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# Breeding Migrations, Survivorship, And Obligate Crayfish Burrow Use By Adult Crawfish Frog (Lithobates Areolatus)

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# BREEDING MIGRATIONS, SURVIVORSHIP, AND OBLIGATE CRAYFISH BURROW USE BY ADULT CRAWFISH FROGS (*LITHOBATES AREOLATUS*)

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by Jennifer L. Heemeyer

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# ABSTRACT

Movements are risky behaviors to animals, and amphibians are no exception. Being unable to cover long distances quickly, amphibians may find migrations challenging, yet many if not most species exhibit cyclic annual migrations. Crawfish Frogs (*Lithobates areolatus*), are a relatively understudied species of North American amphibian listed as endangered in Indiana and Iowa, and considered a species of conservation concern throughout much of their range. To better understand the biology of this species, and in particular, to assess the role that movements play in affecting survivorship, I radio tracked 48 Crawfish Frog adults, in 2009 and 2010. My study encompassed a total of 7,898 telemetered-frog days; single frogs were tracked for up to 606 days. These data demonstrate two behaviors previously undocumented in this species: 1) migration distances that averaged nearly ½ km, and for one frog was > 1,187 m; and 2) fidelity to upland burrows excavated by crayfish. Together, these findings indicate that Crawfish Frogs have a remarkable ability to home to distant upland burrow sites. Burrow fidelity in Crawfish Frogs involves, in part, frogs following similar migration routes to and from breeding wetlands. Burrow fidelity also occurs after ranging movements, and often involves individual frogs following the same circuit across years. Further, I demonstrate that movements are risky for Crawfish Frogs (about 12 times riskier than burrow dwelling), and therefore have survival consequences. My data also suggest that adult Crawfish Frogs are likely not dispersing to colonize new sites; instead, it seems more likely that juveniles represent the dispersing stage.

To ensure the least impact to Crawfish Frog populations several conservation measures should be taken.  First, core habitat and buffers should be established that exclude or limit roads for at least a 1.1-km radius around breeding wetlands.  Secondly, burrow destruction should be minimized by limiting new cultivation and other ground disturbance within the core habitat and buffer.  Thirdly, prescribed burns should be avoided from mid-March to mid-May, when frogs are out of their burrows migrating to and from wetlands.

# PREFACE

## *A Brief History of Radiotelemetry*

The study of amphibian movement behavior has long been of interest to researchers; however, only recently has technology caught up with our research ambitions. Monitoring amphibian movements began as early as 1941 by measuring distances between repeated captures of individually marked animals (Raney 1941). Other methods of tracking terrestrial amphibians that then arose include radioisotope tags (Madison & Shoop 1970), florescent powder (Rittenhouse et al. 2006), thread bobbin tracking (Heyer et al. 1994), radiotelemetry (Dodd 2010), and harmonic radar detection (Rowley & Alford 2007).

Radiotelemetry was first used for wildlife tracking purposes in the early 1960s (Millspaugh & Marzluff 2001). Initially, transmitter size limited the application to large game animals; however, once the transistor was introduced, which allowed battery size and thus transmitter size to decrease, telemetry became applicable for tracking smaller animals such as amphibians (Millspaugh & Marzluff 2001). Telemetry studies have allowed for the detailed documentation of microhabitat use, activity, movement patterns, and home ranges of various amphibian species (Wells 2007).

The earliest amphibian telemetry studies were on toads (*Anaxyrus americanus* [Tester 1963]; *Bufo b. bufo* [Van Nuland & Claus 1981]). Since then, telemetry has been used to study frogs (*Lithobates pipiens* [Dole 1968]; *Rana muscosa* [Mathews & Pope 1999]; *L. sevosus* [Richter et al. 2001]; *L. clamitans* [Lamoureux et al. 2002]; *L. sylvaticus* [Rittenhouse &

Semlitsch 2007]; *Hyla versicolor* [Johnson et al. 2008]; *L. capito* [Roznik et al. 2009]), toads (*B. spinulosus* [Sinsch 1989]; *B. calamita* [Sinsch 1992]; *Rhinella marina* [Seebacher & Alford 1999]; and *A. boreas* [Bartelt et al. 2004]),and various salamanders (*Cryptobranchus a. alleganiensis* [Stouffer et al. 1983]; *Dicamptodon tenebrosus* [Johnston & Frid 2002]; *Ambystoma jeffersoni*, *A. maculatum* [Faccio 2003]; and *A. tigrinum* [Steen et al. 2006]).

In order for telemetry studies to be successful, transmitters must be attached in such a way that they remain on the animal while not disturbing or injuring it. There is an ongoing discussion about whether internal (surgical) or external (belts or harnesses) transmitter attachment best meets these demands. Internal transmitter attachment involves invasive, and sometimes risky, surgery to implant the transmitter into the coelomic cavity. Shedding of internal transmitters is rare but does occur (Weick et al. 2005; Tracy et al. 2011). External transmitters are less risky to attach, but are shed if tied too loose; or cause abrasions which may alter movement and/or lead to infection if tied too tight (Long et al. 2010). While many types of external attachment have been attempted (Van Nuland & Claus 1981; Bull 2000; Goldberg et al. 2002; Weick et al. 2005), most comparisons of external to implanted transmitters recommend implanted transmitters as the safest and most reliable (Werner 1991; Weick et al. 2005; Long et al. 2010). Indeed, internal transmitters have been used successfully to track a variety of frog, toad, and salamander species (*C. a. alleganiensis* [Stouffer et al. 1983]; *B. spinulosus* [Sinsch 1989]; *B. calamita* [Sinsch 1992]; *R. marina* [Seebacher & Alford 1999]; *L. clamitans* [Lamoureux et al. 2002]; *D. tenebrosus* [Johnston & Frid 2002]; *A. jeffersonianum*, *A. maculatum* [Faccio 2003]; *H. versicolor* [Johnson et al. 2008]; and *A. tigrinum* [Steen et al. 2006]). In the following two chapters, I will tell how I used radiotelemetry to describe migration patterns and burrow use of Crawfish Frogs.

## ACKNOWLEDGMENTS

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# CHAPTER 1

## BREEDING MIGRATIONS AND SURVIVORSHIP IN CRAWFISH FROGS (*LITHOBATES AREOLATUS*): LONG-DISTANCE MIGRATIONS, BURROW PHILOPATRY, AND THE COST OF MOVEMENT IN A SPECIES OF CONSERVATION CONCERN

### INTRODUCTION

Animal movements are typically made to acquire resources such as food, water, mates, and habitat. However, movements are risky behaviors; costs include energy expenditure, increased vulnerability to predators, and exposure to unfavorable environmental conditions (Wells 2007). When assessing threats to species, especially species of conservation concern, there is considerable value in knowing the consequences associated with movements.

Animal movements outside of their home ranges can be defined in two general categories: migrations and ranging. Migration has been broadly defined as a "regular seasonal movement that has evolved in response to predictably changing food sources" such that "animals move in order to place themselves in optimum conditions for as long as possible" (Sinclair 1983). Migration has also been defined in a negative sense—"a mechanism by which organisms avoid unfavorable environments for more auspicious ones" (Elewa 2005). Ranging is the term used by Dingle (1996) and Wells (2007) to define movements outside of a home range to explore new resource patches (termed forays by Conradt et al. 2003). Ranging movements tend to be shorter in length than migrations; they may or may not be shorter in time.

Being unable to cover long distances quickly, amphibians may find migrations challenging, yet many if not most species exhibit cyclic annual migrations. These generally occur to and from breeding wetlands (Russell et al. 2005; Wells 2007; Semlitsch 2008). For example, Semlitsch (2008) defines amphibian migrations as movements primarily by resident adults toward and away from aquatic breeding sites. Other types of amphibian migrations include movements to hibernation sites (Wells 2007). I feel a general definition of migration applicable to all amphibian behavior should include three concepts: 1) seasonality—especially, but not exclusively in the spring and fall; 2) directed movements (taxis) beyond the vicinity of the home range; and 3) movements to an area previously known to the animal. In contrast, ranging movements occur outside of the spring breeding and fall hibernation movements, are usually non-directed (kinetic), and are exploratory, typically into areas previously unknown or not recently explored.

Crawfish Frogs (*Lithobates areolatus* [*Rana areolata*]) are members of a four-species clade contained within the *Nenirana* subgenus of Hillis and Wilcox (2005) that includes Pickerel Frogs (*L.* [*R.*] *palustris*), Gopher Frogs (*L.* [*R.*] *capito*), and Dusky Gopher Frogs (*L. sevosus*; [*R. sevosa*]). All three Gopher Frog/Crawfish Frog species are imperiled. Dusky Gopher Frogs are Federally Endangered; extirpated from both Louisiana and Alabama, and one historic population persists in Mississippi (Richter & Jensen 2005; USFWS 2001). Repatriated populations are in the process of being established near this site (USFWS 2010*b*). Gopher Frogs are known from fewer than 20 populations in any state where they occur except Florida (Jensen & Richter 2005); collectively, outside of Florida there may be fewer than 5,000 Gopher Frog adults (SEPARC

2010). Crawfish Frogs are also thought to be in decline throughout large portions of their range (Minton 2001), although due to their cryptic upland habits (considered by some to be the most secretive of North American *Rana*; Smith 1950), their status had been more difficult to determine (Parris & Redmer 2005).

In the present study, I use radiotelemetry techniques to describe the movement patterns of Crawfish Frogs. To date, no studies of movement or migratory behavior have been conducted on this species. While Gloyd (1928), working in Kansas, reported a Crawfish Frog found in a burrow 400 m from the nearest breeding wetland, members of this clade are known to migrate farther. Gopher Frogs, for example, have been reported as far as 1.6 km (Carr 1940; Franz et al. 1988) from breeding wetlands. More recently, radiotelemetry studies have described the movements of Dusky Gopher Frog adults (≤ 300 m; Richter et al. 2001) and Gopher Frog adults (≤ 102 m [Phillips 1995]; ≤ 286 m [Blihovde 2006]; ≤ 600 m [Neufeldt & Birkhead 2001]; ≤ 730 m [Roznik et al. 2009]; and nearly 5 km [Humphries & Sessoin pers. com.]) and Gopher Frog juveniles (≤ 691 m; Roznik & Johnson 2009*a*&*b*). In particular, I report here on the pre- and post-breeding migrations of Crawfish Frogs at the northern extent of their range. I describe two years of post-breeding migrations from wetlands to upland burrow sites (crayfish burrows), one year of pre-breeding migration, and the risks associated with these movements. I also document ranging behaviors including movements to hibernation burrows. Finally, I compare incoming and outgoing migration routes, describe burrow sharing, and document philopatry of Crawfish Frogs to their upland crayfish burrows.

# METHODS

## *Field Site*

My study site, Hillenbrand Fish and Wildlife Area, is located approximately 5 km south of Jasonville, Indiana in Green County (39.120275°N, 87.222187°W). From 1976–1982, Hillenbrand was surface mined for coal (Lannoo et al. 2009). Afterwards, the site was re-contoured and seeded to non-native vegetation. In 1988, the Indiana Department of Natural Resources (IDNR) purchased the land and began converting the vegetation to native prairie species using seedings and regular controlled burns. Hillenbrand is composed of two sections; my study site was located on the 729 hectares of Hillenbrand Fish and Wildlife Area-West (HFWA-W)—the only portion of the property that supports Crawfish Frogs (Lannoo et al. 2009).

