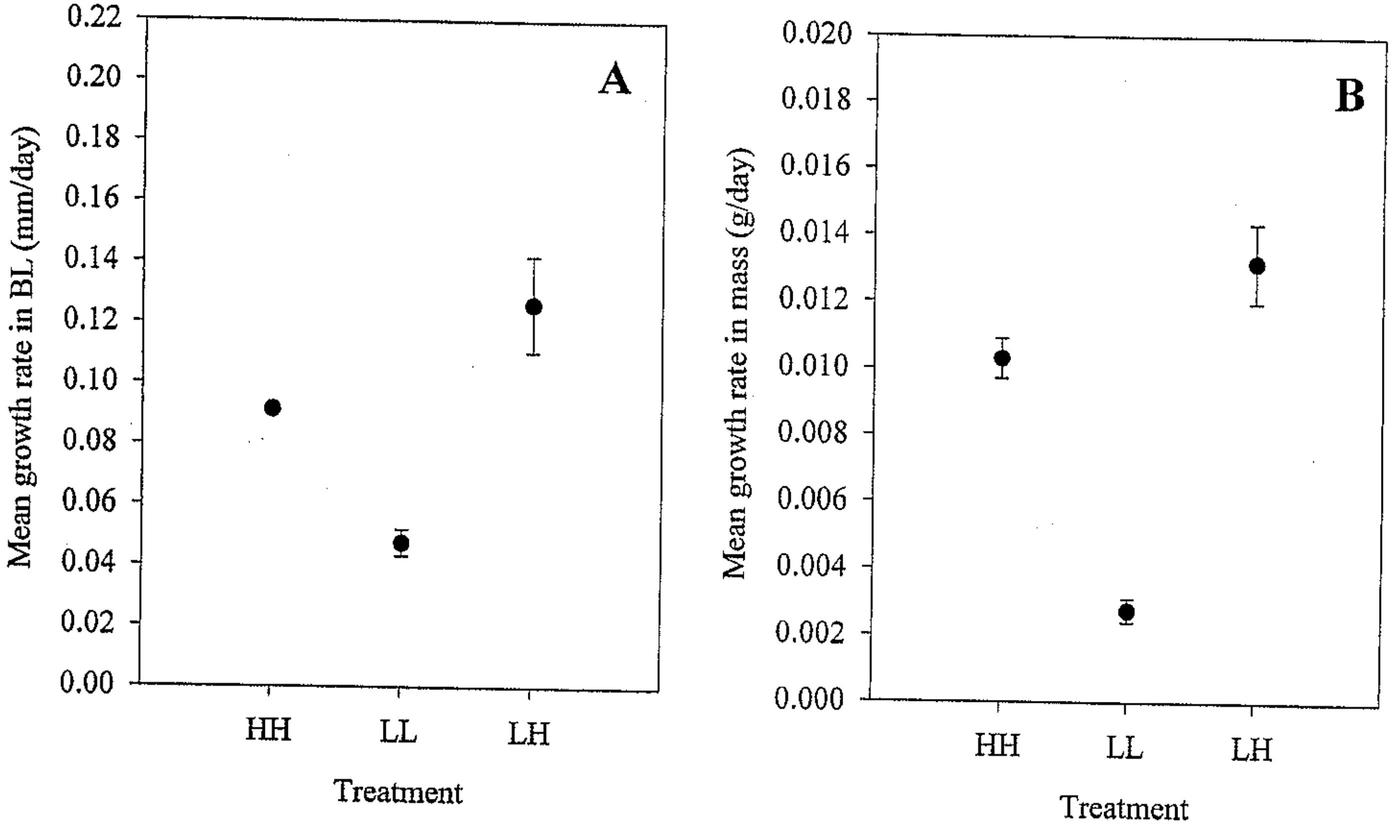


Fig. 4-2. Means comparisons of growth rates for remaining branchiates among three treatments after the switch in food levels. A) Growth rates in body length (BL). B) Growth rates in mass. The HL treatment is excluded because all newts in this treatment transformed shortly after the food-level switch. Differences in BL and mass growth rates were significant. Refer to methods for an explanation of how growth rates were calcualted. Error bars are +/- 1 SE.

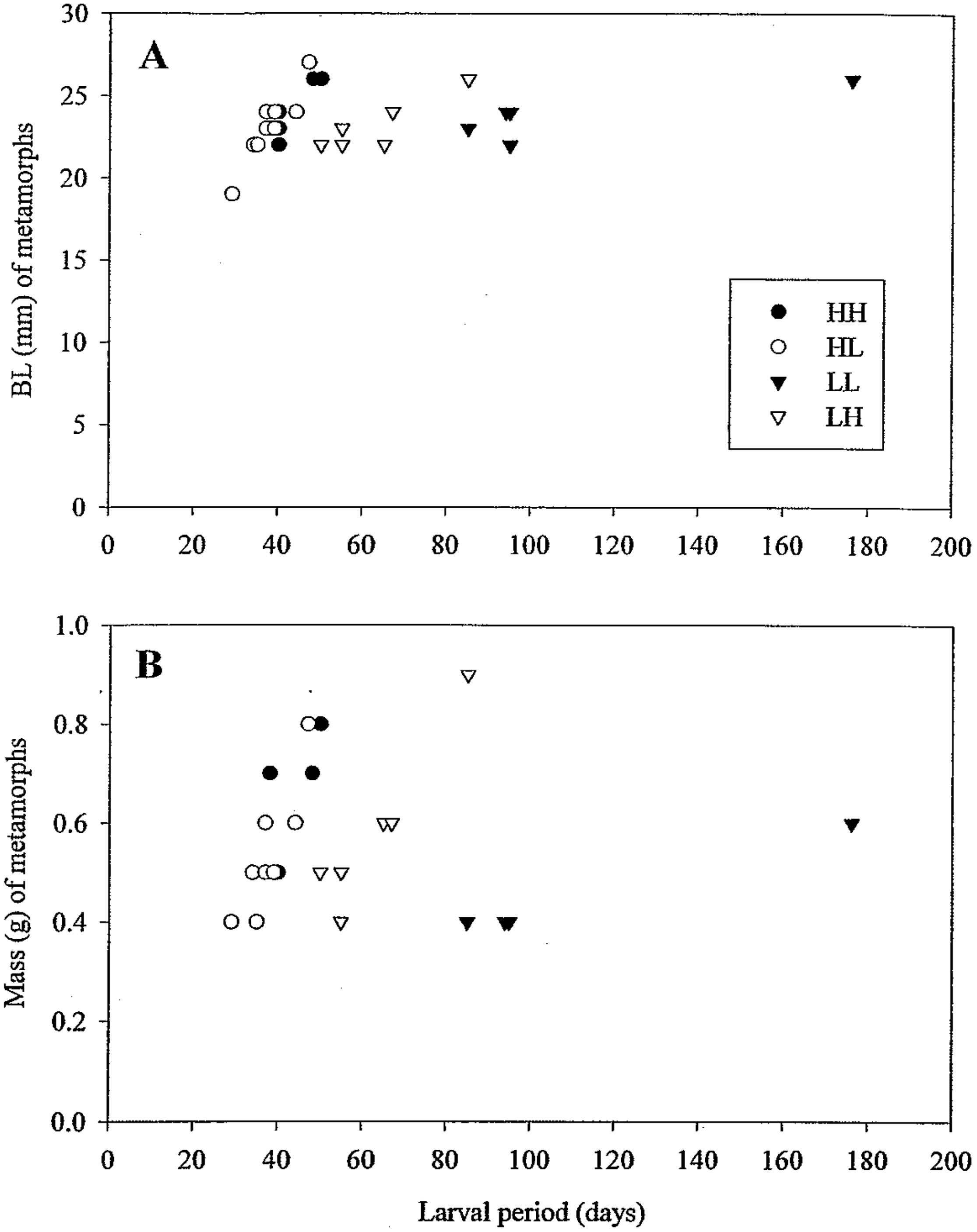


Fig. 4-3. Sizes of metamophic striped newts in each of the four treatments. A) Body length (BL) of newts. B) Mass of newts. Neither measure of body size was significantly different among treatments. Mean larval periods of the HH and HL treatment newts did not differ significantly, but larval periods for both of these treatments were significantly shorter than the LH treatment, which was significantly shorter than the LL treatment. Some symbols overlap.

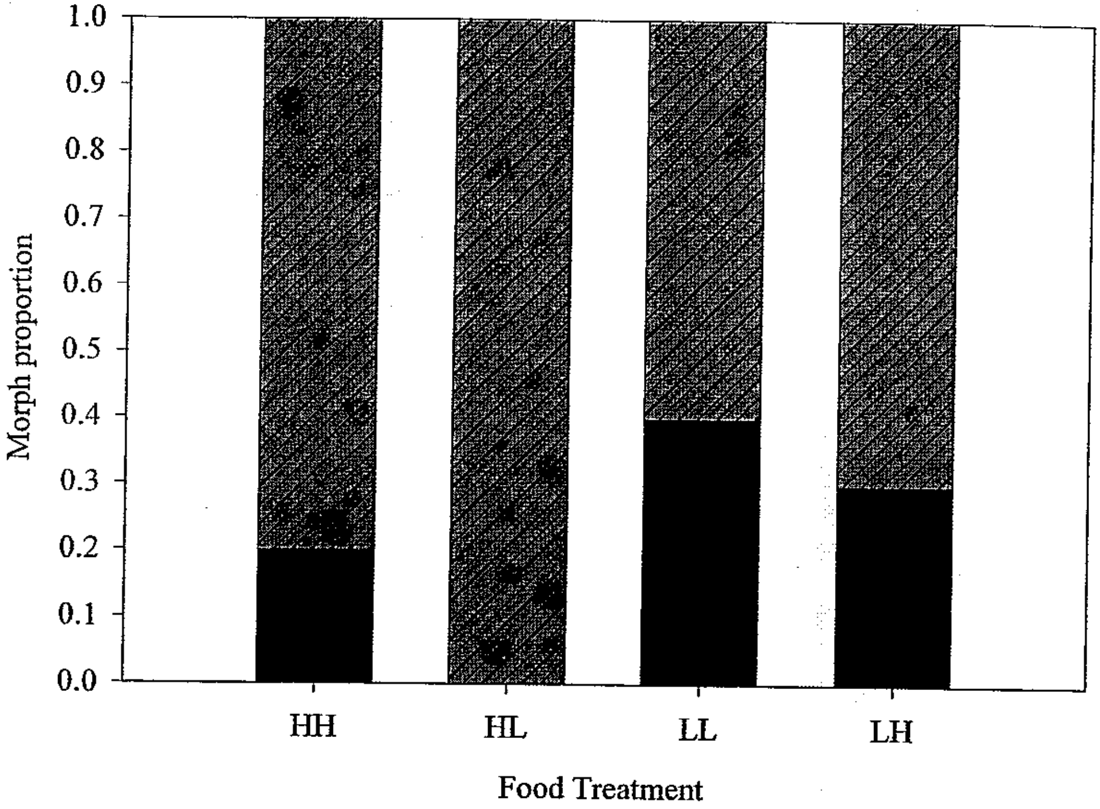


Fig. 4-4. Distribution of life-history pathway expression in striped newts among the four food treatments. Paedomorphs are indicated by the black portions of the bars and metamorphs by the diagonal lines. The effect of food treatment on pathway expression was not significant.

