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Adult Survivorship and Juvenile Recruitment in Populations of Crawfish Frogs (Lithobates Areolatus), With Additional Consideration of the Population Sizes of Associated Pond Breeding Species

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ADULT SURVIVORSHIP AND JUVENILE RECRUITMENT IN POPULATIONS OF CRAWFISH FROGS (*LITHOBATES AREOLATUS*), WITH ADDITIONAL CONSIDERATION OF THE POPULATION SIZES OF ASSOCIATED POND BREEDING SPECIES

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ABSTRACT

Crawfish Frog populations have declined significantly in both the northeastern and southwestern portions of their range, and are listed as state endangered in both Iowa and Indiana. They are animals with a secretive nature, and comparatively little is know about their basic life history and natural history. To address this gap, and to obtain the information necessary to manage for this species in areas of decline, I studied the breeding biology of two Crawfish Frog populations during 2009 and 2010. Using data collected from drift fence and pitfall trap arrays around breeding wetlands, I estimated breeding population sizes, operational sex ratios, breeding adult size ranges, egg and larval survivorship, juvenile recruitment, and adult within-season and between-year survivorship. I also documented the timing of breeding and metamorphosis, spatial patterns of immigration and emigration from breeding sites by adults and recently metamorphosed juveniles, and the diversity and abundance of associated pond breeding species. Crawfish Frog sex ratios were approximately 1:1 (M:F), with male-biased operational sex ratios. Adult sizes were comparatively larger than those reported in other areas of their range, as were sizes of newly metamorphosed juveniles. Breeding occurred from March through May during both years, and metamorphosis occurred from June through August. The number of eggs deposited per wetland ranged from 45,000 to 189,000. Thirteen associated amphibian species (18,109 individuals) and 14 reptile species (435 individuals) were captured at the breeding wetlands. Crawfish Frog survivorship estimates suggest that mortality is high during the larval stage and relatively low during the egg, juvenile and adult stages. Thus, the adult population is

likely regulated by larval survivorship. To help manage for declining populations, captive rearing of larvae could be used to help offset the high mortality experienced during the larval stage and be used to help restore and/or repatriate populations at suitable sites.

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CHAPTER 1

ADULT SURVIVORSHIP AND JUVENILE RECRUITMENT IN POPULATIONS OF CRAWFISH FROGS (*LITHOBATES AREOLATUS*), A SPECIES OF CONSERVATION CONCERN

INTRODUCTION

Amphibians represent a significant proportion of the taxa associated with the Earth's next (sixth) mass extinction (Wake and Vredenburg, 2008). What separates this current mass extinction from previous occurrences is that this one is being anthropogenically driven, and could possibly be reversed given societal and political will. But any desire to halt amphibian declines or restore populations must be accompanied by the knowledge of what is causing these declines and what steps must be undertaken to recover populations. For many species, the lack of basic natural history information is a barrier to management, and is the first knowledge gap that should be addressed in conservation efforts.

Crawfish Frogs (*Lithobates areolatus*) and their closest relatives, Gopher Frogs (*L. capito*) and Dusky Gopher Frogs (*L. sevosus*), together with Pickerel Frogs (*L. palustris*), form the *Nenirana* subgenus of Hillis and Wilcox (2005). While Pickerel Frog populations seem relatively robust (Redmer, 2005), populations of both Gopher Frog species and Crawfish Frogs appear to have experienced and/or are experiencing declines (Jensen and Richter, 2005; Parris and Redmer, 2005; Richter and Jensen, 2005). Dusky Gopher Frogs are U.S. federally listed as endangered (USFWS, 2001), Gopher Frogs are IUCN Red Listed as near threatened (http://www.iucnredlist.org; accessed 7 Dec. 2010), and Crawfish Frog populations have declined significantly in both the northeastern and southwestern portions of their range (SEPARC, 2010). In Indiana, Crawfish Frogs are state endangered, and recent surveys suggest there may be fewer than 1,000 breeding adults in the entire state (Engbrecht, 2010).

Adding to the challenge of evaluating the status and managing for Crawfish Frogs is the inability to detect these frogs for most of the year. According to Smith (1950) "no other species of *Rana* in the country exhibits such secretive habits." When not breeding, Crawfish Frogs obligately inhabit burrows dug by crayfishes (J. L. Heemeyer, *unpubl. data*). Crayfish burrows have the advantage of extending down a meter or more to the water table, and thus offer Crawfish Frogs access to a nearby water source when occupying upland sites. When outside burrows, Crawfish Frogs position themselves on a "feeding platform" adjacent to the burrow entrance. Except when lunging at distant prey, Crawfish Frogs outside of their burrow remain on this platform, and retreat quickly into their burrow when disturbed (Hoffman et al., 2010). Given this wariness, population assessments of Crawfish Frogs can only be realistically accomplished during immigration and emigration at breeding wetlands (Engbrecht, 2010).

Using data obtained from a variety of sampling techniques employed at two breeding wetlands over two years, I offer the first systematically collected data addressing the population biology of Crawfish Frogs. In particular, I document population sizes, operational and absolute sex ratios, survival rates of eggs and tadpoles, juvenile recruitment, and adult survivorship. I also describe triggers to final immigration and emigration movements, timing of breeding and metamorphosis, male/female size differences, and the effect of pond temperature on egg hatching times. Finally, I make comparisons of Crawfish Frog breeding success between wetlands within years, and within wetlands across years. These data identify potential sources of life history elasticities that may be important for management and restoration of Crawfish Frog populations.

MATERIALS AND METHODS

Study Site

My field site is located on the western portion of Hillenbrand Fish and Wildlife Area (HFWA-W) in Greene County, Indiana. HFWA-W comprises 729 hectares that was historically eastern deciduous forest containing scattered pocket prairies (Transeau, 1935; Jones and Cushman, 2004) converted to agricultural fields prior to being mined. Following re-contouring and recovering of this area after mining, it was seeded with prairie species such as big bluestem (*Andropogon gerardii*), little bluestem (*Schizachyrium scoparium*), indian grass (*Sorghastrum nutans*), partridge pea (*Chamaecrista fasciculata*), black-eyed susan (*Rudbeckia hirta)*, and common milkweed (*Asclepias syriaca*). HFWA-W is now managed as prairie by the Indiana Department of Natural Resources' (IDNR) Division of Fish and Wildlife (Lannoo et al., 2009).

As a result of mining activities and post-mining habitat restoration, HFWA-W now includes several bodies of water ranging in hydroperiod from highly ephemeral wetlands, through semi-permanent wetlands, to large final-cut lakes. I have heard Crawfish Frog males calling at seven of these wetlands, and have observed egg masses (evidence of successful breeding) at five. The two study ponds, Nate's Pond and Cattail Pond, are located approximately 0.9 km from each other; both were monitored throughout the periods of Crawfish Frog breeding and metamorphosis in 2009 and 2010.

Nate's Pond is an ephemeral wetland, approximately 0.14 ha in size, that reaches a maximum depth of about 0.5 m in the spring. It was formed unintentionally at the initial site of mining excavation. On the southeast side of the wetland is a large hill where the first spoils were dumped. The wetland itself lies on re-contoured ground that creates a slight slope facing the hill, causing water to accumulate in the resulting depression. Woody vegetation in the pond includes numerous willows (*Salix spp.)* and a few cottonwoods (*Populus deltoides*); understory woody species include introduced bush honeysuckle (*Lonicera maackii*) and raspberries (*Rubus spp*.). Within the wetland, at the north and south ends, willows and hybrid cattails (*Typha angustifolia x latifolia*) predominate; the center of the wetland is characterized by a small open-water area with scattered rushes *(Scirpus* sp.) and aquatic macrophytes. This is where Crawfish Frogs breed. Uplands surrounding the wetland basin consist of herbaceous prairie plantings.

Cattail Pond is a larger, semi-permanent wetland approximately 0.33 ha, with a maximum depth of 1 m. Cattail Pond was also formed unintentionally from either a depression created by uneven contouring during the reclamation process or slumping afterward. Cattail Pond is circular with one large willow at the eastern edge of the pond alongside one bush honeysuckle. Hybrid cattails predominate, occurring densely everywhere except in the center of the pond where there is a roughly circular opening of deeper water. Upland vegetation is reclaimed prairie, similar to the vegetation surrounding Nate's Pond.

Sampling Techniques

I used drift fences paired with pitfall traps to monitor the movement of Crawfish Frogs into and out of wetlands (Gibbons and Bennett, 1974; Gibbons and Semlitsch, 1981; Dodd and Scott, 1994). Full drift fences were installed around Nate's and Cattail ponds in February 2009 when the ground had thawed enough to dig. Fencing was placed about 5 m from the wetland edge. Fence material consisted of woven polypropylene composite fence, 1-m high and buried roughly 10–15 cm below ground, with support stakes placed every 5 m. Hardware cloth was later installed in sections at drainage areas to prevent the washing out of drift fences due to flooding (Lamoureux et al., 2002; Heemeyer et al., 2010). In 2010, I used a more durable monofilament silt fence reinforced by wooden 5 x 60 cm laths. Pitfall traps consisted of 15-L white square buckets placed every 10 m along the inside and outside of the fencing (Heemeyer et al., 2010). Each bucket was fitted with a half lid (open side closest to the fence) to provide shade for trapped animals and deter predators (raccoons, skunks, opossums, feral cats). A sponge was placed in each trap to help prevent desiccation of animals during warm weather, and provide a floating substrate for animals when buckets flooded. A 2.5 cm x 2.5 cm x 40 cm stake was placed in each bucket to facilitate small mammal escape (Dodd and Scott, 1994).

Nate's Pond was enclosed with 270 m of fencing and 26 pairs of pitfall traps; Cattail Pond was enclosed with 280 m of fencing and 27 pairs of pitfall traps (later, one of these pitfall traps located in a perennially wet area was removed). In 2009, pitfall traps were opened from 5 March–16 October. In 2010, pitfall traps were opened from 1 March–19 August. Throughout the breeding season, pitfall traps were checked once daily immediately after sunrise and on rainy nights were checked multiple times (Heemeyer et al., 2010).

Captured frogs were weighed to the nearest 0.5 g (Pesola® spring scale), measured (snout-vent length [SVL]; mm), and sexed (adults); male Crawfish Frogs have vocal sacs and enlarged thumbs, females were either notably gravid or notably spent (assuming the "Gibson Girl" morphology described by Goin and Netting; 1940). Crawfish Frogs were then given individual Passive Integrated Transponder (PIT) tags inserted subcutaneously (Christy, 1996). Adults also received a cohort toe-clip that represented the year the animal was caught; this clip provided redundancy—used to denote recaptured animals if the PIT tag was lost (Richter and Seigel, 2002). Juvenile Crawfish Frogs were also given a cohort toe-clip. The juvenile cohort-clip consisted of two toe-clips: one representing the year, the other representing the pond where captured. All clipped toes were saved; a subset were sent to Dr. Stephen Richter of Eastern Kentucky University for genetic analysis.

In 2010, I surveyed wetlands for Crawfish Frog egg masses. New egg masses were flagged (Forestry Suppliers Inc., Jackson, MS) with the date written on the flag, and monitored daily to determine hatching period and fate (some egg masses never hatched; see below). Characteristics of each egg mass were measured, as follows: maximum diameter; total water depth; depth of egg deposition (measured from the bottom of the egg mass to the bottom of the pond; Palis, 1998). After hatching, a subset of egg masses (n = 5) were brought into the laboratory and the number of undeveloped eggs in each mass was counted (Richter et al., 2003).

Weather data were collected from a portable weather station (HOBO® Micro Station; Onset Computer Corporation, Pocasset, MA), which logged temperature and rainfall data, located at a secure site approximately 3.5 km from Nate's Pond and 3.2 km from Cattail Pond. Additionally, rainfall at each wetland was monitored using a rain gauge situated within 10 m of the wetland edge. Pond water temperatures were recorded using a submerged Hobo® data logger.

Data Analysis

Sizes of breeding adults.—From the raw data I calculated a body mass index (BMI), where mass (g) of the frog was divided by length (SVL; mm). I used a t-test and Wilcox rank-sum test to compare body sizes of individuals that were captured in 2009 and recaptured in 2010. A regression was run on sizes of recaptured individuals to look at between-year growth.

Estimated clutch size and number of deposited eggs.—Clutch sizes were estimated for each spent female using data collected by Redmer (2000), who noted a strong positive correlation between female SVL and clutch size in Crawfish Frogs. From these data I calculated the regression:

$$\text{Clutch size} = -11{,}104.2 + 173.5 * \text{SVL}.$$

Clutch sizes were estimated by entering female SVL into this equation. Total numbers of eggs laid at each wetland both years were estimated by summing the estimated clutch sizes of all spent females at each wetland each year.

Larval developmental period.—Larval developmental periods were estimated at each pond by counting the number of days between: (1) the first female entering and the first juvenile exiting, (2) the first female entering and the last juvenile exiting, (3) the last female entering and the first juvenile exiting, and (4) the last female entering and the last juvenile exiting. These four counts provided a range of days from egg to juvenile metamorphosis. To derive estimates of the length of the tadpole stage, I subtracted from each number 7 d—the mean number of days after oviposition it took an egg mass to hatch.

Adult within-season survivorship.—I estimated within-season survivorship for adult Crawfish Frogs at Nate's Pond and Cattail Pond for 2009 and 2010. Within-season survivorship was calculated for each wetland each year by dividing the number of individuals that exited the wetland by the number that entered. In 2010, at Nate's Pond I recaptured two individuals that were not captured exiting the wetland in 2009; at Cattail Pond I recaptured four individuals that were not captured exiting the wetland in 2009. The 2009 data were adjusted (corrected within-season survivorship) to account for these recaptured individuals.

Adult return rates.—Between-year survivorship was estimated by calculating the return rates (%; 2010 data) of previously marked (2009 data) breeding Crawfish Frogs at each wetland (Elmberg, 1990). This estimate relies on two assumptions: 1) that all Crawfish Frog adults breed every year, and 2) that Crawfish Frogs exhibit breeding site philopatry. Telemetry studies (J. L. Heemeyer, *unpubl. data*) support the first assumption, and generally support the second assumption. Telemetry data revealed that 2/12 (17%) Crawfish Frogs that bred in 2009 changed breeding wetlands in 2010. Therefore, to estimate survivorship from return rates, return rates were adjusted to account for these animals.

Estimated larval survivorship.—In 2009, the egg-to-juvenile survivorship was estimated by dividing the number of juveniles produced by the estimated number of eggs deposited in the wetland (see above). After noting high mortality in wetlands, I wished to know whether embryos, larvae, or both stages were most vulnerable. Therefore, in 2010, in addition to counting spent females and estimating clutch size from SVLs, I located egg masses (see above) and monitored them for hatching success. I estimated hatching success (embryonic survivorship) among viable egg masses (three were not viable) by subtracting the mean number of estimated undeveloped eggs per egg mass (135), then divided this number by the estimated number of viable eggs laid in the wetland. In 2010, I estimated larval survivorship by dividing the number of juvenile recruits by the estimated number of hatchlings.

Estimated mortality rates.—Percent morality was determined for each life history stage (embryonic, larval, juvenile-to-adult, and adult) using 2010 survivorship estimates. Morality rates were calculated by dividing morality counts or estimates for each life history stage by the length (days) of each stage.

Directionality.—I used circular statistics to analyze directional movements into and out of wetlands by Crawfish Frog adults, and movements out of wetlands by newly metamorphosed juveniles. Specifically, I calculated the directions of movements using angle measurements (degrees) of pitfall trap directions taken from the center of the wetland, and used the Rayleigh test (Batschelet, 1981) to determine whether movements were random or directed.

All means were calculated using Program R® (Program R® 2.10.1, The R Foundation for Statistical Computing, Vienna, Austria), and the regression was run using STATISTICA® (STATISTICA® 8.0, StatSoft, Inc., Tulsa, OK). Circular statistics (mean angle and Rayleigh test) were computed using the Program R CircStats Package (package author: Claudio Agostinelli; see Jammalamadaka and SenGupta, 2001). Oriana software (Version 3.21, Kovach Computing Services) was used to graphically display directional data.

RESULTS

Sizes of Breeding Populations and Percent Recaptures

During 2009 and 2010, 127 individual adult Crawfish Frogs were captured at breeding wetland drift fences: 88 at Nate's Pond, 39 at Cattail Pond. At Nate's Pond, 69 breeding adults (38 males, 31 females) were captured in 2009, 42 (22 males, 20 females) were captured in 2010 (Table 1). At Cattail Pond, 28 breeding adults were captured in 2009 (14 males, 14 females), 21 in 2010 (14 males, 7 females; Table 1). Breeding populations were smaller at both wetlands in 2010. The ratio of males to females during each breeding season was approximately 1:1 at both wetlands, with the exception of a 1.8:1 ratio at Cattail Pond in 2010. At Nate's Pond, one sub-adult was captured in 2009; two were captured in 2010 (Table 1).

In 2010, 55% (23/42) of breeding Crawfish Frogs captured at Nate's Pond were recaptures from 2009 (11 males, 12 females; 55% recapture rates for both males and females; Table 2). Of the 19 new animals in 2010, 9 were males, 10 were females (Table 2). At Cattail Pond, 48% (10/21) of breeding adults in 2010 were recaptures (50% of males and 43% of females; Table 2). Of the 11 new animals captured in 2010, 7 were males, 4 were females (Table 2).

Sizes of Breeding Adults

Over the course of this study, male Crawfish Frogs averaged (± SD) 96.2 ± 8 mm SVL, and weighed on average 104.3 ± 23 g entering breeding wetlands and 96.5 ± 19 g exiting (Table 3). Female Crawfish Frogs averaged 102.0 ± 7 mm SVL, and weighed on average 124.8 ± 25 g entering wetlands (gravid) and 90.0 ± 15 g exiting (spent; Table 3). Subadults were 68, 62, and 64 mm SVL; and weighed 40, 22, 26 g entering the wetland and 22 g and 25 g exiting the wetland (Table 3). Body mass indices (BMI) for males averaged 1.05 at Nate's Pond and 1.16 at Cattail Pond (Table 4). BMIs for pre-breeding females averaged 1.18 at Nate's Pond, 1.36 at Cattail Pond; BMIs for post-breeding females averaged 0.87 at Nate's Pond, 0.92 at Cattail Pond. BMIs tended to be higher for pre-breeding females than males; they were much lower for post-breeding females. BMIs of all breeding adult categories were higher at Cattail Pond (Table 4).

In general, results indicate Crawfish Frogs in wetlands lost weight. The mean difference between exit and entry weights of males was -7.8 ± 10 g (Table 3). The mean difference between the entry and exit weights of females was -34.8 ± 15 g (Table 3) and approximates the weight of deposited eggs. Differences between exit and entry weights of the two subadults that exited were 0 g and -1.0 g (Table 3).

Nate's Pond.—At Nate's Pond males averaged 94.4 ± 7 mm SVL (Table 3; Fig. 1). In 2009 males averaged 93.4 ± 7 mm SVL, and in 2010 males averaged 96.0 ± 7 mm SVL (Table 3; Fig. 1). Overall, females averaged 100.7 ± 7 mm SVL (Table 3; Fig. 1). In 2009 females averaged 100.3 ± 6 mm SVL, and in 2010 females averaged 101.2 ± 8 mm SVL (Table 3; Fig. 1). The one subadult captured in 2009 was 68 mm SVL; the two subadults captured in 2010 were 62 and 64 mm SVL (Table 3).

At Nate's Pond, males averaged 99.0 ± 19 g entering wetlands and 93.0 ± 16 g exiting (Table 3). Males lost 3.5 ± 10 g in 2009, and 10.3 ± 10 g in 2010; on average males lost 6.1 ± 10 g while in breeding wetlands. Females averaged 119.0 ± 23 g entering wetlands and 87.8 ± 15 g exiting (Table 3). Weight loss in females at Nate's Pond averaged 33.1 ± 12 g in 2009, and 28.2 ± 12 g in 2010; on average females lost 31.2 ± 12 g while in breeding wetlands (Table 3).

Cattail Pond.—At Cattail Pond males averaged 100.9 ± 7 mm SVL (Table 3; Fig. 2). In 2009 males averaged 102.8 ± 6 mm SVL, and in 2010 males averaged 97.6 ± 8 mm SVL (Table 3; Fig. 2). Overall, females averaged 107.1 ± 7 mm SVL (Table 3; Fig. 2). In 2009 females averaged 106.4 ± 5 mm SVL, and in 2010 females averaged 108.0 ± 9 mm SVL (Table 3; Fig. 2).

At Cattail Pond, males averaged 117.5 ± 27 g entering wetlands and 105.6 ± 23 g exiting (Table 3). Males lost 11.4 ± 12 g in 2009, and 12.7 ± 8 g in 2010; on average males lost 11.9 ± 10 g while in breeding wetlands (Table 3). Females at Cattail Pond averaged 146.4 ± 21 g entering wetlands and 98.1 ± 13 g exiting (Table 3). Weight loss averaged 46.9 ± 18 g in 2009 and 49.8 ± 16 g in 2010; on average females lost 48.2 ± 16 g while in breeding wetlands (Table 3).

Between-year recaptures.—Comparisons of size measurements were made for individuals captured in both years to assess annual growth. At Nate's Pond the SVLs of males recaptured in 2010 (100.6 ± 3 mm) were significantly longer ($\bar{x}$ = 7.6 mm) than when first captured in 2009 (96.4 ± 16 mm; $t = -3.6$, $df = 8$, $p = 0.008$). The mean entry weight was larger in 2010 (110.3 ± 14 g) compared to 2009 (97.9 ± 16 g), but the difference was not significant ($t = -2.7$, $df = 8$, $p =$

0.02). Recaptured females at Nate's Pond did not differ in length or weight between years. The SVLs of females recaptured in 2010 (104.5 ± 6 mm) were not significantly different from 2009 (102.2 ± 5 mm; $t = -1.9$, $df = 11$, $p = 0.09$). The mean entry weight in 2010 (125.0 ± 18 g) was not significantly larger than in 2009 (123.0 ± 21 g; $t = -0.7$, $df = 11$, $p = 0.51$).

At Cattail Pond, the SVLs of males recaptured in 2010 (103.8 ± 4 mm) were not significantly different than when captured in 2009 (101.0 ± 7 mm; $t = -0.4$, $df = 5$, $p = 0.67$). Weight differences between 2009 (124.0 ± 36 g) and 2010 (122.8 ± 21 g) also did not differ significantly between years ($V = 10$, $p = 1.00$). The number of recaptured females between years at Cattail Pond ($n = 3$) was too small for statistical comparison.

Between-year growth was dependent on adult size ($r^2 = 0.57$, $p < 0.001$; Fig. 3); in general, the smaller the adult, the more it grew.

Timing of Breeding

Crawfish Frog breeding occurred simultaneously at Nate's Pond and Cattail Pond during both years of this study. Breeding lasted from 7 March−15 May in 2009, and from 12 March−20 May in 2010 (Figs. 4, 5). The length of the breeding season—number of days from when the first frog entered until the last frog exited—was 70 days both years. Male Crawfish Frogs entered the wetlands one day before females in 2009 (7 March versus 8 March), and nine days before females in 2010 (12 March versus 21 March; Figs. 4, 5).

Peak breeding.—In 2009, peak breeding (defined as the time when the highest number of Crawfish Frogs were present in wetlands) occurred from 31 March–6 April, with 90% of observed individuals in the wetland during this time (Fig. 4). Most individuals entered the wetlands on 2 and 3 April: six frogs (two males, four females) on 2 April, and 42 frogs (27 males, 15 females) on 3 April (Fig. 4). On the night of 2 April, air temperatures were warm and it was rainy; the mean temperature was 14°C and the daily high was 29°C; rainfall for the day totaled 1.9 cm (Fig. 4). Animals continued to move into the wetland until the early hours of 3 April, after rainfall had stopped; the mean temperature for 3 April was 8°C and the daily high was 19°C (Fig. 4). At Nate's Pond the operational sex ratio (OSR; ratio of males to gravid females) prior to peak breeding was 0.8:1. After the large influx of individuals on 2 April, the OSR increased to 1.6:1, and three days later reached its maximum of 2.5:1. At Cattail Pond the OSR was 0.5:1 prior to peak breeding, after 2 April it was 1.2:1. Sixteen females left during peak breeding, another 11 left on 9 April, when the daily high reached 27°C and rainfall was 1.5 cm. Ten days later, on 19 April, the majority (19 of 28) of males exited. On 19 April, air temperatures were warm and it was rainy; the mean temperature was 15°C and the daily high reached a maximum of 21°C, with daily rainfall totaling 1.8 cm (Fig. 4).

In 2010, breeding peaked five days earlier than in 2009 and occurred during 25–31 March, with 52% of individuals observed present in the wetland (Fig. 5). Most individuals entered the wetlands on 25 and 28 March: six frogs (three males, three females) on 25 March; eight frogs (two males, six females) on 28 March (Fig. 5). On the night of 25 March it was raining and air temperatures were warm; the mean temperature was 9°C and the daily high reached 15°C, with daily rainfall totaling 2.6 cm (Fig. 5). Weather conditions were similar on 28 March, with mean air temperatures of 10°C and the daily high reached 14°C; daily rainfall totaled 0.1 cm (Fig. 5). At Nate's Pond prior to peak breeding the male-female OSR was 8:1. After the influx of individuals on 25 and 28 March, the ratio was 1.3:1. At Cattail Pond prior to peak breeding the OSR was 5:1 and after the nights of 25 and 28 March, the ratio was 3:1. At Cattail Pond the peak breeding OSR of 3:1 and the overall breeding season sex ratio of 2:1 were both male-biased, contrasting with the nearly 1:1 overall sex ratio of 2009. Following peak breeding in 2010, most females were captured exiting the pond on 1 April (two males, seven females). On 1 April mean air temperatures were warm (22°C) and the daily high reached 34°C, with no rainfall (Fig. 5). The last big surge of exiting frogs (six males, three females) was on the night of 7 April (Fig. 5). On 7 April mean air temperature was 19°C, the daily high reached a maximum of 24°C and daily rainfall totaled 1.7 cm (Fig. 5).