As a part of a larger study, two Crawfish Frog breeding wetlands, Nate's Pond and Cattail Pond, were encircled with drift fences (V.C. Kinney, *unpubl. data*). Frogs were captured at these drift fences in 2009 and 2010 as they began post-breeding migrations from wetlands to upland burrows. I also captured frogs at a third pond, Big Pond, in unbaited mesh traps. Animals were chosen for telemetry opportunistically, although I attempted to get animals of both sexes in equal numbers at all three wetlands. Frogs were implanted with temperature-sensitive 3.8 g PD-2T radio transmitters, equipped with internal helical antennae (Holohil, Ontario, Canada). Crawfish Frogs are large (in this study frogs averaged 98.5 mm SVL ± 23.8, with an average mass of 108.8 g ± 6.8), and therefore can accommodate relatively long-lasting transmitters requiring large batteries. Transmitters accounted for 2–5% of the frog's total body weight, below the recommendation of Goldberg et al. (2002) of $\leq 5\%$ and Richards et al. (1994) of $\leq 10\%$ of total body weight.

### *Surgeries*

I implanted transmitters into the coelomic cavity following procedures outlined in Johnson (2006). Knowing the potential negative effects of anesthesia on anurans (Goldberg et al. 2002), we started with a concentration of 200 mg/L MS-222 (ethyl 3-aminobenzoate methanesulfonic acid salt; Sigma-Aldrich, St. Louis, MO) dissolved in a buffer solution (500 ml phosphate buffered saline [PBS], pH 7.2, giving the anesthetic solution a pH of 6.8) at room temperature. We observed the animal for 20–30 min and if it was still responsive we added 200 mg/L MS-222. This continued every half hour until the animal became fully anesthetized, indicated by loss of righting reflex and lack of pain response to toe pinching (Johnson 2006). After several surgeries, we were able determine that a concentration of 600 mg/L was optimal. At this concentration, animals usually took 20–30 min to become anesthetized and remained anesthetized through the duration of the surgery (~30 min). Transmitters were placed intraperitoneally by making a left side, off-midline abdominal incision through the skin and a parallel incision through the rectus abdominus (Johnson 2006). After transmitter insertion, the rectus abdominus was closed with five or six continuous (Weick et al. 2005) sutures (Vicryl™ [polyglactin 910] 5-0 RB1, #36; Ethicon, Somerville, NJ), and the skin was closed with five or six continuous sutures (Vicryl™) and glued (Vetbond™ [n-butyl cyanoacrylate] adhesive). Postoperatively, animals were placed in deionized water and observed until they awoke. They were allowed to recover overnight in a cold, dark environment (a cooler placed in a refrigerator) to minimize stress, and then released on the inside (opposite side) of the drift fence, or near the minnow trap, where they were captured.

Between March 2009 and July 2010, I performed 68 surgeries on 49 frogs. I re-implanted 15 frogs with new transmitters after the batteries in their original transmitters failed;

two frogs were implanted three times (Appendix 1). After surgeries, frogs were allowed to recover overnight in a cool dark environment (a cooler in the refrigerator) to minimize stress, and were released under surface cover at the site of capture in the morning of the following day.

Sixty-one surgeries were successful. Of the seven unsuccessful operations, three frogs died as a direct result of the surgery, as follows: Frog 4 died due to herniation of the viscera through the anterior abdominal wall (Heemeyer et al. 2010*a*); Frog 28 never regained consciousness after surgery, possibly from an overdose of MS-222 (see Goldberg 2002); Frog 13 bled out when an artery in the anterior abdominal wall was nicked during surgery. The other four unsuccessful surgeries (Frogs 15, 18, 42, and 54) were halted due to bleeding; in each case, I stopped the bleeding and closed the incisions. These frogs awoke normally and were active; I allowed them to recover overnight then returned them to their site of capture without a transmitter. Several of these frogs were later observed at the drift fences where they appeared to be behaving normally. Additionally, I removed the transmitter from Frog 2 after repairing its anterior wall herniation (Heemeyer et al. 2010*a*).

### ***Belt Harnesses***

I put transmitter belt harnesses on 18 frogs. In 2009, four frogs (Frogs 5, 12, 22, 25) were belted using a design similar to that described by Roznik and Johnson (2009*a&b*) and Muths (2003) where the 3.8g PD-2T transmitters (Holohil, Ontario, Canada) were attached to elastic threaded through glass beads. I quickly discovered this technique led to irritation and skin abrasions and I promptly removed the belts, sutured the abrasions, and released the frogs without transmitters. In 2010, I attached belt transmitters using metal beaded chains (Rathburn & Murphey 1996; Mathews & Pope 1999; similar to the plastic beaded chain that is currently being used successfully by J. Humphries [pers. com.] to track Gopher Frogs) on 14 frogs (Frogs 26, 30, 33, 34, 35, 36, 37, 38, 39, 43, 48, 49, 50, and 55). I never observed abrasions, but seven frogs (Frogs 35, 36, 38, 39, 41, 43, and 48) slipped their belts. Eight frogs were tracked using transmitter belt harnesses and implanted transmitters in series (Appendix 1); at no point did any frog have two functional transmitters.

### *Telemetry*

Crawfish Frogs were tracked from 21 March 2009 to 3 December 2010 using an R-1000 receiver (Communication Specialists, Orange, CA) and a Yagi© unidirectional antennae. I located frogs once a day during times of movement. When frogs settled into burrows during the summer and fall, I decreased tracking frequency to every other day. Under winter conditions, I tracked once a week. Each time an individual was located, I used a handheld Kestrel Tracker® weather meter to measure air temperature, relative humidity, and wind speed at the site. A HOBO® weather station located approximately 3.2 km from the field site recorded rainfall and comparative air temperature, relative humidity, and wind speed data. All positions were recorded using a Garmin® GPSMAP 76CSx, and geospatially referenced using Geographic Information System (GIS) software (ArcMap 9.3©). Distances traveled by individual frogs were measured using Hawthe's Tools (Spatial Ecology LLC©).

### *Enclosures*

During the winter of 2009–2010, I erected enclosures composed of 60-cm tall, 1-cm mesh hardware cloth around 10 burrows known or suspected to contain a Crawfish Frog. As the weather warmed during early and mid-March, I monitored enclosures nightly for Crawfish Frog emergence. Crawfish Frogs without transmitters or with non-functioning transmitters were equipped with external belt harnesses. I then tracked each frog from its overwintering burrow to the drift fence surrounding its breeding wetland. When frogs reached the drift fence, I removed their transmitter belts to avoid interfering with breeding activity. Upon exiting breeding wetlands, frogs were implanted with new transmitters and tracked back to their upland burrows.

### ***Survivorship***

I used two methods for calculating survivorship. Kaplan-Meier survival estimates (Mills 2007) were utilized to calculate the overall survival over the course of the study. The Kaplan-Meier method calculates the percent survival for every one-week period given a changing population size. To compute the cumulative probability of survival, the percent survival is determined by multiplying the percent survival of the previous week by the current population size. This technique allows censoring of individuals whose fates are unknown, and the addition of new animals to the census.

Kaplan-Meier is useful when calculating survival within populations over the entire study period. However, because of its reliance on a common, weekly, time scale for all animals followed, it becomes less useful when calculating survival in a specific behavioral context (e.g., migrations, burrow dwelling, ranging) when different animals within the population are exhibiting different behaviors. For example, if a population of Crawfish Frogs during the week of 1–7 April had 15 animals in a breeding wetland and 15 animals migrating to the breeding wetland, and two of the migrating frogs were killed, Kaplan-Meier could not distinguish migration-associated deaths from breeding-associated deaths. In making management recommendations, it is often important to identify the cause and behavioral context in which death occurs.

The second method of calculating survivorship I utilized was stage-specific survivorship, which accounted for specific behavioral circumstances. Unlike Kaplan-Meier, stage-specific survivorship does not rely on a common calendar, but rather on a specific behavioral context. In particular, I divided behaviors into four stages (pre-breeding, breeding, post-breeding, and burrow dwelling). For each stage, I calculated the number of frogs that began the period (N), by subtracting the number of frogs that were censored (C) from the number of animals that were tracked (T). To determine the number of frogs alive at the end of the stage (n), I then subtracted the number of animals that died (D) from N.

$$N = T - C \qquad \text{and} \qquad n = N - D$$

Finally, I calculated survival (S) by dividing n by N.

$$S = \frac{n}{N}$$

I then calculated the daily mortality rate per stage by dividing the proportion of frogs that died (D/N) by the average duration of each stage (Days).

$$\text{Daily Mortality Rate per Season} = \frac{(D/N)}{\text{Days}}.$$

Weick et al. (2005) and Tracy et al. (2011) determined that frogs can expel implanted transmitters; therefore, in order to produce a conservative survival estimate, frogs were considered dead only if a carcass was found ($n = 14$), and not if the transmitter was found on the ground ($n = 6$).

### ***Statistics***

I used program R for all statistical analyses and SPSS to calculate means and standard deviations. Spearman rank correlation matrices (Program R) were used to determine if there were particular variables that influenced the movement distances, or the number of frogs that moved any given day. I compared the daily value of six weather variables (minimum relative humidity, maximum relative humidity, minimum temperature, maximum temperature, total rain, and total rain the day before) as well as Julian date to determine which best described the variation in the average distance that the frogs moved and the number of times each frog moved. I performed correlations using all movement data for each migratory season. The pre-breeding 2010 migration was evaluated from when the first frog left its burrow to when the last frog reached the wetland. Both of the post-breeding migrations were evaluated from when the first frog left the wetland to when the last frog reached its primary burrow.

To evaluate the total distance traveled by frogs from the breeding wetlands to the upland burrows I generated maximum likelihood generalized linear mixed-effects models (GLMMs) using the lmer function in R. I included individual frog as a random independent variable to control for non-independence of data points from the same individual (Zuur et al. 2009). I also included six fixed independent variables: frog metrics—sex, length [SVL] and mass [g], migration year, migration start date, and number of moves made. To select models, I followed Zuur et al. (2009) and then compared the relative fits of these models using Akaike's information criterion ($AIC_C$). I compared the $AIC_C$ scores of the GLMMs to determine the model that best described the variation in total distance traveled, as denoted by the model with the lowest $AIC_C$ score and the highest Akaike weight (w) based on the $\Delta$ $AIC_C$ (Anderson et al. 2001).

## RESULTS

In total, I tracked 48 individual Crawfish Frogs for up to 606 days (as of 30 November 2010, continuing) and up to 1.2 km away from breeding wetlands (Appendix 1), as follows. In 2009, I tracked 26 Crawfish Frogs during the post-breeding migration stage and while overwintering. In 2010, I tracked 12 Crawfish Frogs (11 were animals previously tracked in 2009) from their overwintering burrows towards the breeding wetlands (pre-breeding migration stage); I tracked 30 Crawfish Frogs during the post-breeding migration stage and while burrow-dwelling (Table 1). Eight frogs were tracked from the beginning of post-breeding migrations in

2009, through pre-breeding migrations in 2010, and until after post-breeding migrations in 2010 (≤ 606 d). I tracked an additional three frogs through two migrations, from the beginning of the post-breeding migration in 2009 through the pre-breeding migration in 2010 (335–354 d). One frog was tracked through the 2010 pre-breeding migration as well as the 2010 post-breeding migration (97 d). Other frogs were tracked for shorter durations. As of 30 November 2010, I tallied a total of 7,898 "telemetered-frog days" (number of frogs tracked multiplied by the numbers of days each frog was tracked).

### *2009 Movements*

In 2009, I tracked 26 post-breeding frogs; 20 were followed to their primary burrows (Table 1; Fig. 1), one frog was implanted after it had migrated, it was captured while occupying its primary burrow. Ten Crawfish Frogs exhibited ranging behaviors after establishing primary burrows, three established new primary burrows prior to overwintering, as detailed below.

