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

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Abstract - I studied the life history of Striped Newts (*Notophthalmus perstriatus*) at a breeding pond in north-central Florida. Newts were captured in pitfall traps at a drift-fence as they migrated into and out of the pond basin. During the 2-year study, I recorded 10,290 captures (8,127 individuals) of newts at the drift-fence. Newts were active during each month of the study, but there were four peak activity periods, each of which included immigration and emigration events. Immigration events were almost exclusively comprised of adults, whereas emigration events were comprised of adults and recently transformed larvae. I documented 5,296 recently transformed, immature larvae (efts) and 435 recently transformed mature larvae (paedomorphs) during four distinct periods of emigration. Efts matured in the uplands before returning to the pond to breed. In the uplands, male efts (n = 16) grew 0.0183 mm/day on average, whereas average female (n = 24) growth was 0.0167 mm/day. Immigrating adults of both sexes were significantly smaller than emigrating adults. Emigrating efts were smallest, followed by emigrating paedomorphs, immigrating adults, then emigrating adults. The overall adult sex ratio was 1:1.25 (m:f). Sex ratio of emigrating paedomorphs was highly skewed towards females, with one male for every 4.43 females. Newts tended to move during wetter periods, and captures were significantly correlated with rainfall, but rainfall was a poor predictor of the magnitude of newt movements.

INTRODUCTION

Salamanders of the genus *Notophthalmus* occur exclusively in North America with three extant species: *N. viridescens* (Rafinesque), Eastern Newt; *N. meridionalis* (Cope), Black-spotted Newt; and *N. perstriatus* (Bishop), Striped Newt. *Notophthalmus viridescens* ranges throughout the eastern United States and into southeastern Canada, whereas *N. meridionalis* is confined to extreme southeastern 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, 1978b; Harris 1987; Harris et al. 1988; Healy 1970, 1973, 1974a, 1974b, 1975; Hurlbert

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1969; Pope 1924). On the other hand, far less research has focused on *N. meridionalis* or *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 legal status is under review by the U.S. Fish and Wildlife Service (pers. comm., L. LaClaire, Jackson, MS). 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 the life history of *N. perstriatus*, Dodd (1993) monitored Striped Newt demography at a 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 recently metamorphosed 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 Newts.

To gain a better understanding of the life history of this species, I conducted a 2-year study at a breeding pond in north-central Florida. I used a drift fence with pitfall traps 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 size-structure and sex ratios of the population, and 4) to evaluate the influence of hydroperiod and rainfall on Striped Newt movements and reproduction.

FIELD-SITE DESCRIPTION

The study was conducted at One Shot Pond (OSP), an isolated body of water surrounded by 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. 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 (the number of consecutive days a pond holds water) of the pond is variable and the pond dries periodically. Because of drying, OSP does not support fish, and many species of amphibians use the pond (Table 1).

METHODS

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 with pitfall traps (after Gibbons and Semlitsch 1982) that completely encircled the pond. The galvanized metal fence was buried in the ground approximately 15 cm with 35 cm extending above ground. The circumference of the fence was 190 m, with 38 pitfall traps (19 pairs of 19-l plastic buckets) buried flush with the ground at intervals of approximately 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, cushion-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 three times per week and daily during periods of warm weather and/or high rainfall. Because predation by vertebrates and invertebrates was minimal and the foam sponges retained adequate moisture, checking traps on this schedule was frequent enough to keep mortality of trapped newts low (< 2% mortality of trapped newts). The drift fence was monitored from 7 October 1996 to 11 September 1998. 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).

Table 1. Amphibians known to use One Shot Pond, Putnam County, FL during the 2-year study.