Residency.— At Nate's Pond, mean residency (defined as the number of nights spent in the wetland between the first entry and exit dates) for males was 17.6 ± 10 nights (range = 0–51) and for females was 8.4 ± 8 nights (range = 0–43). Three individuals at Nate's Pond—two males and one female—entered and exited within the same day. At Cattail Pond, mean residency for males was 13.0 ± 5 nights (range = 2–19) and for females was 15.0 ± 14 nights (range = 1–52).

Egg Mass Counts and Estimated Clutch Sizes

In 2010 at Nate's Pond, 17 of 19 females exited spent and 16 egg masses were found (Table 5). At Cattail Pond all six females exited spent and five egg masses were found (Table 5). Egg masses were laid from 25 March–12 April at Nate's Pond, and from 27 March–2 April at Cattail Pond (Fig. 6). Maximum daily pond temperatures during oviposition at Nate's Pond averaged 16.8 ± 6°C (range = 8.0–28.4°C) and were higher than those at Cattail Pond (11.8 ± 3°C, range = 7.8–16.2°C; Fig. 6). The minimum daily pond temperatures averaged 10.2 ± 3°C (range = 5.2–16.6°C) at Nate's Pond and 9.0 ± 3°C (range = 4.0–14.9°C) at Cattail Pond (Fig. 6).

Egg masses were typically found floating in shallow water (Fig. 7), or resting on debris at the bottom of the pond, not on vegetation. Mean total water depth at oviposition sites was 18.4 ± 2 cm at Nate's Pond and 16.0 ± 2 cm at Cattail Pond (Table 6). Water depth from the bottom of the egg mass to the floor of the pond averaged 12.8 ± 4 cm at Nate's Pond and 12.0 ± 2 cm at Cattail Pond (Table 6); most egg masses were suspended in the water column when first deposited, and later, when closer to hatching, rested on the wetland bottom. Egg mass diameter averaged 13.5 ± 1 cm at Nate's Pond and 14.1 ± 0.6 cm at Cattail Pond (Table 6; Fig. 8).

Egg masses began hatching approximately within one week after deposition. Number of days until hatching averaged 6.3 ± 2 days at Nate's Pond and 7.5 ± 3 days at Cattail Pond (Table 6).

Estimated clutch sizes.—The estimated clutch size (based on female SVL) at Nate's Pond in 2009 averaged 6,303 ± 1,065 eggs; in 2010 the average was 6,724 ± 1,063 eggs (Table 5). In 2009 at Cattail Pond the estimated mean clutch size was 7,002 ± 1,012 eggs; in 2010 clutch size averaged 7,633 ± 1,492 eggs (Table 5). Based on totals from clutch sizes in 2009, an estimated 189,079 eggs were deposited in Nate's Pond, and 77,020 eggs were deposited in Cattail Pond (Table 5a). In 2010, an estimated 114,316 eggs were deposited in Nate's Pond, and 45,796 eggs were deposited in Cattail Pond (Table 5b).

Length of Larval Period and Timing of Metamorphosis

Metamorphosis occurred from 19 June–16 August in 2009, and from 5 June−30 July in 2010 (Figs. 9, 10). The period of metamorphosis—number of days between when the first and last juvenile exited—was 59 days in 2009 and 56 days in 2010. Based on these data, the overall estimated larval developmental period was 91 ± 37 days. Juveniles exited wetlands following large rain events. In 2009, the first juvenile was captured on 19 June following a 3.7 cm rainfall the previous day—this was the largest rainfall during the time of metamorphosis in 2009 (Fig. 9). The largest number of juveniles (46) captured during this period of metamorphosis was on 4 July, total daily rainfall was 2.1 cm (Fig. 9). In 2010, the first juvenile was captured (5 June) two days after a 3.9 cm rainfall (Fig. 10). The largest number of juveniles captured within a day (298) was on 12 June, a day when total daily rainfall was 2.7 cm (Fig. 10).

Juvenile Recruitment

Juvenile Crawfish Frogs metamorphosed successfully from both Nate's Pond and Cattail Pond in 2009, but only from Nate's Pond in 2010. In 2009, 286 juvenile Crawfish Frogs exited Nate's Pond, 11 exited Cattail Pond (Table 1). In 2010, 2,103 juveniles exited Nate's Pond; no juveniles exited Cattail Pond. The 2010 increase at Nate's Pond reflected a 7-fold jump in juvenile recruitment (Table 1).

Sizes of juveniles.—Newly metamorphosed juveniles averaged 33.2 ± 2 mm SVL and 3.5 ± 0.6 g when exiting wetlands (Table 3). At Nate's Pond, in 2009 juveniles averaged 34.4 ± 2 mm SVL and 4.6 ± 0.6 g; in 2010, they averaged 33.1 ± 2 mm SVL and 3.4 ± 0.5 g (Table 3; Fig. 11). Not only were there more juveniles at Nate's Pond in 2010, they were over a millimeter shorter ($V = 2{,}178$, $p < 0.001$; Fig. 11) and weighed less ($V = 38{,}673$, $p < 0.001$; Table 3).

At Cattail Pond, juveniles (only 2009 data were available) had a mean SVL of 29.8 ± 3 mm and a mean weight of 3.0 ± 1 g (Table 3; Fig. 11). Juveniles that exited Cattail Pond were significantly smaller than those that exited Nate's Pond in 2009, both in length ($W = 179.5$, $p < 0.001$) and weight ($W = 261.5$, $p < 0.001$; Table 3).

Adult Within Breeding Season Survivorship

For both ponds both years, within-season survivorship of breeding adults was 81% (128/158). Correcting for trespassers (data available only for 2009), within-season survivorship was 85% (134/158). For Nate's Pond, the within-season survivorship for both years was 87% (97/111); correcting for trespassers, within-season survivorship was 89% (99/111). At Cattail Pond, the within-season survivorship for both years was 66% (31/47); correcting for trespassers, within-season survivorship was 74% (35/47).

Nate's Pond.—In 2009, within-season survivorship was 90%; 62 of 69 Crawfish Frogs that entered to breed exited the wetland (Table 7). In 2010 within-season survivorship was 83%; 35 of the 42 frogs that entered the wetland exited (Table 7). Male within-season survivorship in 2009 was 84% (32/38), in 2010 it was 80% (16/20; Table 7). Female within-season survivorship was 97% (30/31) in 2009 and 86% (19/22) in 2010 (Table 7).

Correcting for trespassers in 2009, within-season survivorship for Nate's Pond was 93% (64/69; Table 7). The 2009 male corrected within-season survivorship was 89% (34/38); two of six males that were not captured exiting Nate's Pond in 2009 were recaptured in 2010 (one entering the wetland, the second exiting—this male likely over-wintered in the pond; Table 7). No unaccounted for females from 2009 were recaptured in 2010, therefore there was no need to correct survivorship numbers (Table 7).

Cattail Pond.—In 2009, within-season survivorship was 70%: 19 of 27 Crawfish Frogs that entered the wetland exited (Table 7). In 2010, within-season survivorship was 60%; 12 of 20 frogs that entered the wetland exited (Table 7). In 2009, male within-season survivorship was 85% (11/13); in 2010 it was 46% (6/13; Table 7). Female within-season survivorship was 57% (8/14) in 2009 and 86% (6/7) in 2010 (Table 7).

Correcting for trespassers, the 2009 within-season survivorship for Cattail Pond was 85% (23/27; Table 7). The male corrected within-season survivorship was 100% (13/13); two males that were not captured exiting Cattail Pond in 2009 were recaptured entering the pond in 2010 (Table 7). The corrected female within-season survivorship was 71% (10/14); two of six females that were not captured exiting the pond in 2009 were recaptured entering the pond in 2010 (suggesting that trespassing occurred; Table 7).

Between pond comparisons.—The total within-season survivorship for both years at Nate's Pond (90%) was significantly higher than that at Cattail Pond (66%; χ^2 = 9.9, df = 1, p = 0.002). The 2009 total corrected within-season survivorship did not significantly differ between Nate's Pond (93%) and Cattail Pond (85%; χ^2 = 1.3, df = 1, p = 0.25).

Adult Between Breeding Season Survivorship

The overall return rate for breeding adult Crawfish Frogs was 34%; 32 of 94 frogs that bred at the wetlands in 2009 were recaptured in 2010. Two frogs are known to have switched breeding wetlands. Factoring these two frogs into the return rate, and assuming remaining frogs died, produces a survivability estimate of 34 of 94 frogs (36%).

At Nate's Pond the total return rate (males and females) was 32%; 22 of the 68 frogs that bred in 2009 returned in 2010 (Table 2). The return rate for males was 29% (11/38), for females 37% (11/30; Table 2).

At Cattail Pond the total return rate (males and females) was 38%; 10 of the 26 frogs that bred in 2009 returned in 2010 (Table 2). The return rate of males was 54% (7/13), for females 23% (3/13; Table 2).

Estimated Oviposition to Larval Survivorship 2009

As noted above, in 2009, egg-to-juvenile survivorship was estimated by dividing the number of juveniles recruited by the estimated number of eggs deposited in the wetland. At Nate's Pond estimated survivorship was 0.2% (286 juveniles/189,079 eggs; Table 5a). Egg-to-juvenile survivorship at Cattail Pond in 2009 was 0.01% (11 juveniles/77,020 eggs; Table 5a).

Estimated Embryonic Survivorship 2010

In 2010, I monitored 16 egg masses at Nate's Pond and five egg masses at Cattail Pond. Three failed egg masses were observed at Nate's Pond; none were observed at Cattail Pond

(Table 5b). Among viable clutches, I counted an average of 135 ± 115 (range = 55–339) undeveloped/dead embryos per egg mass (n = 5; Table 5b). Adjusting the total number of eggs deposited to account for both failed clutches and eggs, I estimated the number of hatchlings at Nate's Pond to have been 91,984; at Cattail Pond, to have been 44,986 (Table 5b).

Estimated Larval Survivorship 2010

At Nate's Pond estimated larval survivorship was 2.3% (2,103 juveniles/91,984 hatchlings; Table 5b). Cattail Pond had zero recruitment (0/44,986; Table 5b).

Comparisons Between 2009 and 2010 Egg to Metamorphosis Survivorship

In 2009 at Nate's Pond, 286 of 189,079 eggs survived to metamorphosis (0.2%); during the 2010 field season, 2,103 of 94,144 eggs survived to metamorphosis (2.2%)—a 15.3 fold increase. In 2009 at Cattail Pond, 11 of 77,020 eggs survived to metamorphosis (0.01%), none survived in 2010.

Estimated Mortality Rates for 2010

Mortality rates were estimated from survivorship data of each life history stage: embryonic, larval, juvenile-to-adult, and adult (Table 8). Embryonic mortality was 1.9% at Nate's Pond, and mortality rate per day was 0.2% (1.9%/7 d). At Cattail Pond embryonic mortality was 1.8%, and mortality rate per day was 0.3% (1.8%/7 d; Table 8b).

Larval mortality was 97.7% at Nate's Pond, and estimated mortality rate per day was 1.1% (97.7%/91 d). At Cattail Pond larval mortality was 100%, and rate per day was a conservative 1.1% (100%/91 d; Table 8b).

No juveniles were recaptured between years (as expected; males are estimated to breed when 2 years old, females at 3; Redmer, 2000). To estimate juvenile-to-adult mortality I calculated a range of survival estimates from data on number of juveniles that metamorphosed in

2009 (286) and 2010 (2,103), and number of new adults (19) that first bred in Nate's Pond in 2010 (0.9%, 6.6%). Therefore, juvenile to adult mortality per day is approximately 0.1% ([93.4%/780 d]; [99.1%/780 d]; Table 8b).

At Nate's Pond 46 of 68 adults did not return in 2010, thus between-year mortality was 68%, an estimated 0.2% per day (68%/350 d; Table 8b). At Cattail Pond, 16 of 26 adults did not return in 2010, thus estimated adult mortality was 62%, approximately 0.2% per day (62%/350 d; Table 8b). Overall, mortality rates were consistent between ponds.

Directionality

Adult Crawfish Frogs immigrated into the wetland from random directions at both ponds both years. When emigrating, Crawfish Frogs showed directionality at both ponds in 2009, however not in 2010. Juveniles from Nate's Pond dispersed non-randomly both years; however juveniles at Cattail Pond dispersed randomly in 2009.

A low percentage of individuals (0–11%) exited wetlands at their point of entry. The majority of frogs exited from 8.0–45.0° relative to where they entered at Nate's Pond, however at Cattail Pond, adult frogs tended to exit further (95.5–178.2°) from their point of entry.

Habitat orientation.—In 2009 at Nate's Pond, the mean direction (93.3°) of immigrating adult Crawfish Frogs was from the east, though this direction did not differ from random ($r = 0.10$, $p = 0.50$; Figs. 12, 13a). Emigrating Crawfish Frogs, however, were significantly oriented towards the southwest (mean direction = 206°; $r = 0.26$, $p = 0.01$; Figs. 12, 13a).

At Nate's Pond in 2010, the mean direction (166°) of immigrating adult Crawfish Frogs was from the south-southeast, though this direction did not differ from random ($r = 0.06$, $p = 0.87$; Figs. 12, 13a). The mean direction (182°) of emigration was towards the south (Figs. 12, 13a), and also did not show significant directionality ($r = 0.07$, $p = 0.83$; Fig. 12).

In 2009 at Cattail Pond, the mean direction (335°) of immigrating adult Crawfish Frogs was from the northwest, and did not differ from random ($r = 0.38$, $p = 0.02$; Figs. 13b, 14). Emigrating Crawfish Frogs, however, were significantly oriented towards the northeast (mean direction = 62°; $r = 0.58$, $p < 0.001$; Fig. 14).

At Cattail Pond in 2010, the mean direction (33°) of immigrating adult Crawfish Frogs was from the northeast; this orientation was not significant and did not differ from random ($r = 0.35$, $p = 0.10$; Figs. 13b, 14). The mean direction (77°) of emigration was towards the east-northeast (Figs. 13b, 14); adults exiting the wetland did not show directionality ($r = 0.46$, $p = 0.05$; Fig. 14).

Juveniles dispersing from Nate's Pond in both years showed directionality; juveniles dispersing from Cattail Pond did not (Figs. 12, 14). At Nate's Pond in 2009 juvenile dispersal showed significant orientation towards the west (mean direction = 262°; $r = 0.17$, $p < 0.001$; Fig. 12). In 2010 at Nate's Pond the mean direction (313°) of juvenile dispersal was significantly oriented towards the northwest ($r = 0.14$, $p < 0.001$; Fig. 12). In 2009 at Cattail Pond, the only year juveniles were captured, the mean direction (262°) of dispersal was toward the west, though this preference was not significantly different from random ($r = 0.43$, $p = 0.13$; Fig. 14).

Individual directedness.—At Nate's Pond in 2009, five individuals exited the wetland at the same point of entry (8%, 5/63). The majority (36%, 23/63) of individuals exited the wetland within 10.5–44.4° from where they entered, and 21 individuals (33%, 21/63) exited from 46.4–90° relative to their point of entry. The remaining 14 individuals that exited the wetland, exited from 93.7–166.1° relative to where they entered (22%, 14/63). Seven frogs were not recaptured exiting Nate's Pond in 2009: six males, and one female exited and later re-entered the wetland—this female was not captured again.

In 2010 at Nate's Pond, two individuals exited the wetland at the same point of entry (6%, 2/36). The majority (44%, 16/36) of individuals exited from 8.8–44.4° relative to where they entered the pond, and seven individuals (19%, 7/36) exited from 47.5–80.0° of their point of entry. The remaining 11 individuals (30%, 11/36), exited from 103.9–176° from where they entered. Five frogs were not recaptured exiting Nate's Pond in 2010: two males and three females.

At Cattail Pond in 2009, two individuals (11%, 2/18) exited the wetland at the same point of entry. Four (22%, 4/18) frogs exited the wetland from 14.3–33.6° relative to where they entered the pond. The remaining 12 individuals (67%, 12/18) exited from 95.5–177.0° relative to their point of entry. Eight frogs were not recaptured exiting Cattail Pond in 2009: two males and five females, and one female entered and exited the wetland several times—this female was not captured again after entering the wetland the fourth time. Three females trespassed entering the wetland, or were in the wetland before the drift fence was installed, as they were captured exiting the wetland with no PIT tag or toe-clip.

In 2010 at Cattail Pond, no adults exited at the same point of entry. Three individuals (25%, 3/12) exited from 16–45.4° relative to where they entered the pond, and five individuals (42%, 5/12) exited from 47.4–90.3° relative to their point of entry. The remaining four frogs (33%, 4/12) that exited the wetland, exited from 96.5–178.2° relative to their point of entry. Six frogs were not recaptured exiting Cattail Pond in 2010: five males and one female. Two individuals, one male and one female, trespassed, or were in the wetland before the drift fence was installed, as they were captured exiting the wetland with no PIT tag or toe-clip.

DISCUSSION

This study represents the first detailed examination of the population biology of Crawfish Frogs. Here I report data from two wetlands over two years on sizes of breeding populations, sizes of breeding adults, timing of breeding, survivorship in egg and larval life history stages as well as in adults between years and while in breeding wetlands. From these data, I also estimate juvenile-to-breeding adult survivorship. I report directionality of entering and exiting breeding adults, and newly metamorphosed juveniles. Data presented support the idea that Crawfish Frogs are explosive breeders, with an overall sex ratio of 1:1, but have a male-biased operational sex ratio during most of the breeding period. Fecundity is high at both study sites; however, only one of our two sites (Nate's Pond) appeared to be acting as a population source during the two study years. Cattail Pond appeared to behave as a population sink. In general, counts and estimates of survivability suggest that mortality is comparatively low during egg, juvenile (although these estimates have the most uncertainty), and adult stages. In contrast, mortality is high during the larval stage. I elaborate on these findings, below.

Size of Breeding Populations

Nate's Pond and Cattail Pond represent small- to medium-sized populations by historical standards, but relatively large populations under the current status of Crawfish Frogs. For example, Smith et al. (1948) collected 432 frogs on consecutive nights in a population in southern Illinois, and IDNR reported an historic population of 100 frogs within a single wetland in southern Indiana (IDNR Amphibian and Reptile Technical Advisory Committee, 1987). In contrast, Nate's Pond and the comparably sized Big Pond (also at HFWA-W, too big to drift fence) are likely the largest contemporary Crawfish Frog breeding sites in Indiana (Engbrecht, 2010; Engbrecht and Lannoo, 2010). Given their status as relatively large Crawfish Frog populations, it is worrisome that both Nate's Pond and Cattail Pond experienced sharp drops in breeding adult numbers in 2010 compared with 2009 (39% drop at Nate's Pond, 25% at Cattail Pond). I show elsewhere (Kinney et al., 2011) that a portion of this mortality is due to the presence of the amphibian chytrid fungus, *Batrachochytrium dendrobatidis* (Bd), which, due to the abnormally wet fall of 2009, may have become fulminant and developed into chytridiomycosis in many frogs during the winter of 2009/2010. The known mortality rate at HFWA-W due to chytridiomycosis since 2009 has been 12%.

Amphibian population sizes are known to fluctuate among years (Pechmann et al., 1991; Pechman and Wilbur, 1994; Green, 2005). The question these studies generally do not address (because they sample single wetlands, and/or are not combined with radiotelemetry studies) is whether absent adults skip reproduction or breed elsewhere. Concurrent tracking data on the same HWFA-W Crawfish Frog populations suggests that male and female frogs breed every year, and that fidelity to breeding wetlands is high, although not without exception (J. L. Heemeyer, *unpubl. data*).

Sizes of Breeding Adults

At HFWA-W, Crawfish Frog adults ranged from 76–121 mm SVL. Adult Crawfish Frogs at our study site were larger than those reported in other regions. Snout-vent length ranges (from south to north) include 72–108 mm (males) in Oklahoma (Bragg, 1953), 51–76 mm in Kentucky (Barbour, 1971), 64–118 mm in southern Illinois (Smith et al., 1948; Redmer, 2000), 75–114 mm in Missouri (Johnson, 2000), and 41–122 mm in Kansas (Smith, 1934; Collins, 1993; Collins et al., 2010). While the lengths of Crawfish Frog adults at HFWA-W fall within the known range for the species, SVLs at HFWA-W were at the upper limits of ranges reported. These data support the observations by Goin and Netting (1940), Bragg (1953), and Engbrecht et al. (2011) of a latitudinal gradient in Crawfish Frog sizes. The pattern in the body size of adult frogs likely reflects the climate, quality, and length of the active season (Martof and Humphries, 1959). The latitudinal pattern in Crawfish Frog sizes may result from a shorter active season due to cooler temperatures in the northern portions of the species range. It has been shown that a shorter active season can lead to delayed maturity in Green Frogs (*Lithobates clamitans*; Martof and Humphries, 1959; Berven et al., 1979); these adults are larger in their first year of breeding than adults located in regions with a longer active season. Larger body size is also advantageous for preventing water loss through evaporation (Thorson, 1955).

In Crawfish Frogs, females are generally thought to be larger than males (Smith et al., 1948; Barbour, 1971; Collins, 1993; Johnson, 2000; Redmer, 2000; Parris and Redmer, 2005). At HFWA-W, while females tended to be longer (SVL) than males, they were only marginally so. Further, body mass indices show that pre-breeding females were more similar in weight to males than to post-breeding females. It is this post-breeding female morphology that Goin and Netting (1940) termed "Gibson Girl."

I also compared size metrics of individuals that were captured in both 2009 and 2010 to detect growth between years. Means were higher for recaptured individuals in 2010, however only in one instance were the differences significant. Recaptured males at Nate's Pond were significantly longer in SVL in the second year; overall mean growth was 7.6 mm (96.4 versus 100.6 mm). Growth between years was inversely correlated with SVL, with small individuals having the greatest increase in length (Fig. 3). Individuals with SVL of 100 mm or greater had the least amount of growth between years; indeed several larger animals did not appear to grow at all.

Timing of Breeding

In 2009 and 2010, Crawfish Frogs at HFWA-W began entering breeding wetlands in early March and finished exiting by the second week in May. This timing is consistent with other studies, when accounting for latitude. Crawfish Frogs are reported to breed from January to March or April in Louisiana (Dundee and Rossman, 1996) and Arkansas (Trauth et al., 2004); as early as mid-late February to April in Illinois (Smith et al., 1948; Phillips et al., 1999), Missouri (Johnson, 2000), and Oklahoma (Bragg, 1953); early March through April in Kentucky (Barbour, 1971); March through early July in Kansas (Collins, 1993; Busby and Brecheisen, 1997; Collins et al., 2010); and mid-April in Iowa (Christiansen and Bailey, 1991).

In 2009, males and females began migrating into Nate's Pond on the same day; in 2010 males moved into both wetlands 4–12 days earlier than females. Smith et al. (1948) observed that male Crawfish Frogs tended to outnumber females for the first 5–6 days of the breeding season. I calculated OSRs for each wetland each year and found that this early male bias continued through peak breeding. Peak breeding lasted for approximately seven days, and involved about half of the individuals in each population. At HFWA-W, breeding peaks corresponded to peak calling activity (Engbrecht, 2010), similar to the observations of Busby and Brecheisen (1997). These observations are consistent with characteristics of explosive breeders, where male competition for mates is high (Wells, 2007).

The total length of the breeding season (animals in breeding wetlands) at HFWA-W was 70 days during both years, however most individuals exited the pond soon after peak breeding, with females tending to exit first (Smith et al., 1948). Length of the breeding season in other regions ranges from 22–63 days (Smith et al., 1948; Bacon and Anderson, 1976; Busby and Brecheisen, 1997). When making these comparisons, breeding activity can be estimated by calling activity, however, it is evident that some animals, especially males, may linger in breeding wetlands after calling has ceased (indeed in 2009, one male never left Nate's Pond but did leave in 2010). Additionally, drift fence-pitfall trap arrays may inhibit post-breeding migrations (Heemeyer et al., 2010). The length of the breeding season (as judged by calling behavior) has recently been tied in a proportional way to the number of breeding adults, with larger populations calling longer (Engbrecht, 2010).

Breeding Sites, Egg Mass Counts and Clutch Sizes

Crawfish Frogs bred in shallow areas of ponds, with chorusing and egg laying occurring within these locations. The number of egg masses found (21) approximated the number of spent females (23), with one egg mass unaccounted for at each pond. Heavy vegetation at the wetland edge may have concealed the unaccounted for egg masses. These data indicate that female Crawfish Frogs deposit one egg mass per breeding season, and egg mass counts provide an estimate of breeding females. Assuming a sex ratio of 1:1 allows for the number of males to be estimated, and from these two estimates, an overall population estimate can be generated.

Egg masses were typically observed floating in shallow water or resting on debris at the bottom of the pond, and tended not to be attached to aquatic vegetation. This observation is consistent with other studies (Smith, 1934; Busby and Brecheisen, 1997; Johnson, 2000). Water depth at oviposition sites (range = 12–22 cm) was consistent across the two wetlands and consistent with previously reported depths (range = 15–20 cm; Bragg, 1953). The maximum depth of Nate's Pond was 0.5 m, and Cattail Pond was 1 m; measured depths at oviposition sites emphasize the use of shallow water by breeding Crawfish Frogs.

Eggs hatched approximately seven days after deposition, similar to the timing reported for Missouri populations (range = 7–10 days; Johnson, 2000). The small difference in hatching time between Nate's Pond (6.3 d) and Cattail Pond (7.5 d) may be related to temperature; water temperatures were lower at Cattail Pond, possibly delaying hatching. In 2010, three egg masses (out of 21) never hatched; I suspect they were not fertilized. Estimated clutch sizes at HFWA-W (based on a regression calculated from data presented in Redmer [2000]) ranged from 4,163–9,194 eggs per clutch. These clutch sizes were either within the reported range for Crawfish Frogs or high, due to the fact that HFWA-W females were large. For example, Redmer (2000) reports a range from 3,208–6,807 eggs/clutch in Illinois. Wright and Myers (1927), Bragg (1953) and Collins (1993) each report clutch sizes of about 7,000. Most clutch sizes were estimated visually or by water displacement techniques, although Redmer (2000) counted embryos. Bragg (1953) reported that egg mass counts for *L. a. circulosus* (present in Indiana) were up to twice as large as for *L. a. areolatus*.