**Post-breeding Migrations to Upland Burrows.** The 2009 post-breeding migration began on 2 April, when the first animal exited its breeding wetland, and ended 25 June, when the last animal entered its burrow. I define the end of an animal's post-breeding migration as the time when the frog becomes sedentary in association with a burrow. The first Crawfish Frog reached its primary burrow on 2 April, while the last breeding Crawfish Frog did not leave its wetland until 15 May—demonstrating substantial overlap in the timing of the post-breeding migration stage. Frogs traveled an average of 493.1 m (SD = 258.6; range = 32.6–1,043.6), took an average of 29.8 days (SD = 20.2; range = 1–67), and used an average of 12.6 moves (SD = 9.3; range = 1–36). For example, Frog 11, a female, left Nate's Pond on 5 April 2009 and traveled 604.7 m, making 10 movements, until she reached her primary burrow on 26 April (21 d later). She remained at this burrow for exactly 11 mo (334 d), until she left to breed the following year, on 26 March 2010 (see below; Appendix 1; Fig. 1). Females moved an average of 458.1 m (SD = 218.7; range = 123.2–793.3), males moved an average of 520.6 m (SD = 291.1; range = 32.6–1,043.6), a difference that was not significant (*p* = 0.6092). As Crawfish Frogs migrated from breeding wetlands to upland sites, they used grass clumps, a variety of holes, puddles, scrapes, and burrows as temporary retreat sites.

Crawfish Frogs exhibited one of several movement patterns when migrating from wetlands to burrows, as follows. Pattern 1: animals migrate straight away from wetlands, they do not reverse course, they exhibit movements in the general direction of burrow, and turns at angles > 90 degrees. Frogs 1, 5, 6, 7, 8, 11, 19, 20, 21, 27, 29, and 31 (n = 12) exhibited this pattern of movement (Fig. 2). These frogs took an average of 17.0 d (SD = 15.7; range = 1–56) to reach their primary burrows, traveling an average of 451.4 m (SD = 283.6; range = 32.6–1,043.6) and making an average of 6.8 movements (SD = 4.4; range = 1–14).

Pattern 2: animals reversed directions or made turns with angles < 90 degrees prior to burrowing. Frogs 3, 9, 10, 12, 14, 16, 17, 22, 24, 26, and 30 (n = 11) exhibited this pattern of movement. These frogs took an average of 45.1 d (SD = 12.9; range 25–67) to reach their primary burrows traveling an average of 527.5 m (SD = 248.0; range = 174.3–896.1) and making an average of 19.3 movements (SD = 8.4; range 8–36). Frogs exhibiting post-breeding migration Patterns 1 and 2 had significantly different durations (*p* = 0.0012) and numbers of moves (*p* = 0.0007; Fig. 3 and Fig. 4A, B, & C) but not distances traveled (*p* = 0.3679). A subset of Pattern 2 frogs (Subset A: Frogs 9, 17, 22, 26, and 30) migrated straight away from breeding wetlands in the general direction of their burrow, then, in the vicinity of their future burrow, changed directions frequently over short distances (Fig. 3). These frogs took an average of 51.4 d (SD = 11.5; range 40–67) to reach their primary burrows traveling an average of 617.1 m (SD = 252.9;

range = 278.5–896.1) and making an average of 22.2 movements (SD = 8.9; range 8–36). A second subset of Pattern 2 frogs (Subset B: Frogs 12, 16, and 24) migrated straight out from breeding wetlands, passed their future burrow, then turned around and doubled back. These frogs took an average of 38 d (SD = 13.5; range 25–52) to reach their primary burrows traveling an average of 616.5 m (SD = 161.1; range = 432.8–733.6) and making an average of 14.0 movements (SD = 6.0; range 8–20). A third subset of Pattern 2 frogs (Subset C: Frogs 3, 10, and 14) changed directions frequently over short distances almost immediately after leaving their breeding wetlands. The duration, distance, and movements of these frogs were not calculated because two of the three frogs died during migration. One of these frogs (Frog 10) tested positive for the chytrid fungus *Batrachochytrium dendrobatidis* (Bd; Kinney et al. 2011) and the other two frogs' migration patterns were likely influenced by hernias (Heemeyer et al. 2010*a*).

**Ranging from Upland Burrows.** Of the 20 frogs that I located at primary burrows post-breeding in 2009, six (Frogs 3, 9, 11, 24, 27, and 29) remained at their primary burrows without ranging until their 2010 pre-breeding migration (for 280–334 d); four frogs (Frogs 5, 17, 20, and 32) were caught after migrating or their transmitters failed; and ten frogs (Frogs 6, 7, 8, 12, 16, 19, 21, 25, 26, and 30) made ranging movements from their primary burrows out to other retreats/burrows then either returned to their primary burrows or established new burrows. Not all of these spring and fall ranging movements occurred when the frog had an active transmitter. However, of those that did (9 frogs), on average (including spring and fall ranging) the frogs moved 3.7 times (SD = 2.5, range = 2–9) covering 98.36 m (SD = 115.2, range = 17.8–311.4) over the course of 38 d (SD = 48.7, range = 1–137). For example, in 2009, Frog 26 left his primary burrow three times for periods of 16, 17, and 15 days (in June, July, and September, respectively), returning to his primary burrow each time. In contrast, Frogs 6, 7, and 25 made fall ranging movements from their primary burrows to new burrows, where they overwintered.

**Movements Specific to Wetlands.** In 2009, I tracked 11 frogs (6 males: Frogs 3, 12, 21, 23, 30, and 31; 5 females: Frogs: 1, 7, 10, 11, and 29) from Nate's Pond. These frogs moved from 1–29 times, with an average of 12.7 (SD = 8.9). They moved an average distance of 490.1 m within a range of 32.6–1,043.6 m (SD = 322.7). Seven frogs from Nate's Pond established primary burrows; four frogs died or were not found and thus I could not identify their primary burrows. Frogs that I tracked from Nate's Pond emigrated in almost all directions except for southeast (Fig. 5).

I tracked eight frogs from Cattail Pond (5 males: Frogs 5, 24, 26, 27, and 32; 3 females: Frogs 20, 22, and 25). Seven of these frogs established primary burrows during the period in which I tracked them. Whereas Frog 22, a female, never established a primary burrow during the period that I tracked her. These frogs made 1–36 movements ($\bar{x}$ = 11.1; SD = 12.1) for distances from 278.5–793.3 m and an average distance of 470.7 m (SD= 164.0). All frogs from Cattail Pond migrated north or east, crossing one or two roads (Fig. 6).

I tracked seven frogs (4 males: Frogs 6, 9, 14, and 16: 3 females: Frogs 8, 17, and 19) from their point of capture at Big Pond. They made from 1–24 movements ($\bar{x}$ = 12.3, SD= 8.1) and traveled 174.3–896.1 m ($\bar{x}$ = 532.0 m, SD= 279.5). I tracked six frogs from Big Pond to their primary burrows; one frog died after herniation and was censored (Heemeyer et al. 2010*a*). The majority of these frogs migrated either north, across the road, or south, into what was at the time a recently burned area, out of Big Pond (Fig. 7).

### *2010 Movements*

In 2010, I tracked 12 frogs from their overwintering burrows as they migrated to their breeding wetlands (pre-breeding stage). Eight frogs had functioning internal transmitters while in breeding wetlands. In breeding wetlands, transmitters were checked daily for function, but frogs were not specifically located in order to prevent interfering with breeding behaviors or retreat sites. Thirty frogs were tracked emigrating from their wetland (post-breeding stage); 16 of these animals were followed to primary burrows (Appendix 1).

**Pre-breeding Migrations to Wetlands.** In 2010, I tracked 12 frogs from their overwintering burrows towards their breeding wetlands. One of these frogs died after being attacked by a predator but was not eaten (Table 1; Fig. 8; Frog 29, see below), the remaining 11 frogs reached wetlands and presumably participated in breeding activities. The 2010 pre-breeding migration period began on 11 March, when the first frog left its overwintering burrow, and ended on 7 April, when the last frog reached its breeding wetland. On average, pre-breeding migrations lasted 5 d (SD = 4.6; range = 1–16) and frogs covered a distance of 314.6 m (SD = 167.4; range = 110.7–660.4) using 2.7 moves (SD = 1.2; range = 1–5). Males moved an average of 248.7 m (SD = 139.5; range = 110.7–530.0); females moved an average of 406.8 m (SD = 171.9; range = 201.2–660.4), a difference that was not significant ($p = 0.438$).

During the 2010 pre-breeding migration, four frogs (Frogs 6, 7, 26, and 29) out of the 12 followed occupied burrows they had used either during the previous summer or during their 2009 post-breeding migration. All pre-breeding movements were in the direction of the frogs' breeding wetlands with the exception of one pre-breeding ranging movement made by Frog 29. After overwintering, Frog 29 moved to a new, previously unoccupied burrow approximately 120 m west of her primary burrow then moved back east to her primary burrow before migrating south towards Nate's Pond to breed.

**Breeding.** The eight frogs in breeding wetlands with functioning internal transmitters were located to wetlands on a daily basis but not tracked to a specific location. In this way, I discovered the remains of Frog 21 along the shoreline on the morning after a raccoon preyed upon it (Heemeyer et al. 2010b).

**Post-breeding Migrations to Upland Burrows.** In 2010, I tracked 30 post-breeding frogs, 16 to their primary burrows (Fig. 9). The post-breeding migration stage began on 22 March, when the first animal left its breeding wetland, and ended on 16 June, when the last migrating frog settled into a burrow. Post-breeding migrations lasted, on average 13.2 d (SD = 12.5, range = 1–39), and frogs moved on average 376.9 m (SD = 297.9, range = 28.1–1,187.8) using 6.9 movements (SD = 6.8, range = 1–27). Females moved an average of 360.7 m (SD = 184.7; range = 86.8–709.5), males moved an average of 387.8 m (SD = 359.1; range = 28.1–1,187.8); this difference was not significant ($p = 0.6566$).

In 2010, 10 frogs (Frogs 3, 6, 7, 8, 37, 40, 44, 47, 53, and 55) followed movement Pattern 1 and migrated straight to primary burrows (Fig. 10). These frogs took on average 12.7 d (SD = 13.4; range 1–39), and moved 324.2 m (SD = 112.5; range 91.4–469.8) using 4.2 movements (SD = 3.7; range 1–10).

Eleven frogs (Frogs 11, 16, 26, 30, 33, 45, 49, 50, 51, 52, and 56) followed movement Pattern 2, exhibiting some sort of wandering and turning at angles of < 90 degrees (Fig. 11). These frogs moved an average of 514.4 m (SD = 372.3, range = 76.0–1,187.8) in 14.0 d (SD = 12.2, range = 2–31) and 11.1 moves (SD = 8.7, range = 3–27). Frogs exhibiting post-breeding migration Patterns 1 and 2 did not differ significantly in distance, duration, or number of moves (at a alpha of 0.01 $p > 0.01$; Fig. 4C) however there was a lot of variation in the pattern 2 movements.

As was the case in 2009, a subset of Pattern 2 frogs (Subset A: Frogs 11, 26, 33, 51, and 56) migrated straight away from their breeding wetlands, and when they reached the area of their future burrow, changed directions frequently over short distances. These frogs took an average of 11.8 d (SD = 11.2; range 2–27) to reach their primary burrows, traveling an average of 464.0 m (SD = 244.1; range = 163.4–709.5) and making an average of 9.2 movements (SD = 6.6; range 3–19). A second subset of Pattern 2 animals (Subset B: Frogs 16, 30, and 52) migrated straight out from breeding wetlands past their future burrows, then doubled back. These frogs took an average of 18.5 d (SD = 17.7; range 6–31) to reach their primary burrows traveling an average of 711.2 m (SD = 427.2; range = 362.6–1,187.8) and making an average of 13 movements (SD = 12.3; range 4–27). A third subset of frogs changed directions frequently and over short distances almost immediately after leaving breeding wetlands (Subset C: Frogs 45, 49, and 50). These frogs traveled an average of 401.7 m (SD = 554.9; range = 76.0–1,042.4) and made an average of 12.3 movements (SD = 11.2; range 4–25). None of these frogs reached primary burrows; all three tested positive and had high zoospore equivalents (>1,000) of the chytrid fungus (Bd; Kinney et al. 2011) and died from either chytridiomycosis or predation.