Common name	Scientific name
Anurans	
Southern Cricket Frog	*Acris gryllus*
Oak Toad	*Bufo quercicus*
Southern Toad	*Bufo terrestris*
Eastern Narrow-mouthed Toad	*Gastrophyrne carolinensis*
Pine Woods Treefrog	*Hyla femoralis*
Barking Treefrog	*Hyla gratiosa*
Squirrel Treefrog	*Hyla squirella*
Spring Peeper	*Pseudacris crucifer*
Little Grass Frog	*Pseudacris ocularis*
Gopher Frog	*Rana capito*
American Bullfrog	*Rana catesbeiana*
Pig Frog	*Rana grylio*
Southern Leopard Frog	*Rana sphenocephala*
Eastern Spadefoot	*Scaphiopus holbrookii*
Caudates	
Dwarf Salamander	*Eurycea quadridigitata*
Striped Newt	*Notophthalmus perstriatus*

Newts Caught at the Drift Fence

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 July 1998 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, measured to the posterior edge of the vent) was measured to the nearest 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 (Johnson 2001). All 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 (non-gilled, sexually mature newts), efts (immature larvae that recently metamorphosed), and paedomorphs (sexually mature larvae that had recently metamorphosed, Johnson 2001, in press). Although paedomorph refers to an aquatic life stage, I use the term to refer to paedomorphic newts that recently initiated metamorphosis and left the pond. Recently metamorphosed newts (efts and paedomorphs) 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 as they moved toward OSP. Data from newts captured in drift fences that were located in the uplands surrounding OSP are presented in Johnson (2001, in review). 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. I limited data to initial captures because many of these individuals were recaptured in pitfall traps on the outside of the fence soon after they exited the pond basin. Individuals were sometimes captured several times over the course of a few days as they moved back and forth at the fence before finally dispersing into the uplands. 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 were used to test for differences between data sets (Hollander and Wolfe 1999). All statistical analyses, with the exception of χ^2 tests, were performed using SPSS ver. 10.0. I used χ^2 tests to test for departure of 1:1 sex ratios for adults and paedomorphs.

RESULTS

Seasonal Activity

During the 2-year study, 10,290 Striped Newt captures (8,127 individuals) 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. 1). Activity during these four peaks included newts moving into (immigration) and away from (emigration) the pond.