Length of Larval Period and Timing of Metamorphosis

The mean larval developmental period was 91 days, longer than that previously reported of 63–75 d (Bragg, 1953; Parris and Redmer, 2005). In artificial ponds, Parris and Semlitsch (1998) found that when raised at high and low densities Crawfish Frog tadpoles metamorphosed within 68–71 d. However, when reared with other ranids, such as Plains Leopard Frog (*L. blairi*) tadpoles, larval period increased to 81–87 d. Therefore, the longer larval period observed at HFWA-W could be a result from competition with other ranid tadpoles (e.g. Southern Leopard Frogs [*L. sphenocephalus*], Green Frogs [*L. clamitans*], Bullfrogs [*L. catesbeianus*]) present in the breeding wetlands.

Emigration of post-metamorphic juveniles began in June during both years and was completed by mid-August. Wright and Wright (1933) noted Crawfish Frog metamorphosis occurring during the first week in July, and Johnson (2000) reported that metamorphosis usually occurs from mid-May to mid June. At HFWA-W, metamorphosis began 11 days earlier in 2010 compared to 2009. At Cattail Pond in 2009 (the only year juveniles were recruited), juveniles began exiting the wetland 15 days after the first juvenile had exited Nate's Pond. This delayed metamorphosis could be related to differences in pond temperatures, since maximum pond temperatures at Cattail Pond are significantly cooler than those at Nate's Pond.

Once metamorphosis began it was continuous and tended to peak following rainy nights (Figs. 9, 10). Juveniles appeared to disperse from wetlands at night; they were typically found along drift fences during the first hours of daylight. Newly metamorphosed Northern Leopard Frogs (*L. pipiens*) are noted to follow similar patterns in timing of dispersal from wetlands; large numbers of juveniles were captured emigrating on nights with favorable climatic conditions (Dole, 1971).

Juvenile Recruitment and Size

Juvenile recruitment and body size varied between years and between ponds. The number of juveniles that exited Nate's Pond was 7 times greater in 2010 compared to 2009 (from 286 to 2,103). In contrast, recruitment at Cattail Pond decreased from 11 juveniles in 2009 to zero in 2010. Similar fluctuations were observed for Dusky Gopher Frogs, with recruitment ranging from 221–2,248 juveniles (in one year recruitment was zero due to pond drying; Richter et al., 2003). Juvenile recruitment is known to vary widely year to year in amphibian populations (Pechmann and Wilbur, 1994), with pond breeding amphibians varying more than direct developing species (Green, 2005).

At HFWA-W, newly metamorphosed juvenile Crawfish Frogs ranged from 22–44 mm SVL. This range is greater than the 22–24 mm reported by Smith (1961). Other reports are 22 mm (Cagle, 1942), 24 mm (Mittleman, 1947), 30 mm (Wright and Myers, 1927), 31 mm

(Crawford et al., 2009), and 20, 26, 33, and 35 mm by Wright and Wright (1949). All of these values fall within the range observed at HFWA-W, with the exception of 20 mm by Wright and Wright (1949). Berven (1990) found a positive correlation between size at metamorphosis and juvenile survival in Wood Frogs (*L. sylvaticus*). The larger sizes reported here for juvenile Crawfish Frogs at HFWA-W may aid in adult recruitment and the persistence of populations at this site.

In 2009 metamorphosing juveniles at Nate's Pond were longer (34 mm) and heavier (4.6 g) than individuals captured in 2010 (33 mm, 3.4 g). Earlier work by Parris and Semlitsch (1998) showed that the body mass of juvenile Crawfish Frogs reared in artificial ponds was approximately 0.8 g less (2.5 g versus 3.3 g) when reared at a high versus low density. Similarly, Berven (1990) noted the effect of density dependence on the size of newly metamorphosed Wood Frogs, finding a negative correlation between total number of eggs deposited and size at metamorphosis. Therefore, given that a larger number of eggs were deposited in Nate's Pond in 2009, one may expect juveniles in 2009 to be smaller in size than juveniles in 2010, however this was not observed. Instead, juveniles from 2009 were larger in size and fewer metamorphosed. It is possible that this resulted from high early-stage larval mortality, which decreased the number of larvae present in the wetland, and reduced the effect of density dependence, thus producing larger juveniles (Vonesh and Cruz, 2002).

In comparison, the few juveniles that emerged from Cattail Pond (11 in 2009, 0 in 2010) were shorter (30 mm) and weighed less (3.0 g) than juveniles at Nate's Pond, suggesting that in 2009 and 2010 conditions for both growth and survival at Cattail Pond were less favorable than at Nate's Pond.

Directionality

The populations of Crawfish Frogs at Nate's Pond and Cattail Pond immigrated from all directions. Additionally, Crawfish Frogs tended to emigrate in all directions randomly, with the exception of adults exiting wetlands in 2009. This result is not surprising given that habitat surrounding the wetlands consist primarily of open prairie habitat and may potentially be areas were burrows are located.

Data from a telemetry study on these same populations of Crawfish Frogs at HFWA-W found that individual frogs show burrow site fidelity (J. L. Heemeyer, *unpubl. data*). However, when captured at drift fences, individual frogs generally did not use the same entry and exit point when moving into and out of wetlands. The majority of frogs at Nate's Pond left from 10–45° relative to where they entered wetlands, and the majority of frogs at Cattail Pond left from 90–180°. Ideally, directionality is best explored in circular drift fence arrays, and while Cattail Pond approaches this shape, Nate's Pond is more linear (Fig. 10). Although the telemetry data would lead to the prediction that animals would exit at, or near, the same traps—a straight line between the wetland and their burrow—my data do not fully support this. It is possible that frogs attempting to enter the wetlands move laterally along the drift fence, possibly missing a few pitfall traps, until they eventually fall into one, or a researcher finds them against the fence (Heemeyer et al., 2010). This type of behavior would compromise directional results.

Juvenile Crawfish Frogs showed directionality when exiting Nate's Pond, but not at Cattail Pond. Juveniles that dispersed from Nate's Pond oriented towards the west-northwest. Non-random dispersal in juvenile amphibians is well documented (Dodd and Cade, 1998; Walston and Mullin, 2008; Roznik and Johnson, 2009a). However, in most studies habitat surrounding breeding wetlands is heterogeneous, and results show juvenile habitat preferences

(Walston and Mullin, 2008; Roznik and Johnson, 2009a). Both Nate's Pond and Cattail Pond are surrounded by open prairie habitat, thus, the lack of obvious habitat landmarks (e.g. transition from grassland to forested area) makes habitat preference likely not the reason for directionality observed in juvenile Crawfish Frogs. It is possible that directionality in juveniles at Nate's Pond reflects the side of the pond where tadpoles were concentrated, and thus from where most juveniles emerged (Berven, 1990), or that juveniles were using indirect cues to find suitable habitat (Patrick et al., 2007).

Adult Within Breeding Season Survivorship

Within breeding seasons, corrected survivorship for Crawfish Frogs was 85%. Survivorship varied between years and between sites, although the differences were not statistically significant. There were no differences between the survivorship of males and females. Crawfish Frog breeding season survivorships observed across the two years of this study (76%–91%) are comparable to those observed across three years for Dusky Gopher Frogs (68%–85%; Richter and Seigel, 2002).

Adult Between Breeding Season Survivorship

Assuming that all adult Crawfish Frogs breed and that Crawfish Frogs show breeding site fidelity, it is possible to estimate between-year survivorship from return rates (Richter and Seigel, 2002). Telemetry data from HFWA-W (J. L. Heemeyer, *unpubl. data*) completely supports the first assumption and strongly supports the second (2 out of 12 radiotracked animals changed wetlands, one of which attempted to breed at a newly formed wetland on his migration route to Nate's Pond).

In total, 34% (32 out of 94) of the frogs captured in 2009 returned to breed in 2010. Return rates were consistent between wetlands, and between males and females (Table 2). The return rate observed in this study is comparable to those reported for other ranids, such as 16.3–21.8% for Dusky Gopher Frogs (Richter and Seigel, 2002), 31% for Common Frogs (*Rana temporaria*; Elmberg, 1990), and 53% for Cascade Frogs (*R. cascadae*; Briggs and Storm, 1970). Richter and Seigel (2002) speculate that low return rates for Dusky Gopher Frogs reflect low across-year survivorship in this species. Between-year survivorship values for Crawfish Frogs are low for a species projected to live up to five years (Redmer, 2000). Although 50% of the animals captured in 2010 were recaptures, fewer Crawfish Frogs bred in 2010, suggesting that the 2009–2010 adult mortality was uncompensated by recruitment.

Hatching Success and Larval Survivorship

Estimated hatching success was high (98%) at both breeding wetlands. Three out of 21 egg masses failed to develop, possibly due to not being fertilized. Of the viable egg masses (18) approximately 135 (eggs/mass) did not hatch. The estimated mortality for egg masses (2%; Table 8b) is lower than that reported for the related Dusky Gopher Frog (from 1996–1998; 5%, 37%, 25% respectively; Richter et al., 2003). Caddisfly infestations are reported to have contributed to embryonic mortality for Dusky Gopher Frogs (Richter, 2000; Richter et al., 2003). Crawfish Frog egg mortality (2%) is comparable to that observed for Wood Frogs (4%; Herreid and Kinney, 1966), and Northern Red-legged Frogs (2.4%; *R. aurora*; Calef, 1973). In these two studies, egg mortality was due to fungal infection, death due to desiccation or freezing, abnormal eggs, or failure in fertilization.

Estimated larval survivorship was low, ranging from 0.2–2.3% at Nate’s Pond, and from 0–0.01% at Cattail Pond (Table 5). Similarly, Dusky Gopher Frogs (0.4–5.4% when the pond held water) and Wood Frogs (1–8%) experience low larval survivorship (Berven, 1990; Richter et al., 2003). Larval amphibians are susceptible to competition, predation, desiccation, and disease among other factors when in the larval stage, with larval survivorship often not exceeding 10% (Herreid and Kinney, 1966; Calef, 1973; Berven, 1990; Richter et al., 2003; Wells, 2007).

Competition has been shown to play an important role in Crawfish Frog larval mortality. Parris and Semlitsch (1998) suggest that Crawfish Frog tadpoles reduce foraging in the presence of both inter- and intraspecific competitors. Data from Nate's Pond support this, as juvenile size was inversely proportional to juvenile number.

Predation may also account for low larval survivorship. Known predators of anuran larvae at Nate's and Cattail ponds included: Marbled Salamander larvae (*Ambystoma opacum*), Eastern Newts (*Notophthalamus viridescens*), backswimmers (*Notonecta* spp.), and dragonfly larvae (*Odonata*; Morin, 1983; Cronin and Travis, 1986; Skelly, 1994).

High mortality and annual variation in larval survivorship for some amphibian species has been linked to weather conditions—specifically those that affect hydroperiod—such as rainfall (Pechmann et al., 1989; Berven, 1990; Richter et al., 2003; Daszak et al., 2005). The direct effect of desiccation was not an important factor in the mortality of Crawfish Frog larvae during this study. For example, the complete lack of juvenile recruitment at Cattail Pond in 2010 was not due to pond drying (as this pond held water throughout the larval developmental period). Nate's Pond, which is shallower, is more vulnerable to desiccation, and indeed nearly dried once in late March 2009 and once in April 2010. It is possible that in some years Nate's Pond dries causing complete larval mortality.

Disease is known to play a major role in amphibian population and species declines (Green et al., 2002; Daszak et al., 2003; Muths et al., 2003; Greer et al., 2005). Diseases of amphibians include Bd, *Ranavirus*, mycoplasma infections and others. Crawfish Frogs at

HFWA-W are infected with Bd, and I have estimated elsewhere (Kinney et al., 2011) that 12% of adults develop chytridiomycosis and die. Amphibian larvae that are infected with Bd experience de-keratinization of mouthparts, but the disease is not fatal to tadpoles (Fellers et al., 2001). Despite the prevalence of Bd among breeding adults, newly metamorphosed juveniles only exhibit a 1% infection rate (Kinney et al., 2011). These observations, coupled with the fact that tadpoles at HFWA-W were never observed with de-keratinized mouth parts, suggest that Bd is not responsible for low larval survivorship in these populations. *Ranavirus* is also known to decimate amphibian larval populations (Greer et al., 2005), and mycoplasma has caused deaths in related Dusky Gopher Frog tadpoles (MGFRAP, 2009). To date we have not tested for the presence of *Ranavirus* or mycoplasma at HFWA-W.

Comparisons With the Closely Related Gopher Frog Species

A comparison between Crawfish Frogs and closely related Gopher Frogs species gives perspective (there are no comparative data for Gopher Frogs; Table 9). Data on Dusky Gopher Frogs (there is only one reasonable robust population remaining) are reported by Richter and Seigel (2002) and Richter et al. (2003). HFWA-W Crawfish Frog breeding populations were smaller, and therefore fewer egg masses were laid. However, because Crawfish Frog fecundity is high, Crawfish Frogs deposited a greater number of eggs. Larval survivorship was higher in Dusky Gopher Frogs, and therefore the number of juvenile recruits was similar (Table 9). Adult within-breeding season survivorship was similar, although between-year adult survivorship for Crawfish Frogs was almost double that of Dusky Gopher Frogs (Table 9). This comparison suggests larval survivorship is lower in Crawfish Frogs but adult survivorship is higher. Sample sizes (years) are low, however, and additional data may reveal other trends.

Although the same types of data are not available for Gopher Frogs, populations are reported to be small and to vary in number between years, even in undisturbed habitats (Semlitsch et al., 1995; Greenberg, 2001). Semlitsch et al. (1995) reported that at Savannah River site the yearly number of breeding adults was small (10 or fewer) and juvenile recruitment (46–50) was low at monitored wetlands, however populations were stable across 25 years. A larger breeding population of Gopher Frogs has been observed (n = 301) at a pond in Florida (Palis, 1998). A recent study on survival of newly metamorphosed Gopher Frogs found that mortality was high (88%) within the first month after emergence (Roznik and Johnson, 2009b).

Given the status of both Gopher Frog species, conservation initiates are currently in place to help restore populations (Amphibian Ark, 2006; Mississippi Gopher Frog Recovery Action Plan [MGFRAP], 2009). To help improve the status of Dusky Gopher Frogs, tadpoles are being head-started and released at the two existing population sites, and at new sites (MGFRAP, 2009). Goals for this species include protecting the known isolated populations, establishing new populations, and restoring the status from declining to stable (MGFRAP, 2009). To improve Gopher Frog populations, egg masses collected from breeding sites are being captive reared until metamorphosis, and juveniles are batch marked and released onto habitat managed by The Nature Conservancy (Amphibian Ark, 2006). Starting this year through 2012, the release site will be monitored to determine whether captive reared individuals return to breed (Amphibian Ark, 2006).

Given the status of Crawfish Frogs compared to the two closely related Gopher Frog species, I recommend similar conservation initiatives be put into place to secure the status of this species.

Conservation Implications

Crawfish Frogs have experienced severe declines in both the northeastern and southwestern portions of their range. Equally disturbing, estimates of population sizes are relatively unknown in many states where they occur (e.g. Mississippi; SEPARC, 2010). The majority of populations occur primarily in Oklahoma, southern Illinois, western Kentucky, Missouri, and Indiana (SEPARC, 2010). In Indiana, Crawfish Frogs are state endangered; and recent surveys (Engbrecht, 2010) suggest there may be fewer than 1,000 breeding adults in the entire state. Data from the present study highlight aspects of Crawfish Frog population biology that can be useful in its recovery. While adult survivorship and egg hatching success are relatively high, most mortality occurs during the larval period (Table 8).

Captive rearing and release is currently being used to assist in the recovery of both Dusky Gopher Frogs and Gopher Frogs (Amphibian Ark, 2006; MGFRAP, 2009). I suggest the same approach be used with Crawfish Frogs—that captive rearing be employed to help recover existing populations and repatriate others. If done well it should work; Crawfish Frogs have shown an ability to colonize and inhabit highly disturbed habitats such as reclaimed mine spoil prairies (Lannoo et al., 2009; Engbrecht and Lannoo, 2010). The ultimate goal is to secure this species' future before heroic measures become necessary.

CHAPTER 2

POPULATION SIZE, TIMING OF BREEDING, AND JUVENILE RECRUITMENT IN POND BREEDING AMPHIBIANS ON A RECLAIMED MINE SPOIL PRAIRIE

INTRODUCTION

Amphibians are facing an extinction crisis, with nearly 25% of species globally facing extirpation, and another 25% of species threatened (Stuart et al., 2004). Habitat destruction, disease, invasive species, pollution, and the pet trade are all factors known to negatively influence amphibian populations (Collins and Storfer, 2003; Stuart et al., 2004; Daszak et al., 2005). From among these insults, habitat loss has been proposed as the most important cause of amphibian declines (Collins and Storfer, 2003; Gallant et al., 2007). Land use accounts the most in affecting the persistence of amphibian populations within the United States, affecting 77% of anurans and 91% of caudates (Bradford, 2005).

In the midwestern United States, specifically within the area encompassed by the coalfields of the Illinois Basin, amphibian habitat has been altered and in some cases destroyed by surface mining. However, following the implementation of the Surface Mining Control and Reclamation Act (SMCRA) of 1977, areas surface-mined across the United States are required to comply with national reclamation standards (Office of Surface Mining Reclamation and Control, 2008). Habitats destroyed as a result of coal mining are to be restored to their previous use, historical use, or to a standard that is equally or more economically productive (Office of Surface Mining Reclamation and Control, 2008). In practice, this means that mined sites are frequently restored to grasslands (Bajema et al., 2001). This emphasis has, somewhat unexpectedly, expanded the available prairie habitat in Indiana into the southwestern portion of the state (Lannoo et al., 2009).

The ability of wildlife to colonize reclaimed mine spoil prairies has been reported for several birds (DeVault et al., 2002; Scott et al., 2002; Scott and Lima, 2004), small mammals (Hingtgen and Clark, 1984; Stone, 2007), amphibians (Myers and Klimstra, 1963; Timm and Meretsky, 2004; Anderson and Arruda, 2006), and reptiles (Myers and Klimstra, 1963). Previous studies on amphibian and reptile occurrence on reclaimed coal mines have primarily focused on documenting species presence, diversity, and abundance (Myers and Klimstra, 1963; Galán, 1997; Timm and Meretsky, 2004; Loughman, 2005; Lannoo et al., 2009; Carrozzino, 2009). Fewer studies have reported on the population size and reproductive potential of amphibians and reptiles found on reclaimed mine sites (but, see Galán, 1997; Loughman, 2005).

Over the past two years, my colleagues and I published on the diversity and abundance of herptofauna observed on a reclaimed mine spoil prairie in southwest Indiana (see Lannoo et al., 2009; Kinney et al., 2010). As a follow-up to these studies, I report here the diversity and abundance of amphibian and reptile species found at four monitored wetlands on the same reclaimed mine spoil prairie in southwestern Indiana. In particular, I go beyond our initial surveys to report on the population size, timing of breeding and metamorphosis, and juvenile recruitment of the amphibian species present. My data show that areas once stripped of their ecology and reclaimed can be colonized by amphibians and reptiles to the point of producing successfully breeding and presumably sustainable populations.

MATERIALS AND METHODS

Study Site

My field site is located on the western portion of Hillenbrand Fish and Wildlife Area (HFWA-W) in Greene County, Indiana. HFWA-W comprises 729 hectares that was historically eastern deciduous forest containing scattered pocket prairies (Transeau, 1935; Jones and Cushman, 2004) converted to agricultural fields prior to being mined. Following re-contouring and recovering of this area after mining, it was seeded with prairie species such as big bluestem (*Andropogon gerardii*), little bluestem (*Schizachyrium scoparium*), indian grass (*Sorghastrum nutans*), partridge pea (*Chamaecrista fasciculata*), black-eyed susan (*Rudbeckia hirta)*, and common milkweed (*Asclepias syriaca*). HFWA-W is now managed as prairie by the Indiana Department of Natural Resources' (IDNR) Division of Fish and Wildlife (Lannoo et al., 2009).

As a result of mining activities and post-mining habitat restoration, HFWA-W now includes several bodies of water ranging in hydroperiod from highly ephemeral wetlands, through semi-permanent wetlands, to large final-cut lakes. As part of a larger collaborative project to study the biology of Crawfish Frogs (*Lithobates areolatus*) at HFWA-W in 2009, the presence of other amphibian and reptile species was monitored at four of these wetlands (Nate's Pond, Cattail Pond, Willow Pond, Hill Pond). Because Nate's Pond and Cattail Pond supported Crawfish Frog breeding, they were monitored during both the 2009 and 2010 field seasons; Willow Pond and Hill Pond were only monitored during 2009.

Nate's Pond is an ephemeral wetland, approximately 0.14 ha in size. It was formed unintentionally at the initial site of mining excavation. On the southeast side of the wetland is a large hill where the first spoils were dumped. The wetland itself lies on re-contoured ground that creates a slight slope facing the hill, causing water to accumulate in the resulting depression.

Woody vegetation in the pond includes numerous willows (*Salix* sp.) and a few cottonwoods (*Populus deltoides*); understory woody species include introduced bush honeysuckle (*Lonicera maackii*) and raspberries (*Rubus* sp.). Within the wetland, at the north and south ends, willows and hybrid cattails (*Typha angustifolia x latifolia*) predominate; the center of the wetland is characterized by a small open-water area with scattered rushes (*Scirpus* sp.) and aquatic macrophytes. Uplands surrounding the wetland basin consist of herbaceous prairie plantings.

Cattail Pond is a larger, semi-permanent wetland approximately 0.33 ha. Cattail Pond was also formed unintentionally from either a depression created by uneven contouring during the reclamation process or slumping afterward. Cattail Pond is circular with one large willow at the eastern edge of the pond alongside one bush honeysuckle. Hybrid cattails predominate, occurring densely everywhere except in the center of the pond where there is a roughly circular opening of deeper water. Upland vegetation is reclaimed prairie, similar to the vegetation surrounding Nate's Pond.

Willow Pond is an ephemeral wetland, approximately 0.06 ha. This pond is closest to the woodland edge (that surrounds the open prairie habitat of HFWA-W), and is a depression created from uneven contouring during the reclamation process, or slumping afterwards. Willow Pond is a woodland pond with emergent trees including willows, maples (*Acer* sp.), sycamores (*Platanus occidentalis*), shingle oaks (*Quercus imbricaria*), red oaks (*Quercus rubra*) and locusts (*Gleditsia* sp.). The western edge of the wetland backs up to the forest edge; elsewhere the wetland is bordered by restored prairie.

Hill Pond is an ephemeral wetland, covering approximately 0.07 ha. This wetland is essentially a wet meadow filled with hybrid cattails. There is one honeysuckle on the northwest side, and vegetation immediately surrounding the wetland includes rushes and bush clover (*Lespedeza* sp.). Upland vegetation is reclaimed prairie.

Sampling Techniques

I used drift fences paired with pitfall traps to monitor amphibian and reptile movement into and out of wetlands (Gibbons and Bennett, 1974; Gibbons and Semlitsch, 1981; Dodd and Scott, 1994). Full drift fences were installed around ponds in February 2009 when the ground had thawed enough to dig; fencing was placed approximately 5 m from the wetland edge. Fence material consisted of woven polypropylene composite fence, 1-m high and buried roughly 10–15 cm below ground, with support stakes placed every 5 m. Hardware cloth was later installed in sections at drainage areas to prevent the washing out of drift fences due to flooding (Lamoureux et al., 2002; Heemeyer et al., 2010). In 2010, I used a more durable monofilament silt fence reinforced by wooden 5 x 60 cm laths. Pitfall traps consisted of 15-L white square buckets placed every 10 m along the inside and outside of the fencing (Heemeyer et al., 2010). Each bucket was fitted with a half lid (open side closest to the fence) to provide shade for trapped animals and deter predators (raccoons, skunks, opossums, feral cats). A sponge was placed in each trap to help prevent desiccation of animals during warm weather, and provide a floating substrate for animals when buckets flooded. A 2.5 cm x 2.5 cm x 40 cm stake was placed in each bucket to facilitate small mammal escape (Dodd and Scott, 1994).

Nate's Pond was enclosed with 270 m of fencing and 26 pairs of pitfall traps; Cattail Pond was enclosed with 280 m of fencing and 27 pairs of pitfall traps (later, one of these pitfall traps located in a perennially wet area was removed). Willow Pond was enclosed with 240 m of fencing and 23 pairs of pitfall traps; and Hill Pond was enclosed with 160 m of fencing and 15 pairs of pitfall traps. In 2009, pitfall traps were opened from 5 March–16 October at Nate's and

Cattail ponds, from 27 February–12 August at Willow Pond, and from 5 March–12 August at Hill Pond. In 2010, pitfall traps were opened from 1 March–19 August at Nate's and Cattail ponds. Pitfall traps were checked once daily immediately after sunrise and again on rainy nights—perhaps several times—during the breeding season (Heemeyer et al., 2010).

All captured amphibians were sexed, aged, and those in the families Ambystomatidae, Ranidae and Bufonidae were given a cohort clip. The cohort clip consisted of two toe clips: one representing the year, the other representing the pond where captured. The pond clip differed for adults and newly metamorphosed animals so that age classes could be distinguished during future encounters when juveniles had matured. Reptiles were not given an identification mark.

RESULTS

Species Diversity and Abundance

Thirty-three species of amphibians and reptiles were found at Hillenbrand FWA-W, 10 species were new county records for Green County (Lannoo et al., 2009; Kinney et al., 2010). Twenty eight—14 amphibian species and 14 reptile species—of the 33 species found were captured at the drift fences (Table 10). Five additional species were found opportunistically while conducting other research activities at the study site (e.g. telemetry study). A total of 18,109 amphibians and 435 reptiles were captured at drift fences across the two years of this study. Amphibians captured at the wetlands included five salamander species, eight frog species, and one toad species (Table 10). The five salamander species captured included three ambystomatids, one salamandrid, and one plethodontid (Table 10). The eight frog and one toad species captured included four hylids, four ranids, and one bufonid (Table 10). Reptiles captured at the wetlands included eight snake, five turtle, and one lizard species (Table 10). The eight snake species were in three families—five natricids, two xenodontids, and one colubrid (Table

10). The five species of turtles captured were in three familes—one chelydrid, three emydids, and one kinosternid (Table 10). The one species of lizard was in the family Scincidae (Table 10).