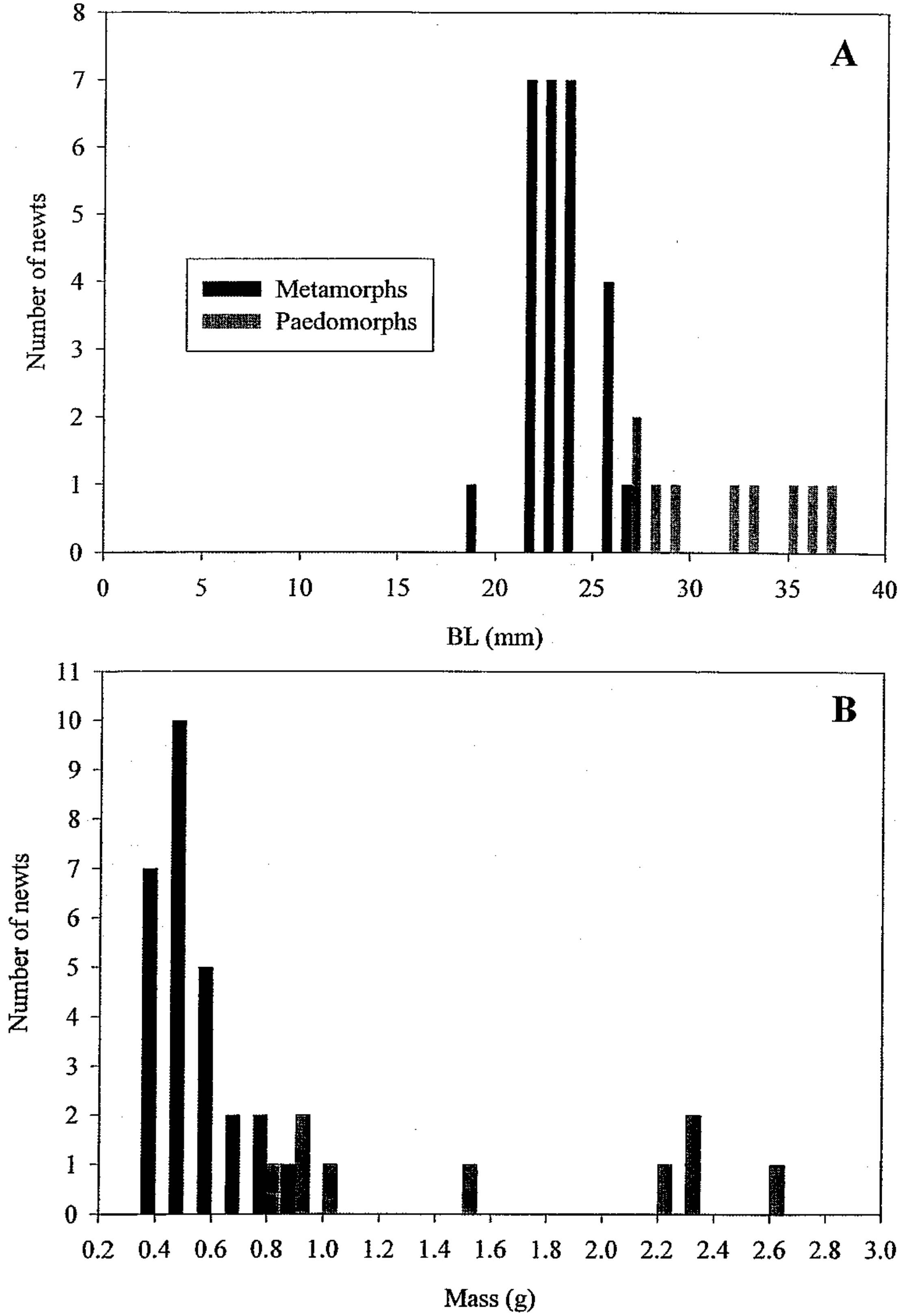


Figure 4-5. Size of metamorphic and paedomorphic newts at the end of the experiment. A) Body length (BL) of newts. B) Mass of newts.

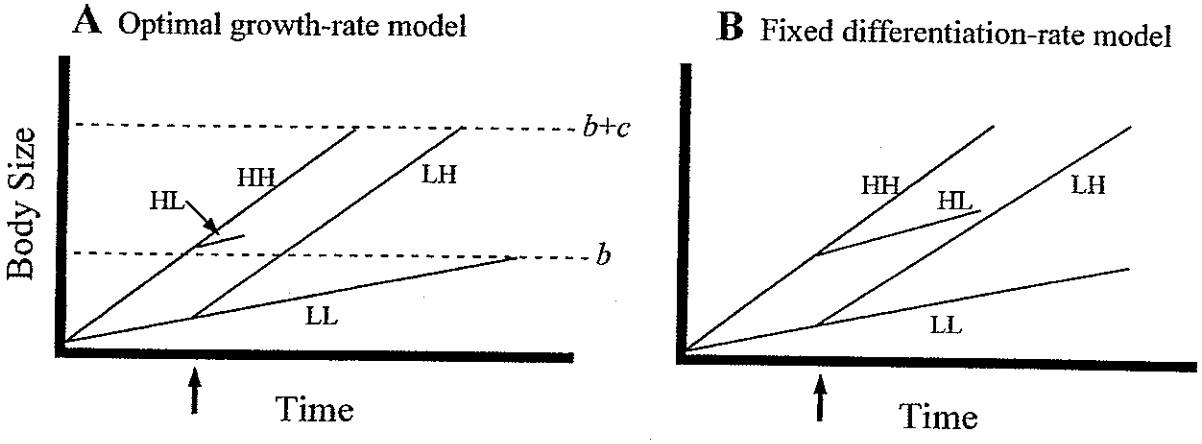


Fig. 4-6. Predictions of size at metamorphosis and larval period for two different models of amphibian metamorphosis. A) The optimal growth-rate model (Wilbur and Collins, 1973). B) The fixed differentiation-rate model (Smith-Gill and Berven, 1979; Travis, 1984). The figures were modified from Alford and Harris (1988), and Hensley (1993). Predictions are based on the expected outcome of the four treatments used in my experiment. Slopes indicate relative growth rates and the lines end at metamorphosis. The dashed lines indicated by "*b*" and "*b+c*" in model "A" represent the minimum and maximum size thresholds for metamorphosis as presented in the Wilbur-Collins model. The bold arrows along the "Time" axes indicate when the food level switch occurred.

CHAPTER 5
CONSERVATION GENETICS AND PHYLOGEOGRAPHY OF THE STRIPED NEWT

Introduction

The striped newt (*Notophthalmus perstriatus*) is a salamander endemic to north-central Florida and southeastern Georgia (Conant and Collins, 1991). Individuals inhabit xeric upland habitats (e.g., sandhill and scrub communities) and breed exclusively in temporary ponds that lack predatory fishes (Carr, 1940; Christman and Means, 1992; Dodd and LaClaire, 1995; Franz and Smith, 1999). The uplands inhabited by striped newts are fire climax communities (Myers, 1990), and fire appears to be crucial for the persistence of striped newts.

Little has been published about the striped newt's ecology (Christman and Means, 1992; Dodd, 1993; Dodd and LaClaire, 1995). Most literature on striped newts is limited to survey results and species accounts (Bishop, 1941a, 1943; Carr, 1940; Christman and Means, 1992; Dodd and LaClaire, 1995; Franz and Smith, 1999; Hipes and Jackson, 1996; Meecham, 1967). Studies of striped newt feeding habits (Christman and Franz, 1973), natural history at a breeding pond (Dodd, 1993), and orientation to and from a breeding pond (Dodd and Cade, 1998) represent the only published works focusing on this species. Nothing has been reported about population genetics of the striped newt.

Striped newts have declined throughout their range (Dodd and LaClaire, 1995; Franz and Smith, 1999). Reduction of the longleaf pine/wiregrass ecosystem, fire suppression, and the natural patchy distribution of upland habitats (i.e., sandhill and scrub communities) required by striped newts have resulted in a fragmented and patchy distribution of the species. A complex life history (Fig. 1-1) makes striped newts vulnerable to threats at breeding ponds (e.g., ditching and draining of temporary ponds) as well as in the surrounding uplands (e.g., silviculture practices, fire suppression). Densities of striped newts are very low at most sites where they persist (Dodd and LaClaire, 1995; S. A. Johnson, B. Means, K. Greenberg, and D. Stevenson, unpubl. data). Because of historical declines and current low population densities, the striped newt is recognized as a rare species in both Florida and Georgia (Christman and Means, 1992; Cox and Kautz, 2000; Jensen, 1999) and its biological status is under review by the U.S. Fish and Wildlife Service (L. LaClaire, pers. comm.).

Determining population genetic structure is an essential foundation for conservation and management of striped newt populations. Striped newt populations persist at only a few "stronghold" locations (areas where, according to recent surveys, newts are known to persist) throughout the range of the species. Most stronghold locations have multiple breeding ponds with appropriate upland habitat that allows dispersal to occur among the ponds. In Florida, these include Ocala National Forest, Katharine Ordway Preserve, Camp Blanding Training Site, and Apalachicola National Forest. In Georgia, "strongholds" include the Joseph Jones Ecological Research Center property, Fort Stewart Military Instillation, and possibly a suite of ponds in Jenkins Co.. Significant genetic divergence among these locations would indicate restricted contemporary gene flow, meaning that exchange of individuals among populations is minimal or nonexistent. Consequently, if local extinctions were to occur, it is unlikely that extirpated locations would be recolonization by individuals from other populations.

If this is the case, each population should be viewed and managed as an independent demographic unit. Identifying such "management units" (Moritz 1994a) is a powerful and practical application of molecular techniques "to define the appropriate geographic scale for monitoring and management" (Moritz 1994b). Moritz (1994a, b) defined management units as populations that differ significantly in allele frequencies at nuclear or mitochondrial loci. Population genetic structure must be resolved to identify appropriate management units for striped newt conservation.

The objectives of this study were to 1) determine population genetic structure of striped newts to identify potential management units as targets for conservation, 2) infer historical biogeographic patterns based on a mitochondrial DNA (mtDNA) gene genealogy, 3) test Dodd and LaClaire's (1995) biogeographic hypothesis, which predicts that genetic differences exist between western and eastern striped newt populations, and 4) provide management agencies with conservation recommendations for the striped newt based on genetic data. Gene flow among locations sampled was estimated with ϕST and *Nm* values, and divergence among haplotypes was estimated with the Kimura two-parameter model.