Five out of eight frogs exhibited the same post-breeding movement pattern in both 2009 and 2010: Frogs 6, 7, and 8 followed movement Pattern 1; Frog 26 followed movement Pattern 2A; and Frog 16 followed movement Pattern 2B. The remaining three frogs altered their migration patterns between years; Frog 3 (recovering from a post-herniation repair in 2009) shifted from Pattern 2C in 2009 to Pattern 1 in 2010; Frog 11 shifted from Pattern 1 to Pattern 2A; and Frog 30 shifted from Pattern 2A to 2B.

**Movements Specific to Wetlands.** I tracked 14 frogs (8 males: Frogs 3, 34, 44, 46, 49, 50, 52, and 55; 6 females: Frogs 7, 11, 37, 40, 48, and 53) from Nate's Pond (Fig. 12). These frogs made from 1–27 movements with an average of 7 moves (SD = 8.5). They traveled an average distance of 380.4 m (SD = 351.7) with a range of 28.1–1,187.8 m. I tracked nine of these frogs to their primary burrows; the remaining five animals either died or were not found. Similar to 2009, frogs from Nate's Pond migrated out in all directions except for southeast. Two frogs established burrows in a mowed lawn southeast of the pond (Fig. 12).

Ten frogs from Cattail were tracked (5 males: Frogs 26, 39, 43, 47, and 58; 5 females: Frogs 33, 41, 45, 51, and 56; Fig. 13). These frogs made 1–19 movements ($\bar{x}$ = 7; SD= 5.9) over distances that ranged from 86.8 –709.5 m ($\bar{x}$ = 318.5; SD = 209.9). I tracked five of these frogs to their primary burrows; the remaining five went missing after their transmitters failed or were removed. As in 2009, all frogs from Cattail Pond traveled in a general northeast direction from the wetland (Fig. 13).

I tracked six frogs (5 males: Frogs 6, 16, 30, 35, and 57; 1 female: Frog 8) from their point of capture at Big Pond (Fig. 14). They made from 1–12 movements ($\bar{x}$ = 6; SD= 3.9); and traveled 76.0–1,000.1 m ($\bar{x}$ = 466.3 m; SD = 311.8). I tracked three of these frogs to their primary burrows, whereas the other three frogs died or were not found. Frogs from Big Pong tended to move either north or south from the pond following breeding (Fig. 14).

**Ranging from Upland Burrows.** In 2010, eight frogs (Frogs 3, 6, 7, 8, 11, 26, 51 and 58) out of 16 exhibited ranging behaviors in the spring/summer; one frog was caught too late in the season; and seven frogs remained at their primary burrows without ranging for periods of 167–241 d (as of 30 November, continuing). Not all of these ranging movements occurred when the frog had an active transmitter. However, those that did (6 frogs), on average moved 14 times

(SD = 6.2, range = 4–22) covering 302.8 m (SD = 100.9, range = 168.6–415.7) over the course of 47 d (SD = 33.3, range = 15–112). For example, as in 2009, Frog 26 left his primary burrow three times, for periods of 10, 10, and 6 days (in March, March, and July, respectively). Unlike in 2009, no frogs moved in the fall from primary burrows to overwintering burrows.

### ***Burrow Philopatry***

Of eight frogs tracked from primary burrows in 2009 through overwintering, pre-breeding migrations, breeding, then back to burrows in 2010, six (Frogs 3, 6, 7, 8, 11, and 16) returned to their 2009 primary burrows. For example, Frog 3 moved directly out of his breeding wetland to his 2009 primary burrow, 91.4 m distant, in one night's movement. Frog 44 was implanted on 6 April, released on 7 April, and by 8 April had migrated 469.8 m to his primary burrow, which he inhabited until he began his 2010 pre-breeding migration. The remaining two frogs migrated to the vicinity of their 2009 primary burrows: Frog 30 was preyed upon by an Eastern Gartersnake (*Thamnophis s. sirtalis*) within 7.1 m of his 2009 burrow; Frog 26 occupied the burrow of a neighboring frog (Frog 33; see Burrow Sharing and Ranging from Upland Burrows sections, below) within 5.8 m of his 2009 burrow.

### ***Burrow Sharing***

Over the course of this study, encompassing a total of 7,898 telemetered-frog days, there were only four nonconsecutive days (or 8 telemetered-frog days) where I documented a single pair of frogs sharing the same burrow at the same time. During the fall of 2009, a female Crawfish Frog without a transmitter (Frog 33) was discovered in a burrow 5.8 m from the burrow of a radio-implanted male (Frog 26). These two frogs overwintered in their respective burrows; then in the spring of 2010, Frog 33 was fitted with a belt harness and I tracked both frogs to Cattail Pond. Following breeding, Frog 33 was implanted and Frog 26 was re-implanted. Frog 26 left the wetland first and inhabited Frog 33's overwintering burrow on 23 April 2010. Seven days later, Frog 33 migrated to within 25 cm of the burrow, but did not enter; Frog 26 could be seen at the burrow entrance. Frog 26 left this burrow on 17 May (after inhabiting it for 24 d); Frog 33 moved into it on 25 May (eight days later). On 28 May, Frog 26 returned and both frogs inhabited this burrow. The following day (29 May) Frog 26 left, Frog 33 remained. Frog 33's transmitter failed on 5 June. Frog 26 returned to this burrow four days later (9 June), at which point I was able to verify (visually) the presence of both frogs. These frogs shared this burrow for three days, until 11 June, when Frog 26 left. I saw Frog 33 at the burrow just once more (13 June); when Frog 26 returned again to this burrow (19 June) I was unable to confirm Frog 33's presence due to transmitter failure. It seems likely Frog 33 left sometime after 13 June. Utilizing wildlife cameras (Hoffman et al. 2010), I determined that Frog 26 had been occupying this burrow alone since at least 25 June 2010.

### ***Movement Triggers***

The number of frogs that made post-breeding movements in 2009 negatively correlated with Julian date (Rho = -0.73) and negatively correlated with maximum relative humidity and maximum temperature (Rho = -0.25 and -0.18). Post-breeding movements in 2009 were also positively correlated with total rain and total rain the day before (Rho = 0.25, and 0.29; Table 2, Fig. 15 A&C). Pre-breeding movements in 2010 were positively correlated with all of the weather variables, though not all tests were statistically significant (Table 2). Post-breeding movements in 2010 were negatively correlated only with Julian date (Rho = -0.30; Table 2, Fig. 15 B & D).

I compared 26 maximum likelihood generalized linear mixed-effects models (GLMMs) to explain the most variation in the distance traveled of post-breeding distances of 2009 and

2010. The lowest scoring GLMM included the variables “individual frog”, “mass”, “migration year”, and “number of moves” (model 1, Table 3). This indicates that these four variables are important in describing the distance that frogs traveled.

### ***Mortality and Survivorship***

Over the course of this study, 14 Crawfish Frogs with implanted transmitters died from “natural” causes (i.e., not directly related to implantation surgery): 11 frogs died from predation (Engbrecht & Heemeyer 2010; Heemeyer et al. 2010*b*), two died from chytridiomycosis (Kinney et al. 2011), and one died from winterkill (Table 4; Heemeyer & Lannoo *submitted*). Seven frogs died during post-breeding migrations (two in 2009; five in 2010), five frogs died after establishing primary burrows (three in 2009; two in 2010), one frog died during the 2010 pre-breeding migration, and one frog died in a breeding wetland (Table 4). Predators included snakes (Eastern Hog-nosed Snake [*Heterodon platyrhinos*], Eastern Gartersnakes [*T. s. sirtalis*], Black Racer [*Coluber constrictor*]), raccoons (*Procyon lotor*), and unknown predators). Based on the Kaplan-Meier estimate, adult Crawfish Frogs had a 42% chance of surviving the 21 months (continuing) of this study (Table 4).

From these data, it may be assumed that post-breeding migrations and burrow dwelling are high-risk behaviors, but not all of these seasonal stages are of equal duration—migrations and breeding occur on a scale of days to weeks, while burrow dwelling occurs on a scale of months to nearly a year. Considering this, I calculated a Daily Mortality Rate, which adjusted the mortality data for the mean time animals spent in each stage. Examining these data, burrow dwelling was clearly the safest period for Crawfish Frogs. In 2009, the calculated mortality rate of burrow dwellers was seven deaths every 10,000 days (27.4 years) or a rate of about one death every four years. In 2010, the rate was of the same magnitude, 12 deaths every 10,000 days, or about one death every 2.3 years. Further, of the five burrow-associated deaths, only two animals were actually killed while occupying burrows; the other three were killed while ranging.

Movements and breeding were riskier behaviors. The Daily Mortality Rate of the 2010 pre-breeding migration was 170 deaths every 10,000 days, a rate of one death every 59 days (roughly every two months)—17.5 times riskier than burrow dwelling (Table 5). Similarly, the mortality rate of post-breeding frogs was 32 deaths per 10,000 in 2009, and 166 deaths per 10,000 in 2010, a combined rate of about one frog death every 101 days—10 times riskier than burrow dwelling (Table 5). Occupying breeding wetlands was associated with a mortality rate of 80 deaths per 10,000 days, or one every 125 days, a rate 8.4 times higher than burrow dwelling (Table 5). On average, breeding migrations and breeding resulted in a daily mortality rate 11.7 times higher than burrow dwelling. Of the 12 deaths due to predation (two other animals died from disease), 10 were associated with activities outside of burrows (migration, ranging movements, and breeding; Table 4). Of the two deaths that occurred while frogs were in burrows, one was from predation (Engbrecht & Heemeyer 2010), and one was from winterkill (Heemeyer & Lannoo *submitted*).

## DISCUSSION

Results from 48 radio tracked Crawfish Frog adults at HFWA-W during 2009 and 2010, encompassing a total of 7,898 telemetered-frog days, demonstrated two behaviors previously undocumented in this species: 1) migration distances that averaged nearly ½ km, and for one frog was > 1 km; and 2) fidelity to upland burrows. Together, these findings indicate that Crawfish Frogs have a remarkable ability to home to distant upland burrow sites. This conclusion supports the observation of Richter et al. (2001) on related Dusky Gopher Frogs (*L capito*); the authors tracked an individual 236 m during two consecutive migration periods to the same mammal burrow that it inhabited. Blihovde (2006) also documented site fidelity and ranging behavior in Gopher Frogs in which frogs moved up to 10 m away from their burrows or were displaced 10 m and returned to their burrow. This conclusion does not support the idea of Neufeldt and Birkhead (2001) who suggested Gopher Frogs migrate out from breeding wetlands until they encounter a suitable retreat site, and then settle in, an explanation used to account for the long migration distances (nearly 600 m) that they observed.

Burrow fidelity in Crawfish Frogs involves, in part, frogs following similar migration routes, which I observed during both pre-breeding and post-breeding migrations within years and during post-breeding migrations across years. Burrow fidelity also occurs after ranging movements, and often involves individual frogs following the same ranging circuit across years. Further, I demonstrate that both migration and ranging are risky behaviors for Crawfish Frogs (about 12 times riskier than burrow dwelling), and therefore that movements have survival consequences for this at-risk species.