Each wetland had different species compositions and relative abundances (Table 10), but in general Nate's Pond and Willow Pond had similar species compositions, and Cattail Pond and Hill Pond had similar species compositions. Marbled Salamanders (*Ambystoma opacum*) were the most abundant salamander captured at Nate's (2009, n = 1,479; 2010, n = 904) and Willow (2009, n = 1,557) ponds; Small-mouthed Salamanders (*A. texanum*) were the most abundant at Cattail (2009, n = 579; 2010, n = 597) and Hill (2009, n = 123) ponds (Table 10).

The most abundant frog species captured differed between ponds. At Nate's Pond in 2009, Southern Leopard Frogs (*L. sphenocephalus*; n = 947) were the most abundant; in 2010 Crawfish Frogs (*L. areolatus*; n = 2,161) were the most abundant (Table 10). At Cattail Pond, Green Frogs (*L. clamitans*) were the most abundant both years (2009, n = 1,980; 2010, n = 506; Table 10). At Willow Pond, Western Chorus Frogs (*Pseudacris triseriata*; n = 250) were the most abundant. At Hill Pond, Southern Leopard Frogs (n = 374) were the most abundant.

Reptile abundances were low at the drift fences, with several species represented by only one individual (Table 10). In 2009, Eastern Ribbonsnakes (*Thamnophis saurtius*; n = 3) were the most frequently captured snake at Nate's Pond. Common Gartersnakes (*T. sirtalis*) were most frequently captured at Cattail (n = 5), Willow (n = 1), and Hill ponds in 2009 (n = 1; Table 10). In 2010, fewer snakes were captured. Dekay's Brownsnakes (*Storeria dekayi*) were most commonly captured at Nate's Pond (n = 13). At Cattail Pond, Common Gartersnakes were the only captured snakes (n = 4; Table 10).

In general, Painted Turtles (*Chrysemys picta*) were the most commonly captured turtles. But in 2009 at Willow Pond, Eastern Box Turtles (*Terrapene carolina*; n = 46) were most common (Table 10). Similarly, in 2010 at Nate's Pond there were slightly more Eastern Box Turtles (n = 17) captured than Painted Turtles (n = 14; Table 10). The Common Five-lined Skink (*Plestiodon fasciatus*) was the only species of lizard found at HFWA-W, and it was found only at Willow Pond.

Amphibian Breeding

Amphibian breeding assemblages were consistent across years, but varied between the four ponds (Tables 11–14). Predominate species during the breeding season at all wetlands were Marbled Salamanders, Small-mouthed Salamanders, Eastern Newts (*Notophthalmus viridescens*), and Western Chorus Frogs. The four ranids captured (Crawfish Frogs, American Bullfrogs [*L. catesbeianus*], Green Frogs, Southern Leopard Frogs) were common but adults were not present in large numbers (Tables 11–14). At Nate's and Cattail ponds, where species population sizes were monitored for two years, numbers of adults varied between years, with some species fluctuating more than others (Tables 11, 12).

At Nate's Pond, breeding population sizes fluctuated the most for Marbled Salamanders, Small-mouthed Salamanders, and Southern Leopard Frogs (Table 11). The number of female Marbled Salamanders decreased from 133 in 2009 to 46 in 2010 (65%), and the number of males decreased from 254 in 2009 to 62 in 2010 (76%; Table 11). The number of adult Small-mouthed Salamanders increased between years. There was approximately a twofold increase (from 131 to 248; 89%) in the number of females, and an increase in the number of males (from 159 to 251; 58%) in 2010 (Table 11). The number of adult Southern Leopard Frogs decreased between years at Nate's Pond, with the number of females down from 54 in 2009 to 13 in 2010 (76%), and males down from 71 in 2009 to 23 in 2010 (67%; Table 11). The breeding population sizes of other amphibian species at Nate's Pond fluctuated less between the 2009 and 2010 field seasons (Table 11).

At Cattail Pond, adult population sizes fluctuated the most between years for all four species of salamanders and for two frog species, as follows. The numbers of female Marbled Salamanders decreased from 22 (2009) to 11 (2010; 50%) and decreased from 22 to 8 (64%) for males (Table 12). The number of Small-mouthed Salamanders increased from 155 (2009) to 275 (2010) for females and from 243 to 272 for males (Table 12). A small population of Tiger Salamanders (*A. tigrinum*) bred at the pond during both years; the number of females increased from two to four, and number of males decreased from 10 to two between 2009 and 2010. Fewer breeding Eastern Newts were captured in 2010; the numbers of females captured decreased from 110 to 51 (54%), males decreased from 88 to 37 (58%; Table 12).

Among frogs at Cattail Pond, populations sizes of Green Frogs and Southern Leopard Frogs fluctuated the most. Numbers of adult Green Frogs captured more than doubled (for females, from 11 to 34; for males, from 18 to 42). Numbers of captured Southern Leopard Frogs varied: females increased (from 18 to 33 individuals), males decreased (from 98 to 34 individuals; Table 12). The breeding population sizes of other amphibian species were generally consistent between the two years (Table 12).

At Willow Pond, Marbled Salamanders (30 females, 24 males) and Small-mouthed Salamanders (44 females, 67 males) had the largest salamander populations, and Western Chorus Frogs (157 females, 86 males) had the largest frog population (Table 13).

Hill Pond had the smallest numbers of breeding amphibians of all four ponds. Small-mouthed Salamanders (43 females, 27 males) had the largest salamander population, and Western Chorus Frogs (13 females, 19 males) had the largest frog population (Table 14).

Between-year Recaptures

Between-year recaptures at Nate's Pond and Cattail Pond (Willow Pond and Hill Pond were not sampled in 2010) were low among species given cohort clips (Tables 6, 7). Small-mouthed Salamanders, Crawfish Frogs, and Green Frogs tended to have the highest percentages of recaptures between years, as follows.

Of the eight species given cohort clips at Nate's Pond in 2009, Marbled Salamanders, Small-mouthed Salamanders, Crawfish Frogs and Southern Leopard Frogs had individuals return to the wetland in 2010 (Table 6). Thirty-one Marbled Salamanders from 2009 returned to the pond in 2010: seven females (5.3%), 13 males (5.1%), and 11 juveniles (1.2%). Of the 11 juvenile Marbled Salamanders that exited Nate's Pond and returned in 2010, three were sexually mature females, seven were sexually mature males, and one was a subadult (Table 15). Sixty Small-mouthed Salamanders marked in 2009 returned in 2010: 13 females (9.9%), 46 males (29%), and one juvenile (0.5%). The one juvenile that exited in 2009 returned as a sexually mature male (Table 15). Adult Crawfish Frogs were recaptured, but are discussed in Chapter 1. Lastly, 11 Southern Leopard Frogs were recaptured entering in 2010: one female (1.8%), five males (7.0%), and five juveniles (0.8%). The five juvenile Southern Leopard Frogs that exited the pond in 2009 all returned as sexually mature males (Table 15).

Of the eight species given cohort clips at Cattail Pond in 2009, seven—Marbled Salamanders, Small-mouthed Salamanders, Tiger Salamanders, Crawfish Frogs, Bullfrogs, Green Frogs, and Southern Leopard Frogs—had individuals return to the wetland in 2010 (Table

16). Only one male Marbled Salamander (out of 22; 4.5%) returned in 2010. Forty-three Small-mouthed Salamanders returned: 16 females (10%), 27 males (11%). Only one male Tiger Salamander (out of 10; 10%) returned. Adult Crawfish Frogs were recaptured (see Chapter 1). One female Bullfrog (out of 6; 17%) returned. Five Green Frogs returned: four males (22%) and one juvenile (0.1%); the juvenile returned as a sexually mature male (Table 16). Eight Southern Leopard Frogs returned: two females (11%), four males (4.1%), and two juveniles (4.3%); one juvenile returned as a sexually mature female, the other as a sexually mature male (Table 16).

Timing of Breeding

In 2009, the timing of breeding for each species was simultaneous at each of the four wetlands (Figs. 15–20). In 2010, the timing of breeding for each species was comparable between Nate's and Cattail ponds with the exception of Green Frogs, which began immigrating into Nate's Pond approximately 30 days later than they began entering Cattail Pond (Figs. 16, 18).

Adult amphibians moved into the wetlands mostly from early March through June—with the exception of fall breeders (Marbled Salamanders). The following species tended to enter and exit wetlands between early March–mid-May: Small-mouthed Salamanders, Eastern Tiger Salamanders, Eastern Newts, Spring Peepers (*P. crucifer*), Western Chorus Frogs, and Southern Leopard Frogs (Figs. 15–20). Northern Cricket Frogs (*Acris crepitans*), Bullfrogs, and Green Frogs tended to enter wetlands in mid-April, and movement across the drift fences lasted through early July (Figs. 15–19). Fall breeding for Marbled Salamanders ranged from August to mid-October (Figs. 15–20). Eastern Newts, Western Chorus Frogs, and Southern Leopard Frogs were often caught immigrating back into the wetlands during early fall.

Juvenile Recruitment

The majority of amphibians that bred at monitored wetlands had successful juvenile recruitment. Recruitment for Marbled Salamanders, Bullfrogs, and Green Frogs occurred the year following breeding since larvae of these species overwinter in wetlands. The exception was at Nate's Pond, where juvenile Green Frogs could not overwinter because of pond drying, and thus emerged during the same year.

Nate's Pond produced ten species of juvenile amphibians in 2009 (Table 11a). Numbers of juveniles produced varied between species, ranging from 1–943 individuals (Table 11). Also in 2010, ten species of juveniles exited the wetland, with numbers ranging from 1–2,103 newly metamorphosed individuals (Table 11b). Numbers of juveniles produced decreased between years at Nate's Pond for Marbled Salamanders (943 to 751; 20%), Small-mouthed Salamanders (199 to 12; 94%), Eastern Newts (667 to 519; 22%), Northern Cricket Frogs (1 to 0), Spring Peepers (35 to 5; 86%), Western Chorus Frogs (32 to 6; 81%), Green Frogs (47 to 21; 55%), and Southern Leopard Frogs (625 to 243; 61%). Recruitment for two species increased from 2009 to 2010: Crawfish Frogs (286 to 2,103; 635%) and Cope's Gray Treefrogs (*Hyla chrysoscelis*; 0 in 2009, 1 in 2010; Table 11b). Juveniles of 11 species in 2009 and 10 species in 2010 were captured immigrating into Nate's Pond; predominately Marbled Salamanders, Green Frogs, and Southern Leopard Frogs (Table 11).

At Cattail Pond in 2009 all eleven amphibian species captured produced juveniles, ranging from 1–1,507 newly metamorphosed individuals (Table 12a). In 2010, the eight species captured successfully produced juveniles, ranging from 1–86 individuals (Table 12b). Juvenile recruitment decreased at Cattail Pond between years for the following species: Small-mouthed Salamanders (59 to 13; 75%), Northern Cricket Frogs (4 to 0; no recruitment), Spring Peepers (1 to 0; no recruitment), Western Chorus Frogs (10 to 9; 10%), Crawfish Frogs (11 to 0; no recruitment), Bullfrogs (4 to 1; 75%), and Green Frogs (1,507 to 34; 98%). Three species had an increase in the number of juveniles produced: Marbled Salamanders (15 to 48; 153%), Tiger Salamanders (from 1 to 2; 100%), and Eastern Newts (from 49 to 86 76%; Table 12). Southern Leopard Frogs had the same number of juveniles metamorphose, 47, in 2009 and in 2010 (Table 12). Juveniles of ten different species were captured immigrating into Cattail Pond both years; predominately Green Frogs and Southern Leopard Frogs (Table 12).

At Willow Pond, six species successfully reproduced; numbers of juveniles ranged from 1–1,382 (Table 13). Juveniles produced were predominately Marbled Salamanders (1,382; Table 13). Juveniles of nine species were captured immigrating into the wetland, predominantly Marbled Salamanders, Green Frogs and Southern Leopard Frogs (Table 13).

At Hill Pond, seven species successfully reproduced, numbers of juveniles ranged from 1–49 (Table 14). Juveniles produced were predominately Marbled Salamanders (39) and Southern Leopard Frogs (49; Table 14). Juveniles of nine different species immigrated into Hill Pond; predominately Green Frogs and Southern Leopard Frogs (Table 14).

Timing of Metamorphosis

The earliest juveniles to emerge from all four wetlands were Marbled Salamanders, and metamorphosis occurred from late April–mid June (Figs. 15–20). Only in a few instances did juveniles of other species—Eastern Newts (Figs. 16, 18) and Southern Leopard Frogs (Fig. 17)—emerge earlier. Metamorphosis of other juvenile species occurred mostly between late May and early August, with timing of emergence partially overlapping for all species (Figs. 15–20). In 2009, metamorphosis occurred later at Hill Pond compared to the other three wetlands (Figs. 15, 18–20). Timing of metamorphosis was similar at Nate’s and Willow ponds in 2009 (Figs. 15, 19), however timing was different for juveniles at Nate's and Cattail ponds (Figs. 15, 17). At Nate's Pond in 2009, juvenile salamanders tended to emigrate earlier than at Cattail Pond, however juvenile frogs emigrated later (Figs. 15, 17). Green Frog tadpoles at Nate's Pond metamorphosed later in the year as a result of pond drying in late August. Juveniles at Cattail Pond emerged earlier since they had overwintered from the previous year. The timing of metamorphosis for each species differed little between years at Nate's and Cattail ponds (Figs. 15–18).

DISCUSSION

This study demonstrates an important aspect of amphibian and reptile conservation biology, namely the ability of these animals to colonize highly disturbed—but restored—habitats. The diversity of amphibians and reptiles detected in this study is surprising given the ecological history of the site (Lannoo et al., 2009), and my data show that, at least for amphibians, these species are successfully reproducing.

These data follow up a previous report by Lannoo et al. (2009), by examining the diversity, population sizes, and juvenile recruitment in amphibians at four monitored wetlands within HFWA-W in Indiana. During this study, 28 species of amphibians and reptiles (18,544 captures) were observed. Abundance at HFWA-W was comparable to that documented at constructed wetlands on a conservation preserve, with juveniles accounting for the majority of captures (Palis, 2007). I found 13 species of pond-breeding amphibians (and one terrestrial breeder, Red-backed Salamander), similar to species richness previously noted at other wetlands. For example, Brodman et al. (2006) reported 10 species at a restored prairie in northwestern Indiana, Timm and Meretsky (2004) documented nine species at a reclaimed mine area in Indiana (near HFWA-W), Walston and Mullin (2007) reported 10 species at a pond in Illinois, and Hocking et al. (2008) reported 15 species at ponds located within an oak-hickory forest in Missouri.

Some species favored certain pond types (e.g. semi-permanent vs. ephemeral). Species preferring more permanent bodies of water, such as American Bullfrogs, Green Frogs, and Snapping Turtles (Minton, 2001), were more common at Cattail Pond. Species associated with ephemeral wetlands (e.g. Marbled Salamanders) were more abundant at the other three ponds. These observations are consistent with the results of Pechmann et al. (1989), who noted that pond hydroperiod is a determining factor in amphibian species diversity and community structure. It is likely that the amphibian diversity documented at HFWA-W stems in part from the assorted wetland types present.

Although recaptures were low between years for species given cohort clips, several species had a least one individual return. Southern Leopard Frogs and Marbled Salamanders had juveniles from 2009 return as mature adults in 2010. Juveniles were also recruited at ponds through dispersal, as newly metamorphosed individuals were captured immigrating into each wetland. This type of dispersal among wetlands at HFWA-W possibly works to create a metapopulation dynamic for each species (Sinsch, 1997; Semlitsch, 2008). Population connectivity between the wetlands, likely a result from juvenile dispersal, helps populations persist and recover when disturbed or extirpated (Marsh and Trenham, 2000; Semlitsch, 2000; Semlitsch, 2008).

Juvenile dispersal may be how Hillenbrand was colonized following the restoration process. Indeed, Galán (1997) reported that during the first three years following mining, the first individuals captured for each species of amphibian were juveniles, and breeding was not detected until five years after reclamation. Galán (1997) also suggested that more than ten years are needed for amphibian and reptile communities to reach pre-disturbance diversity and abundance levels. Given that HFWA-W was in agricultural use prior to being mined (Lannoo et al., 2009), amphibian and reptile diversity is probably higher now than prior to mining. The subsequent diversity and abundance of amphibians and reptiles at HFWA-W may be attributed to proper ecosystem management by the IDNR, the inadvertent creation of a diversity of wetland types, expansive upland habitat, and/or the presence of off site source populations.

Conclusions

The findings in this study follow up on our previous work (Lannoo et al., 2009; Kinney et al., 2010), emphasizing the value of mine spoil prairies as critical habitat for amphibian and reptile species. Not only are amphibians and reptiles able to colonize these areas (Timm and Meretsky, 2004; Loughman, 2005; Carrozzino, 2009), but they are also able to use them as successful breeding sites. These data demonstrate that both wetland and upland habitats can be recovered following severe degradation, and that amphibians and reptiles will respond.

REFERENCES

AMPHIBIAN ARK. 2006. *Ex situ* program progress: *Lithobates capito*. <http://www.amphibianark.org/exsituprogress/Lithobates%20capito.htm>. Accessed on 25 January 2011.

ANDERSON, L. R., AND J. A. ARRUDA. 2006. Land use and anuran biodiversity in southeast Kansas, USA. Amphibian and Reptile Conservation 4:46–59.

BACON, E. J., AND Z. M. ANDERSON. 1976. Distributional records of amphibians and reptiles from the Coastal Plain of Arkansas. Proceedings of the Arkansas Academy of Science 30:14–15.

BAJEMA, R. A., T. L. DEVAULT, P. E. SCOTT, AND S. L. LIMA. 2001. Reclaimed coal mine grasslands and their significance for Henslow's Sparrows in the American Midwest. Auk 118:422–431.

BARBOUR, R.W. 1971. Amphibians and Reptiles of Kentucky. University Press of Kentucky, Lexington, Kentucky.

BATSCHELET, E. 1981. Circular Statistics in Biology. Academic Press, London.

BERVEN, K. A. 1990. Factors affecting population fluctuations in larval and adult stages of the Wood Frog (*Rana sylvatica*). Ecology 71:1599–1608.

BERVEN, K. A., D. E. GILL, AND S. J. SMITH-GILL. 1979. Countergradient selection in the Green Frog, *Rana clamitans*. Evolution 33:609–623.

BRADFORD, D. F. 2005. Factors implicated in amphibian population declines in the United States. *In* M. J. Lannoo (ed.) Amphibian Declines: The Conservation Status of United States Species, pp. 915–925. University of California Press, Berkeley, California.

BRAGG, A. N. 1953. A study of *Rana areolata* in Oklahoma. The Wasmann Journal of Biology 11:273–319.

BRIGGS, J. L., AND R. M. STORM. 1970. Growth and population structure of the Cascade Frog, *Rana cascadae* Slater. Herpetologica 26:283–300.

BRODMAN, R., M. PARRISH, H. KRAUS, AND S. CORTWRIGHT. 2006. Amphibian biodiversity recovery in a large-scale ecosystem restoration. Herpetological Conservation and Biology 1:101–108.

BUSBY, W. H., AND W. R. BRECHEISEN. 1997. Chorusing phenology and habitat associations of the Crawfish Frog, *Rana areolata* (Anura: Ranidae), in Kansas. Southwestern Naturalist 42:210–217.

CAGLE, F. R. 1942. Herpetological fauna of Jackson and Union counties, Illinois. American Midland Naturalist 28:164–200.

CALEF, G. W. 1973. Natural mortality of tadpoles in a population of *Rana aurora*. Ecology 54:741–758.

CARROZZINO, A. L. 2009. Evaluating wildlife response to vegetation restoration on reclaimed mine lands in southwestern Virgina. Unpubl. Master's Thesis, Virgina Polytechnic Institute and State Univ.

CHRISTIANSEN, J. L., AND R. M. BAILEY. 1991. The Salamanders and Frogs of Iowa. Iowa Department of Natural Resources, Des Moines, Iowa.

CHRISTY, M.T. 1996. The efficacy of using passive integrated transponder (PIT) tags without anesthetic in free-living frogs. Australian Zoologist 30:139–142.

COLLINS, J. T. 1993. Amphibians and Reptiles of Kansas. Third edition, revised. Natural History Museum, University of Kansas, Lawrence, Kansas.

COLLINS, J. P., AND A. STORFER. 2003. Global amphibian declines: sorting the hypotheses. Diversity and Distributions 9:89–98.

COLLINS, J. T., S. L. COLLINS, AND T. W. TAGGART. 2010. Amphibians, Reptiles, and Turtles in Kansas. Eagle Mountain Publishing, LC, Kansas.

CRAWFORD, J. A., D. B. SHEPARD, AND C. A. CONNER. 2009. Diet composition and overlap between recently metamorphosed *Rana areolata* and *Rana sphenocephala*: implications for a frog of conservation concern. Copeia 2009:642–646.

CRONIN, J. T., AND J. TRAVIS. 1986. Size-limited predation on larval *Rana areolata* (Anura: Ranidae) by two species of backswimmer (Insecta: Hemiptera: Notonectidae). Herpetologica 42:171–174.

DASZAK, P., A. A. CUNNINGHAM, AND A. D. HYATT. 2003. Infectious disease and amphibian population declines. Diversity and Distributions 9:141–150.

DASZAK, P., D. E. SCOTT, A. M. KILPATRICK, C. FAGGIONI, J. W. GIBBONS, AND D. PORTER. 2005. Amphibian population declines at Savannah River Site are linked to climate, not chytridiomycosis. Ecology 86:3232–3237.

DEVAULT, T. L., P. E. SCOTT, R. A. BAJEMA, AND S. L. LIMA. 2002. Breeding bird communities of reclaimed coal mine grasslands in the American Midwest. Journal of Field Ornithology 7:268–275.

DODD, C. K., JR., AND D. E. SCOTT. 1994. Drift fences encircling breeding sites. *In* W. R. Heyer, M. A. Donnelly, R. W. McDiarmid, L-A. C. Hayek, and M. S. Foster (eds.), Measuring and Monitoring Biological Diversity. Standard Methods for Amphibians, pp. 125–130. Smithsonian Institution Press, Washington, D.C.

DODD, C. K., JR., AND B. S. CADE. 1998. Movement patterns and the conservation of amphibians breeding in small, temporary wetlands. Conservation Biology 12:331–339.

DOLE, J. W. 1971. Dispersal of recently metamorphosed Leopard Frogs, *Rana pipiens*. Copiea 2:221–228.

DUNDEE, H. A., AND D. A. ROSSMAN. 1996. The Amphibians and Reptiles of Louisiana. Louisiana State Univserity Press, Baton Rouge and London.

ELMBERG, J. 1990. Long-term survival, length of breeding season, and operational sex ratio in a boreal population of common frogs, *Rana temporari*a L. Canadian Journal of Zoology 68:121–127.

ENGBRECHT, N. J. 2010. The status of Crawfish Frogs (*Lithobates areolatus*) in Indiana, and a tool to assess populations. Unpubl. Master's Thesis, Indiana State Univ.

ENGBRECHT, N. J., AND M. J. LANNOO. 2010. A review of the status and distribution of Crawfish Frogs (*Lithobates areolatus*) in Indiana. Proceedings of the Indiana Academy of Science 119:64–73.

ENGBRECHT, N. J., S. J. LANNOO, J. O. WHITAKER, AND M. J. LANNOO. 2011. Comparative morphometrics in ranid frogs (Subgenus *Nenirana*): are apomorphic elongation and a blunt snout responses to small-bore burrow dwelling in Crawfish Frogs (*Lithobates areolatus*)? Copeia *in press*.

FELLERS, G. M., D. E. GREEN, AND J. E. LONGCORE. 2001. Oral chytridiomycosis in the Mountain Yellow-legged Frog. Copeia 2001:945–953.

GALÁN, P. 1997. Colonization of spoil benches of an opencast lignite mine in Northwest Spain by amphibians and reptiles. Biological Conservation 79:187–195.

GALLANT, A. L., R. W. KLAVER, G. S. CASPER, AND M. J. LANNOO. 2007. Global rates of habitat loss and implications for amphibian conservation. Copeia 2007:967–979.

GIBBONS, J. W., AND D. H. BENNETT. 1974. Determination of anuran terrestrial activity patterns by a drift fence method. Copeia 1974:237–243.

GIBBONS, J. W., AND R. D. SEMLITSCH. 1981. Terrestrial drift fences with pitfall traps: an effective technique for quantitative sampling of animal populations. Brimleyana 7:1–16.

GOIN, C. J., AND M. G. NETTING. 1940. A new gopher frog from the Gulf Coast, with comments upon the *Rana areolata* group. Annals of the Carnegie Museum 28:137–168.

GREEN, D. E., K. A. CONVERSE, AND A. K. SCHRADER. 2002. Epizootiology of sixty-four amphibian morbidity and mortality events in the USA, 1996–2001. Annals of the New York Academy of Sciences 969:323–339.

GREEN, D. M. 2005. Biology of amphibian declines. *In* M. J. Lannoo (ed.), Amphibian Declines: The Conservation Status of United States Species, pp. 28–33. University of California Press, Berkeley, California.

GREENBERG, C. H. 2001. Spatio-temporal dynamics of pond use and recruitment in Florida Gopher Frogs (*Rana capito aesopus*). Journal of Herpetology 35:74–85.

GREER, A. L., M. BERRILL, AND P. J. WILSON. 2005. Five amphibian mortality events associated with ranavirus infection in south central Ontario, Canada. Diseases of Aquatic Organisms 67:9–14.

HEEMEYER, J. L., V. C. KINNEY, N. J. ENGBRECHT, AND M. J. LANNOO. 2010. The biology of Crawfish Frogs (*Lithobates areolatus*) prevents the full use of telemetry and drift fence techniques. Herpetological Review 41:42–45.