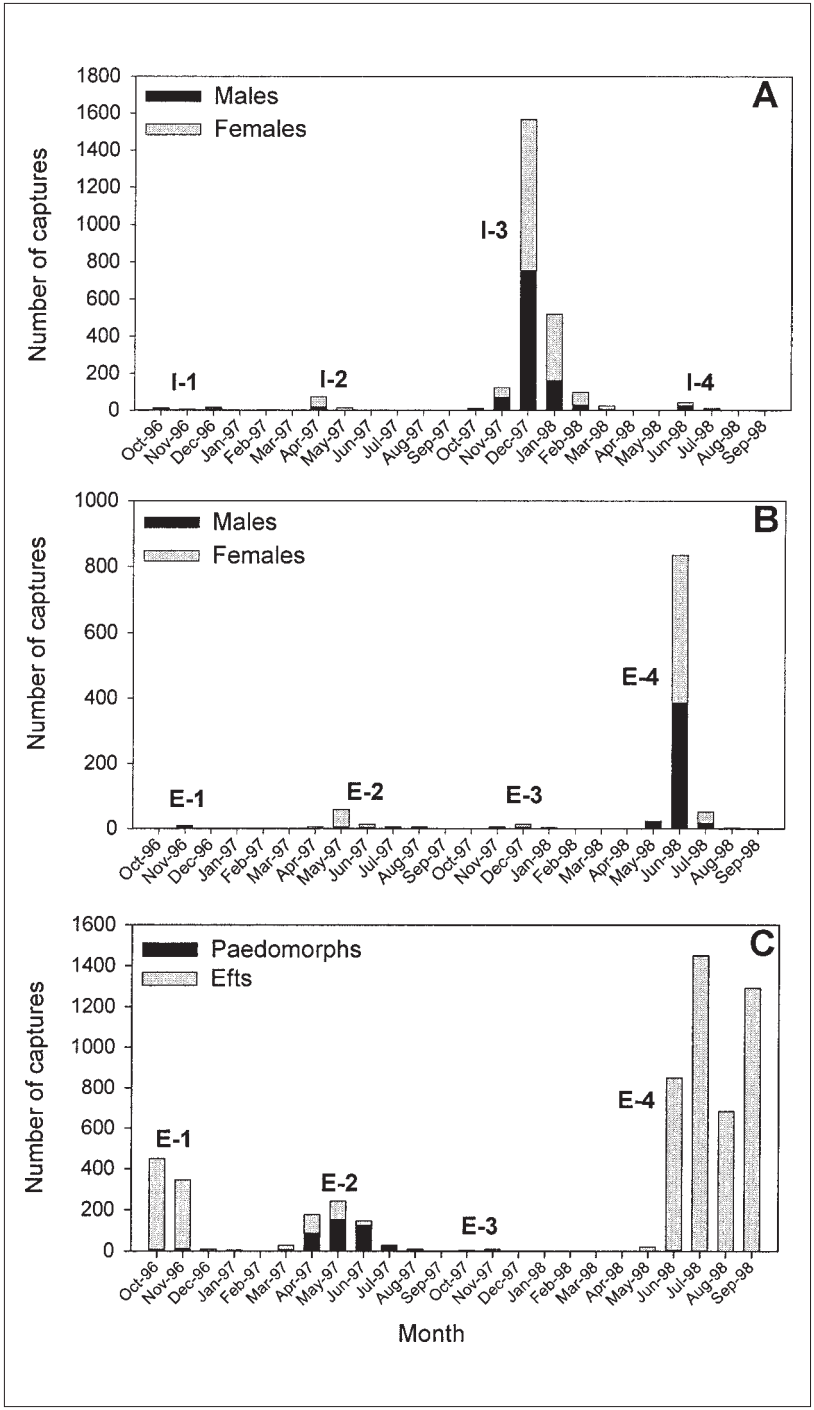
Immigration

Immigration was almost exclusively comprised of breeding migrations of adult Striped Newts, and there were four distinct adult immigrations during the study (Table 2, Fig. 1A). The largest and most prolonged immigration event was immigration Event I-3, which lasted for sixmonths. Peak movement during this event occurred in December 1997 (Fig. 1A). During this month, 1,567 adults were captured entering the pond basin. 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. 1A).

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


A
Males
Females
Number of captures
I-1
I-2
I-3
I-4
B
Males
Females
Number of captures
E-1
E-2
E-3
E-4
C
Paedomorphs
Efts
Number of captures
E-1
E-2
E-3
E-4
Month
Oct-96
Nov-96
Dec-96
Jan-97
Feb-97
Mar-97
Apr-97
May-97
Jun-97
Jul-97
Aug-97
Sep-97
Oct-97
Nov-97
Dec-97
Jan-98
Feb-98
Mar-98
Apr-98
May-98
Jun-98
Jul-98
Aug-98
Sep-98

(Table 2). Similar to immigration, there were four distinct periods of adult emigration (Table 2, Fig. 1B). The largest of these (E-4) occurred toward the end of the study (Fig. 1B). This emigration event accounted for 88% of all emigrating adults with more adults captured leaving the pond in June 1998 than any other month of the study. Female and male adults emigrated during the same times of the year (Fig. 1B).

Efts metamorphosed and emigrated during all months of the year except February, but there were four distinct periods of emigration (Table 2, Fig. 1C). Most efts (81%) emigrated during the last five months of the study period (eft emigration Event E-4). Recently metamorphosed paedomorphs were captured during three emigration events (Table 2, Fig. 1C). Most (94%) were captured from March 1997 through August 1997 (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 course of the study. These individuals likely represented successful reproduction of four distinct breeding bouts, as indicated by emigration of recently transformed newts throughout the study (Fig. 1C). The first evidence of successful reproduction was provided by captures of emigrating efts (E-1, Table 2) and paedomorphs (E-1, Table 2) during the first few months of the study (Fig. 1C). During this period, 776 efts and 25 recently transformed paedomorphs were captured while migrating from OSP (Fig. 1C). The second period of eft and paedomorph production occurred in spring and early summer of 1997. During this time, 214 efts

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

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

Figure 1, facing page. Captures of adult male, adult female, recently transformed eft, and recently transformed paedomorphic Striped Newts at One Shot Pond, Putnam County, FL. Immigrating adults are shown in "A", emigrating adults in "B," and emigrating efts and paedomorphs in "C." Note differences in scales along the Y-axes. Four distinct periods of immigration (I) and emigration (E) are indicated.