Methods

Sample Collection

Samples were collected from 10 locations throughout the range of *N. perstriatus*, with the exception the Tifton and Vidalia Uplands of Georgia (Table 5-1, Fig. 5-1). Newts were captured mainly with dip nets, although in a few cases seine nets or wire-screen funnel traps were used. A relatively small section (based on the size of the animal) of the distal end of the tail of each individual was removed and placed in a uniquely labeled vial containing saturated salt buffer (NaCl; 25mM EDTA pH 7.5; 20% DMSO; protocol modified from Amos and Hoelzel, 1991). Tail sections, which usually amounted to less than 15% of an individual's total length, were removed with dissection scissors; scissors were cleaned and sterilized with alcohol between individuals. This tail-clip method is nonlethal and individuals were released shortly after the sample was taken. Samples were stored at room temperature until used for DNA extraction.

DNA Isolation and Sequencing

Whole genomic DNA was isolated from each sample using standard phenol/chloroform extraction followed by ethanol precipitation and storage in Tris/EDTA buffer (Hillis et al., 1996). A 790 base-pair fragment located in the cytochrome b (*cytb*) gene of the mitochondrial DNA (mtDNA) genome was amplified by polymerase chain reaction (PCR) methodology using primers H14447 (Edwards et al., 1991) and MVZ15 (Moritz et al., 1992). Amplifications were carried out in 25 µl reactions containing: 1x buffer, 3 µM MgCl2, 200 µM each dNTP, 0.25 µM each primer, 1 U Taq polymerase (Sigma), and 2-5 ng of template DNA. All amplifications were performed in a Biometra UNO thermocycler. Following an initial denaturation at 94°C for 3 min, 35 cycles of polymerase chain reaction (PCR) were ran under the following conditions: denaturing for 1 min at 94°C, annealing for 1 min at 54°C, and extension for 1 min at 72°C. PCR products were purified with 30,000 MW filters (Millipore, Inc., Bedford, MA). At the University of Florida's DNA Sequencing Core, sequencing reactions were conducted with Big Dye technology (Applied Biosystems, Inc., Foster City, CA) using a robotic workstation (ABI model 800), and the fragments were gel-separated using an automated sequencer (ABI model 377). Ambiguous sequences were re-amplified and sequenced to confirm the accuracy of the nucleotide sequence designations. Sequences of haplotypes from the western portion of the species's range (haplotype F) and the eastern portion of the range (haplotype C) were submitted to GenBank (accession numbers AF380362 and AF380363, respectively).

Data Analysis

Chromatograms were checked against computer base designations, then aligned using Sequencher version 3.1 (Genes Codes Corp., Ann Arbor, MI). Divergence among haplotypes (*d*) was estimated with the two-parameter model of Kimura (1980). Nucleotide diversity (π; Nei, 1987) and haplotype diversity (*h*; Nei, 1987) were calculated with the program Arlequin, version 1.1 (Schneider, et al., 1997). I estimated the proportion of gene diversity within and between collection sites with ϕ_{ST} values based on the AMOVA (Excoffier et al., 1992) function in Arlequin. Pair-wise estimates of gene flow among sites (*Nm*: number of migrants per generation) were determined using the formula $Nm = (1/\phi_{ST}-1)/4$ (Slatkin, 1993). The average migration rate (*Nm*) between the sampled sites was calculated with the private-allele method (Slatkin, 1985) using equation 14 of Slatkin and Barton (1989). Sites with sample sizes less than five (i.e., JSF, n = 1; and NSJC, n = 2) were excluded in pair-wise calculations of ϕ_{ST} and *Nm* values. These samples were included, however, in species-wide estimates of genetic diversity. To reveal relationships among haplotypes, phylogenetic trees were generated using the parsimony option in PAUP* version 4.016 (Swofford, 1998). An unrooted parsimony network of haplotypes was constructed and imposed on a map to visualize phylogeographic patterns.

Results

A 593 bp fragment of the *cytb* gene was aligned for 86 samples collected throughout most of the range of the striped newt (Table 5-1, Fig. 5-1). Comparisons among the sequences revealed 53 variable nucleotide sites including 37 transitions and 17 transversions (Table 5-3; nucleotide site 95 contained both a transition and a transversion). Twenty-seven haplotypes were identified among the 86 samples (Table 5-4). The percent sequence divergence (d) among the haplotypes ranged from $d = 0.00169$ to $d = 0.03879$. The number of haplotypes identified at each collection location ranged from one (ONF, JSF) to seven (CBTS), and overall haplotype diversity (h) was 0.8996 (Table 5-4). Overall nucleotide diversity (π) among the 27 haplotypes was $\pi = 0.00091$ (Table 5-4).

Most sample locations contained endemic haplotypes, and only haplotypes A, B, and C were found at more than one site. Haplotype C was the most widespread, but was shared among only three of the ten locations (KOP, NSJC, and ODNA; Table 5-4), occurring with the greatest frequency (62.5%) at the ODNA site in Georgia. Haplotype A was the most common and was found at sites KOP and CBTS, both in north central Florida. Eighty-three percent of individuals at KOP had haplotype A, whereas only 18.2% of individuals from CBTS had haplotype A (Table 5-4). Haplotype B was shared between RSPSR and ONF at the southern end of the range of *N. perstriatus*. All individuals analyzed from the three ponds representing the ONF site had haplotype B, whereas 60% of the individuals from the single pond sampled at RSRSP showed haplotype B. The remaining 24 haplotypes were endemic to single locations, although multiple individuals within a location had the same haplotype in some instances (Table 5-4).

Haplotype diversity varied considerably among sites. CBTS had the greatest h (0.867), with seven unique haplotypes among 11 individuals. At two sites, ONF and JSF, only a single haplotype was observed. In many instances haplotypes differed by only a single nucleotide position and corresponding nucleotide diversity "π" was relatively low (Table 5-4).. Haplotypes S, M, and N were the most divergent from the consensus sequence, differing at 14, 11, and nine nucleotide positions, respectively.

The distribution of haplotypes indicates very strong genetic differentiation among collection sites. Overall $\phi_{ST} = 0.67$; a value that indicates highly significant population structure across the range of this species and very restricted gene flow among sites. Pair-wise comparisons of ϕ_{ST} values between sites are presented in Table 5-5. With the exception of sites excluded because of small sample size (JSF and NSJC), all pair-wise ϕ_{ST} values were significantly different ($P < 0.05$), based on 100 permutations for each comparison.

The estimated number of migrants per generation (Nm) among sites is presented in Table 5-5. Because ϕ_{ST} values were used to calculate the Nm values, these two measures of population divergence are directly related. Nevertheless, Nm values provide perspective on the estimated exchange of individuals among sites in a management context. The overall migration value (excluding the JSF and NSJC sites) was $Nm = 0.265$.

A geographic distribution of the 27 haplotypes illustrates the limited number of haplotypes shared among collection sites (Fig. 5-2). The topology produced by a neighbor-joining analysis (Fig. 5-3) was consistent with a manually constructed parsimony network (Fig. 5-4). There are distinct western (i.e., ANF and JJEC sites) and eastern phylogroups, which are separated by a hiatus in the species's range of about 120 km (Figs. 5-3 and 5-4). The eastern phylogroup is further partitioned into at least two, and possibly three, sub-groups. Numerous branch lengths in Fig. 5-3 are relatively short because of the low sequence divergence among some of the haplotypes, but nonetheless indicate a phylogeographic signal.

Discussion

Population Structure

Significant population genetic structure was revealed throughout the range of the striped newt. An overall high AMOVA estimate of $\phi_{ST} = 0.67$ and corresponding low estimate of migration rate among locations sampled ($Nm = 0.265$) indicates a high degree of genetic divergence because of restricted contemporary gene flow. The low *Nm* value demonstrates the high degree of isolation among the locations sampled since migration between populations in excess of four migrants per generation ($Nm \geq 4$) is required to homogenize populations at mitochondrial loci (Birky et al., 1983). Gene flow is severely restricted and, consequently, population differentiation has likely occurred through genetic drift.

Both genetic data and mark-recapture studies (Chapter 3) indicate that relatively low vagility of striped newts and the patchy distribution of sandhill and scrub habitats limit long distance dispersal. However, within an area of contiguous, suitable habitat, individuals disperse hundreds of meters and they occasionally colonize or recolonize isolated ponds (Chapter 3). For example, of the areas sampled, the KOP site is best represented. I analyzed sequences of 24 individuals from seven ponds (numbers 4, 5, 6, 7, 9, 10, 11) at the KOP site (Table 5-1; Fig 5-5.). Four haplotypes were revealed among the 24 samples, with haplotype A found at all ponds (Tables 5-2, 5-4). Sharing of haplotype A among the ponds indicates that they are tightly connected by recent gene flow. Moreover, a mark-recapture study demonstrated movement of a newt between two of the ponds that are separated by almost 700 m, and newts commonly dispersed hundreds of meters from their pond (Chapter 3).

Genetic data show strong separation between habitat fragments across the range of *N. perstriatus* and a mark-recapture study has revealed considerable movement within at least one of these fragments (e.g., KOP site). I therefore hypothesize that the KOP site supports a metapopulation (Hanski and Simberloff, 1997) of striped newts and that striped newts may persist at most locations as metapopulations. I suggest that within a metapopulation, ponds act as focal points for demes (i.e., subpopulations) and that there are periods of extirpation and recolonization that characterize each deme over time. The same focal pond may serve as a source at one point and a sink at another. A pond at which newts arrive to breed but where they are unsuccessful because of a short hydroperiod or high predation level could act as a sink. Successful reproduction in the pond may occur during wet periods or when predators are sparse. Over time, a specific deme of newts may decline (Dodd, 1993), and possibly become extirpated. Recolonization is possible by dispersal through contiguous upland habitat. Although dispersal occurs at a local scale (i.e., metapopulation scale) as shown by mark-recapture study, the pair-wise and overall ϕ_{ST} values indicate that gene flow between metapopulations is severely restricted.

Testing a Biogeographic Hypothesis

Dodd and LaClaire (1995) hypothesized that striped newts colonized Georgia via two separate corridors, along sandy river terraces in the west, and along marine terraces (primarily Trail Ridge) in the east. If this supposition is correct, they predicted that "genetic differences may exist between western striped newt populations and the eastern striped newt populations." There is an apparent large (ca. 125 km) hiatus in the distribution of striped newts in Florida, separating the Florida animals into eastern and western clusters (Dodd et al., in press; Franz and Smith, 1999).