HERREID, C. F., AND S. KINNEY. 1966. Survival of Alaskan Woodfrog (*Rana sylvatica*) larvae. Ecology 47:1039–1041.

HILLIS, D. M., AND T. P. WILCOX. 2005. Phylogeny of the new world true frogs (*Rana*). Molecular Phylogenetics and Evolution 34:299–314.

HINGTGEN, T. M., AND W. R. CLARK. 1984. Small mammal recolonization of reclaimed coal surface-mined land in Wyoming. Journal of Wildlife Management 48:1255–1261.

HOCKING, D. J., T. A. RITTENHOUSE, B. B. ROTHERMEL, J. R. JOHNSON, C. A. CONNER, E. B. HARPER, AND R. D. SEMLITSCH. 2008. Breeding and recruitment phenology of amphibians in Missouri Oak-Hickory Forests. American Midland Naturalist 160:41–60.

HOFFMAN, A. S., J. L. HEEMEYER, P. J. WILLIAMS, J. R. ROBB, D. R. KARNS, V. C. KINNEY, N. J. ENGBRECHT, AND M. J. LANNOO. 2010. Strong site fidelity and a variety of imaging techniques reveal around-the-clock and extended activity patterns in Crawfish Frogs (*Lithobates areolatus*). Bioscience 60:829–834.

INDIANA DEPARTMENT OF NATURAL RESOURCES. 1987. Amphibian and Reptile Technical Advisory Committee Meeting Notes. Unpublished data. Indianapolis, Indiana.

JAMMALAMADAKA, R.S., AND A. SENGUPTA. 2001. Topics in Circular Statistics; World Scientific Publishing Co. Pte. Ltd., Singapore.

JENSEN, J. B., AND S. C. RICHTER. 2005. *Rana capito*. *In* M. J. Lannoo (ed.) Amphibian Declines: The Conservation Status of United States Species, pp. 536–538. University of California Press, Berkeley, California.

JOHNSON, T. R. 2000. The Amphibians and Reptiles of Missouri. Second edition. Missouri Department of Conservation, Jefferson City, Missouri.

JONES, S. R., AND R. C. CUSHMAN. 2004. *The North American Prairie*; Peterson Field Guide Series; Houghton Mifflin, New York, New York.

KINNEY, V. C., J. L. HEEMEYER, A. P. PESSIER, AND M. J. LANNOO. 2011. Seasonal Pattern of *Batrachochytrium dendrobatidis* infection and mortality in *Lithobates areolatus*: affirmation of Vredenburg's "10,000 zoospore rule." PLoS One 6:e16708.

KINNEY, V. C., N. J. ENGBRECHT, J. L. HEEMEYER, AND M. J. LANNOO. 2010. New records for amphibians and reptiles in southwest Indiana. Herpetological Review 41:387.

LAMOUREUX, V. S., J. C. MAERZ, AND D. M. MADISON. 2002. Premigratory autumn foraging forays in the Green Frog, *Rana clamitans*. Journal of Herpetology 36:245–254.

LANNOO, M. J., V. C. KINNEY, J. L. HEEMEYER, N. J. ENGBRECHT, A. L. GALLANT, AND R. W. KLAVER. 2009. Mine spoil prairies expand critical habitat for endangered and threatened amphibian and reptile species. Diversity 1:118–132.

LOUGHMAN, Z. J. 2005. Natural History and Conservation Biology of a Southern West Virginia Contour Surface Mine Reptile and Amphibian Community. Unpubl. Master's Thesis, Marshall Univ.

MARSH, D. M., AND P. C. TRENHAM. 2000. Metapopulation dynamics and amphibian conservation. Conservation Biology 15:40–49.

MARTOF, B., AND R. L. HUMPHRIES. 1959. Geographic variation in the Wood Frog *Rana sylvatica*. American Midland Naturalist 61:350–389.

MGFRAP (MISSISSIPPI GOPHER FROG RECOVERY ACTION PLAN). 2009. U. S. Fish and Wildlife Service, Southeast Region. Mississippi Ecological Services Field Office, Jackson, Mississippi.

MINTON, S. A., JR. 2001. Amphibians and Reptiles of Indiana. Second Edition. Indiana Academy of Science, Indianapolis, Indiana.

MITTLEMAN, M. B. 1947. Miscellaneous notes on Indiana amphibians and reptiles. American Midland Naturalist 38:466–484.

MORIN, P. J. 1983. Predation, competition, and the composition of larval anuran guilds. Ecological Monographs 53:119–138.

MUTHS, E., P. S. CORN, A. P. PESSIER, AND D. E. GREEN. 2003. Evidence for disease-related amphibian decline in Colorado. Biological Conservation 110:357–365.

MYERS, C. W., AND W. D. KLIMSTRA. 1963. Amphibians and reptiles of an ecologically disturbed (strip-mined) area in southern Illinois. American Midland Naturalist 70:126–132.

OFFICE OF SURFACE MINING RECLAMATION AND CONTROL. 2008. Surface Mining Control and Reclamation Act of 1977 (Public Law 95-87). U.S. Department of Interior, Washington, D.C., USA. Available at: < http://www.osmre.gov/topic/SMCRA/SMCRA.shtm>.

PALIS, J. G. 1998. Breeding biology of the Gopher Frog, *Rana capito*, in western Florida. Journal of Herpetology 32:217–223.

PALIS, J. G. 2007. If you build it, they will come: herpetofaunal colonization of constructed wetlands and adjacent terrestrial habitat in the Cache River drainage of southern Illinois. Transactions of the Illinois State Academy of Science 100:177–189.

PARRIS, M. J., AND M. REDMER. 2005. *Rana areolata*, Crawfish Frog. *In* M. J. Lannoo (ed.) Amphibian Declines: The Conservation of United States Species, pp. 256–258. University of California Press, Berkeley, California.

PARRIS, M. J., AND R. D. SEMLITSCH. 1998. Asymmetric competition in larval amphibian communities: conservation implications for the northern crawfish frog, *Rana areolata circulosa*. Oecologia 116:219–226.

PATRICK, D. A., A. J. K. CALHOUN, AND M. L. HUNTER JR. 2007. Orientation of juvenile Wood Frogs, *Rana sylvatica*, leaving experimental ponds. Journal of Herpetology 41:158–163.

PECHMANN, J. H. K., AND H. WILBUR. 1994. Putting declining amphibian populations in perspective: natural fluctuations and human impacts. Herpetologica 50:65–84.

PECHMANN, J. H. K., D. E. SCOTT, J. W. GIBBONS, AND R. D. SEMLITSCH. 1989. Influence of wetland hydroperiod on diversity and abundance of metamorphosing juvenile amphibians. Wetlands Ecology and Management 1:3–11.

PECHMANN, J. H. K., D. E. SCOTT, R. D. SEMLITSCH, J. P. CALDWELL, L. J. VITT, AND J. W. GIBBONS. 1991. Declining amphibian populations: the problem of separating human impacts from natural fluctuations. Science 253:892–895.

PHILLIPS, C. A., R. A. BRANDON, AND E. O. MOLL. 1999. Field Guide to Amphibians and Reptiles of Illinois. Illinois Natural History Survey Manual 8. Champaign, Illinois.

REDMER, M. 2000. Demographic and reproductive characteristics of a southern Illinois population of the Crayfish Frog, *Rana areolata*. Journal of the Iowa Academy of Science 107:128–133.

REDMER, M. 2005. *Rana palustris*, Pickerel Frog. *In* M.J. Lannoo (ed.), Amphibian Declines: The Conservation Status of United States Species. p. 568–570. University of California Press, Berkeley, California.

RICHTER, S. C. 2000. Larval caddisfly predation on the eggs and embryos of *Rana capito* and *Rana sphenocephala*. Journal of Herpetology 34:590–593.

RICHTER, S. C., J. E. YOUNG, G. N. JOHNSON, AND R. A. SEIGEL. 2003. Stochastic variation in reproductive success of a rare frog, *Rana sevosa*: implications for conservation and for monitoring amphibian populations. Biological Conservation 111:171–177.

RICHTER, S. C., AND J. B. JENSEN. 2005. Dusky Gopher Frog. *In* M. J. Lannoo (ed.), Amphibian Declines: The Conservation Status of United States Species, pp 584–586. University of California Press, Berkeley, California.

RICHTER, S. C., AND R. A. SEIGEL. 2002. Annual variation in the population ecology of the endangered Gopher Frog, *Rana sevosa*, Goin and Netting. Copeia 2002:962–972.

ROZNIK, E. A., AND S. A. JOHNSON. 2009a. Canopy closure and emigration by juvenile Gopher Frogs. Journal of Wildlife Management 73:260–268.

ROZNIK, E. A., AND S. A. JOHNSON. 2009b. Burrow use and survival of newly metamorphosed gopher frogs (*Rana capito*). Journal of Herpetology 43:431–437.

SEMLITSCH, R. D., J. W. GIBBONS, AND T. D. TUBERVILLE. 1995. Timing of reproduction and metamorphosis in the Carolina Gopher Frog (*Rana capito capito*) in South Carolina. Journal of Herpetology 29:612–614.

SEPARC (SOUTHEASTERN PARTNERS IN AMPHIBIAN AND REPTILE CONSERVATION). 2010. Meeting Workshop: Conserving the Gopher Frog/Crawfish Frog Complex: What do we know, what do we need to know? February 18th–21st, Ocala, Florida.

SCOTT, P. E., T. L. DEVAULT, R. A. BAJEMA, AND S. L. LIMA. 2002. Grassland vegetation and bird abundances on reclaimed midwestern coal mines. Wildlife Society Bulletin 30:1006–1014.

SCOTT, P. E., AND S. L. LIMA. 2004. Exotic grasslands on reclaimed midwestern coal mines: an ornithological perspective. Weed Technology 18:1518–1521.

SEMLITSCH, R. D. 2000. Principles for management of aquatic-breeding amphibians. Journal of Wildlife Management 64:615–631.

SEMLITSCH, R. D. 2008. Differentiation migration and dispersal processes for pond-breeding amphibians. Journal of Wildlife Management 72:260–267.

SINSCH, U. 1997. Postmetamorphic dispersal and recruitment of first breeders in a *Bufo calamita* metapopulation. Oecologia 112:42–47.

SKELLY, D. K. 1994. Activity level and the susceptibility of anuran larvae to predation. Animal Behavior 47:465–468.

SMITH, H. M. 1934. The amphibians of Kansas. American Midland Naturalist 15:377–527.

SMITH, H. M. 1950. Handbook of Amphibians and Reptiles of Kansas. University of Kansas Museum of Natural History, Miscellaneous Publication, Number 2, Lawrence, Kansas.

SMITH, H. M., C. W. NIXON, AND P. E. SMITH. 1948. A partial description of the tadpole of *Rana areolata circulosa* and notes on the natural history of the race. American Midland Naturalist 39:608–614.

SMITH, P. W. 1961. The amphibians and reptiles of Illinois. Bulletin of the Illinois Natural History Survey, Number 28, Urbana, Illinois.

STONE, E. R. 2007. Measuring impacts of restoration on small mammals in a mixed-grass Colorado prairie. Ecological Restoration 25:183–190.

STUART, S. N, J. S. CHANSON, N. A. COX, B. E. YOUNG, A. S. L. RODRIGUES, D. L. FISCHMAN, AND R. W. WALLER. 2004. Status and trends of amphibian declines and extinctions worldwide. Science 306:1783–1786.

THORSON, T. B. 1955. The relationship of water economy to terrestrialism in amphibians. Ecology 36:100–116.

TIMM, A., AND V. MERETSKY. 2004. Anuran habitat use on abandoned and reclaimed mining areas of southwestern Indiana. Proceedings of the Indiana Academy of Science 113:140–146.

TRANSEAU, E. N. 1935. The prairie peninsula. Ecology 16:423–437.

TRAUTH, S. E., H. W. ROBISON, AND M. V. PLUMMER. 2004. The Amphibians and Reptiles of Arkansas. The University of Arkansas Press, Fayetteville, Arkansas.

USFWS (UNITED STATES FISH AND WILDLIFE SERVICE). 2001. Endangered and threatened wildlife and plants; final rule to list the Mississippi Gopher Frog distinct population segment of dusky gopher frog as endangered. Federal Register 66:62993–63001.

VONESH, J. R., AND O. D. L. CRUZ. 2002. Complex life cycles and density dependence: assessing the contribution of egg mortality to amphibian declines. Oecologia 133:325–333.

WAKE, D. B., AND V. T. VREDENBURG. 2008. Colloquium paper: Are we in the midst of the sixth mass extinction? A view from the world of amphibians. Proceedings of the National Academy of Sciences 105:11466–11473.

WALSTON, L. J., AND S. J. MULLIN. 2007. Responses of a pond-breeding amphibian community to the experimental removal of predatory fish. American Midland Naturalist 157:63–73.

WALSTON, L. J., AND S. J. MULLIN. 2008. Variation in amount of surrounding forest habitat influences the initial orientation of juvenile amphibians emigrating from breeding ponds. Canadian Journal of Zoology 86:141–146.

WELLS, K. D. 2007. The Ecology and Behavior of Amphibians. The University of Chicago Press, Chicago, Illinois.

WRIGHT, A. H., AND A. A. WRIGHT. 1933. Handbook of Frogs and Toads. Comstock Press, Ithaca, New York.

WRIGHT, A. H., AND A. A. WRIGHT. 1949. Handbook of Frogs and Toads of the United States and Canada. Third Edition. Comstock Publishing Associates, Ithaca, New York.

WRIGHT, H. P., AND G. S. MYERS. 1927. *Rana areolata* at Bloomington, Indiana. Copeia 159:173–175.

Table 1. Total number of Crawfish Frogs captured at drift fences during 2009 and 2010, and differences in population sizes between years.

	Nate's Pond		Difference between years	Cattail Pond		Difference between years
	2009	2010	2009–2010	2009	2010	2009–2010
Males	38	20	- 18	14	14	0
Females	31	22	- 9	14	7	- 7
Subadults	1	2	+ 1	—	—	—
Juveniles	286	2103	+ 1817	11	—	- 11

Table 2. Estimated adult survivorship between years at Nate's Pond and Cattail Pond. Data include: percent animals recaptured in 2010 and return rate (percentage of animals from 2009 that returned in 2010). Data on return rate offer the best estimates of adult survivorship.

Pond	Sex	Percent of Recaptures in 2010	Return Rate
Nate's Pond	Male	**55 %** (11/20)	**29%** (11/38)
	Female	**55 %** (12/22)	**37%** (11/30*)
	Total	**55 %** (23/42)	**32%** (22/68)
Cattail Pond	Male	**50 %** (7/14)	**54 %** (7/13†)
	Female	**43 %** (3/7)	**23 %** (3/13†)
	Total	**48 %** (10/21)	**38 %** (10/26)
Overall	Total	**52%** (33/63)	**34%** (32/94)

* one female was censored due to complications with surgery for telemetry
† one male was censored due to complications with surgery for telemetry

Table 3. Measurements (SVL [mm], entry weight [g], exit weight [g]) of adult, subadult, and juvenile Crawfish Frogs at Nate's Pond and Cattail Pond during the 2009 and 2010 seasons. Mean differences between the entry and exit weights are given for adult and subadult Crawfish Frogs. Weight differences in females are attributed to weight of deposited eggs. Data are presented as the mean ± SD, range, and the sample size (n).

	Males				Females				Subadults				Juveniles	
Pond	SVL (mm)	Entering Mass (g)	Exiting Mass (g)	Difference in Mass (g)	SVL (mm)	Entering Mass (g)	Exiting Mass (g)	Difference in Mass (g)	SVL (mm)	Entering Mass (g)	Exiting Mass (g)	Difference in Mass (g)	SVL (mm)	Mass (g)
Nate's 2009	**93.4** ± 7 76–103 (29)	**97.1** ± 16 58–126 (29)	**93.5** ± 15 66–118 (29)	**-3.5** ± 10 -30–+12 (29)	**100.3** ± 6 88–115 (29)	**120.8** ± 21 77–158 (29)	**87.6** ± 15 60–116 (29)	**-33.1** ± 12 ˉ65–ˉ14 (29)	**68** (1)	**40** (1)	—	—	**34.4** ± 2 28–39 (284)	**4.6** ± 0.6 3.1–6.4 (284)
Nate's 2010	**96.0** ± 7 81–103 (18)	**102.1** ± 23 46–150 (18)	**91.8** ± 19 43–123 (18)	**-10.3** ± 10 -27–+11 (18)	**101.2** ± 8 84–117 (19)	**116.3** ± 26 62–154 (19)	**88.1** ± 16 65–110 (19)	**-28.2** ± 12 -40–+3 (19)	**62, 64** (2)	**22, 26** (2)	**22, 25** (2)	**0,-1** (2)	**33.1** ± 2 28–44 (2043)	**3.4** ± 0.5 2.0–6.4 (2043)
Nate's total	**94.4** ± 7 76–103 (47)	**99.0** ± 19 46–150 (47)	**93.0** ± 16 43–123 (47)	**-6.1** ± 10 -30–+12 (18)	**100.7** ± 7 84–117 (48)	**119.0** ± 23 62–158 (48)	**87.8** ± 15 60–116 (48)	**-31.2** ± 12 -65–+3 (48)	**62, 63, 68** (3)	**22, 26, 40** (3)	**22, 25** (2)	**0,-1** (2)	**33.2** ± 2 28–44 (2327)	**3.5** ± 0.6 2.0–6.4 (2327)
Cattail 2009	**102.8** ± 6 96–112 (12)	**125.6** ± 25 69–156 (12)	**114.2** ± 18 68–142 (12)	**-11.4** ± 12 -30–-5 (12)	**106.4** ± 5 99–115 (7)	**149.0** ± 20 126–188 (7)	**102.1** ± 11 88–120 (7)	**-46.9** ± 18 -78–-23 (7)	—	—	—	—	**29.8** ± 3 22–33 (11)	**3.0** ± 1 1.9–4.8 (11)
Cattail 2010	**97.6** ± 8 88–107 (7)	**103.6** ± 27 73–140 (7)	**90.9** ± 23 65–116 (7)	**-12.7** ± 8 -24–-2 (7)	**108.0** ± 9 99–121 (6)	**143.3** ± 24 116–177 (6)	**93.5** ± 14 78–117 (6)	**-49.8** ± 16 -79–-34 (6)	—	—	—	—	—	—
Cattail total	**100.9** ± 7 88–112 (19)	**117.5** ± 27 69–156 (19)	**105.6** ± 23 65–142 (19)	**-11.9** ± 10 -30–-2 (19)	**107.1** ± 7 99–121 (13)	**146.0** ± 21 116–188 (13)	**98.1** ± 13 78–120 (13)	**-48.2** ± 16 -79–-23 (13)	—	—	—	—	**29.8** ± 3 22–33 (11)	**3.0** ± 1 1.9–4.8 (11)
Overall total	**96.2** ± 8 76–112 (66)	**104.3** ± 23 46–156 (66)	**96.5** ± 19 43–142 (66)	**-7.8** ± 10 -30–+12 (66)	**102.0** ± 7 84–121 (61)	**124.8** ± 25 62–188 (61)	**90.0** ± 15 60–120 (61)	**-34.8** ± 15 -79–+3 (61)	**62, 63, 68** (3)	**22, 26, 40** (3)	**22, 25** (2)	**0,-1** (2)	**33.2** ± 2 22–44 (2338)	**3.5** ± 0.6 1.9–6.4 (2338)

Table 4. Body mass index (weight [g]/snout-vent length [mm]) calculated for males, pre-breeding females, and post-breeding females.

Pond	Males	Pre-breeding Females	Post-breeding Females
Nate’s	**1.05**	**1.18**	**0.87**
Cattail	**1.16**	**1.36**	**0.92**

Table 5. Egg-to-juvenile survivorship estimates for 2009 (A) and 2010 (B) at Nate's and Cattail ponds. Data include number of females that entered wetlands to breed, exited wetlands, and exited spent. Numbers of eggs deposited were estimated as described in the text. Clutch sizes were totaled to estimate number of eggs laid at each wetland. In 2010 (B), total number of eggs deposited was adjusted to account for failed egg masses, and the mean number of eggs per egg mass that never hatched. In 2009, egg-to-juvenile survivorship was estimated by dividing the number of recruited juveniles by the estimated number of eggs deposited; in 2010, survivorship was estimated by dividing the number of recruited juveniles by the estimated number of hatchlings.

A.

Year	Pond	Total females	Total that exited	Spent females	Mean clutch size	Total eggs deposited	Total juveniles	Egg-to-juvenile survivorship
2009	Nate's	31	31*	30	6,303 ± 1065 4,163–8,847	189,079	286	0.2%
2009	Cattail	14	8†	11	7,002 ± 1,012 5,030–8,847	77,020	11	0.01%

* One female entered and exited the pond several times and was last seen entering the wetland; however she was spent when exiting the pond the first time.
† Two females that never exited were recaptured in 2010 entering the pond to breed, inquiring that trespass occurred. Additionally, one female crossed the fence more than twice and was last seen entering the fence, she was spent when first exiting the pond; therefore these three animals were added to the total number of females that exited the wetland (n=11 instead of n=8)

Table 5 (continued)

B.

Year	Pond	Total females	Total that exited	Spent females	Mean clutch size	Egg masses found	Total eggs deposited	Failed egg masses	Mean # of unhatched eggs per egg mass	Estimated # of hatchlings	Total juveniles	Larval survivorship
2010	Nate's	22	19	17	6,724 ± 1,063 5,030–9,194	16	114,316	3	135 ± 115 55–339	91,984	2,103	2.29%
2010	Cattail	7	6	6	7,633 ± 1,492 6,071–9,888	5	45,796	0	135 ± 115 55–339	44,986	0	0%

Table 6. Data from Crawfish Frog egg mass counts. Total water depth was measured from the surface of the water to the bottom of the wetland. Water depth from the egg mass was measured from the bottom of the egg mass to the bottom of the pond. Egg mass diameter was measured as the widest length across the surface of the egg mass. Not all variables were measured for each egg mass. Data are presented as the mean ± SD and the sample size (n).

Pond	Total egg masses found	Total water depth (cm)	Water depth from egg mass (cm)	Egg mass diameter (cm)	Number of days to hatch
Nate’s	**16**	**18.4** ± 2 15–22 (16)	**12.8** ± 4 8–20 (16)	**13.5** ± 1 10–16 (15)	**6.3** ± 2 4–9 (11)
Cattail	**5**	**16.0** ± 2 12–18 (5)	**12.0** ± 2 10–15 (5)	**14.1** ± 0.6 14–15 (5)	**7.5** ± 3 4–10 (4)

Table 7. Within breeding season survivorships for adult Crawfish Frogs at Nate's Pond and Cattail Pond. Survivorship was calculated by dividing the number of frogs that exited the wetland by the number that entered to breed. Data were corrected for trespassers as described in the text.

Pond and Year	Sex	Within-season survivorship	Corrected within-season survivorship
Nate's Pond 2009	Male	84% (32/38)	89% (34/38)
	Female	97% (30/31)	—
	Total	90% (62/69)	93% (64/69)
Nate's Pond 2010	Male	80% (16/20)	na
	Female	86% (19/22)	na
	Total	83% (35/42)	na
Cattail Pond 2009	Male	85% (11/13*)	100% (13/13*)
	Female	57% (8/14)	71% (10/14)
	Total	70% (19/27)	85% (23/27)
Cattail Pond 2010	Male	46% (6/13†)	na
	Female	86% (6/7)	na
	Total	60% (12/20)	na
Overall	Total	81% (128/158)	85% (134/158)

*one male was censored in 2009 due to complications with surgery for telemetry
† one male was censored in 2010 due to predation prior to entering the drift fenced area

Table 8. Estimated survivorships (A) at each life history stage. Embryonic and larval survivorship are within years. Juvenile survivorship compares breeding adult recruitment in 2010 to juvenile emigration in 2009 and 2010. Adult survivorship is based on between year return rates. Mortality rates (B) were estimated from survivorship and days spent in each life history stage (for adults, days represent one year).

A.

Pond	Embryonic Survivorship	Larval Survivorship	Juvenile to Adult Survivorship	Adult Survivorship
Nate's	98.1%	2.3%	0.9–6.6%	32.3%
Cattail	98.2%	0%	—	38.5%

B.

		Embryonic	Larval	Juvenile to Adult	Annual Adult
Nate's Pond	Mortality (%)	1.9 %	97.7%	93.4–99.1%	68%
	Days	7	91	780	350
	Mortality rate/day	**0.2 %**	**1.1%**	**0.1%**	**0.2%**
Cattail Pond	Mortality (%)	1.8%	100%	—	62%
	Days	7	91	—	350
	Mortality rate/day	**0.3%**	**1.1%**	**—**	**0.2%**

Table 9. Comparisons between Crawfish Frogs and Dusky Gopher Frogs (Richter and Seigel, 2002; Richter et al., 2003). Data in each column are presented as the mean across the study period for each species (Crawfish Frogs [2 years]; Dusky Gopher Frogs [2 years; 1996 was excluded because the pond dried]). Number of egg masses found for Crawfish Frogs only represents data from 2010.

	Adult population	Numbers of egg masses	Numbers of eggs deposited	Numbers of juveniles	Larval survivorship	Within breeding season survivorship	Across season survivorship
Dusky Gopher Frogs	88	48	52,956	1,234	2.3%	80%	20%
Crawfish Frogs (*Nate's Pond*)	56	16	151,698	1,194	1.7%	89%	32%
Crawfish Frogs (*Cattail Pond*)	24	5	61,408	6	0.9^{-5}%	74%	38%

Table 10. Amphibian and reptile species encountered at the drift fences and total numbers of captures during 2009 and 2010. Species with asterisks were given cohort toe clips.