and 407 recently transformed paedomorphs were captured (E-2, Table 2, Fig. 1C). Only 16 efts were produced during the third eft emigration event (E-3, Table 2), but no recently transformed paedomorphs were captured during this period (Fig. 1C). By far, the most successful reproductive bout during the two years was indicated by eft emigration (E-4) that occurred during the last five months of the study. Efts were captured starting in late May 1998, and immature larvae continued to transform and leave the pond until the end of the study (Fig. 1C). I likely did not document the full extent of this emigration event because 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 (Johnson 2001, in press). 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 October 1997 through March 1998, 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. However, of 40 newts for which I was confident of the individual toe clip, 39 had matured (i.e., their vents had become swollen) while they were in the uplands. All of these individuals were immature efts (i.e., vents not swollen) when they were initially marked immigrating from OSP. Based on dissections and examination of gonads (Johnson 2001), 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 (SE = 19.7; range = 359–456 days). The average number of days at large since metamorphosis was similar between the sexes. Males (n = 16) averaged 412 days at large (SE = 22.8; range = 359–440 days), whereas females (n = 24) averaged 419 days (SE = 17.4; range = 394–456 days). Net growth, measured as the difference in SVL (mm) between initial capture during emigration and recapture during immigration, was similar for females and males (Wilcoxon rank sum test; $t_s = 0.815$, $P > 0.4$). Males averaged 0.0183 mm/day (SE = 0.0043; range = 0.0129–0.0306), whereas females averaged 0.0167 mm/day (SE = 0.0054; range = 0.0068–0.0295).

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) and mass (Fig. 3). On average, immigrating females were slightly larger (SVL and mass) than immi-