The genetic data based on *cytb* sequences support this biogeographic hypothesis. A neighbor-joining tree (Fig. 5-3) depicts a distinct western phylogroup, composed of samples from the ANF site in Florida and the JJEC site in Georgia. Some of the haplotypes from these sites were not very divergent (Fig. 5-4) and the pair-wise ϕ_{ST} value between these two sites was the smallest (0.173) of all pair-wise values (Table 5-5). Therefore, gene flow between the sites may have occurred relatively recently. However, the two sites are genetically distinct and they did not share haplotypes (Table 5-4, Fig. 5-2). These two sites comprise a western phylogroup (Fig. 5-3) that is genetically divergent from the eastern phylogroup. The eastern phylogroup appears to be divided into two or thee additional groups (Fig. 5-3), all of which are closely associated with relict coastal ridge systems in peninsular Florida and eastern Georgia. Sequence divergence among most of the eastern haplotypes is relatively shallow, and there is no overt phylogeographic signal that is absolutely parsimonious with the distribution of the several ridge systems that characterize peninsular Florida and eastern Georgia (Hall, 1966; White, 1970). Nonetheless, if newts persist long enough into the future, it is possible that the isolated newt metapopulations associated with the different ridge systems will continue to diverge genetically because of restricted gene flow and lineage sorting (Avise, 1994). Eventually a stronger phylogeographic signal may develop, concordant with the distribution of the different ridge systems, such as has been revealed for the Florida endemic scrub lizard (Clark et al., 1999).

Although samples were analyzed from throughout the range of the striped newt, one area of interest in Georgia was not sampled. Consequently, the genetic affinities of striped newts that persist in apparent isolation within the Tifton Uplands in Irwin Co. (Dodd and LaClaire, 1995) are unknown. However, based on Dodd and LaClaire's interpretation of newt biogeography, I speculate that newts from Irwin Co., may be closely allied with the western phylogroup. Dodd and LaClaire (1995) suggested that newts in the western portion of the specie's range (i.e., western phylogroup) may have dispersed into Georgia along sandy terraces running parallel to rivers that drain into the Gulf of Mexico. On the other hand, newts of the eastern phylogroup in Georgia are thought to have dispersed along the "Trail Ridge and other marine terraces parallel to the coast" and perpendicular to rivers draining into the Atlantic (Dodd and LaClaire, 1995). Newts in Irwin Co. are located close to the Alapaha River (Dodd and LaClaire, 1995), which is part of the Suwannee River basin, a Gulf Coast drainage. If Irwin Co. newts prove to be allied with the western phylogroup, this would further support the Dodd and LaClaire (1995) biogeographic scenario.

Striped Newt Biogeography and Phylogeography

Genetic data have been analyzed for many vertebrate species in the southeastern United States, thus providing a region-wide phylogeographic interpretation across numerous taxa (Avise, 1996, 2000; Walker and Avise, 1998). Most species surveyed show significant phylogeographic structure. The striped newt showed significant mtDNA structure across its range as well. The phylogeographic pattern revealed for striped newts best approximates the category III pattern, "most or all haplotypes are related closely, yet localized geographically", described by Avise (2000). Sequence divergence (*p*) among the 27 haplotypes was ranged from $p = 0.00169$ to $p = 0.03879$. Nevertheless, most haplotypes were endemic, with only three haplotypes shared among sample collection locales (Table 5-4; Fig. 5-2). Another pattern observed in many of the species previously assayed in the Southeast, which included freshwater and terrestrial forms, is the presence of a fundamental phylogeographic split separating species into eastern and western phylogroups. Similar to these species, striped newts showed a pattern in which a western phylogroup, is distinct from an eastern phylogroup.

The location of the split between the eastern and western phylogroups for the striped newt is remarkably concordant with the boundary between eastern and western clades of the gopher tortoise (Osentoski and Lamb, 1995) and the white-tailed deer (Ellsworth et al., 1994). In each of the three species, mtDNA analysis revealed a phylogeographic boundary in panhandle Florida and southeastern Georgia east of the Apalachicola River drainage. In Florida, this area is recognized as a significant zoogeographic boundary, influencing the distribution of freshwater fishes (Gilbert, 1987). Although phylogeographic patterns of other species also show distinct eastern and western genetic assemblages, the precise geographic location and "evolutionary depth" of this east/west split varies among taxa (Avise, 1996).

Changes in sea level and climate influenced Florida's natural communities throughout the Pleistocene (Webb, 1990) and this certainly impacted the present-day genetic population structure of striped newts. The difference in mtDNA sequences between the most divergent striped newt haplotypes was 3.9%. Using an estimate of 0.8% sequence divergence per million years, suggested by Tan and Wake (1995) for North American salamandrids, it is clear that events during the late Pliocene, and especially during the middle Pleistocene, had a major influence on the phylogeography of striped newts. Historical events have led to a patchy distribution of xeric upland habitats required by striped newts presently. Likely having evolved from an ancestor adapted to the xeric conditions of the Madro-Tertiary Geoflora, the range of the striped newt has probably always been linked to the distribution of xeric habitats, mainly scrub and sandhill. Current distribution of scrub communities is just a remnant of a historically much more extensive ecosystem (Myers, 1990). Dry savanna-like habitat (resembling modern sandhill) was also more widespread in Florida during the early Pleistocene (Meylan, 1981; Webb and Wilkins, 1984; Webb, 1990), and certainly xeric habitats predominated across much of the peninsula during the Wisconsinan glaciation (Myers, 1990; Watts and Stuiver, 1980; Webb, 1990). Presently, scrub and sandhill communities occur as isolated habitat islands in panhandle and peninsular Florida (Myers, 1990). The natural patchy distribution of striped newt habitat, probably contributed to the apparent development of metapopulations throughout the range of the species. Much of the naturally fragmented striped newt habitat has been severely impacted by humans reducing the extent of suitable habitat to a mere fraction of what is was just a century ago (Means, 1996; Myers, 1990). Human disturbance has further isolated metapopulations and probably caused the extirpation of some local populations. Considering the fragmented and isolated nature of present striped newt habitat and the relatively limited dispersal abilities of newts, it should not be surprising that significant genetic structure was found across the range of *N. perstriatus*.

Conservation and Management Implications

Genetic and drift-fence data show that gene flow occurs among ponds at a local scale (i.e., within metapopulations). However, as indicated by pair-wise estimates of migration rates between sites (Table 5-5), gene flow is severely restricted between the sites sampled. The fact that only a few haplotypes were shared among populations and the ϕ_{ST} values were significant in all pair-wise comparisons supports the designation of site-specific management units. In fact, each management unit probably represents a different metapopulation. The current patchy distribution of high pine uplands (Myers, 1990) certainly contributes to restricted gene flow observed and probably influence metapopulation structuring across the species range. Based on these data, the sites sampled are demographically isolated from one another and should be considered as management units. Management units are populations recognized to have significant divergence of allele frequencies at nuclear or mitochondrial loci (Moritz, 1994a).

Practical considerations also indicate that each location sampled (i.e., metapopulation) should be managed as an independent demographic unit. As a result of habitat loss and degradation, as well as the patchy distribution of upland xeric habitats required by striped newts, the species is now almost entirely restricted to public lands (Dodd and LaClaire, 1995; Franz and Smith, 1999) and many different organizations are ultimately responsible for management of these public lands (e.g, U.S. Forest Service, U.S. Department of Defense, Florida Division of Forestry, Florida Department of Environmental Protection, Georgia Department of Natural Resources). If striped newts become extirpated at any of these sites, the genetic data indicate that no recolonization will occur within a timeframe meaningful to resource managers. Clearly, most land management practices at one site will have no effect on newt populations at other sites. Although each organization is responsible for making management decisions to secure the long-term persistence of an isolated striped newt metapopulation(s), similar conservation and management procedures should be followed at all sites.

Managing the habitat at a landscape scale (i.e., ecosystem management) will benefit numerous other taxa in addition to the striped newt. Conserving and protecting small, temporary wetlands where striped newts breed, as well as the adjacent uplands, will also enhance populations of the numerous other species that rely on these habitats (Dodd and Charest, 1988; Dodd, 1992; Guyer and Bailey, 1993; Johnson, 1999; Moler and Franz, 1988). Managing upland habitat and restoring historical conditions seem the most effective approach to striped newt conservation. Such an approach will rely heavily on prescribed burn programs. Regular burning of appropriate upland habitat will maintain the dynamics of metapopulations, facilitating dispersal of individuals among demes. In addition to prescribed burning and protecting isolated wetlands, mechanical disturbance of herbaceous ground cover should be avoided or eliminated. Such disturbance, associated with silvicultural practices, is one form of habitat degradation that has contributed to the decline of *N. perstriatus*. If the species becomes federally listed those agencies and organizations responsible for land management will have to become more attentive to these recommendations to ensure that their land management practices enhance the quality of striped newt habitat.

Table 5-1. Locations of striped newt breeding ponds in Georgia and Florida where samples were collected.

Location no.	State	County	No. ponds sampled	Location of pond(s)
1	Florida	Orange	1	Rock Springs Run State Preserve (RSRSP)
				Spears Scrub Pond; Sanford SW Quad.; sec6, T20S, R29E
2	Florida	Marion	2	Ocala National Forest (ONF)
				Neofiber Pond; Lake Delancy Quad.; sec22-23, T12S, R25E
				Mud Bog Pond; Lake Kerr Quad.; sec36, T13S, R25E
		Putnam	1	Greenberg Pond 6; Lake Delancy Quad.; sec36, T12S, R25E
3	Florida	Putnam	7	Katharine Ordway Preserve-Swisher Memorial Sanctuary (KOP)
				Blue Pond; Putnam Hall Quad.; sec15-16, T9S, R23E
				Smith Lake; Putnam Hall Quad.; sec23-24, T9S, R23E
				Harry Prairie Sinkhole Pond; Putnam Hall Quad.; sec15-16, T9S, R23E
				Fox Pond; Putnam Hall Quad.; sec28, T9S, R23E
				Clear Pond; Putnam Hall Quad.; sec24, T9S, R23E
				Breezeway Pond; Putnam Hall Quad.; sec24, T9S, R23E
				One Shot Pond; Melrose Quad.; sec28, T9S, R23E
4	Florida	Clay	1	Camp Blanding Training Site (CBTS)
				unnamed pond; Gold Head Branch Quad.; sec35, T7S, R23E
5	Florida	Clay	1	Jennings State Forest (JSF)
				Franz pond 7; Middleburg Quad.; sec32, T4S, R24E
6	Florida	St. Johns	1	Northern St. Johns County (NSJC)
				unnamed pond; no location available
7	Georgia	Bryan	3	Ft. Stewart Military Installation (FSMI)
				DS pond 1; no location available
				DS pond 2; no location available
				DS pond 3; no location available
8	Georgia	Emanuel	1	Ohoopee Dunes Natural Area (ODNA)
				unnamed pond; Norristown Quad.; 23 36.23' N, 82 24.97' W
9	Florida	Leon	1	Apalachicola National Forest (ANF)
				borrow pit pond; Lake Munson Quad.; sec3, T2S,R1W
10	Georgia	Baker	3	Joseph Jones Ecological Research Center (JJEC)
				Pond 40; Bethany Quad.; 31 15.66' N, 84 31.75' W
				Pond 41; Bethany Quad.; 31 15.65' N, 84 31.74' W
				Rhexia Pond; Elmodel Quad.; 31 16.22' N, 84 29.73' W

Table 5-2. Number of samples analyzed and haplotypes discovered at each location. Individual sample ID numbers are presented so samples can be referenced to stored DNA and tissue samples at the University of Florida.