### ***Migration Triggers***

Pre-breeding migrations in Crawfish Frogs coincided with several factors, including moisture (rain, humidity) and temperature (Table 2, Fig 15 A–D). This finding is similar to those of Busby and Brecheisen (1997), Jensen et al. (2003), and Richter et al. (2001), who found that both temperature and rain triggered breeding migrations in both Gopher Frogs and Dusky Gopher Frogs. I have observed Crawfish Frogs active at their burrow entrance following overwintering, prior to initiating pre-breeding migrations. Specifically, once the ground had thawed, Crawfish Frogs became active at their burrows when temperatures were above freezing, but did not initiate pre-breeding migrations until it began raining. Further, I have observed that while conditions that trigger migrations are favorable during migrations, conditions over the course of long migrations (for example, post-breeding migrations averaged nearly 30 days in 2009 and a little over 13 d in 2010) may deteriorate (becoming cold and/or dry) for periods of time. In particular, rains—which trigger migrations—often accompany cold fronts producing sub-freezing temperatures—which will stop migrations and perhaps stress exposed animals. When in migration stages and not moving, Crawfish Frogs find cover under vegetation, in wet areas, or in holes—including shallow scrapes they excavate using their hind limbs (pers. obs., Engbrecht et al. 2011)—that offer some thermal relief. The same factors (warm rains) that initiate migrations will cause migrations to resume in sheltered mid-migrating frogs. While one element of these migration pauses is undoubtedly to seek protection from unfavorable conditions, a second may be to rest. Despite favorable weather conditions, none of the 48 frogs tracked, exhibited long migration movements on consecutive nights. These movement bursts concur with those reported in Gopher Frogs by Neufeldt and Birkhead (2001).

Several factors, including Julian date, maximum relative humidity, maximum temperature, and total rain, correlated with movement during the post-breeding migration of 2009 (Table 2, Fig 15 A–D). The same factors, although with different rho values, correlated with the pre-breeding migration in 2010. In contrast, only Julian date correlated with post-breeding migrations in 2010 (Table 2). Any discussion of Crawfish Frog movement triggers must account for a substantial amount of variation in environmental conditions across years, and in frog responses to these environmental conditions. For example, warm, rainy days in January did not trigger Crawfish Frog migrations, although individual frogs may be active (I have seen frogs active every month of the year during favorable conditions)—the season is incorrect. Similar conditions towards the end of the breeding season also do not trigger much movement, because many frogs have already returned to burrows. Further, warm rains during peak breeding may trigger post-breeding females to leave wetlands, while males will stay in an attempt to increase breeding opportunities.

### *Migration Distances*

Crawfish Frogs in this study exhibited migration distances that ranged from 28.1–1,187.8 m ($\bar{x}$ = 348.0) between breeding wetlands and upland burrows. While covering the same point-to-point distance from burrows to wetlands, post-breeding migrations tended to be longer than pre-breeding migrations in terms of time, distance traveled, and number of movements, although only the 2009 post-breeding data were significantly different from the 2010 pre-breeding data. Frogs generally took less time to complete pre-breeding migrations ($\bar{x}$ = 5.0 d; range = 1–16 d) than to complete post-breeding migrations (2009: $\bar{x}$ = 29.8 d; range = 1–67 d; 2010: $\bar{x}$ = 13.2 d; range = 1–39; Kruskal-Wallis $p = 0.1386$). Frogs also typically traveled shorter distances during pre-breeding migrations ($\bar{x}$ = 314.6 m; range = 110.7–530.0 m) than post-breeding distances (2009: $\bar{x}$ = 493.1 m; range = 32.6–1,043.6 m; 2010: $\bar{x}$ = 376.9 m; range = 28.1–1,187.8; $p$ = 0.4676). This variation in the distance traveled between individual frogs in the AIC maximum likelihood model was best explained by a model that incorporated “individual frog”, “mass”, “migration year”, and “number of movements”., This indicates that the distances that frogs traveled during migrations are not tied specifically to number of movements, size, or year, but instead are related to a combination of these variables which depends on the individual frog.

The post-breeding migrations of Pattern 1 frogs were more similar in terms of time ($\bar{x}$ = 21 d vs. 4 d) and distance ($\bar{x}$ = 431 m vs. 356 m) to their pre-breeding migrations. In contrast, Pattern 2 frogs that emigrated straight away from breeding wetlands in the general direction of their burrow, then, in the vicinity of their future burrow, changed directions frequently over short distances, took longer time ($\bar{x}$= 31 d vs. 6 d) and moved farther ($\bar{x}$ = 456 m vs. 244 m) than during their pre-breeding migrations. It is possible that these frogs simply could not find their burrow. During pre-breeding migrations, wetlands are large and noisy with several species of frogs calling—wetlands are big targets for migrating frogs. In contrast specific crayfish burrows are small, quiet targets on the landscape, and it may take some frogs a longer time and some searching to find their burrow. Other factors may enter into this apparent searching behavior: one frog (Frog 6) returned from breeding to discover that a crayfish had capped his 2009 primary burrow, and he had to undergo an additional search for a suitable burrow.

### ***Burrow Fidelity and Migration Routes***

Crawfish Frogs demonstrate fidelity to upland crawfish burrows in two ways: by returning to them following long (in terms of both time and distance) breeding migrations, and by usually returning to them following shorter ranging movements. All eight Crawfish Frogs that were tracked from pre-breeding through post-breeding in 2010 returned either to the same primary burrow (six frogs) or to the vicinity of that burrow (two frogs, one of which was preyed upon within 7.1 m of its 2009 primary burrow). Individual frogs often followed a similar route to and from the wetland each year. Overall, three of the eight frogs that were tracked during both post-breeding migrations followed similar routes to and from the breeding wetlands each year. This indicates not only burrow fidelity and philopatry, but also suggests homing, orienteering, and spatial awareness (Twitty 1966; Stebbins & Cohen 1995; Wells 2007). The concepts of homing ability and terrestrial philopatry are not new for amphibians; they have been documented in several species including *Bufo bufo* (Sinsch 1988), *L. clamitans* (Martof 1953), *L. sylvaticus* (Bellis 1965), *Rana temporaria* (Haapanen 1970), and *Atelopus oxyrhynchus* (Dole & Durant 1974). However, to our knowledge, such fine-scale homing to a particular burrow has only been observed in two species (*Scaphiopus holbrooki* [Pearson 1955 & 1957] and *Heleioporus australiacus* [Lemekert & Brassil 2003]).

The post-breeding migrations of Pattern 1 frogs who went straight to their burrows from the breeding wetland are similar to those seen by Muths (2003) and Semlitsch (1981) in Boreal Toads (*Bufo boreas*) and Mole salamanders (*Ambystoma talpoideum*), respectively. The fact that individual post-breeding migration Crawfish Frogs exhibiting Pattern 2 behavior—i.e., indirect routes to burrows—repeated their routes in consecutive years, suggests that Crawfish Frogs may be using terrestrial, local landmarks or magnetic cues rather than celestial cues when migrating. In fact, it would be difficult for frogs to use celestial cues during migrations when rains trigger movements and the clouds that produce rains block the visibility of the nighttime sky.

Once Crawfish Frogs settle into a primary burrow, they will either stay there, or they will exhibit one of several types of ranging movements, including those where: 1) a Crawfish Frog leaves its primary burrow, ventures out for days or weeks then returns to its original burrow; 2) a frog leaves its primary burrow and moves into a new burrow; and/or 3) a frog moves to change burrows in the fall, prior to overwintering. Ranging movements cannot be considered migrations because not all frogs (18/32 that I can verify) exhibited them and the frogs that did usually return to their primary burrow. Instead, they are more similar to the forays described by Conradt et al. (2003). I saw fall ranging movements only in 2009, during which the frogs moved from their primary burrows to overwintering burrows. The fall of 2009 was unusually wet and most Crawfish Frog burrows were flooded to their entrance following rains; one Crawfish Frog (182) either drowned or asphyxiated after its burrow flooded then froze (Heemeyer & Lannoo *submitted*). The summer and fall of 2010, in contrast, were unusually dry, and though frogs ranged in the summer (the last movement of 2010 was on 29 July), they remained associated with their primary burrows; they did not move in the fall to overwintering burrows. Fall ranging movements to overwintering burrows cannot be considered migrations; they were exhibited by only a subset of animals that ranged (3/16) in only one year (2009), a wet year. It may be that frogs moved to avoid overwintering in flooded burrows, which can be fatal (Heemeyer & Lannoo *submitted*).

Typically, telemetry studies are used to define or delimit home ranges; but what is clear from both these data and from imaging (wildlife cameras and video [Hoffman et al. 2010]) is that during the summer, while in upland burrows, the home ranges of a Crawfish Frog consist of a crayfish burrow, its feeding platform, and a small area no more than 20 cm radius beyond the feeding platform. Crawfish Frogs exhibit vertical movements in their burrows more frequently then horizontal movements beyond their feeding platforms. Exceptions to these generalizations occur during ranging movements and migrations, which are not typically thought of as being home range attributes. Applying traditional home range estimation methods (minimum convex polygon, activity kernel, etc.) to ranging and migratory movements would grossly overestimate the amount of area that each frog used (see Wells 2007).

### *Why Home?*

Homing behavior may be the result of the need to ensure resource availability, or it may serve as a mechanism to sort and distribute animals, and in the process decrease intraspecific competition for resources (Russell et al. 2005). Both explanations likely apply at least in part to Crawfish Frogs. By returning to their previous burrow, Crawfish Frogs presumably have access to a resource base similar to the preceding year. It is also true that post-breeding migrations serve to disperse adult Crawfish Frogs in the upland prairie; no two frogs exhibited the same migration route, even though they may have bred in the same wetland and occupied upland burrows in the same vicinity. What is uncertain is how much area an individual Crawfish Frog requires in order to secure adequate resources. Crawfish Frogs that were occupying burrows did not leave their feeding platform unless to lunge at prey. When this occurs, frogs immediately return to their feeding platform or retreat into their burrow (Hoffman et al. 2010).

The bigger question may be why do frogs occupy particular burrows? It is likely that frogs that occupy the same burrows during consecutive years will occupy these burrows for longer periods, perhaps their whole lifetime. If this is the case, and if migrations—in particular post-breeding migrations—increase exposure and reduce survivorship, why occupy (and subsequently home to) burrows that are, on average ½ km distant? One answer might lie in the location of suitable crayfish burrows, another, suggested above, is resource (especially food) availability. It may be that burrows are established during sub-adult life history stages, when resource acquisition is a higher priority than proximity to breeding site. After Crawfish Frogs become mature, distance to breeding wetlands may on average reduce fitness less than resources at the burrow site increase fitness.

### ***Survival***

Long-distance migrations make Crawfish Frogs vulnerable to predation. Adult Crawfish Frogs spend most of their time in one of two specific locations, either their breeding wetland or their crayfish burrow, with relatively brief migrations between. For example, Frog 11 spent 21 d migrating post-breeding in 2009 then spent 334 d in her burrow before leaving to breed in 2010. Frogs that are breeding and migrating are unprotected by a burrow and exposed to predation. My survival estimates clearly indicate that migrating or ranging frogs are at a greater risk of predation than frogs inhabiting burrows.

Movements and breeding are risky behaviors. The 2010 pre-breeding migration was 17.5 times riskier than burrow dwelling (Table 5). Similarly, the two post-breeding migrations were 10 times riskier than burrow dwelling, and simply occupying breeding wetlands was 8.4 times riskier than burrow dwelling (Table 5). Of the 12 deaths due to predation in this study, 10 were associated with movements outside of burrows (Table 4).

Exposure is tied to predation risk, and by late April at this latitude, snakes—Eastern Hog-nosed Snakes, Eastern Gartersnakes, and Black Racers—have emerged from their hibernation sites, are active, and are searching for prey (Minton 2001). Frogs that exhibit post-breeding migration Pattern 1 are likely less vulnerable than Pattern 2 frogs. By following a direct route back to a known burrow, a Crawfish Frog should have reduced risk of predation and increased probability of survival (see Stebbins & Cohen 1995; Russell et al. 2005).