		Total Captures at Each Pond					
Scientific Name	**Common Name**	Nate's 2009	Nate's 2010	Cattail 2009	Cattail 2010	Willow 2009	Hill 2009
Salamanders							
*Ambystoma opacum**	Marbled Salamander	1479	904	75	83	1557	60
*Ambystoma texanum**	Small-mouthed Salamander	646	561	579	597	120	123
*Ambystoma tigrinum**	Eastern Tiger Salamander	4	—	22	12	2	1
Notophthalmus viridescens	Eastern Newt	809	627	297	203	7	5
Plethodon cinereus	Red-backed Salamander	—	1	—	—	—	—
Frogs and Toads							
Acris crepitans	Northern Cricket Frog	11	15	18	21	6	1
Pseudacris crucifer	Spring Peeper	140	73	13	5	1	15
Pseudacris triseriata	Western Chorus Frog	511	372	112	122	250	37
*Lithobates areolatus**	Crawfish Frog	367	2161	42	22	1	1
*Lithobates catesbeianus**	American Bullfrog	8	8	25	47	13	—
*Lithobates clamitans**	Green Frog	149	139	1980	506	107	254
*Lithobates sphenocephalus**	Southern Leopard Frog	947	604	300	209	194	374
Hyla chrysoscelis	Cope's Gray Treefrog	1	11	—	—	2	—
*Anaxyrus fowleri**	Fowler's Toad	2	4	—	—	5	—
Snakes							
Thamnophis sirtalis	Common Garter Snake	1	2	5	4	1	1
Thamnophis sauritus	Eastern Ribbonsnake	3	3	5	—	—	—
Storeria dekayi	Dekay's Brownsnake	1	13	2	—	1	—

Table 10 (continued)

Scientific Name	**Common Name**	Nate's 2009	Nate's 2010	Cattail 2009	Cattail 2010	Willow 2009	Hill 2009
Nerodia sipedon	Northern Water Snake	—	—	1	—	—	—
Diadophis punctatus	Ring-necked Snake	1	—	—	—	2	—
Carphophis amoenus	Worm Snake	1	—	—	—	—	—
Clonophis kirtlandii	Kirtland's Snake	—	—	—	—	1	—
Coluber constrictor	North American Black Racer	1	—	2	—	—	—
Turtles							
Chelydra serpentina	Common Snapping Turtle	5	1	18	4	13	—
Chrysemys picta	Painted Turtle	30	14	117	37	31	7
Terrapene carolina	Eastern Box Turtle	25	17	4	7	46	2
Trachemys scripta	Red-eared Slider	4	2	3	1	3	—
Sternotherus odoratus	Stinkpot	—	—	—	—	1	—
Lizards							
Plestiodon fasciatus	Common Five-lined Skink	—	—	—	—	2	—

Table 11. Amphibians captured at Nate's Pond in 2009 (A) and in 2010 (B) separated into the numbers of individual females, males, subadults, natal juveniles (juveniles that metamorphosed from the wetland), immigrating juveniles, and unknowns (typically animals caught out of their breeding season when physical sexual differentiation is difficult to detect) captured. Species with asterisks were given cohort toe clips.

A.

Scientific Name	**Common Name**	**Female**	**Male**	**Subadult**	**Natal Juveniles**	**Immigrating Juveniles**	**Unknown**	**Total**
*Ambystoma opacum**	Marbled Salamander	133	254	48	943	101	—	1479
*Ambystoma texanum**	Small-mouthed Salamander	131	159	114	199	29	14	646
*Ambystoma tigrinum**	Eastern Tiger Salamander	—	—	—	1	3	—	4
Notophthalmus viridescens	Eastern Newt	41	43	—	667	58	—	809
Plethodon cinereus	Red-backed Salamander	—	—	—	—	—	—	—
Acris crepitans	Northern Cricket Frog	7	3	—	1	—	—	11
Pseudacris crucifer	Spring Peeper	53	51	—	35	1	—	140
Pseudacris triseriata	Western Chorus Frog	279	196	—	32	1	3	511
*Lithobates areolatus**	Crawfish Frog	31	38	1	286	11	—	367
*Lithobates catesbeianus**	American Bullfrog	—	—	—	—	8	—	8
*Lithobates clamitans**	Green Frog	10	4	—	47	88	—	149
*Lithobates sphenocephalus**	Southern Leopard Frog	54	71	14	625	183	—	947
Hyla chrysoscelis	Cope's Gray Treefrog	—	—	—	—	—	1	1
*Anaxyrus fowleri**	Fowler's Toad	—	—	—	—	2	—	2

Table 11 (continued)

B.

Scientific Name	Common Name	Female	Male	Subadult	Natal Juveniles	Immigrating Juveniles	Unknown	Total
*Ambystoma opacum**	Marbled Salamander	46	62	5	751	27	13	904
*Ambystoma texanum**	Small-mouthed Salamander	248	251	42	12	3	5	561
*Ambystoma tigrinum**	Eastern Tiger Salamander	—	—	—	—	—	—	—
Notophthalmus viridescens	Eastern Newt	48	35	15	519	10	—	627
Plethodon cinereus	Red-backed Salamander	—	—	—	—	—	1	1
Acris crepitans	Northern Cricket Frog	3	4	5	—	—	3	15
Pseudacris crucifer	Spring Peeper	36	26	—	5	6	—	73
Pseudacris triseriata	Western Chorus Frog	192	172	1	6	—	1	372
*Lithobates areolatus**	Crawfish Frog	22	20	2	2103	14	—	2161
*Lithobates catesbeianus**	American Bullfrog	1	—	1	1	5	—	8
*Lithobates clamitans**	Green Frog	9	8	1	21	100	—	139
*Lithobates sphenocephalus**	Southern Leopard Frog	13	23	1	243	323	—	603
Hyla chrysoscelis	Cope's Gray Treefrog	—	—	—	1	9	1	11
*Anaxyrus fowleri**	Fowler's Toad	3	—	—	—	1	—	4

Table 12. Amphibians captured at Cattail Pond in 2009 (A) and in 2010 (B), separated into the numbers of individual females, males, subadults, natal juveniles (juveniles that metamorphosed from the wetland), immigrating juveniles, and unknowns (typically animals caught out of their breeding season when physical sexual differentiation is difficult to detect) captured. Species with asterisks were given cohort toe clips.

A.

Scientific Name	Common Name	Female	Male	Subadult	Natal Juveniles	Immigrating Juveniles	Unknown	Total
*Ambystoma opacum**	Marbled Salamander	22	22	—	15	15	1	75
*Ambystoma texanum**	Small-mouthed Salamander	155	243	96	59	21	5	579
*Ambystoma tigrinum**	Eastern Tiger Salamander	2	10	—	1	9	—	22
Notophthalmus viridescens	Eastern Newt	110	88	—	49	45	5	297
Plethodon cinereus	Red-backed Salamander	—	—	—	—	—	—	—
Acris crepitans	Northern Cricket Frog	3	6	—	4	4	1	18
Pseudacris crucifer	Spring Peeper	8	4	—	1	—	—	13
Pseudacris triseriata	Western Chorus Frog	59	41	—	10	1	1	112
*Lithobates areolatus**	Crawfish Frog	14	14	—	11	3	—	42
*Lithobates catesbeianus**	American Bullfrog	6	1	2	4	11	1	25
*Lithobates clamitans**	Green Frog	11	18	17	1507	424	3	1980
*Lithobates sphenocephalus**	Southern Leopard Frog	18	98	4	47	131	2	300
Hyla chrysoscelis	Cope's Gray Treefrog	—	—	—	—	—	—	—
*Anaxyrus fowleri**	Fowler's Toad	—	—	—	—	—	—	—

Table 12 (continued)

B.

Scientific Name	Common Name	Female	Male	Subadult	Natal Juveniles	Immigrating Juveniles	Unknown	Total
*Ambystoma opacum**	Marbled Salamander	11	8	3	48	11	2	83
*Ambystoma texanum**	Small-mouthed Salamander	275	272	29	13	6	2	597
*Ambystoma tigrinum**	Eastern Tiger Salamander	4	2	—	2	4	—	12
Notophthalmus viridescens	Eastern Newt	51	37	7	86	22	—	203
Plethodon cinereus	Red-backed Salamander	—	—	—	—	—	—	—
Acris crepitans	Northern Cricket Frog	6	7	2	—	3	3	21
Pseudacris crucifer	Spring Peeper	3	2	—	—	—	—	5
Pseudacris triseriata	Western Chorus Frog	59	49	3	9	1	1	122
*Lithobates areolatus**	Crawfish Frog	7	14	—	—	1	—	22
*Lithobates catesbeianus**	American Bullfrog	3	4	16	1	23	—	47
*Lithobates clamitans**	Green Frog	34	42	13	34	382	1	506
*Lithobates sphenocephalus**	Southern Leopard Frog	33	34	—	47	95	—	209
Hyla chrysoscelis	Cope's Gray Treefrog	—	—	—	—	—	—	—
*Anaxyrus fowleri**	Fowler's Toad	—	—	—	—	—	—	—

Table 13. Amphibians captured at Willow Pond in 2009 separated into the numbers of individual females, males, subadults, natal juveniles (juveniles that metamorphosed from the wetland), immigrating juveniles, and unknowns (typically animals caught out of their breeding season when physical sexual differentiation is difficult to detect) captured. Species with asterisks were given cohort toe clips.

Scientific Name	**Common Name**	**Female**	**Male**	**Subadult**	**Natal Juveniles**	**Immigrating Juveniles**	**Unknown**	**Total**
*Ambystoma opacum**	Marbled Salamander	30	24	2	1382	119	—	1557
*Ambystoma texanum**	Small-mouthed Salamander	44	67	2	1	4	2	120
*Ambystoma tigrinum**	Eastern Tiger Salamander	2	—	—	—	—	—	2
Notophthalmus viridescens	Eastern Newt	4	—	2	1	—	—	7
Plethodon cinereus	Red-backed Salamander	—	—	—	—	—	—	—
Acris crepitans	Northern Cricket Frog	1	3	—	—	2	—	6
Pseudacris crucifer	Spring Peeper	—	1	—	—	—	—	1
Pseudacris triseriata	Western Chorus Frog	157	86	—	3	2	2	250
*Lithobates areolatus**	Crawfish Frog	—	—	—	—	1	—	1
*Lithobates catesbeianus**	American Bullfrog	6	—	4	—	3	—	13
*Lithobates clamitans**	Green Frog	10	4	2	14	77	—	107
*Lithobates sphenocephalus**	Southern Leopard Frog	17	57	12	17	91	—	194
Hyla chrysoscelis	Cope's Gray Treefrog	—	1	—	—	—	1	2
*Anaxyrus fowleri**	Fowler's Toad	—	1	—	—	4	—	5

Table 14. Amphibians captured at Hill Pond in 2009 separated into the numbers of individual females, males, subadults, natal juveniles (juveniles that metamorphosed from the wetland), immigrating juveniles, and unknowns (typically animals caught out of their breeding season when physical sexual differentiation is difficult to detect) captured. Species with asterisks were given cohort toe clips.

Scientific Name	**Common Name**	**Female**	**Male**	**Subadult**	**Natal Juveniles**	**Immigrating Juveniles**	**Unknown**	**Total**
*Ambystoma opacum**	Marbled Salamander	4	2	—	39	14	1	60
*Ambystoma texanum**	Small-mouthed Salamander	43	27	7	28	18	—	123
*Ambystoma tigrinum**	Eastern Tiger Salamander	—	—	—	1	—	—	1
Notophthalmus viridescens	Eastern Newt	—	—	—	2	3	—	5
Plethodon cinereus	Red-backed Salamander	—	—	—	—	—	—	—
Acris crepitans	Northern Cricket Frog	—	—	—	—	1	—	1
Pseudacris crucifer	Spring Peeper	—	4	—	—	2	9	15
Pseudacris triseriata	Western Chorus Frog	13	19	—	1	3	1	37
*Lithobates areolatus**	Crawfish Frog	—	—	—	—	1	—	1
*Lithobates catesbeianus**	American Bullfrog	—	—	—	—	—	—	—
*Lithobates clamitans**	Green Frog	2	—	—	27	223	2	254
*Lithobates sphenocephalus**	Southern Leopard Frog	6	10	1	49	308	—	374
Hyla chrysoscelis	Cope's Gray Treefrog	—	—	—	—	—	—	—
*Anaxyrus fowleri**	Fowler's Toad	—	—	—	—	—	—	—

Table 15. Numbers of recaptures in 2010 of the species given cohort clips at Nate's Pond in 2009. Superscript letters refer to the identity of juveniles recaptured in 2010 from 2009.

Scientific Name	**Common Name**	**F 2009 recap (enter)**	**F 2009 recap (exit)**	**M 2009 recap (enter)**	**M 2009 recap (exit)**	**Juv. 2009 recap (enter)**	**Juv. 2009 recap (exit)**
Ambystoma opacum	Marbled Salamander	7	—	13	2	11[a]	11[b]
Ambystoma texanum	Small-mouthed Salamander	13	—	46	36	1[c]	1[d]
Ambystoma tigrinum	Eastern Tiger Salamander	—	—	—	—	—	—
Lithobates areolatus	Crawfish Frog	12	12	11	11	—	—
Lithobates catesbeianus	American Bullfrog	—	—	—	—	—	—
Lithobates clamitans	Green Frog	—	—	—	—	—	—
Lithobates sphenocephalus	Southern Leopard Frog	1	1	5	—	5[e]	—
Anaxyrus fowleri	Fowler's Toad	—	—	—	—	—	—

[a] 3 females, 7 males, 1 juvenile; [b] 11 juveniles; [c] 1 male; [d] 1 male; [e] 5 males

Table 16. Numbers of recaptures in 2010 of the species given cohort clips at Cattail Pond in 2009. Superscript letters refer to the identity of juveniles recaptured in 2010 from 2009.

Scientific Name	**Common Name**	**F 2009 recap (enter)**	**F 2009 recap (exit)**	**M 2009 recap (enter)**	**M 2009 recap (exit)**	**Juv. 2009 recap (enter)**	**Juv. 2009 recap (exit)**
Ambystoma opacum	Marbled Salamander	—	—	1	—	—	—
Ambystoma texanum	Small-mouthed Salamander	16	13	27	30	—	—
Ambystoma tigrinum	Eastern Tiger Salamander	—	—	1	1	—	—
Lithobates areolatus	Crawfish Frog	3	3	7	2	—	—
Lithobates catesbeianus	American Bullfrog	1	—	—	—	—	—
Lithobates clamitans	Green Frog	—	—	4	—	1[a]	—
Lithobates sphenocephalus	Southern Leopard Frog	2	—	4	—	2[b]	—
Anaxyrus fowleri	Fowler's Toad	—	—	—	—	—	—

[a] 3 males ; [b] 1 female, 1 male

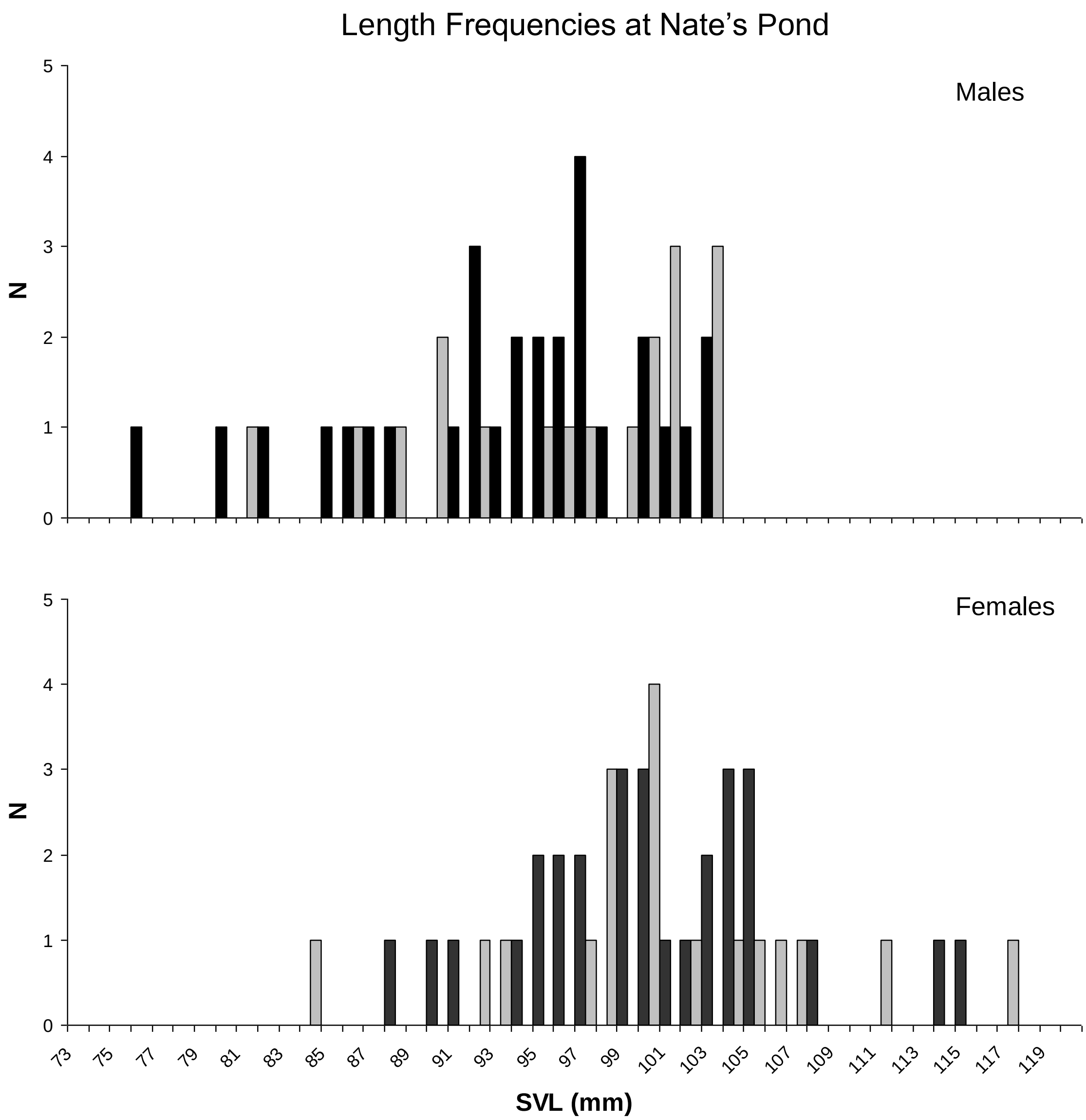


Figure 1. Snout-vent length (mm) frequencies of male (top) and female (bottom) Crawfish Frogs at Nate's Pond (black bars represent animals captured in 2009, gray bars represent animals captured in 2010).

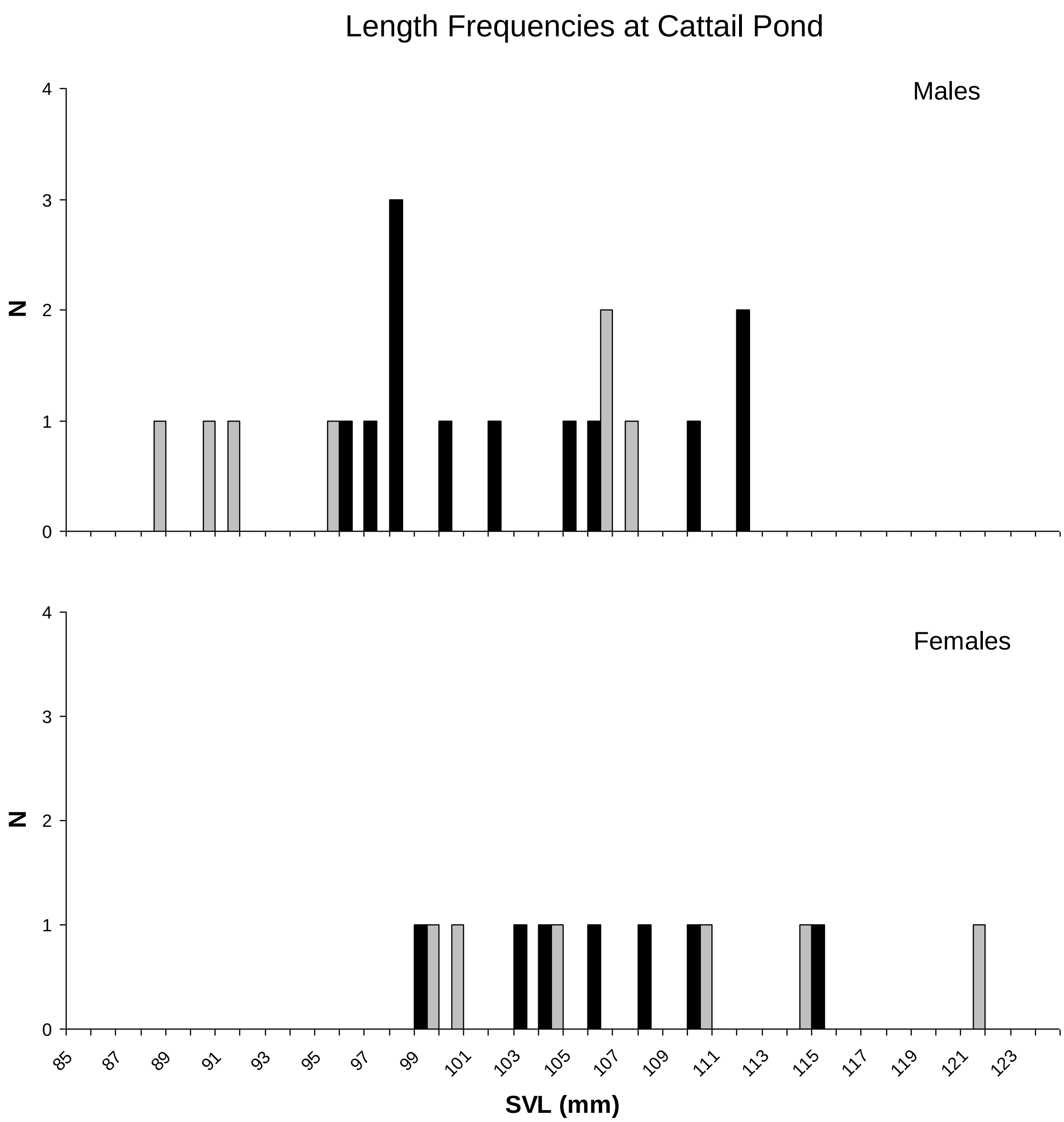


Figure 2. Snout-vent length (mm) frequencies of male (top) and female (bottom) Crawfish Frogs at Cattail Pond (black bars represent animals captured in 2009, gray bars represent animals captured in 2010).

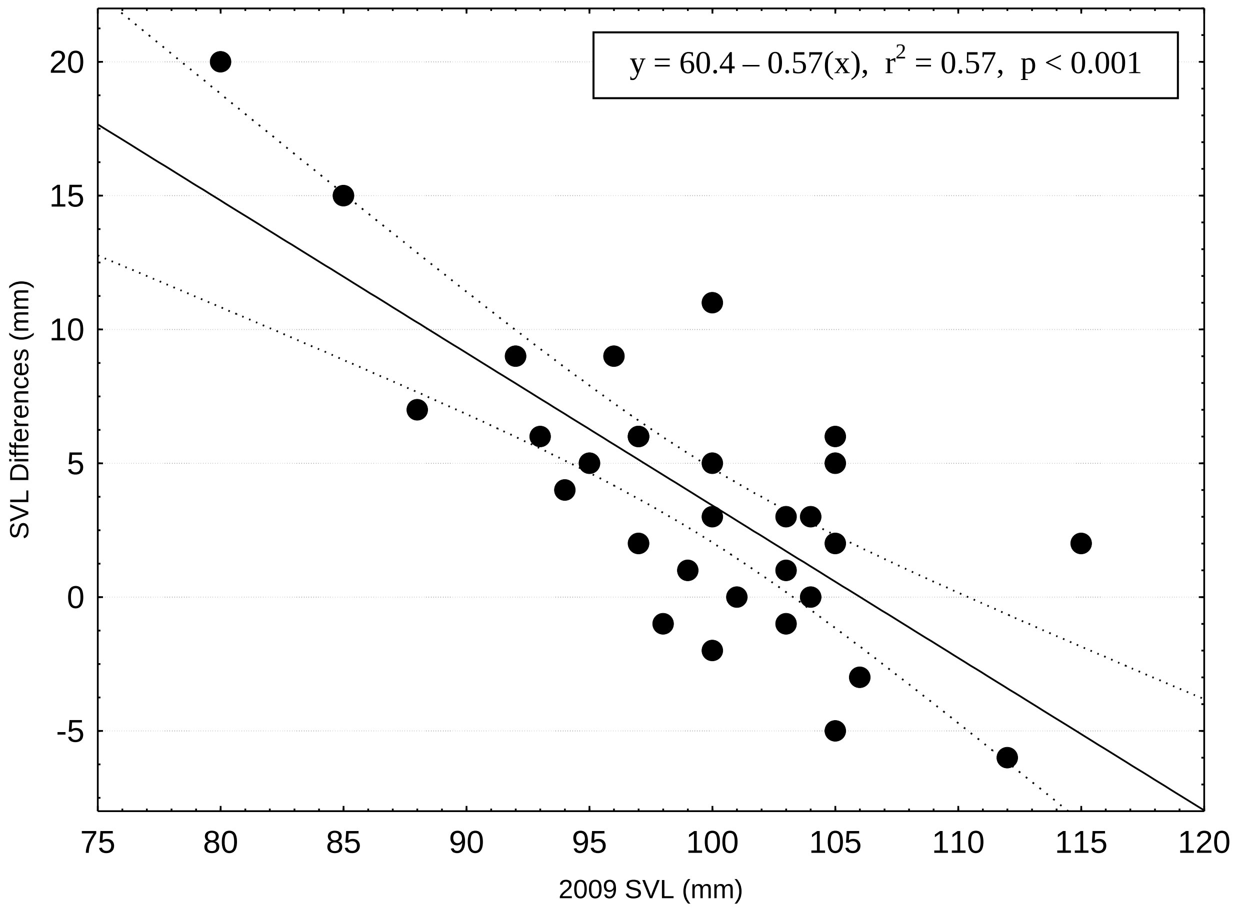


Figure 3. Annual growth measured in Crawfish Frogs captured in 2009 and 2010, x-axis represents 2009 body length, y-axis represents 2009 SVL subtracted from 2010 SVL. Note that larger animals grow less.