Location no.	Location acronym	No. samples analyzed	Haplotypes observed	Sample ID nos.	Pond name(s)
1	RSRSP	5	B	Np47, 48, 50	Spears Scrub Pond
			H	Np49, 54	Spears Scrub Pond
2	ONF	8	B	Np66, 67, 68, 69	Neofiber Pond
				Np80, 81, 82	Mud Bog Pond
				Np26	Greenberg Pond 6
3	KOP	24	A	Np2, 171	Blue Pond
				Np142	Smith Lake
				Np149, 151, 153, 154	Harry Prairie Sinkhole Pond
				Np158, 160, 161, 162	Fox Pond
				Np167	Clear Pond
				Np175, 176, 178, 179	Breezeway Pond
				Np127, 128, 129, 130	One Shot Pond
			C	Np11	Blue Pond
				Np150	Harry Prairie Sinkhole Pond
			R	Np3	Blue Pond
			T	Np159	Fox Pond
4	CBTS	11	A	Np95, 99	unnamed pond
			E	Np93, 100, 102, 104	unnamed pond
			M	Np98	unnamed pond
			N	Np101	unnamed pond
			O	Np103	unnamed pond
			P	Np94	unnamed pond
			Q	Np97	unnamed pond
5	JSF	1	Z	Np16	Franz pond 7
6	NSJC	2	C	Np59	unnamed pond
			U	Np58	unnamed pond
7	FSMI	13	D	Np105-109, 111, 112, 114	DS pond 3
			I	Np4	DS pond 1
				Np116	DS pond 2
			J	Np5	DS Pond 1
			K	Np115	DS Pond 2
			L	Np118	DS Pond 1
8	ODNA	9	C	Np72, 74-77	unnamed pond
			G	Np70, 71, 78	unnamed pond
			AA	Np79	unnamed pond
9	ANF	8	F	Np7, 8, 42, 44, 45	borrow pit pond
			V	Np43	borrow pit pond
			W	Np41	borrow pit pond
			S	Np40	borrow pit pond
10	JJEC	5	X	Np30, 37	Pond 40
			Y	Np31, 38	Pond 41
				Np35	Rhexia Pond

Table 5-3. Variable nucleotide sites found in striped newt cytochrome *b* sequences. The 27 haplotypes are identified by letters followed by numbers (read top to bottom) to indicate nucleotide locations of polymorphic sites within the 593-base sequence.

	2	7	1	2	2	3	3	4	5	6	6	7	8	9	9	9	1	1	1	1	1	1	1	1	2	2	2	2	2	2	2	3	3	3	3	3	3	4	4	4	4	4	4	4	4	4	5	5	5	5	5	5	5
			5	1	3	4	6	0	7	5	6	8	3	5	7	9	1	1	2	2	2	2	4	7	0	0	2	3	4	5	5	3	3	4	6	7	9	0	0	0	4	4	4	5	5	9	0	1	1	1	2	6	7
Haplotypes																	6	7	2	3	8	9	4	2	4	7	3	2	6	1	2	3	5	8	8	5	9	3	7	8	0	7	8	1	6	1	7	0	5	6	9	7	5
Concensus	A	T	T	G	A	A	T	T	T	T	T	T	T	A	A	C	C	T	C	A	T	A	G	G	T	T	A	A	A	T	G	T	G	A	T	T	G	A	A	A	C	A	T	C	C	C	C	T	T	A	T	T	T
AA	-	-	C	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	T	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	G	-	-	-	-	-	-	-	-	-	-	-	-	-
C	-	-	C	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	G	-	-	-	-	-	-	-	-	-	-	-	-	-
B	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	G	-	-	-	-	-	-	-	-	-	-	-	-	-
H	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	G	-	-	-	-	-	-	-	-	-	-	-	C	-
G	-	-	C	-	-	-	-	-	-	-	C	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	G	-	-	-	-	-	-	-	-	-	-	-	-	-
U	-	-	C	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	T	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	G	-	-	-	-	-	-	-	-	-	-	-	-	-
L	-	-	C	-	-	-	-	-	-	-	-	-	-	-	-	-	-	C	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	G	-	-	-	-	-	-	-	-	-	G	-	-	-
O	-	-	C	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	G	-	-	C	-	-	-	-	-	-	-	-	-	G	-	-	-	T	-	-	-	-	-	-	-	-	-
D	-	-	C	-	-	-	-	-	-	-	-	-	-	-	-	-	-	C	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	G	-	-	-	-	-	-	-	-	-	-	-	-	-
I	-	-	C	-	-	-	-	-	-	-	-	-	-	-	-	-	-	C	-	-	-	-	-	-	-	-	-	-	-	-	A	-	-	-	-	-	-	-	-	G	-	-	-	-	-	-	-	-	-	-	-	-	-
J	-	-	C	-	-	-	-	-	-	-	-	-	-	-	-	-	-	C	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	G	-	-	-	-	G	-	-	-	-	-	-	-	-	-	-	-	-	-
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Z	-	-	-	-	-	G	-	-	-	-	-	-	-	-	-	-	T	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	C	A	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-
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F	-	-	-	-	-	G	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	C	-	-	-	-	-	-	-	-	-	G	-	-	-	T	-	-	-	-	-	-	C
Y	-	-	-	-	-	G	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	C	-	-	-	C	-	-	-	-	-	G	-	-	-	T	-	-	-	-	-	-	C
W	C	-	-	-	-	G	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	C	-	-	-	C	-	-	-	-	-	G	-	-	-	T	T	-	-	-	-	-	C
X	-	-	-	-	-	G	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	C	-	-	-	C	-	-	-	-	-	G	-	-	-	-	-	-	-	-	-	-	C

Table 5-4. Striped newt haplotypes, haplotype diversity (h), and nucleotide diversity (π) at each location.

Location	Haplotypes																													
	A	B	C	D	E	F	G	H	I	J	K	L	M	N	O	P	Q	R	S	T	U	V	W	X	Y	Z	AA	Total	h	π
1) Orange Co. RSRSP	—	3	—	—	—	—	—	2	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	5	0.600	0.001
2) Marion Co. ONF	—	8	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	8	1.000	0.000
3) Putnam Co. KOP	20	—	2	—	—	—	—	—	—	—	—	—	—	—	—	—	—	1	—	1	—	—	—	—	—	—	—	24	0.297	0.002
4) Clay Co. CBTS	2	—	—	—	4	—	—	—	—	—	—	—	1	1	1	1	1	—	—	—	—	—	—	—	—	—	—	11	0.867	0.012
5) Clay Co. JSF	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	1	—	1	—	—
6) St. Johns Co. NSJC	—	—	1	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	1	—	—	—	—	—	—	2	—	—
7) Bryan Co. FSMI	—	—	—	8	—	—	—	—	2	1	1	1	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	13	0.628	0.001
8) Emanuel Co. ODNA	—	—	5	—	—	—	3	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	1	9	0.639	0.001
9) Leon Co. ANF	—	—	—	—	—	5	—	—	—	—	—	—	—	—	—	—	—	—	1	—	—	1	1	—	—	—	—	8	0.643	0.008
10) Baker Co. JJEC	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	3	2	—	—	5	0.600	0.001
Totals	22	11	8	8	4	5	3	2	2	1	1	1	1	1	1	1	1	1	1	1	1	1	1	3	2	1	1	86		

Table 5-5. Pairwise *Nm* (above diagonal) and ϕST values among the 10 striped newt sample locations.

Location	1	2	3	4	5	6	7	8	9	10
1) Orange Co. RSRSP	■	0.51	0.06	0.59	—	—	0.08	0.14	0.15	0.02
2) Marion Co. ONF	0.331	■	0.06	0.47	—	—	0.06	0.10	0.12	0.01
3) Putnam Co. KOP	0.797	0.818	■	0.31	—	—	0.04	0.05	0.09	0.03
4) Clay Co. CBTS	0.299	0.347	0.443	■	—	—	0.20	0.31	0.38	0.33
5) Clay Co. JSF	—	—	—	—	■	—	—	—	—	—
6) St. Johns Co. NSJC	—	—	—	—	—	■	—	—	—	—
7) Bryan Co. FSMI	0.748	0.800	0.858	0.557	—	—	■	0.17	0.07	0.02
8) Emanuel Co. ODNA	0.633	0.722	0.831	0.445	—	—	0.599	■	0.10	0.02
9) Leon Co. ANF	0.620	0.675	0.725	0.396	—	—	0.771	0.711	■	1.20
10) Baker Co. JJEC	0.912	0.962	0.817	0.429	—	—	0.920	0.913	0.173	■