The frogs that followed Pattern 2C—the most erratic and unpredictable movement pattern—were frogs that either were recovering from herniation surgery (in 2009; Heemeyer et al. 2010*a*) or tested positive for Bd (in both 2009 and 2010; Kinney et al. 2011). Bd has been a problem at HFWA-W. During 2009 and 2010, 53% of post-breeding Crawfish frogs tested positive for Bd infection; 12% developed chytridiomycosis and died (Kinney et al. 2011). The four Bd positive frogs that exhibited erratic movement patterns (Figs. 3&11), showed movement patterns similar to those of injured frogs (hernias). These infected frogs had very high zoospore equivalents (> 1,000, Kinney et al. 2011). Of the infected frogs, 50% (2/4) died from chytridiomycosis and 50% were eaten by predators (one by a snake and the other mauled by an unknown predator), suggesting that infections may not be directly lethal but cause behaviors that divert Crawfish Frogs from their migration routes and make them susceptible to predation.

Not only do breeding migrations expose Crawfish Frogs to predators (snakes, raccoons, perhaps minks, birds of prey), but with average migration distances approaching 1/2 km across modern landscapes, can force them to cross roads. One frog (Frog 11) was separated from her breeding wetland (Nate's Pond) by two roads. In 2010, one post-breeding Crawfish Frog (not telemetered) was road killed. Fortunately, for Crawfish Frogs and other amphibians, traffic along the roads passing through HFWA tends to be light.

### ***Dispersal***

If my observations of Crawfish Frog upland burrow philopatry generally hold—that is, if breeding Crawfish Frogs typically return to the site of their previous burrow—breeding adults are likely not dispersing and colonizing new sites. The question of dispersal is interesting in the context of the history of our study site; because HFWA-W was surface mined for coal from 1976–1982, when no Crawfish Frogs could have inhabited this site. The populations represented here were established after the site was re-contoured and seeded to herbaceous vegetation, sometime after 1982 (Lannoo et al. 2009).

With no evidence that adults disperse, it seems more likely that juveniles represent the dispersing stage. Working with closely related Gopher Frogs, Roznik et al. (2009) found that post-metamorphic juveniles emigrating from breeding wetlands ranged twice as far as adults, and their observations may hold for Crawfish Frogs. To test this, I attempted to radio track dispersing juveniles using Holohil Systems Ltd. (Carp, Ontario) BD-2 transmitters, with external antennae, attached to animals using elastic belts (described above). However, unlike Gopher Frog juveniles (Roznik et al. 2009; Roznik & Johnson 2009*a&b*), Crawfish Frog juveniles have a narrow pelvis and hind limb articulation (Engbrecht et al. 2011), which makes it easy for them to shed belted transmitters. All juveniles shed their transmitters, usually within 24 hours and a few feet from where they were released. One juvenile retained its transmitter for 9 days and was recorded traveling a distance of 255.2 m.

### ***Conservation***

These data suggest that to ensure the least impact to Crawfish Frog populations several measures should be taken. First, impose buffers that exclude roads for at least a 1.1-km radius around breeding wetlands. If roads cannot be removed or closed, I suggest restricting or slowing traffic during nights in March, April, and May. Secondly, no new cultivation should occur within this buffer zone; Thompson (1915) reported that frogs were unearthed with a plow depth of 15 cm. It is unlikely that crayfish burrows occur in previously cultivated areas such as food plots, and therefore Crawfish Frogs avoid using these sites (although they will migrate through them). In buffer zones, cultivation could continue, but should be restricted to previously cultivated sites. Thirdly, while prescribed burns are essential to maintaining grasslands (and without grassland habitat Crawfish Frog populations will not persist) migrating Crawfish Frogs may be vulnerable and burns should be avoided if possible from (at the latitude of our study site) mid-March to mid-May. Prescribed burns in the fall of 2008 (prior to the start of my study), September 19, 2009, and March 9th, 2010 caused no direct harm to Crawfish Frogs, although they may have affected individuals indirectly by reducing prey availability and increasing exposure to predators.

Table 1. The number of frogs tracked during the 2009 and 2010 migratory seasons. Note that frogs were counted more than once if they were tracked through multiple seasons.

| Year and Migratory Season | No. of Frogs Tracked | (M/F) | No. of Frogs Tracked to Primary Burrow | (M/F) |
|---|---|---|---|---|
| 2009 Post-breeding Migration | 26 | (15/11) | 20 | (11/9) |
| 2010 Pre-breeding Migration | 12 | (7/5) | Not Applicable | --- |
| 2010 Post-breeding Migration | 30 | (18/12) | 16 | (8/8) |

Table 2. Spearman rank correlation values of weather variables that show how they relate to average daily distance and number of frogs that moved per year during the post-breeding migrations of 2009 and 2010. Rho values that have a significant p-value are shaded in gray. Holm's method adjusted p-values *$p < 0.05$, ** $p < 0.01$.

| | 2009<br>Post-breeding | | 2010<br>Pre-breeding | | 2010<br>Post-breeding | |
|---|---|---|---|---|---|---|
| Daily Weather Metric | Rho | P-Value | Rho | P-Value | Rho | P-Value |
| Julian Date | -0.73 | 0.000** | 0.45 | 0.000** | -0.30 | 0.010** |
| Minimum Relative Humidity | -0.34 | 0.000** | 0.31 | 0.019* | -0.07 | 1.000 |
| Maximum Relative Humidity | -0.25 | 0.011** | 0.30 | 0.023* | -0.18 | 0.481 |
| Minimum Temperature | -0.06 | 1.000 | 0.12 | 1.000 | 0.01 | 1.000 |
| Maximum Temperature | -0.18 | 0.099 | 0.42 | 0.000** | -0.04 | 1.000 |
| Total Rain the Day Before | 0.29 | 0.002** | 0.12 | 1.000 | 0.14 | 1.000 |
| Total Rain | 0.25 | 0.009** | 0.24 | 0.136 | 0.08 | 1.000 |

Table 3. Maximum likelihood generalized linear mixed-effects model (GLMM) analysis of distance traveled (y) by Crawfish Frogs as a result of the random variable individual frog (F), and the fixed variables: migration year (Y), sex, length (SVL), mass, migration start date (D), and number of moves made (M). Shown are the 10 lowest $AIC_C$ scoring models.

| # | Model | K | AICc | ΔAICc | w |
|---|---|---|---|---|---|
| 1 | y=F+Y*M+Mass | 6 | 737.75 | 0.00 | 0.074 |
| 2 | y=F+D+Y*M+Mass | 7 | 740.38 | 2.63 | 0.020 |
| 3 | y=F+Y*M+Mass+Sex | 7 | 740.38 | 0.00 | 0.074 |
| 4 | y=F+Y+D*M+Mass | 7 | 740.48 | 0.10 | 0.071 |
| 5 | y=F+Y*M*Mass | 9 | 742.50 | 2.02 | 0.027 |
| 6 | y=F+Y*D*M+Mass | 10 | 746.90 | 4.40 | 0.008 |
| 7 | y=F+M | 3 | 749.77 | 2.87 | 0.018 |
| 8 | y=F+Y+M+Mass | 5 | 751.82 | 2.05 | 0.027 |
| 9 | y=F+Y+M+Mass | 5 | 751.82 | 0.00 | 0.074 |
| 10 | y=F+Y*D*M+Mass+SVL+Sex | 12 | 752.13 | 0.30 | 0.064 |

Table 4. Number of deaths of Crawfish Frogs tracked during this study by seasonal stage and the known causes of death. The Kaplan-Meier estimated probability of survival shows the likelihood of surviving from 21 March 2009 to 30 November 2010.

| Year and Migratory Season | Died (M/F) | Cause | |
|---|---|---|---|
| 2009 Post-breeding Migration | 2 (1/1) | 1 predation [1]<br>1 chytridiomycosis | |
| 2009 Burrow | 3 (1/2) | 2 predation [1, 2A]<br>1 winter kill | |
| 2010 Pre-breeding Migration | 1 (0/1) | 1 predation [1] | |
| 2010 Breeding | 1 (1/0) | 1 predation [3] | |
| 2010 Post-breeding Migration | 5 (3/2) | 4 predation [1, 1, 2B 2C]<br>1 chytridiomycosis | |
| 2010 Burrow | 2 (1/1) | 2 predation [2B 2C] | |
| Total Deaths | 14 (7/7) | Kaplan Meier<br>Probability of Survival | 0.42 |

[1] Unknown predator; [2A] *Heterodon platyrhinos* (Engbrecht & Heemeyer 2010); [2B] *Thamnophis sirtalis*; [2C] *Coluber constrictor*; and [3] Raccoon (Heemeyer et al. 2010*b*)

Table 5. Calculation of the stage-specific survival and the daily mortality rate of frogs in this study per migratory interval.

|  | Tracked | Censored | Deaths | No. at Beginning | No. at End | Probability of Survival | Avg. Duration | No. Deaths per No. Frogs Tracked | Daily Mortality Rate |
|---|---|---|---|---|---|---|---|---|---|
| Year and Migratory Season | T | C | D | N=T-C | n=N-D | S=n/N | Days | D/N | (D/N)/Days |
| 2009 Post-breeding Migration | 26 | 5 | 2 | 21 | 19 | 0.90 | 29.8 | 0.10 | 0.0032 |
| 2009 Burrow | 19 | 5 | 3 | 14 | 11 | 0.79 | 304.0 | 0.21 | 0.0007 |
| 2010 Pre-breeding Migration | 12 | 0 | 1 | 12 | 11 | 0.92 | 5.0 | 0.08 | 0.0167 |
| 2010 Breeding | 11 | 1 | 1 | 10 | 9 | 0.90 | 12.4 | 0.10 | 0.0080 |
| 2010 Post-breeding Migration | 30 | 12 | 5 | 18 | 13 | 0.72 | 16.8 | 0.28 | 0.0166 |
| 2010 Burrow | 13 | 5 | 2 | 8 | 6 | 0.75 | 210.4 | 0.25 | 0.0012 |
| Total | 122 | 38 | 14 | 84 | 70 |  |  | 0.17 |  |

Figure 1. Movements of all frogs from all wetlands tracked post-breeding in 2009. Each color represents a different frog. Colored circles are sites where the frog was associated with a burrow. Minimum dist a frog moved was 32.6 m (Frog 31, brown colored line) maximum distance frog moved was 1043.6 m (Frog 21, yellow colored line). Nine frogs crossed one road, and three frogs crossed two roads.