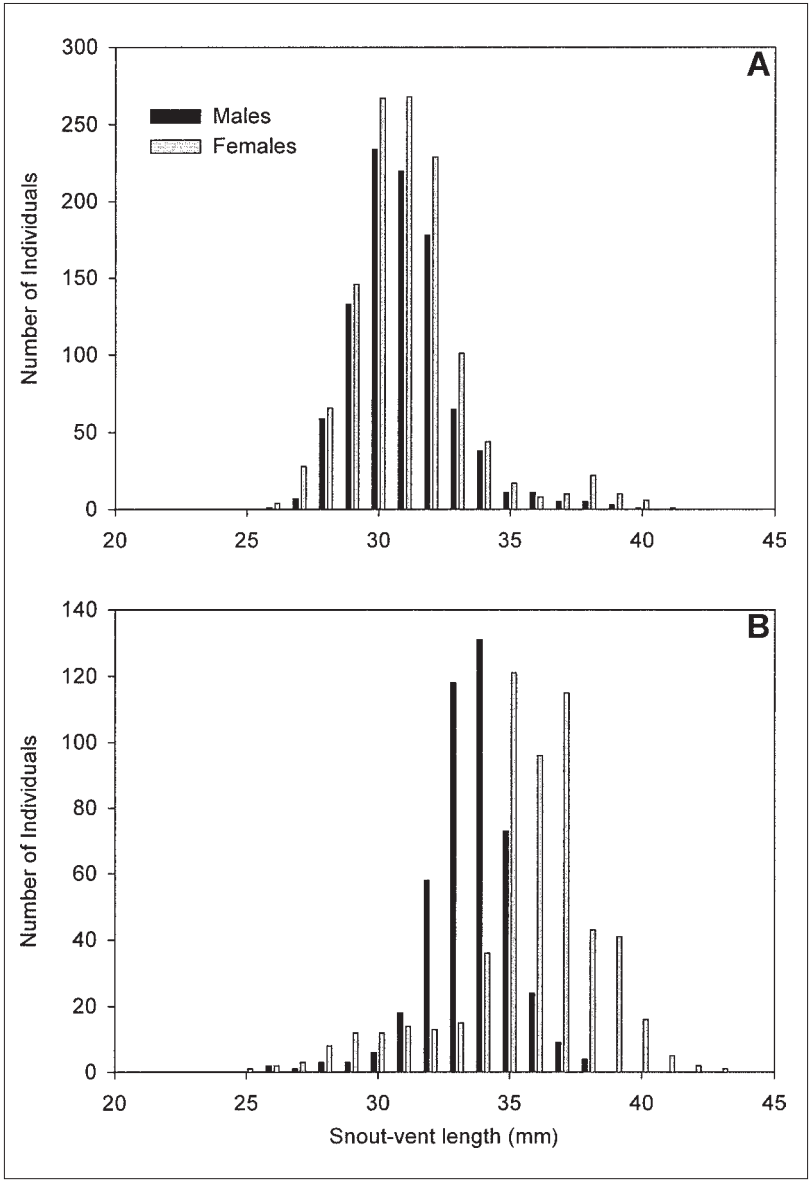


Figure 2. Snout-vent lengths of adult female and male Striped Newts captured at One Shot Pond, Putnam County, FL. Immigrating adults are shown in "A" and emigrating adults in "B."

grating males, and this pattern was evident during immigration Events I-1, I-3, and I-4 (Table 3). During immigration Event I-2, adult males and females were almost the same size (Table 3). Overall differences were not significant for SVL or mass, however (Figs. 2A, 3A). Adult females

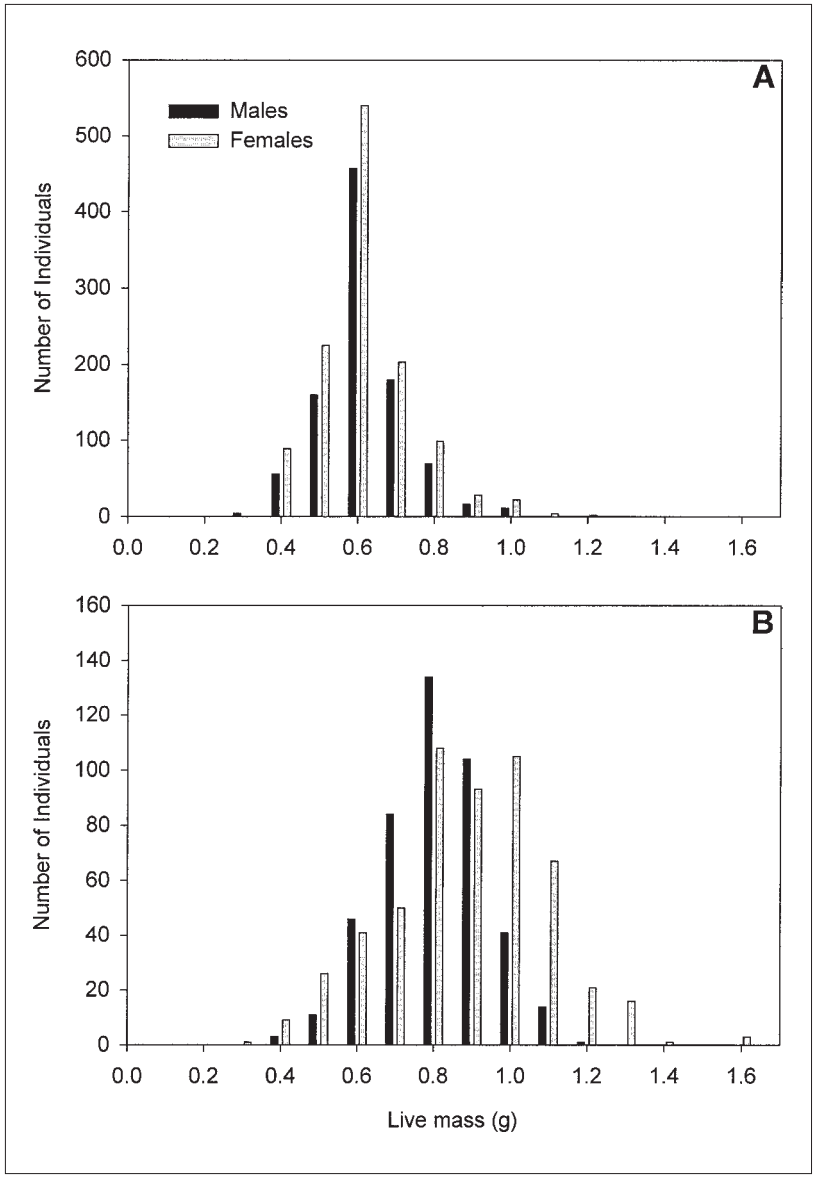


Figure 3. Live mass of adult female and male Striped Newts captured at One Shot Pond, Putnam County, FL. Immigrating adults are shown in "A" and emigrating adults in "B."