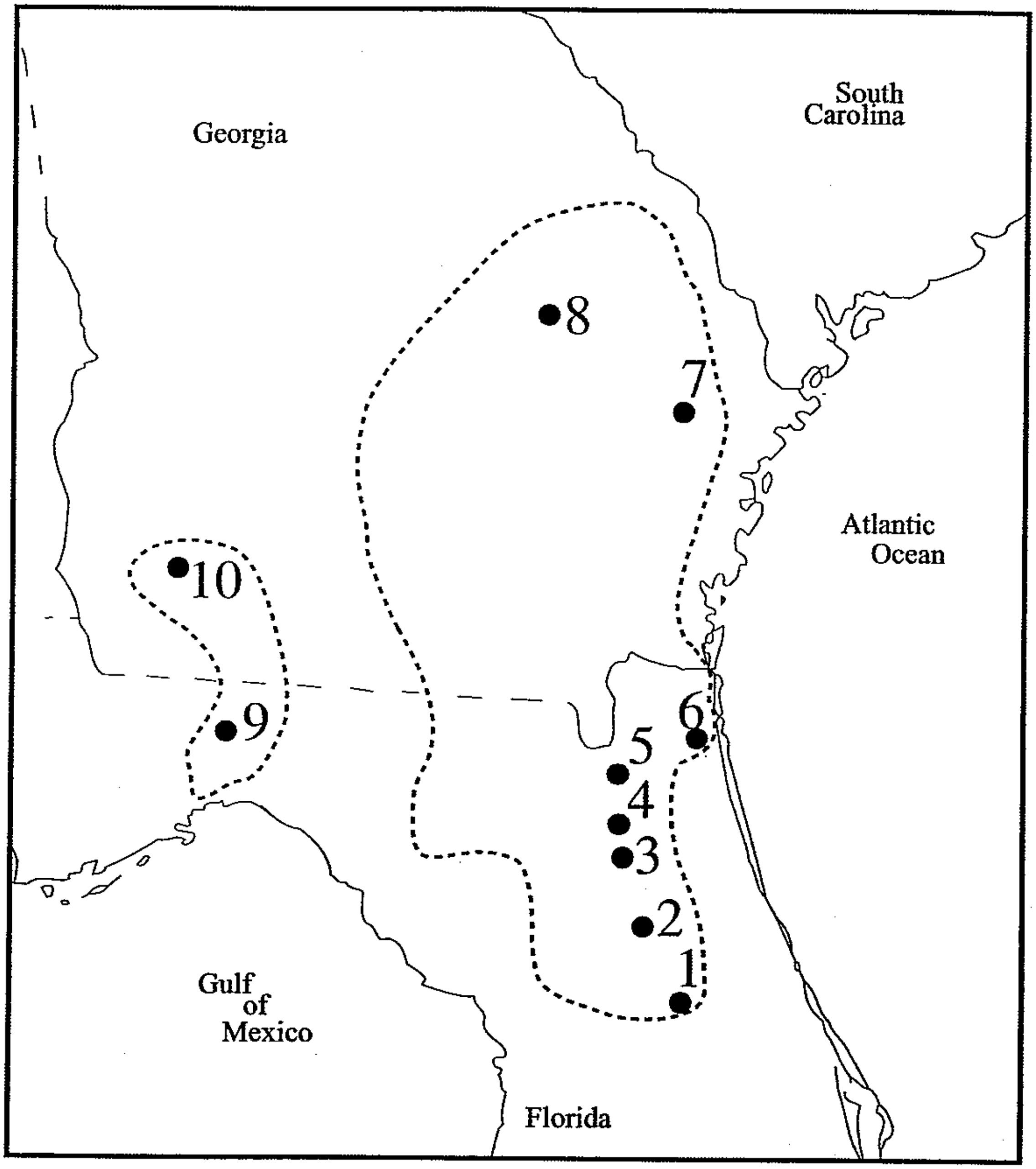

Fig. 5-1. Sampling locations of striped newts in Florida and Georgia. Dots on the map are approximate locations. Refer to Table 5-1 for specific locations. The dashed line shows the present range of the species.

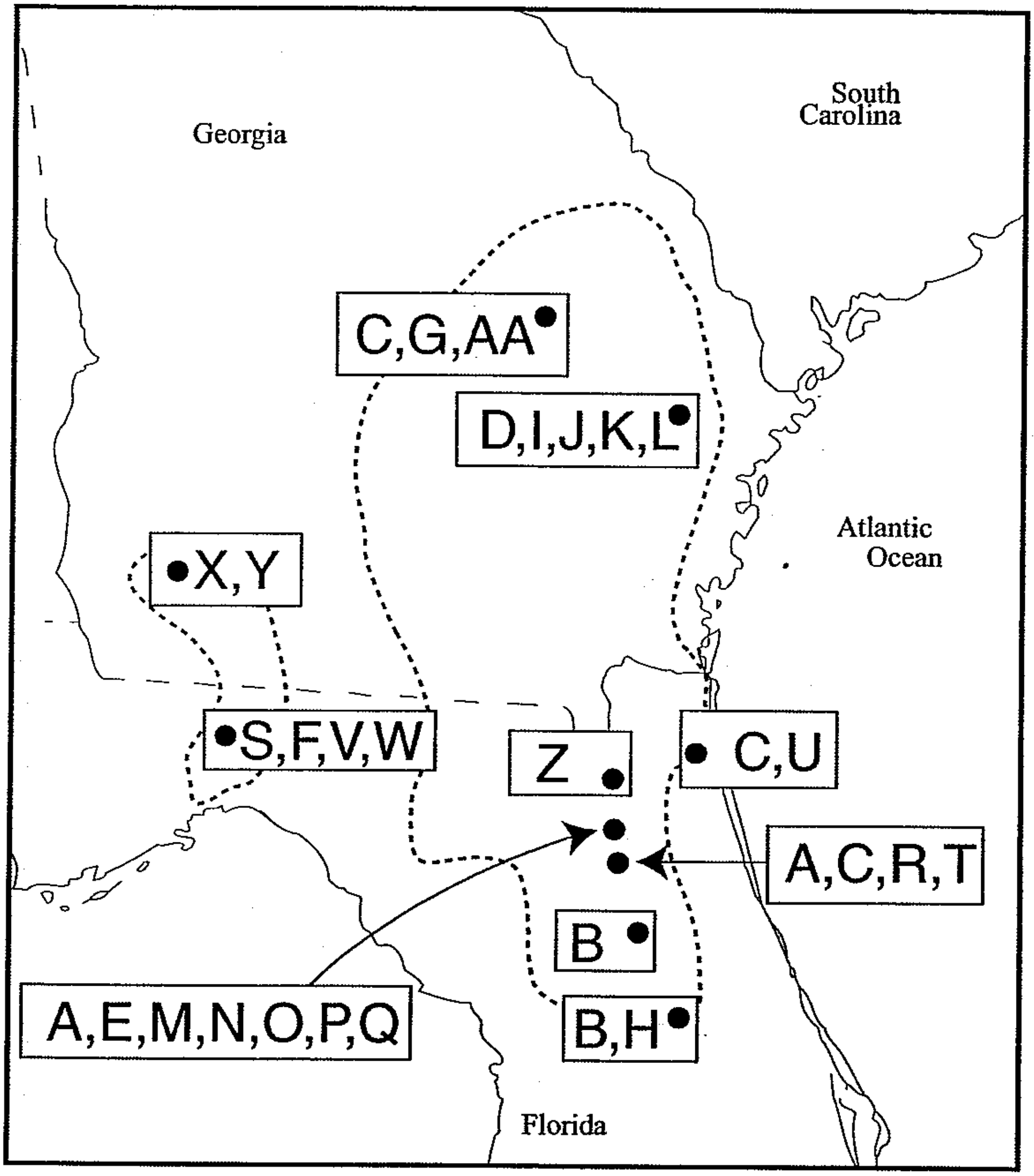

Fig. 5-2. Geographic distribution of the 27 striped newt haplotypes among the 10 sites sampled in Florida and Georgia. Dots on the map are approximate locations. Refer to Table 5-1 for specific locations. The dashed line shows the present range of the species.

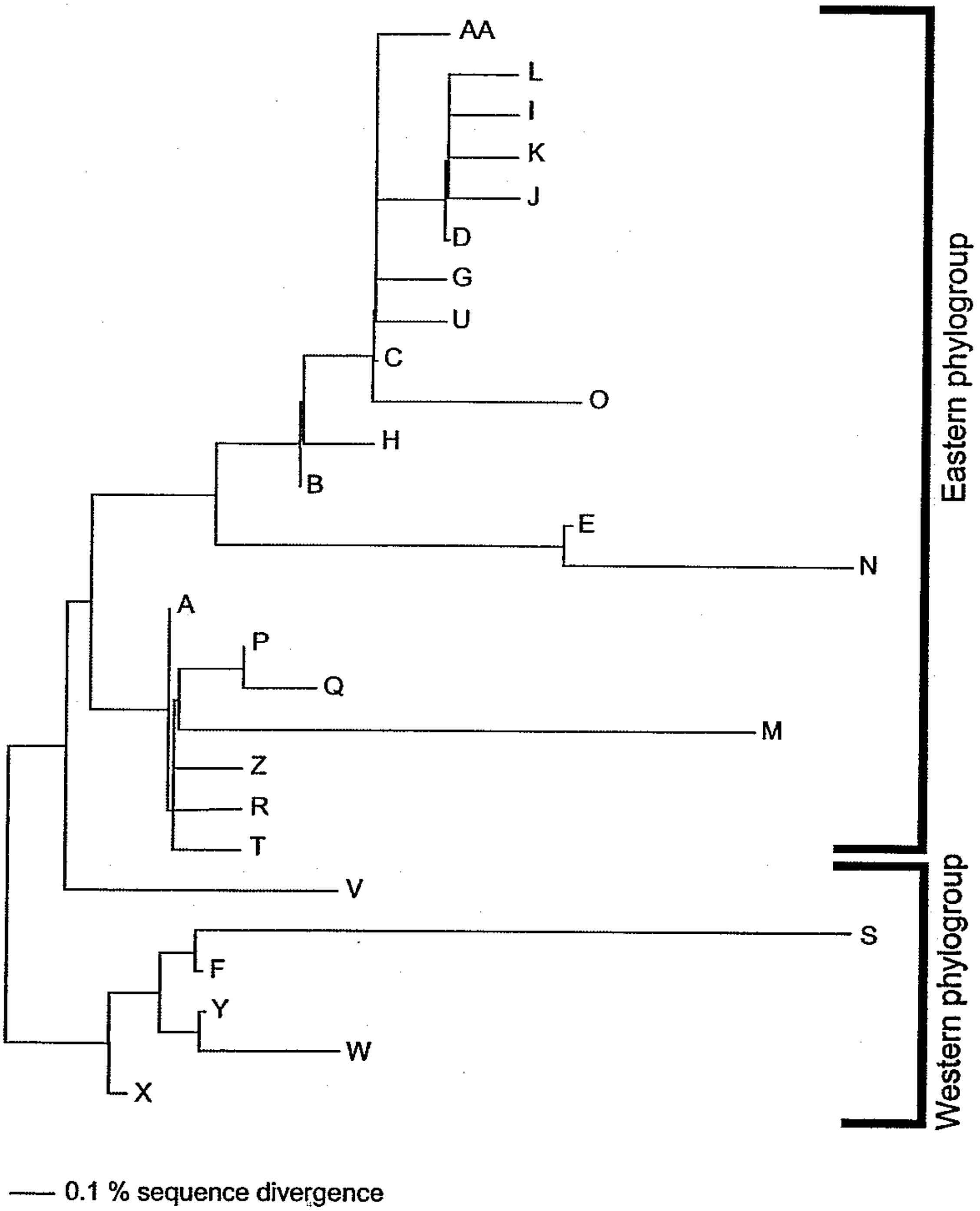

Fig. 5-3. Neighbor-joining tree (midpoint rooted) showing the phylogenetic relationships among the 27 mtDNA haplotypes for the striped newt. Note the two major phylogroups indicated at the right.