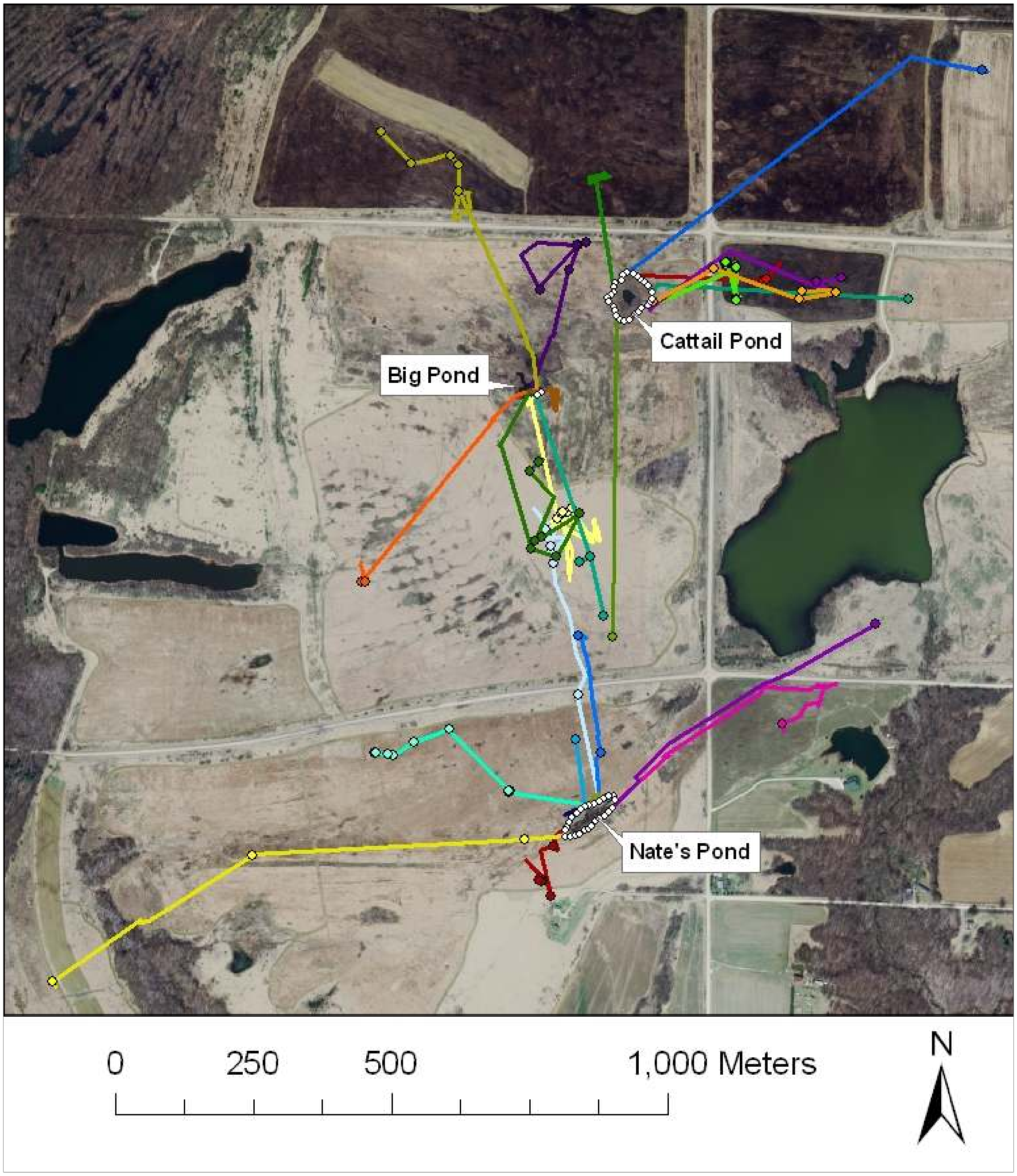


Figure 2. Movements of all frogs tracked post-breeding in 2009 that exhibited movement Pattern 1. Movement Pattern 1 is defined as migrations in which animals migrated straight away from wetlands, did not reverse course, exhibited movements in the general direction of burrow, and turned at angles > 90 degrees. Minimum dist a frog moved was 32.6 m maximum distance frog moved was 1043.6 m.

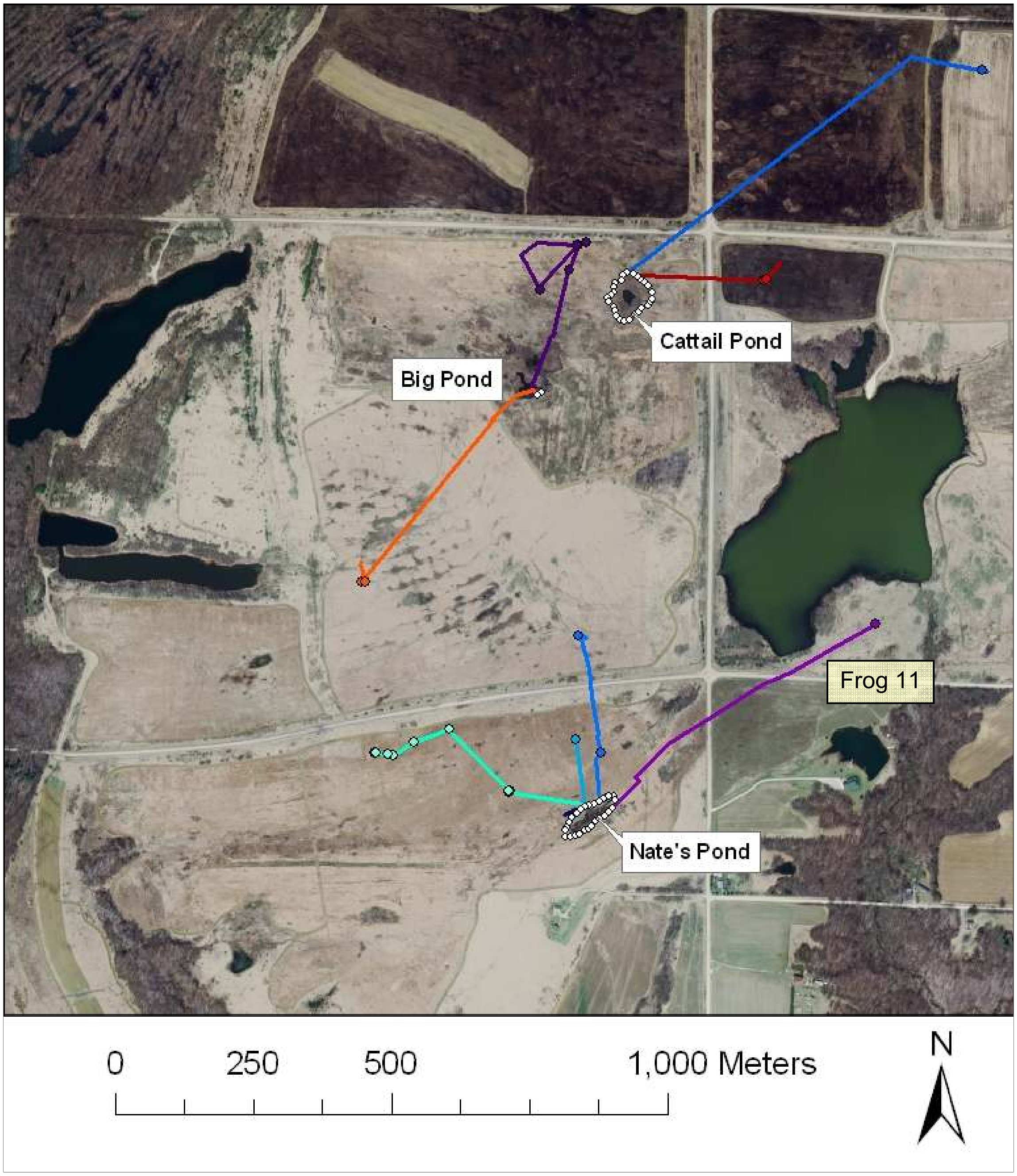


Figure 3. Movements of frogs tracked post-breeding in 2009 that exhibited movement Pattern 2. Movement Pattern 2 is defined as migrations in which animals reversed directions or made turns with angles < 90 degrees prior to burrowing. Minimum dist a frog moved was 174.3 m maximum distance frog moved was 896.1 m.

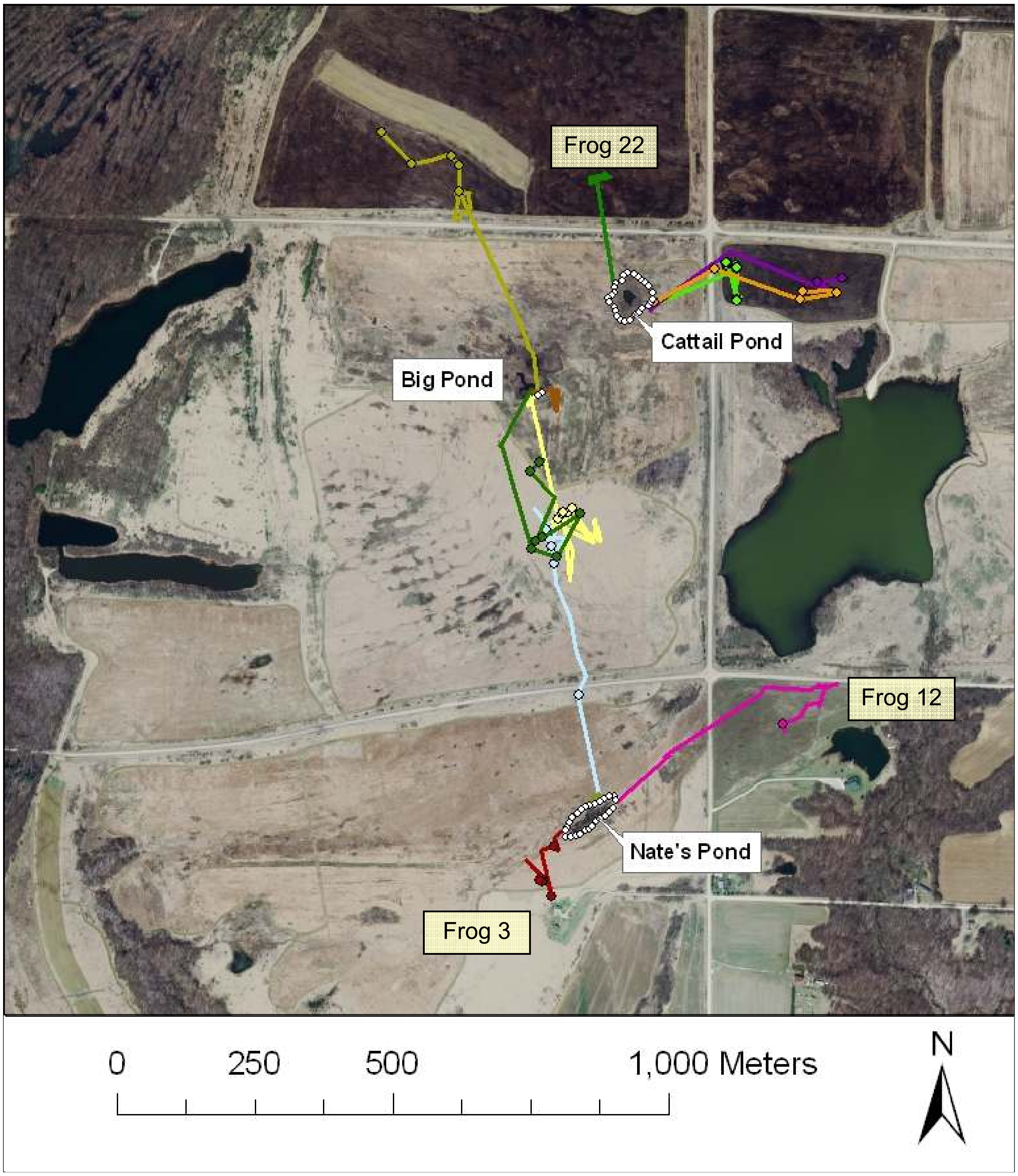


Figure 4. Plot of the average distance (A), duration (B), and number of movements (C) of frogs per season and per movement pattern. Whiskers show the range of the data. Means are represented by the black diamonds. Symbols above represent pairs of means that differ significantly ($p < 0.01$). Pattern 2 movements in 2009 were significantly longer (open circles) and involved more movements (asterisks) than Pattern 1 movements.