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 4). However, SVL and mass were only significantly different between males and females for emigration Event E-4 ($P < 0.0001$). Overall, emigrating females were significantly larger in SVL (Fig. 2B) and mass (Fig. 3B) 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 4). 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 4). *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 4). 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

Table 3. Snout-vent length (SVL) and live mass of adult Striped Newts caught at One Shot Pond, Putnam County, 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
	SE	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
	SE	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
	SE	1.87	0.11	1.66	0.11
I-4	n	10	9	8	6
	Mean	35.60	1.00	34.25	0.90
	Range	33–39	0.8–1.2	33–36	0.8–1.0
	SE	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
	SE	2.24	0.13	1.88	0.11

Table 4. Snout-vent length (SVL in mm) and live mass (g) of adult, recently transformed eft, and recently transformed paedomorph Striped Newts captured at One Shot Pond, Putnam County, FL during four emigration events. Efts were not sexed.

		Adults				Efts		Paedomorphs			
		Females		Males				Females		Males	
Event		SVL	Mass	SVL	Mass	SVL	Mass	SVL	Mass	SVL	Mass
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
	SE	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	31.84	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
	SE	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
	SE	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	–	–	–	–
	SE	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
	SE	2.73	0.21	1.63	0.14	2.33	0.12	2.83	0.19	2.60	0.15

was the same (Table 4). There were no statistical differences in either measure of body size between the sexes (SVL: $t = 1.42$, $P = 0.156$; mass: $t = -0.159$, $P = 0.874$; Table 4). Of the three paedomorph emigrations, Event E-2 had the largest number of individuals (Table 4). 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 4). 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 5). 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 5). 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 5). Overall adult sex ratio (emigrating and immigrating individuals) was female-biased (Table 5; $\chi^2 = 43.9$, 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

Table 5. Sex ratios of adult and recently transformed paedomorph Striped Newts captured at One Shot Pond, Putnam Co., FL. Total values include some individuals not accounted for in the immigration (I) and emigration (E) events listed. Sex ratios are listed as males:females, followed by the number of males and females captured in parentheses.

Event	Adults	Paedomorphs
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
Total-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
Total-E	1:1.22 (469:572)	1:4.43 (81:359)
Grand Total	1:1.25 (1588:1984)	1:4.43 (81:359)

by far the largest of the three events, representing 92% of paedomorph captures. Therefore, E-2 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 ranged from 12–283 mm (Fig. 4). The driest periods were November 1996 through March 1997 and March 1998 through July 1998 (Fig. 4). The wettest period was from June 1997 through February 1998 because of an El Niño/Southern Oscillation event. Rainfall exceeded 100 mm during 13 months of the study period, and beginning in June 1997, there were seven consecutive months 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 = 0.06).

One Shot Pond held water throughout the study period (Fig. 4). Pond depth was lowest (68 cm) in October 1997, but the El Niño rains filled the pond to its greatest depth (275 cm) the following April. Analyses of