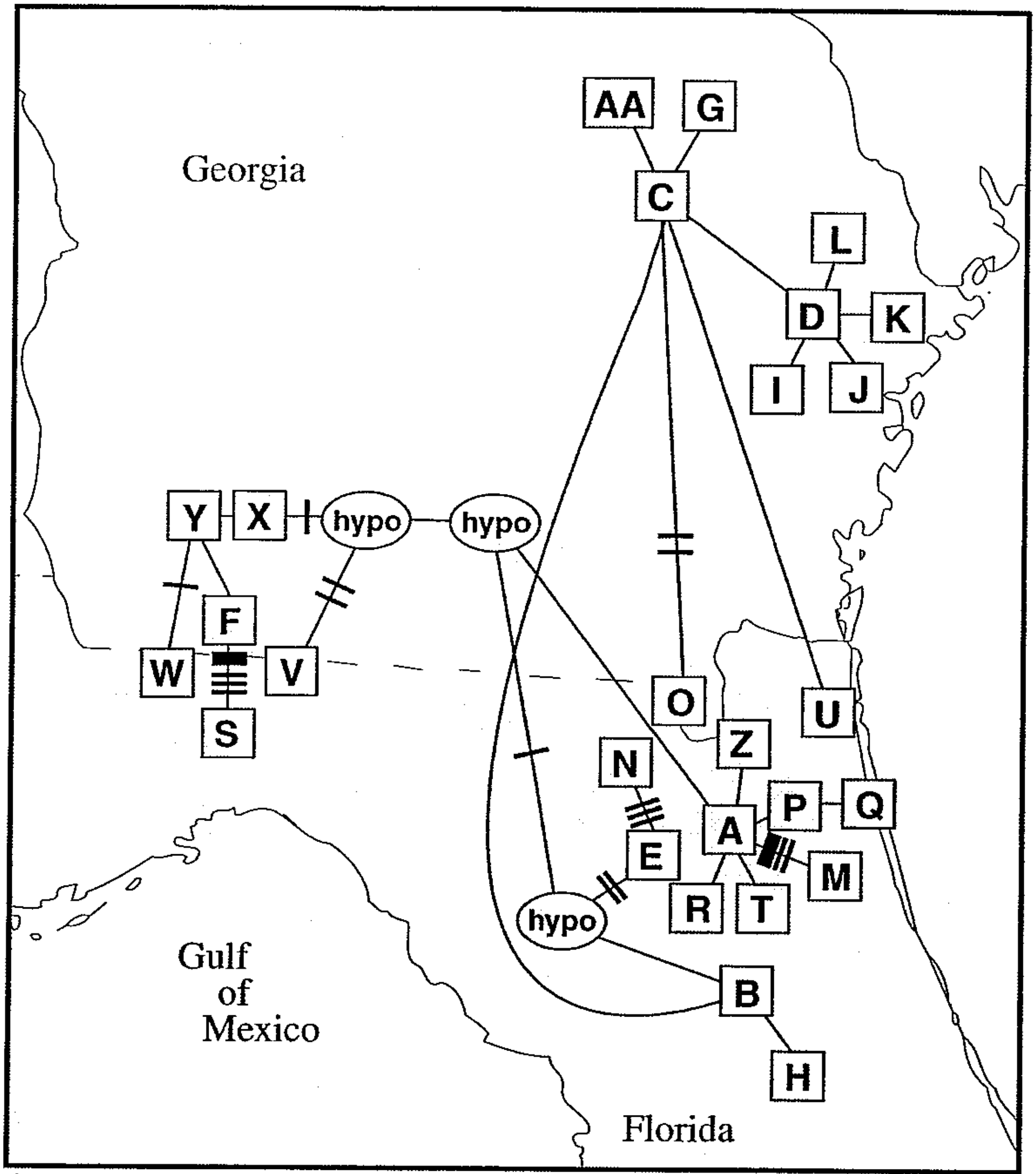

Fig. 5-4. Hand-generated parsimony network showing the number of nucleotide differences between each of the haplotypes. The network is roughly overlaid on the locations where samples were collected. Because of the map's scale, locations of haplotypes are only approximate. Tables 5-1 and 5-2 give specific locations where haplotypes were found. A plain line connecting haplotypes indicates one nucleotide difference between the haplotypes. Thin cross dashes indicate additional nucleotide differences (1 per dash) and thick dashes represent 5 nucleotide differences. Hypothetical haplotypes, or possibly contemporary ones not discovered during sampling, are indicated in the ovals as "hypo".

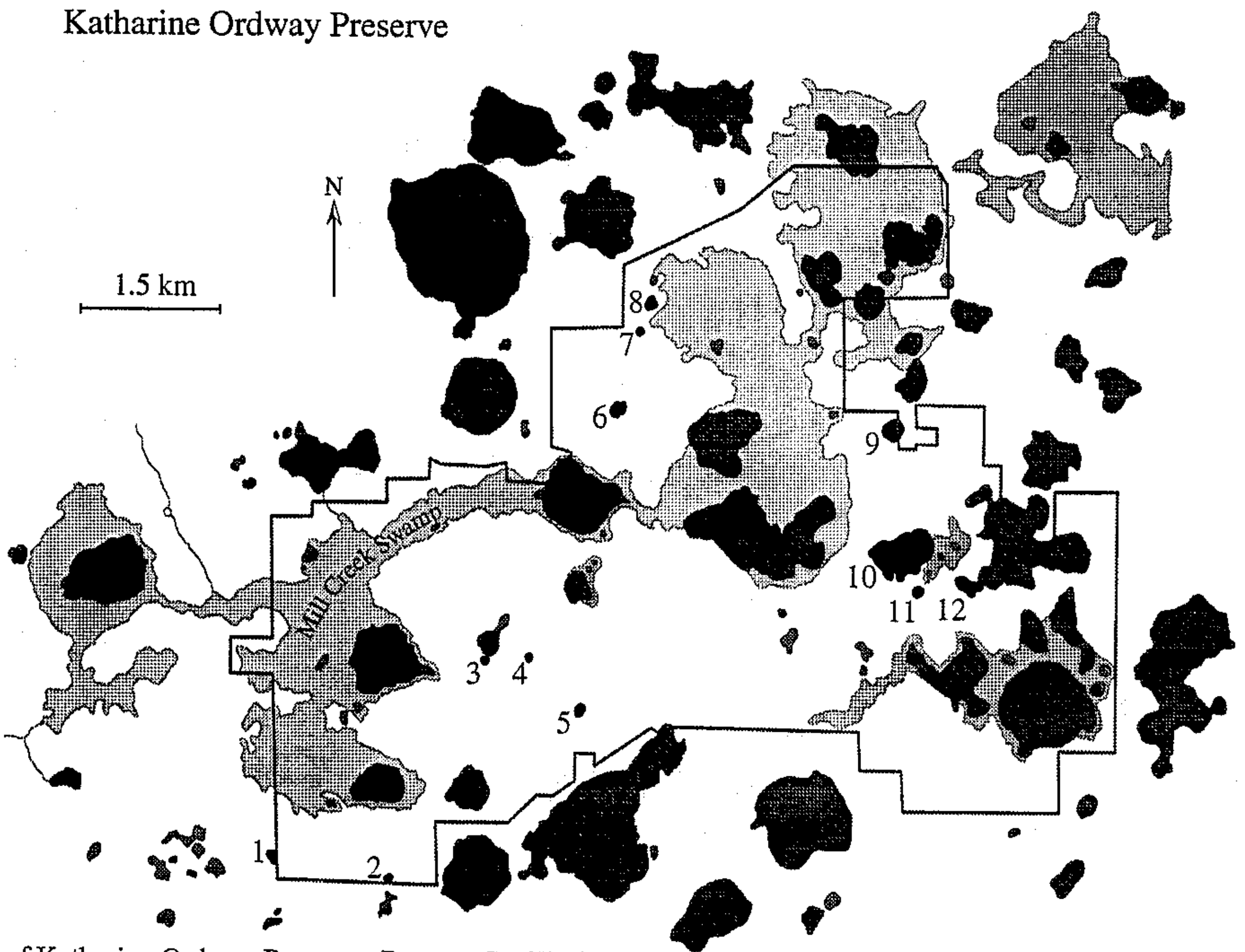

Fig. 5-5. Map of Katharine Ordway Preserve, Putnam Co. Florida (i.e., KOP site). Known striped newt breeding ponds are identified with numbers and are shown in black. These ponds include: 1) Recess, 2) South Fence, 3) Barry, 4) One Shot, 5) Fox, 6) Blue, 7) Harry Prairie Sinkhole, 8) Harry Prairie, 9) Clear, 10) Smith Lake, 11) Breezeway, 12) Breezeway Sandhill. Other ponds and lakes are shown in dark gray with their associated prairies and swamps in light gray.

CHAPTER 6
SUMMARY AND CONCLUSIONS

Life-history Summary

Field-collected data at OSP (Chapter 2) and Breezeway Pond (Dodd, 1993), demonstrate that striped newts have a complex life-cycle involving terrestrial and aquatic stages (Fig. 1-1). Breeding occurs exclusively in aquatic habitats of fishless ponds that are small and have variable hydroperiods (Carr, 1940; Campbell and Christman, 1982; Christman and Means, 1992; Dodd and LaClaire, 1995; Dodd et al., in press; Franz and Smith, 1999; Stout et al., 1988). Larvae feed and grow in ponds until they reach a SVL of 18-20 mm, which appears to be the minimum size necessary for striped newts to initiate metamorphosis (Chapter 2; Dodd, 1993). If metamorphosis is not initiated at this size, an individual will continue to grow and will follow one of two life-history pathways (Chapter 4). After more growth, but before sexual maturation is reached, it may metamorphose (metamorphic pathway) and leave the pond as an immature eft. The other life-history pathway results in maturation while the larval morphology is retained (paedomorphic pathway). Paedomorphs reproduce when they are about 1 year old, then metamorphose and leave the pond, even if the pond holds substantial water. The life-history pathway "decision" appears to be controlled in part by expression of genes that may be influenced by environmental factors (Chapter 4). Striped newts spend much of their lives in uplands surrounding breeding ponds, and individuals disperse hundreds of meters after metamorphosis or reproduction (Chapter 3; Dodd, 1996). The quality of upland habitat has an important influence on the local persistence of striped newts. Fire exclusion in uplands and conversion of native longleaf pine (*Pinus palustris*) uplands to monoculture pine plantations (e.g., slash pine—*P. elliottii*, loblolly pine—*P. taeda*, and sand pine—*P. clausa*), especially if done in conjunction with mechanical site preparation, have contributed to the decline of *N. perstriatus* throughout the species' range (Dodd and LaClaire, 1995; Franz and Smith, 1999; Jensen, 1999; R. C. Means, pers. comm.). Because of the current patchy distribution of localities where striped newts persist, as a result of anthropogenic and natural causes, remaining striped newt populations are effectively isolated. Cytochrome *b* sequence data from samples collected throughout the range of striped newts show that contemporary gene flow between habitat fragments is severely restricted (Chapter 5). On a local scale, gene flow occurs among some breeding ponds. Taken together these data suggest that striped newts form metapopulations and that the long-term survival of the species may depend on preserving existing metapopulations.

Conservation, Management, and Research Prospectus

Current knowledge of striped newt life history, status and distribution, and population genetic structure can be used to make recommendations for the conservation and management of the species. In general, presence of newts at a location (Dodd and LaClaire, 1995; Franz and Smith, 1999) suggests that land managers are managing the habitat effectively. Nevertheless, present management practices may not ensure the long-term persistence of newts where they are currently found. Land managers should consider the following recommendations carefully. Some of the suggestions are not novel; for example, Christman and Means (1992), Dodd (1993), Dodd and LaClaire

(1995), and Franz and Smith (1999). Most of the recommendations which follow are based on the results of my studies, or they reinforce the ideas previously presented.