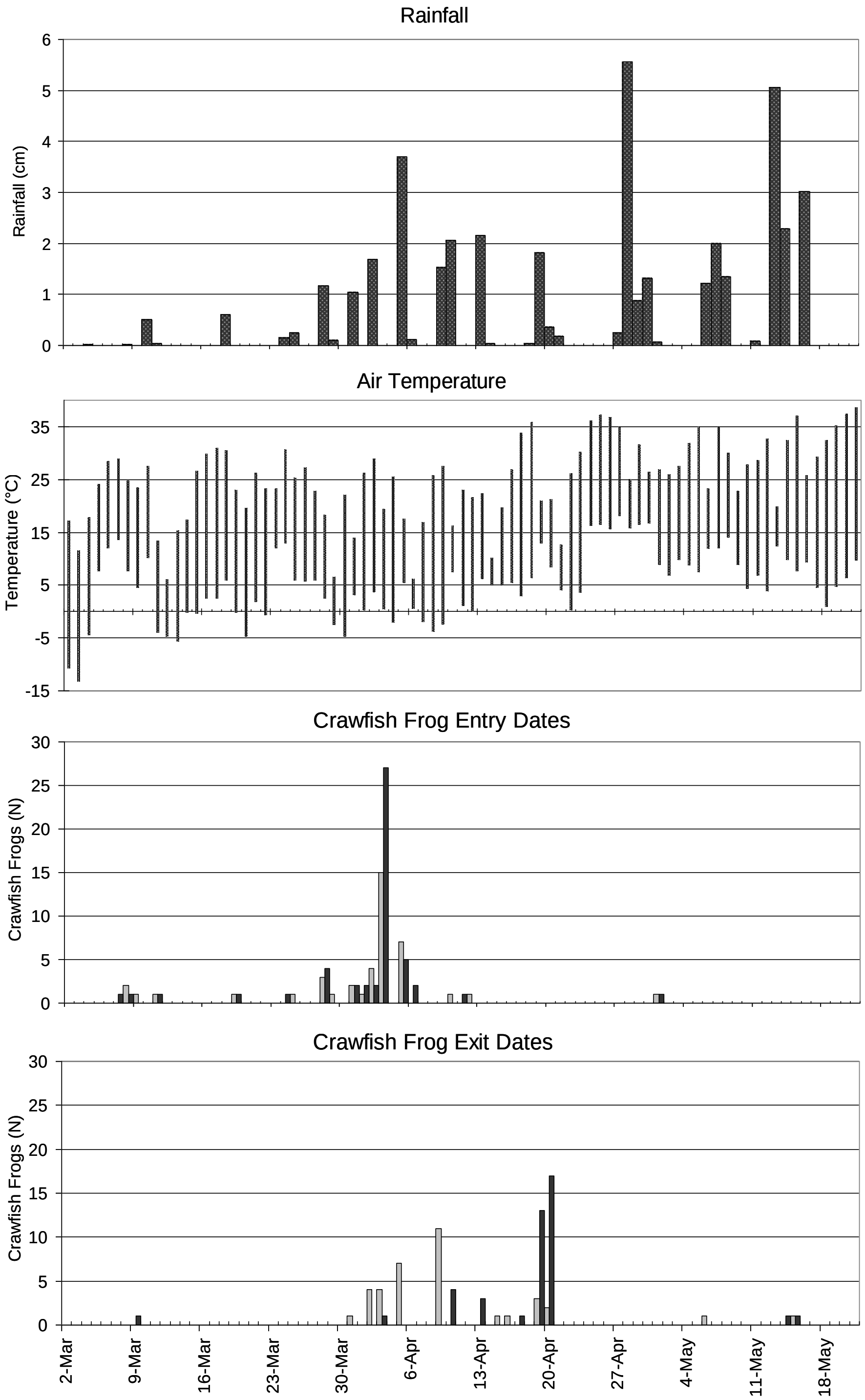


Figure 4. Daily total rainfall (cm), maximum and minimum air temperatures (°C), and dates adults entered and exited wetlands in 2009 (black bars represent males, gray bars represent females).

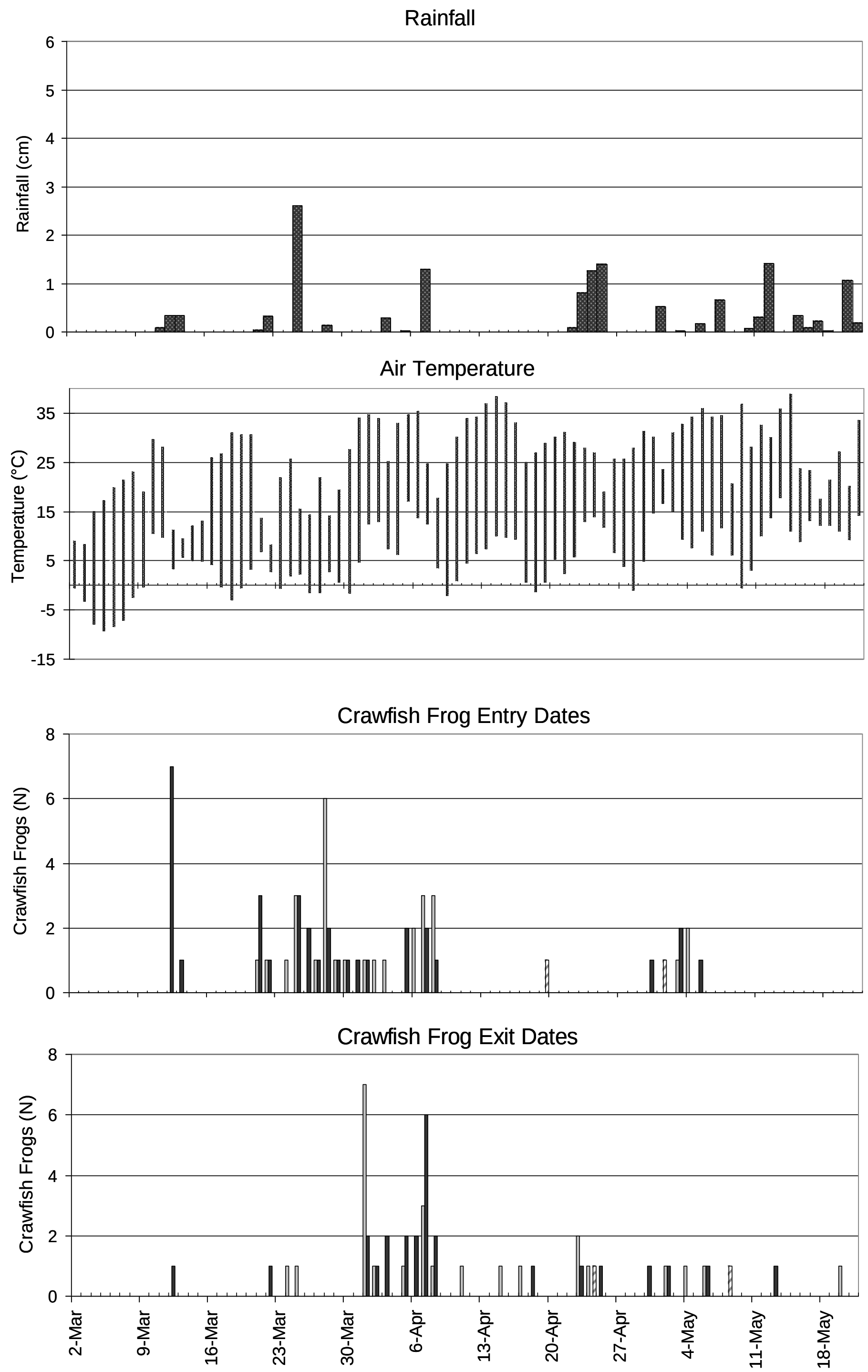


Figure 5. Daily total rainfall (cm), maximum and minimum air temperatures (°C), and dates adults entered and exited wetlands in 2010 (black bars represent males, gray bars represent females, striped bars represent subadults).

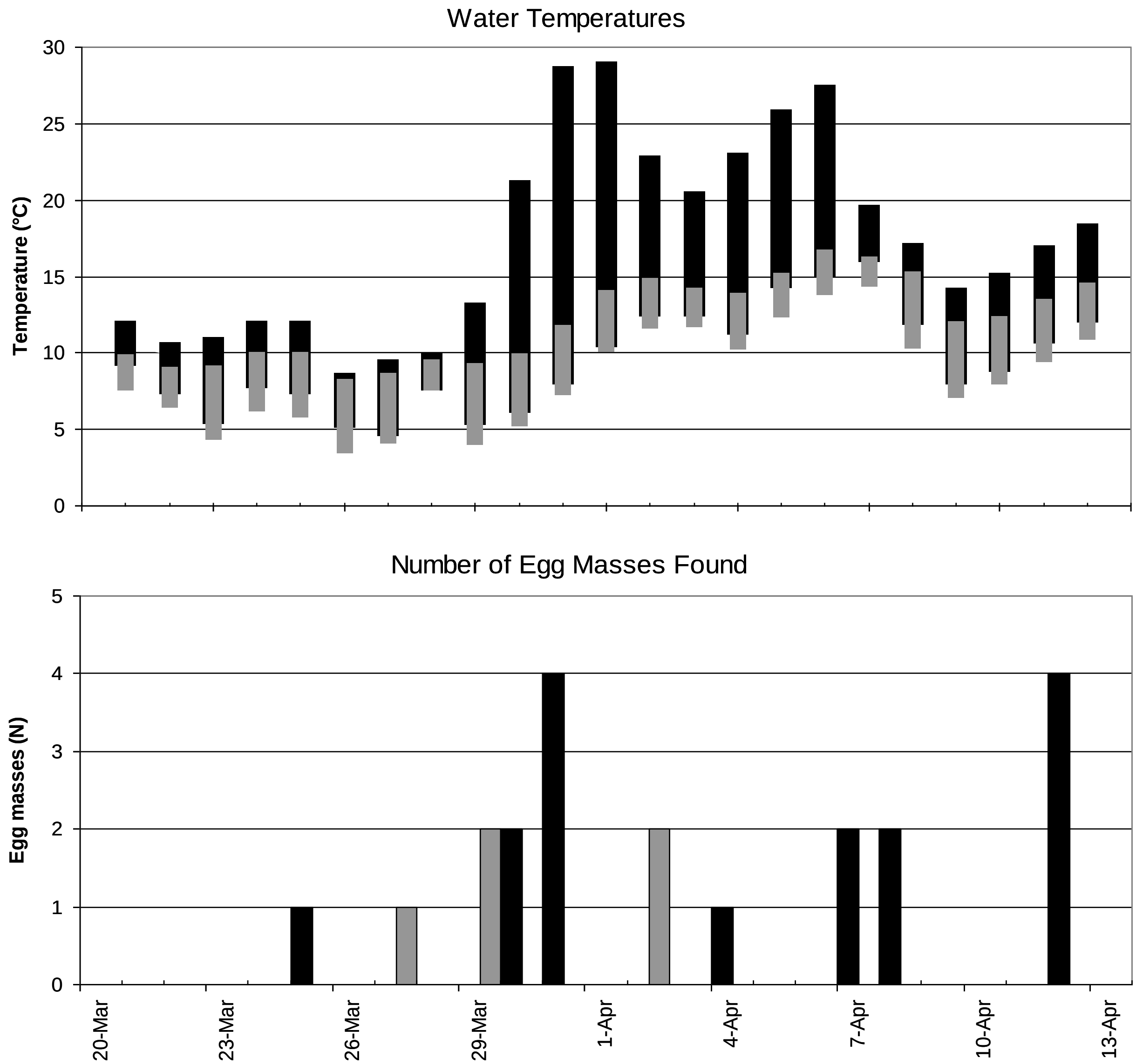


Figure 6. Maximum and minimum water temperatures for Nate's Pond and Cattail Pond (top), and dates when egg masses were found (bottom; black bars represent Nate's Pond, gray bars represent Cattail Pond in both plots).

A.

B.

Figure 7. Breeding area at Nate's Pond (A) and Cattail Pond (B). Orange flags mark egg mass locations. Egg masses were typically found in open shallow areas within each pond.

Figure 8. Photograph of a Crawfish Frog egg mass. Egg masses ranged from 10–15 cm in diameter.

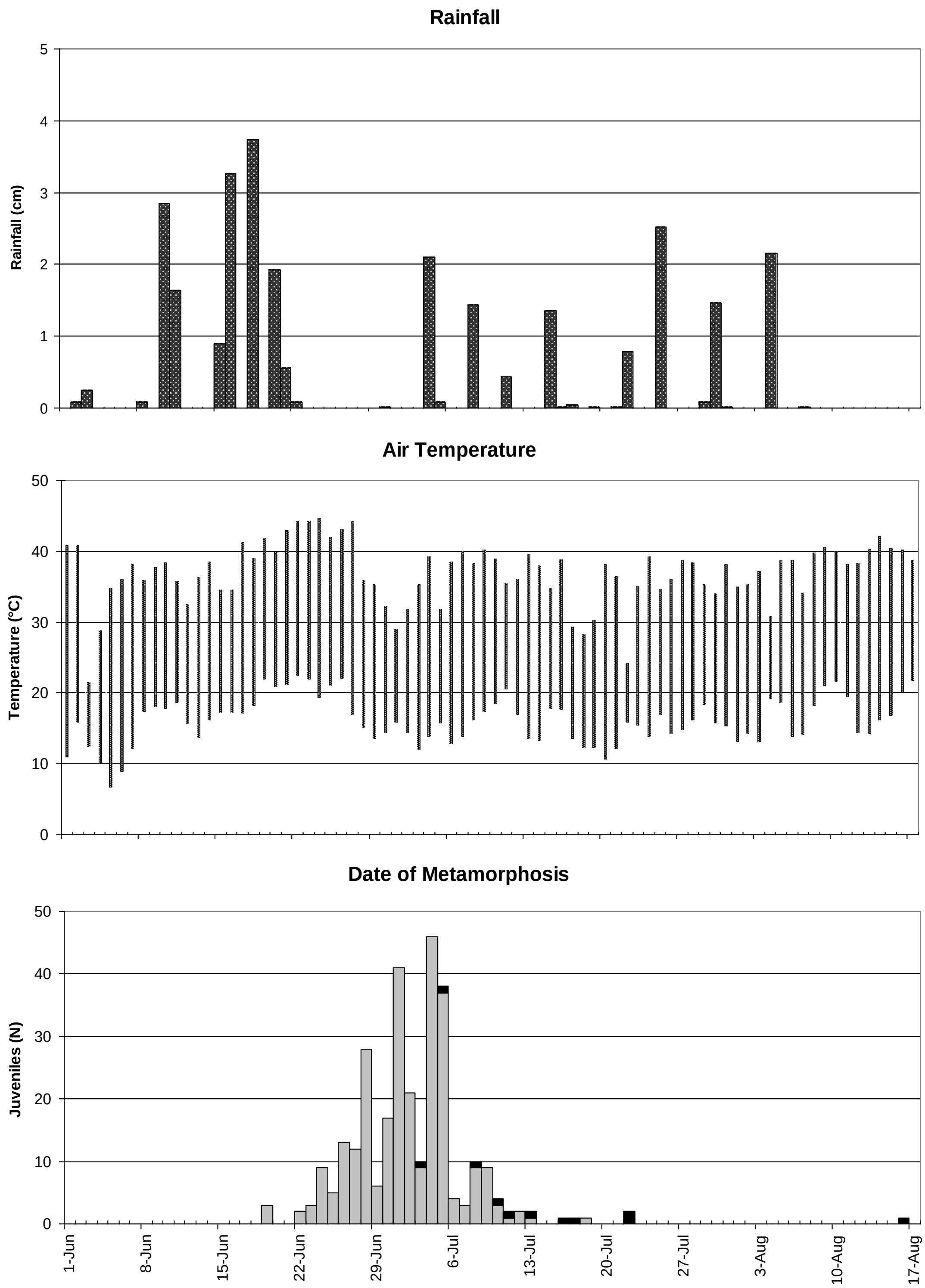


Figure 9. Daily rainfall (cm), maximum and minimum air temperatures (°C), and timing of juvenile Crawfish Frog metamorphosis 2009 (gray bars represent Nate's Pond, black bars represent Cattail Pond).

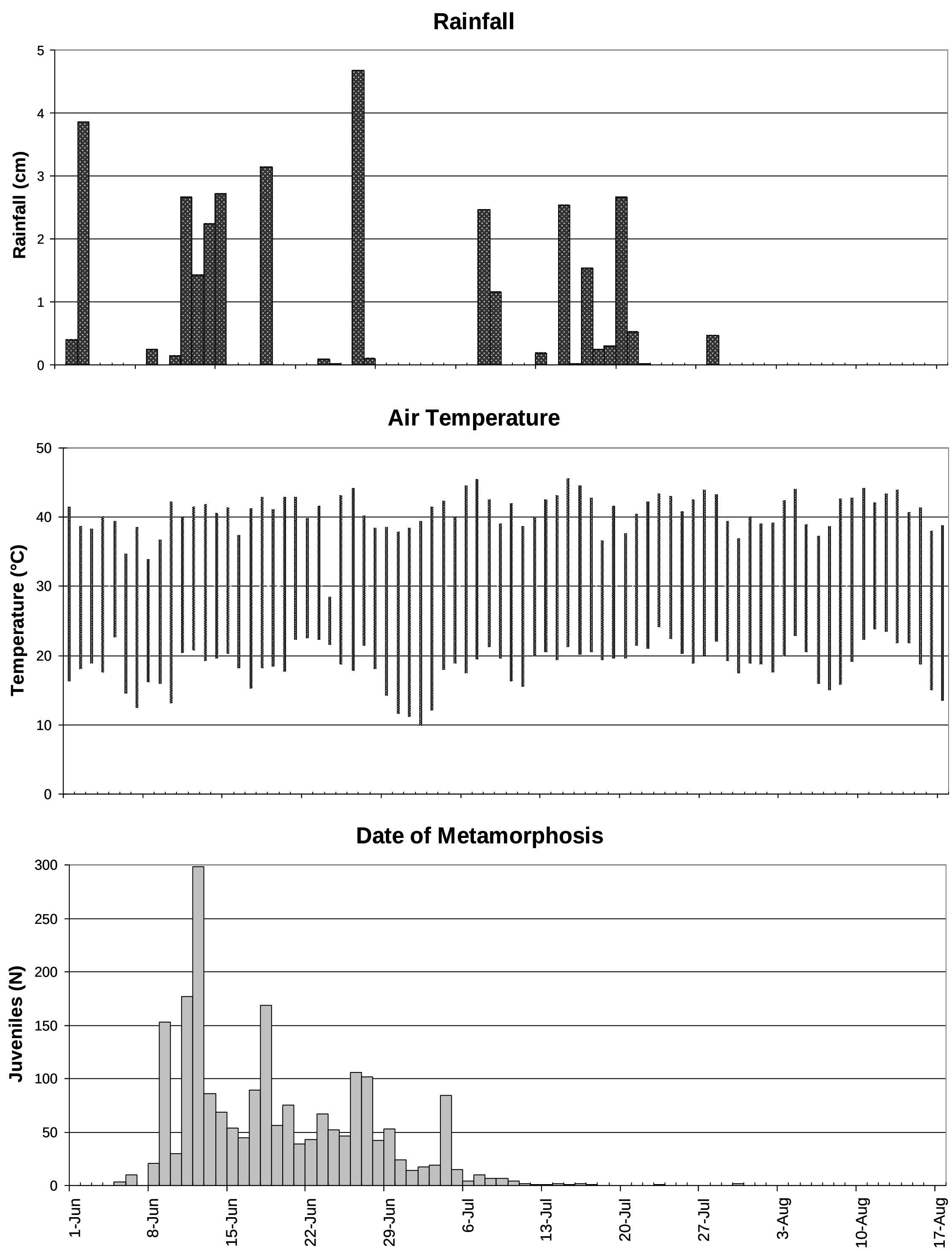


Figure 10. Daily rainfall (cm), maximum and minimum air temperatures (°C), and timing of juvenile Crawfish Frog metamorphosis in 2010 (gray bars represent Nate's Pond, Cattail Pond had no recruitment).

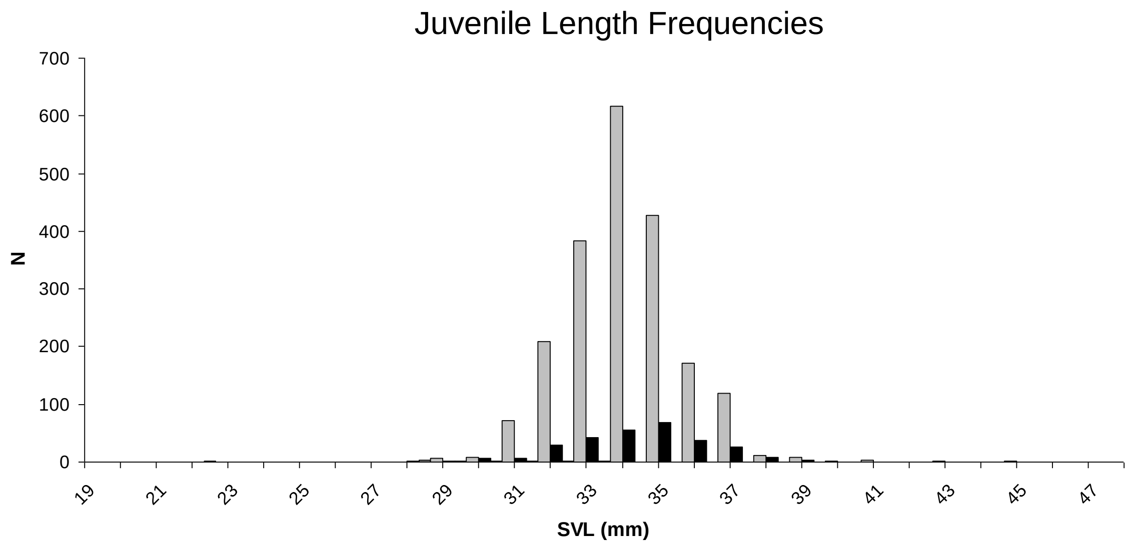


Figure 11. Snout-vent length (mm) frequencies of juvenile Crawfish Frogs that exited from Nate's Pond (black bars represent juveniles from 2009, light gray bars represent juveniles from 2010) and Cattail Pond (dark gray bars represent juveniles from 2009, no juveniles metamorphosed in 2010).

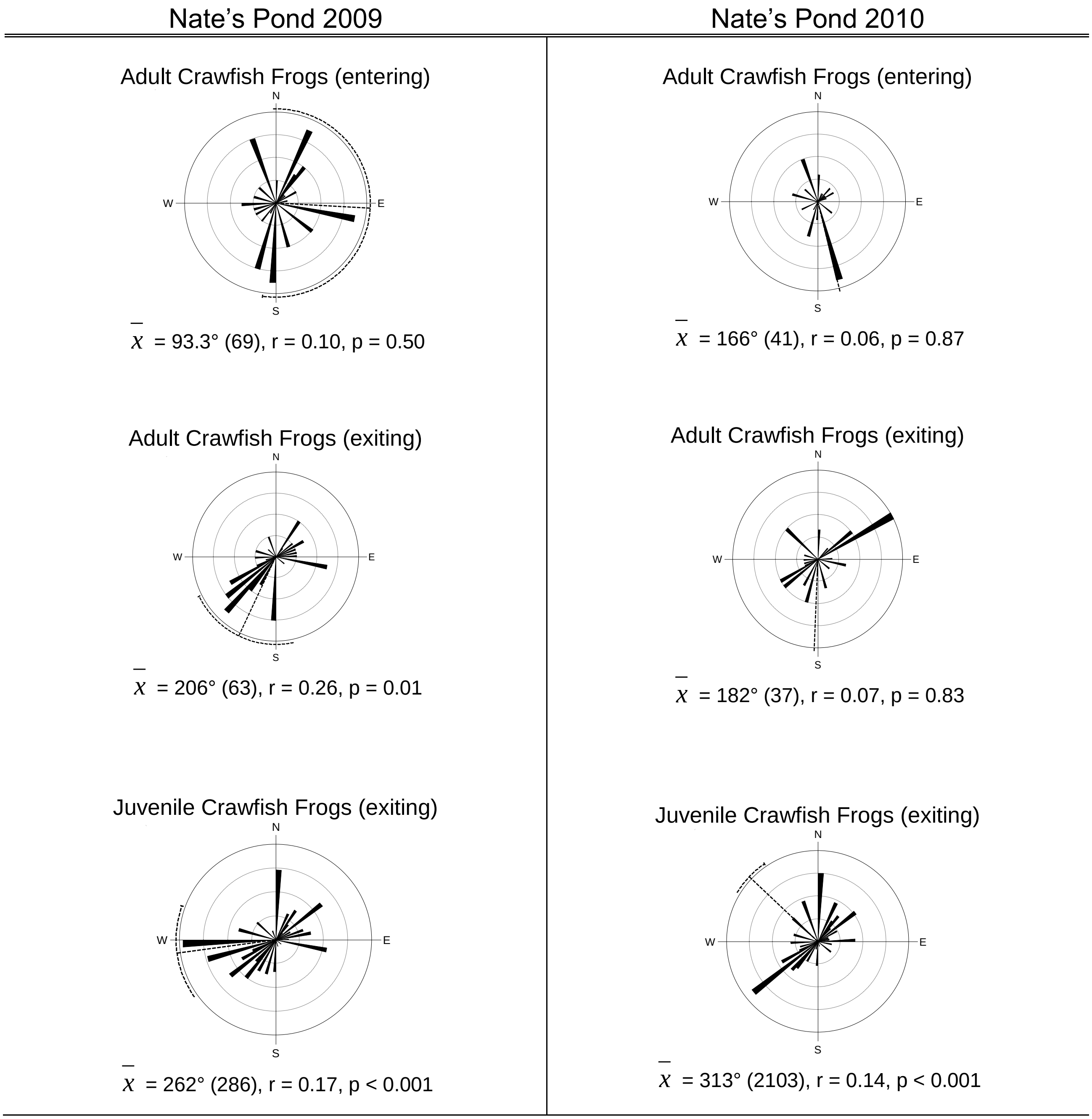
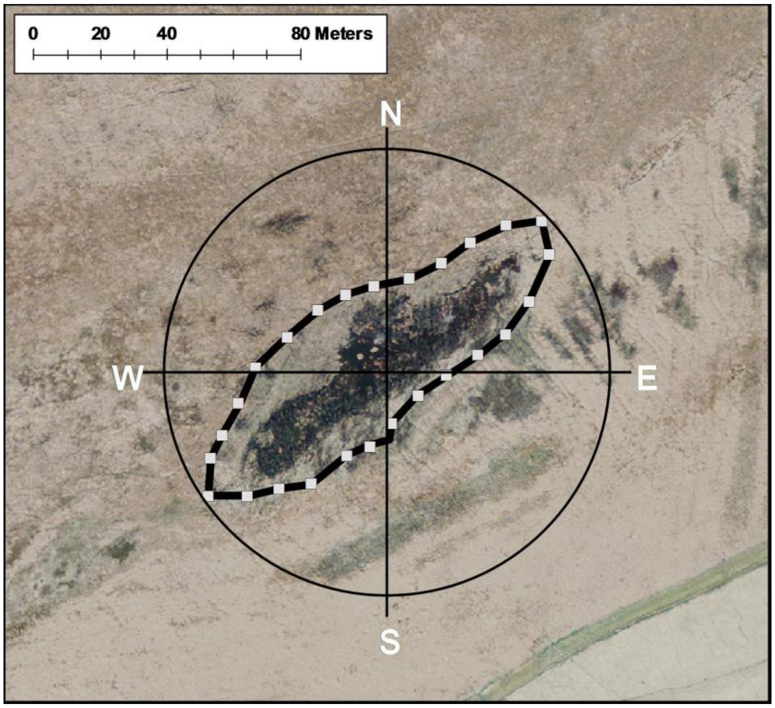


Figure 12. Circular histograms of immigrating/emigrating adults and emigrating juvenile Crawfish Frogs at Nate’s Pond with mean angle° (sample size), rho value, and p-value. Bars represent frequency of captures, dashed line represents mean angle of direction with 95 % confidence intervals.