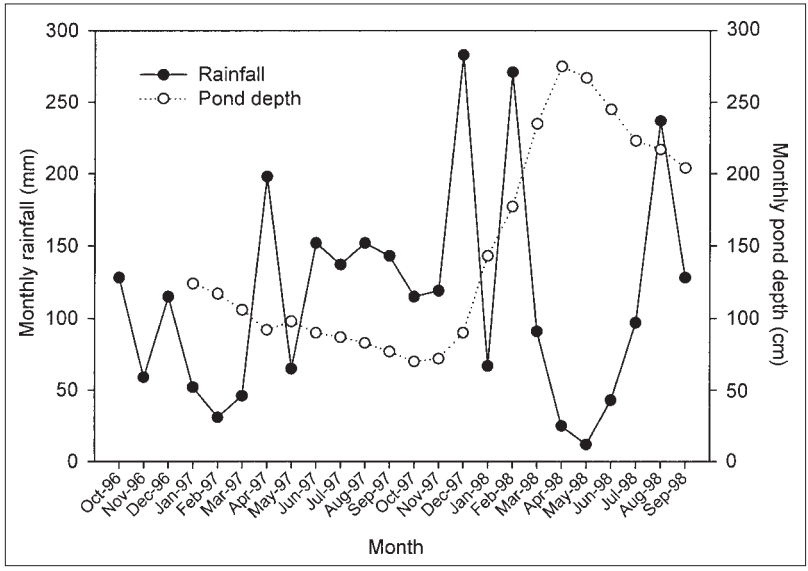


Figure 4. Cumulative monthly rainfall and pond depth recorded at One Shot Pond, Putnam County, FL. Pond depth was not measured until January 1997. Note differences in scale of the Y-axes. Rainfall is reported in mm and pond depth is reported in cm.

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 4), coinciding with the shallowest pond depth during the study (Fig. 4). The largest eft emigration (Event E-4, Table 4) began in May 1998, when pond depth exceeded 260 cm. Pond depth increased steeply during the months before May 1998 (Fig. 4), 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. 1,300 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. 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 October through March and from April through July. At Breezeway Pond, 75% of adults immigrated from January through March (Dodd 1993). Although data collected at OSP support 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 exhibit phenotypic plasticity in the timing of breeding migrations. The only months adults were not documented moving into OSP were August and September. 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 an opportunistic 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, presumably courted and bred, 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 (unpubl. data, S.A. Johnson), 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 (unpubl. data, S.A. Johnson). 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 (Table 2, Fig. 1A, B). 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; pers. comm., B. Means, Tallahassee, FL; pers. comm., K. Greenberg, Arden, NC; pers. comm., D. Stevenson, Ft. Stewart, GA). As a result of a drought, Dodd (1993) only captured 42 recently metamorphosed newts during his entire 5-year study at Breezeway Pond.

Recently transformed efts emigrated in all months except February, but there were periods of concentrated migration, three of which accounted for 99.6% of the captures (Fig. 1C, Table 4). At Breezeway Pond, recently transformed Striped Newts were only captured from June through August 1997. 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 likely resulted from a reproductive event that 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 (Fig. 1A, C). This staggered pattern of adult immigration, later followed by eft emigration, was because larvae apparently required approximately six months to reach metamorphosis. Paedomorphs also likely contributed to the production of larvae in OSP, but the relative contributions of non-gilled adults and paedomorphs are unknown. Data derived from monthly sampling in OSP during the two years of this study support the above supposition (unpubl. data, S. A. Johnson).

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 interpretation is supported by captures at the drift fence encircling OSP (Fig. 1C) as well as monthly samples of newts captured in the pond (unpubl. data, S. A. Johnson). This resulted in a bimodal pattern of emigration of a cohort with immature efts showing up first, followed months later 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. 1C). The few paedomorphs that were caught in June and July 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 (unpubl. data, S. A. Johnson). 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 18–25 mm (n = 47) and 0.1–0.4 g (n = 44). Based on Dodd's (1993) data, a snout-vent length of 18 mm and a mass of 0.1 g may be the 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.

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 25–43 mm, whereas SVL of females at Breezeway Pond ranged from 26–43 mm. One Shot Pond females ranged from 0.3–1.6 g and Breezeway Pond females ranged from 0.3–2.0 g. Adult males at OSP were, on average, slightly smaller than females and ranged in SVL from 26–38 mm with mass ranging from 0.4–1.2 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 two decades it has dried often enough to preclude predatory fishes (pers. comm., R. Franz, Gainesville, FL). 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 his 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-d 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.

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 in breeding ponds. Although Striped Newts of various life-history stages may be found in breeding ponds during all months of the year (unpubl. data, S.A. Johnson), I suggest that spring (April through June) is the best time to conduct aquatic sampling for the species, assuming ponds hold water. Based on captures at the drift fence and monthly samples in the pond, during these months OSP contained all three life-history stages. Sampling for newts during this time of the year should maximize the probability of detecting the species. However, considering the temporary nature of Striped Newt breeding ponds, individuals should conduct surveys whenever breeding ponds hold water, and, as suggested by Dodd (1993), surveys for Striped Newts should include recording biotic and abiotic parameters that might influence the distribution and detection of newts.

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