Managing upland habitats to reestablish historical ecosystem function is the most effective approach to achieve the conservation of striped newts. Such an approach will rely on a prescribed burn program. Managing upland and pond habitats as a unified landscape should prove an effective conservation strategy. Protecting and managing small, seasonally-ponded wetlands where striped newts breed, as well as the adjacent uplands, also will enhance populations of the numerous other species that rely on these habitats (Dodd, 1992; Dodd and Charest, 1988; Guyer and Bailey, 1993; Johnson, 1999; Moler and Franz, 1988). Semlitsch (2000) presented an excellent template for land managers concerned with aquatic breeding amphibians. My recommendations lend support for his protocols.

The order in which the following recommendations are listed does not imply any hierarchy of importance. Suggestions for additional research on striped newts follow most recommendations. Recommendations for management and additional research are often not mutually exclusive.

1. <u>Manage striped newt metapopulations as independent demographic units</u>. Remaining populations in both Florida and Georgia are confined to isolated areas because of the natural patchy distribution of appropriate upland habitats as well as habitat loss and habitat degradation caused by anthropogenic factors. Genetic data (Chapter 5) show strong partitioning of striped newt metapopulations, and there is essentially no contemporary gene flow among metapopulations, as indicated by pairwise values of ϕ_{ST} and an overall ϕ_{ST} of 0.67. These data imply that if a local extinction of a metapopulation

occurs, it will not be recolonized naturally from other metapopulations on a contemporary time scale. Based on the genetic data presented in Chapter 5, the locations sampled meet the requirements of Management Units (Moritz 1994a, b).

Although samples were analyzed from throughout the range of the striped newt, one region of interest in Georgia was not sampled. Consequently, the genetic affinities of striped newts that persist in apparent isolation within the Tifton Uplands in Irwin Co. (Dodd and LaClaire, 1995) are unknown. Based on the biogeographic scenario proposed by Dodd and LaClaire (1995), these newts are probably allied with the western phylogroup (Chapter 5). Tissue samples of newts from this location should be analyzed to determine the genetic relationship of newts in this area.

2. Protect small, isolated wetlands where striped newts are known to occur or may potentially occur. Striped newts breed exclusively in ponds that are devoid of predatory fishes. Such ponds are isolated and usually dry frequently; they are often less than one hectare in extent (LaClaire, 1995; Means et al., 1994). Small, isolated wetlands receive little protection at local or federal levels (Chapter 3; Semlitsch, 2000). If striped newts are to be conserved, small, isolated wetlands must be afforded protection. Furthermore, as initially suggested by Christman and Means (1992), stocking of fish in known or suspected breeding ponds should never be allowed.

Research on striped newt breeding ponds is needed. Dodd and LaClaire (1995) reported biotic and abiotic characteristics of striped newt ponds in Georgia, and LaClaire (1995) presented vegetative and soil characteristics of dry pond basins for several known newt ponds in Florida. Hydroperiods of striped newt breeding ponds vary considerably (R. Means, pers. comm.; K. Greenberg, pers. comm.). A very short a hydroperiod will preclude or negate reproduction, but a long hydroperiod may result in colonization by predatory fishes (Chapter 2; Semlitsch, 2000). The window of hydroperiod lengths that allows local persistence of striped newts is unknown and needs to be established. Such data would be useful to identify potential breeding sites. In addition, wildlife managers need to know which microhabitat features of a breeding pond affect metamorphosis of striped newt larvae (e.g., types of predators, density of larvae, food availability). In captivity, larval striped newts eat zooplankton, but the diet of larvae in natural ponds is unknown. Knowledge of food requirements of larvae could help identify potential breeding ponds.

3. Initiate or continue prescribed burn programs in upland sites near striped newt breeding ponds. Although there has never been an empirical test of the effect of fire suppression on striped newts, surveys conducted by several researchers have suggested that local extinction has occurred at sites where fire has been suppressed (Franz and Smith, 1999; R. Means, pers. comm.; S. A. Johnson, unpubl. data). However, fire suppression at some of these sites has been concurrent with conversion of uplands to pine plantations, so interpreting the direct impact of fire suppression is confounded by silviculture. Fire probably plays a crucial role in maintaining productive breeding ponds for striped newts and other pond-breeding amphibians in the southern Coastal Plain. Periodic burning of dry pond basins may be necessary to maintain the quality of breeding ponds. Fires, as evidenced by charring on the stems of shrubs and trees, frequently occur within the basins of many striped newt breeding ponds. Land management practices that discourage fire in small, isolated wetlands should be discouraged. Studies of the

influence of prescribed fire in breeding ponds are crucial to effective conservation planing for striped newts and other pond-breeding amphibians.

Although regular burning of upland habitat may be essential for the persistence of striped newts, the optimal frequency of prescribed fire is unknown, as is the most appropriate season(s) to burn and the optimal fire intensity. It would be valuable to analyze prescribed burn records from locations that support the highest densities of striped newts, such as the Katharine Ordway Preserve and Ocala National Forest, to determine if there is any correlation between burning regime and striped newt relative abundance at breeding ponds. Experiments that manipulate fire frequency, intensity, and burn season would prove informative for managing striped newts, but will be difficult to undertake because of sample size considerations. Research needs to address the fundamental issue of why striped newts appear to persist only at sites that burn regularly. Research should also determine the direct impact of fire suppression in the absence of confounding factors, especially silviculture.

4. Preserve core areas and buffer zones of protected upland habitat around breeding ponds. Striped newts spend most of their lives in upland habitats. A large percentage of striped newts at OSP, located in a sandhill longleaf pine habitat, dispersed hundreds of meters and many newts (an estimated 16% of the breeding population) exceeded 500 m (Chapter 3). Striped newts have been found as far as 709 m from the closest breeding pond (Dodd, 1996). Protecting adequate upland habitat is crucial for persistence of striped newts. Core areas and their associated buffer zones should be as large as possible, but managers should strive to preserve upland sandhill habitat that extends at least 1000 m from the pond edge. Data from OSP show that protected areas of

this amount of habitat will encompass most of the newts that use the pond. Dispersal distances of striped newts in other upland habitat types (e.g., scrub) and at other breeding ponds needs to be studied. In any case, the extent of upland used by striped newts appears to be much greater than that used by pond-breeding salamanders of the genus *Ambystoma* (Semlitsch, 1998). Therefore, extrapolating data across amphibian genera or species may not be justified.

5. Avoid mechanical disturbance of native vegetation in upland habitats, especially near breeding ponds. Silvicultural practices that disturb the herbaceous ground layer and disrupt the soil (e.g., extensive mechanical site preparation) should be avoided because they appear to lead to local extirpation of striped newts (Dodd and LaClaire, 1995). Protecting the ground cover and subsurface soil structure in established core areas and buffer zones is crucial for the persistence of striped newt populations.

6. Maintain corridors of managed habitat at sites where there are striped newt breeding ponds. Genetic and field data demonstrated that striped newts disperse among breeding ponds (Chapter 5). One individual captured as an eft dispersing from OSP was later captured at a neighboring pond (Fox Pond). The genetic data from the Katharine Ordway Preserve indicate that newts disperse between ponds often enough to homogenize the metapopulation at mitochondrial loci. Throughout their range, striped newts appear to persist mainly at locations where multiple breeding ponds have been identified. In concert with dispersal records from OSP and genetic data, this supports the hypothesis that striped newts occur in metapopulations (Chapter 5) and likely require a metapopulation structure for long-term persistence. Maintaining connectivity among

ponds via upland habitat will facilitate metapopulation function and provide a buffer against local extirpation.

Where connectivity among ponds is maintained with habitat corridors, research needs to determine if newts will use the corridors and what corridor characteristics influence newt dispersal among breeding ponds.

7. Surveys should be conducted to locate aditional striped newt populations. Striped newts have declined throughout their range during the past decades. Therefore, all remaining populations are vital to the long-term persistence of the species. Striped newts may persist in some areas and have not been detected because of low population density or lack of survey effort. Given the imperiled status of the species, it is important to identify all remaining sites that support striped newts so that they can be managed properly. Sites found on private land should be purchased or protected through a conservation easement. Permission to manage the property for striped newts should be guaranteed. Based on a habitat model, the Florida Fish and Wildlife Conservation Commission has identified areas that should contain suitable habitat and could serve as target areas for future surveys (Cox and Kautz, 2000). Dodd and LaClaire (1995) identified areas in Georgia that should be surveyed.

8. Striped newts should be regularly monitored at sites where they occur. Regularly monitoring striped newts will enable biologists to determine “natural” levels of population fluctuation and possibly identify the cause(s) if a decline or local extinction occurs. With this information, declines might be mitigated or prevented at other sites. It is crucial to understand population dynamics so that natural fluctuation can be recognized as distinct from declines caused by human impacts (Pechmann et al., 1991).

In conclusion, an effective conservation strategy for striped newts requires a landscape approach. Large tracts of upland habitats containing multiple breeding ponds of varying hydroperiods must be preserved. These areas should be managed to facilitate natural ecosystem processes—fire in the landscape is crucial. Clearly, more information on the upland habitat requirements of striped newts is urgently needed.

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BIOGRAPHICAL SKETCH

Steve A. Johnson was born 19 April 1966, in St. Petersburg, Florida. He grew up in Orlando, Florida where he attended Boone High School, graduating in 1984. He attended Valencia Community College and transferred to the University of Central Florida, where he graduated with a Bachelor of Science degree in biology in 1990.

While he was an undergraduate, Steve became involved with the U.C.F. Marine Turtle Research Group, under the direction of Dr. L. M. Ehrhart. Steve entered the graduate program at U.C.F. in 1991 and studied sea turtle ecology for his Master of Science research. His thesis was entitled "Reproductive Ecology of the Florida Green Turtle" and he graduated with his Master of Science degree in Biological Sciences in the summer of 1994.

Steve began his Ph.D. program at the University of Florida in the spring of 1994, and thus was dual enrolled at U.F. and U.C.F. for two semesters. His initial research at U.F. was on the effects of organized sea turtles watches on loggerhead nesting behavior and hatchling production. However, to broaden his graduate education and research experience, he initiated studies of the striped newt in 1996. While at U.F., Steve worked as a lab technician, graduate teaching assistant, and graduate research assistant; and was funded for 2 years by a grant from the U.S. Fish and Wildlife Service. He is a member of several professional societies.

Steve is married to his soul mate of ten years and counting, Dale Ann Johnson, a artist and biological illustrator. They live with their four cats (Jojo, Ginger, Jasmine, and Cedar), dog (Dude), parrot (Zipper), and several turtles. Steve plans to fish more after graduation.