A.



B.

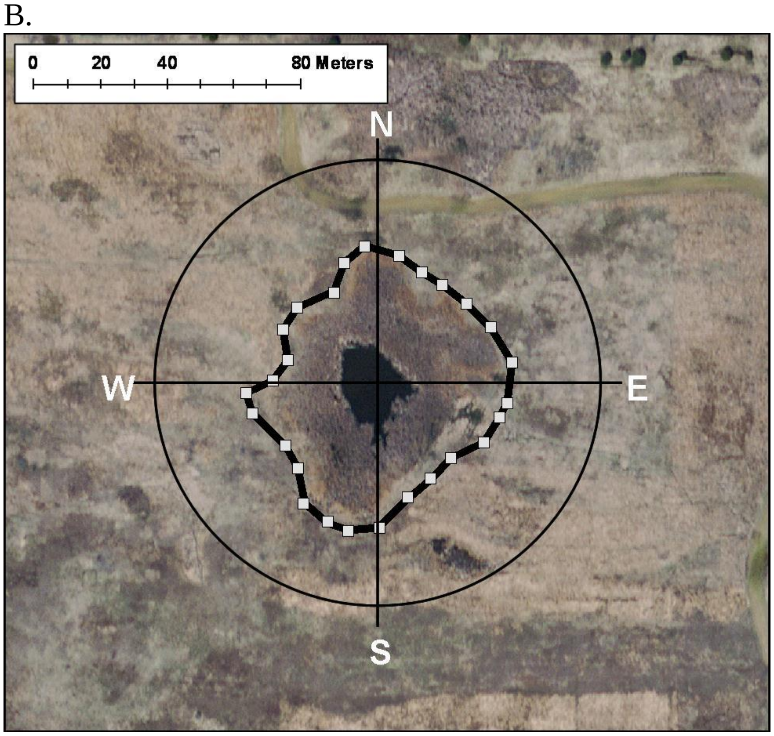


Figure 13. Aerial images of Nate’s Pond (A) and Cattail Pond (B). Irregular black circles indicate drift fence location, white squares indicate pitfall trap locations. Angle measurements, were determined from the center of each wetland.

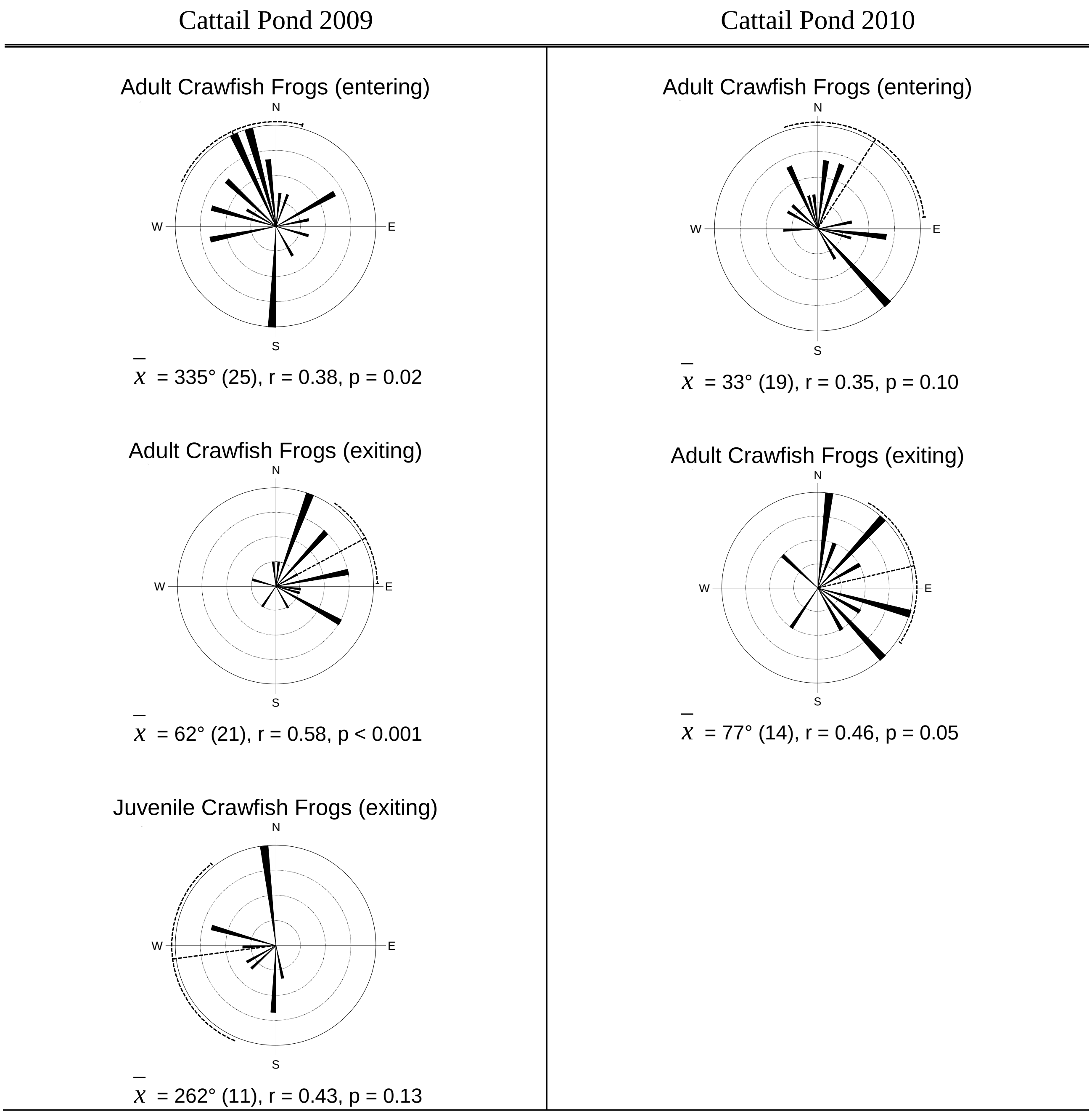


Figure 14. Circular histograms of immigrating/emigrating adults and emigrating juvenile Crawfish Frogs at Cattail Pond with mean angle° (sample size), rho value, and p-value. Bars represent frequency of captures, dashed line represents mean angle of direction with 95 % confidence intervals.

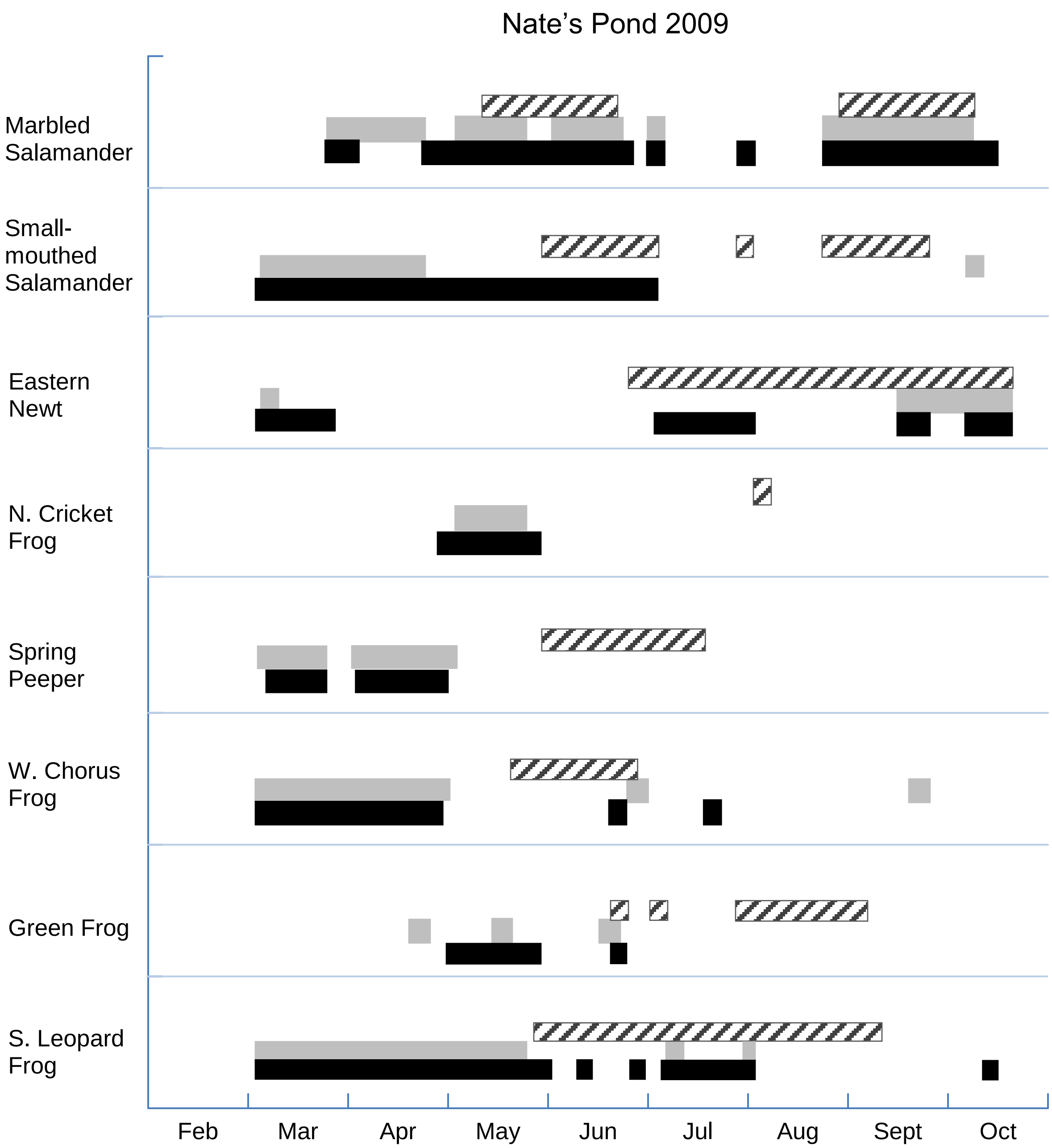


Figure 15. Timing of amphibian breeding and metamorphosis at Nate's Pond in 2009. Bars represent movement across drift fences by each species (black bars represent females, gray bars represent males, gray striped bars represent juveniles).

Figure 16. Timing of amphibian breeding and metamorphosis at Nate's Pond in 2010. Bars represent movement across drift fences by each species (black bars represent females, gray bars represent males, gray striped bars represent juveniles).

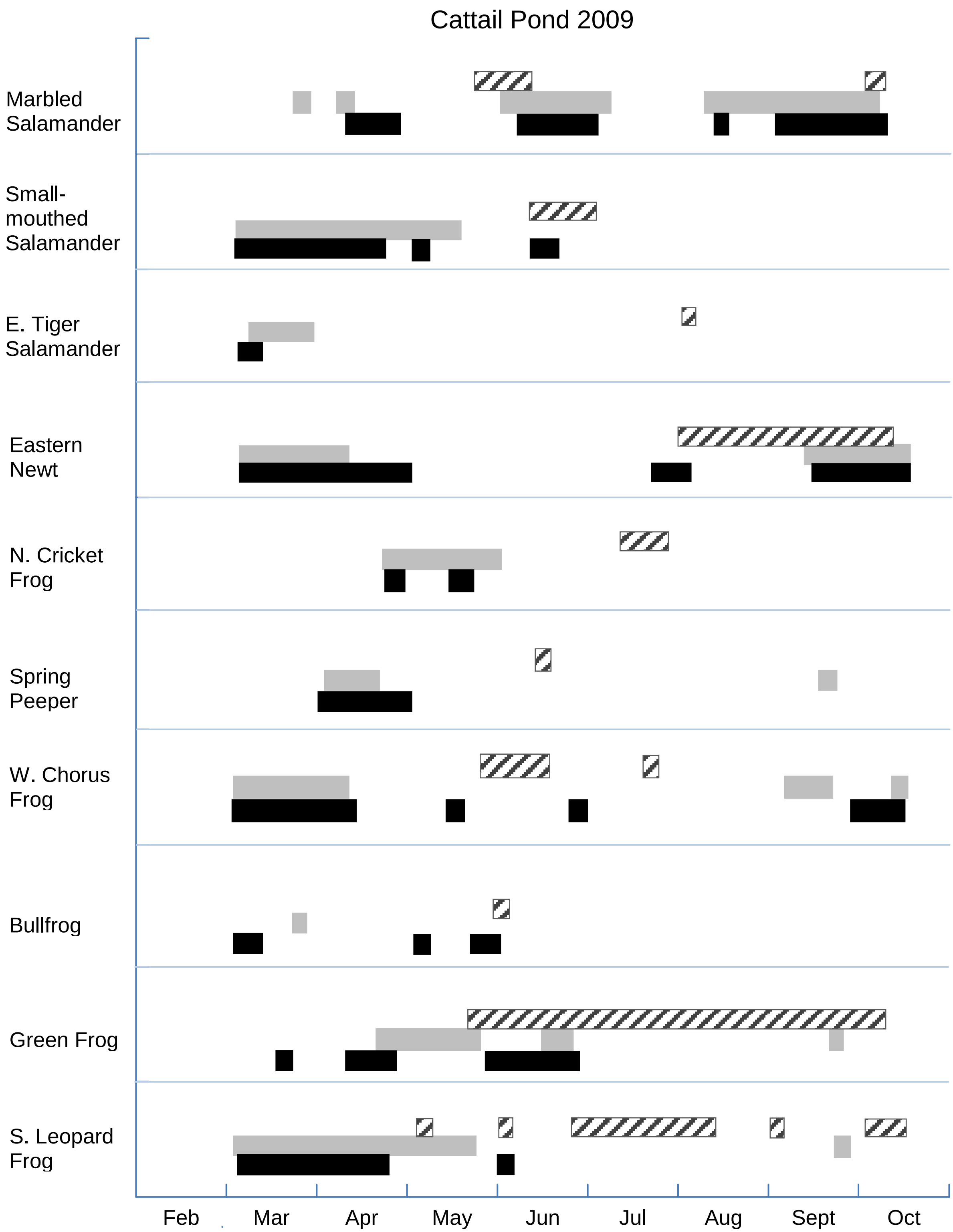


Figure 17. Timing of amphibian breeding and metamorphosis at Cattail Pond in 2009. Bars represent movement across drift fences by each species (black bars represent females, gray bars represent males, gray striped bars represent juveniles).

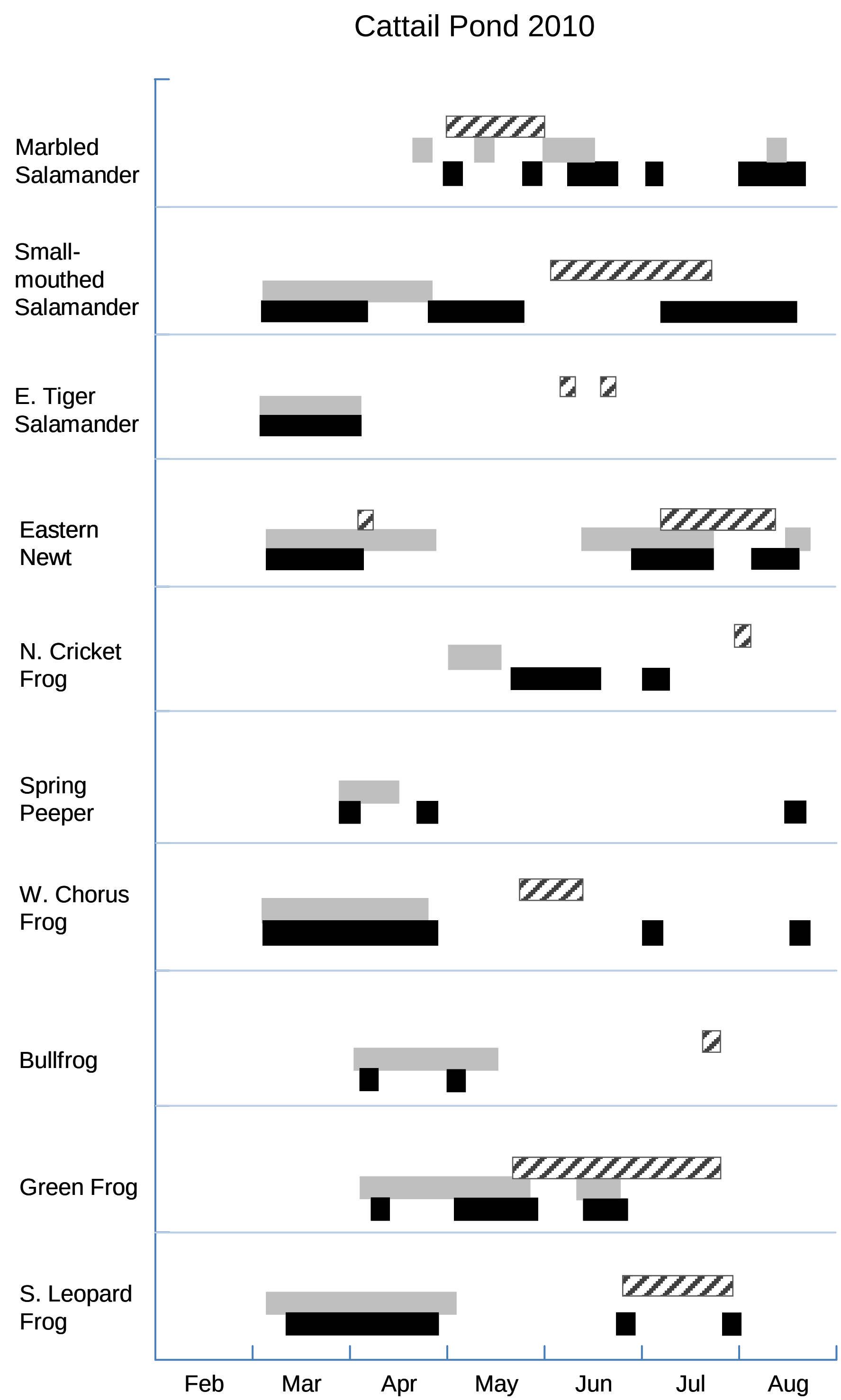


Figure 18. Timing of amphibian breeding and metamorphosis at Cattail Pond in 2010. Bars represent movement across drift fences by each species (black bars represent females, gray bars represent males, gray striped bars represent juveniles).

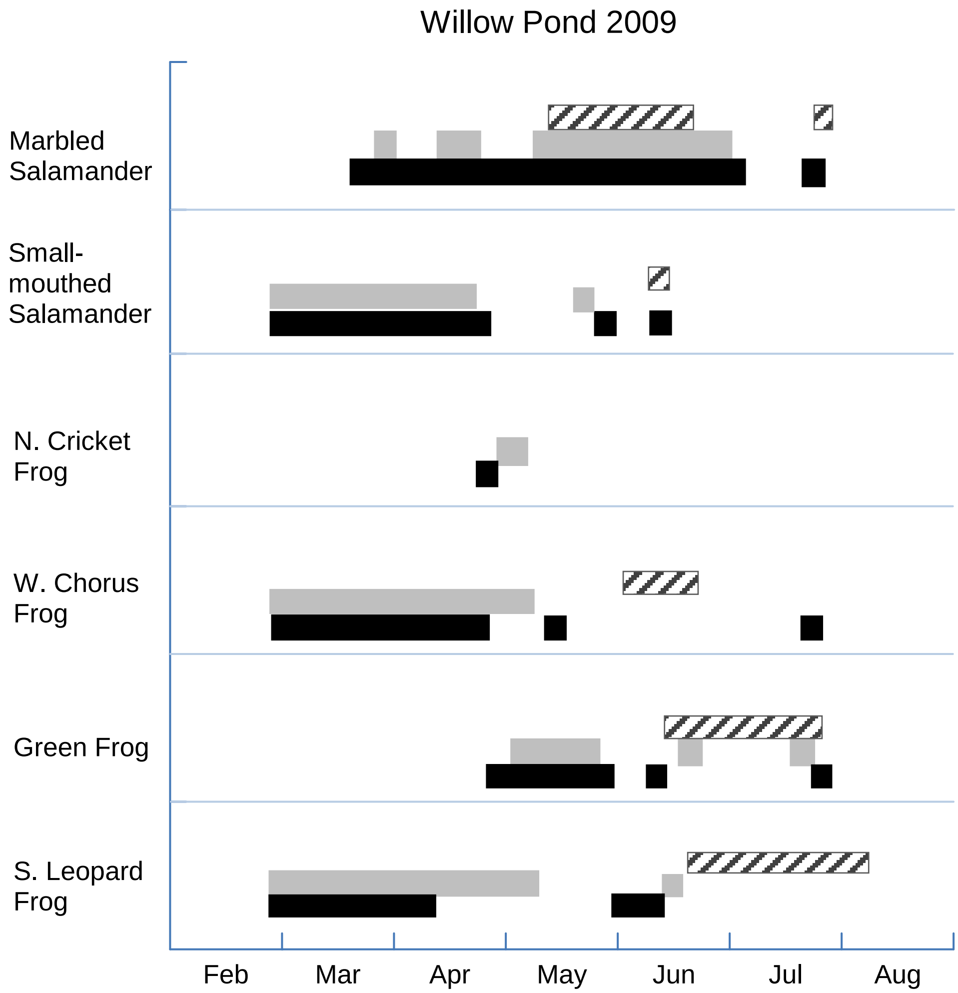


Figure 19. Timing of amphibian breeding and metamorphosis at Willow Pond in 2009. Bars represent movement across drift fences by each species (black bars represent females, gray bars represent males, gray striped bars represent juveniles).

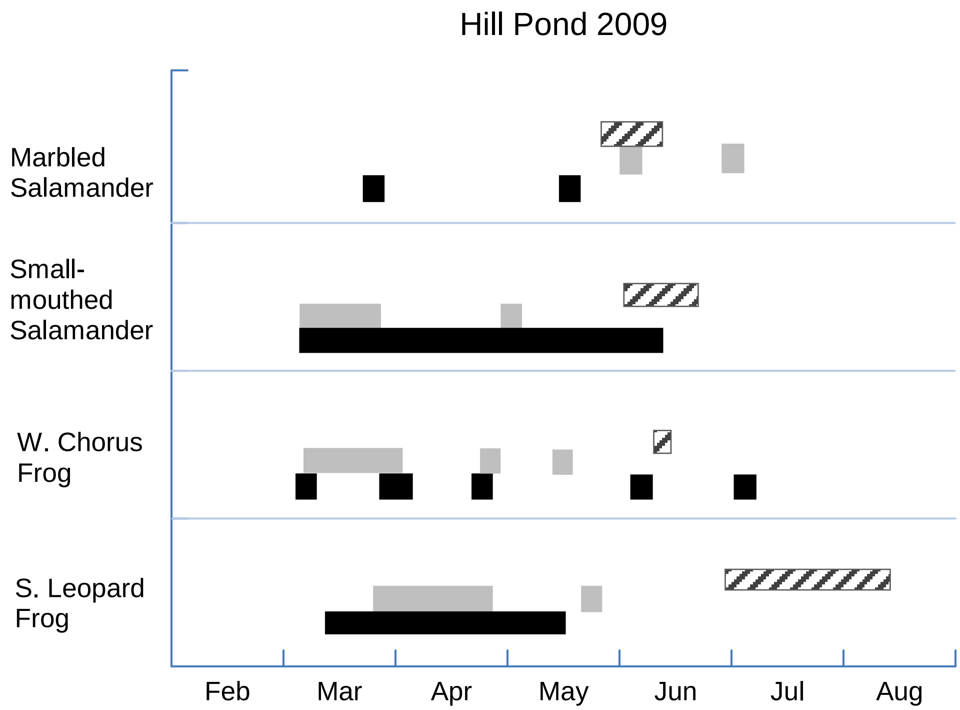


Figure 20. Timing of amphibian breeding and metamorphosis at Hill Pond in 2009. Bars represent movement across drift fences by each species (black bars represent females, gray bars represent males, gray striped bars represent juveniles).