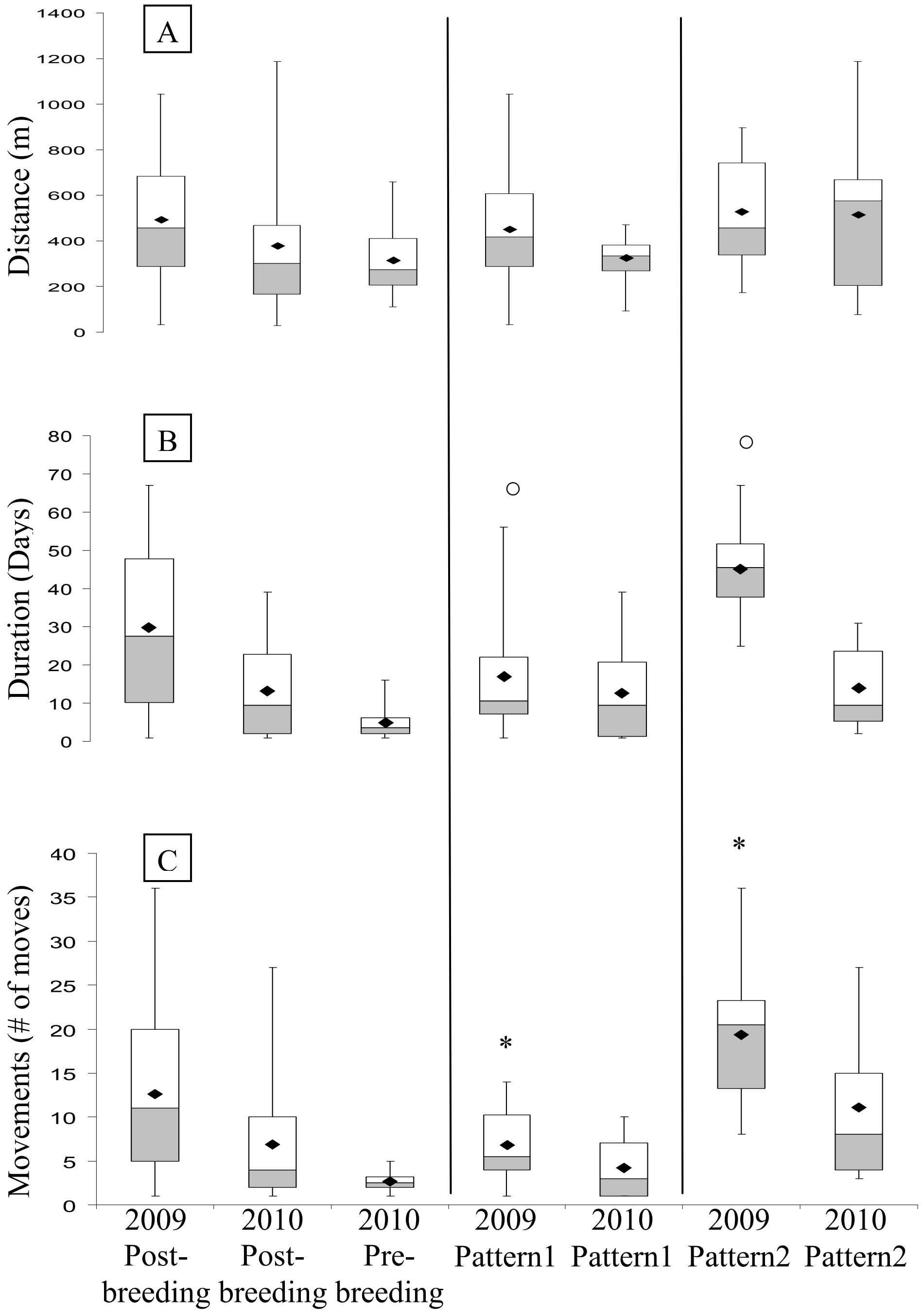


Figure 5. Movements of frogs tracked post-breeding in 2009 from Nate's Pond. Note that frogs moved all directions except southeast. Distances traveled ranged from 32.6–1,043.6 m.

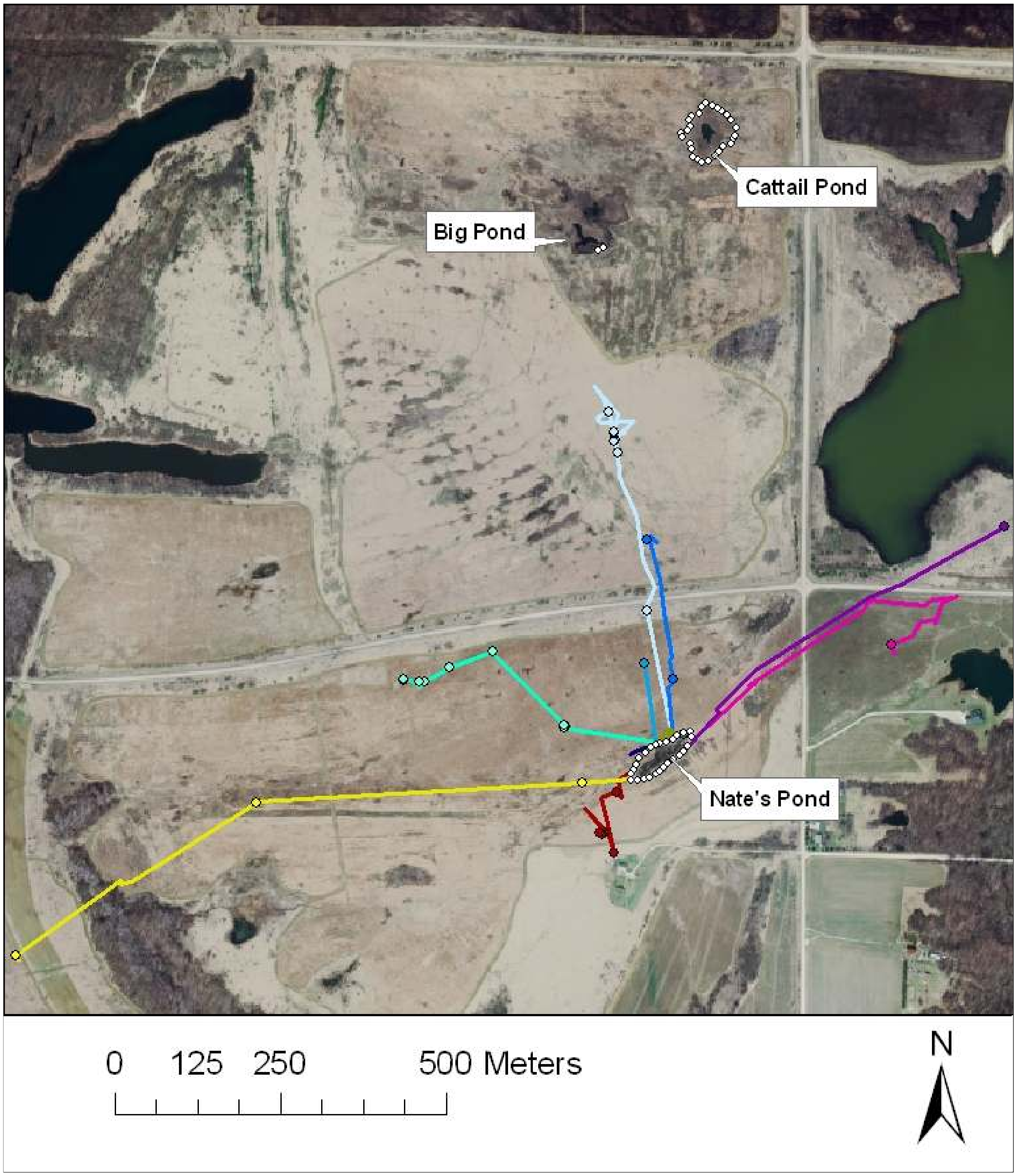


Figure 6. Movements of frogs tracked post-breeding in 2009 from Cattail Pond. Compared with Nate’s pond, directions of tracked frogs were restricted to a cone from north northwest to east. Distances traveled ranged from 278.5–793.3 m.

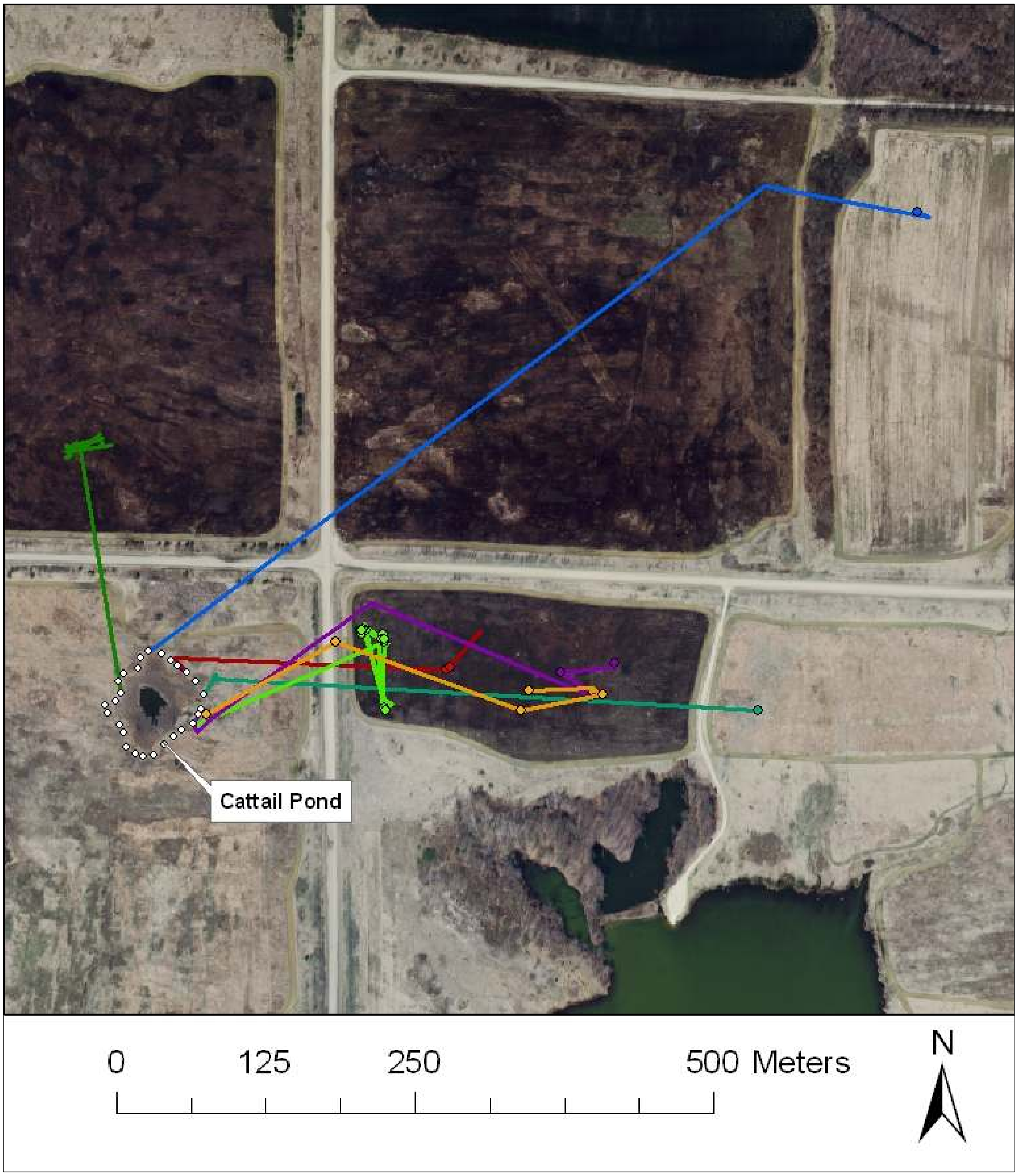


Figure 7. Movements of frogs tracked post-breeding in 2009 from Big Pond. Most frogs either went generally north or generally south. Distances traveled ranged from 174.3–896.1 m.

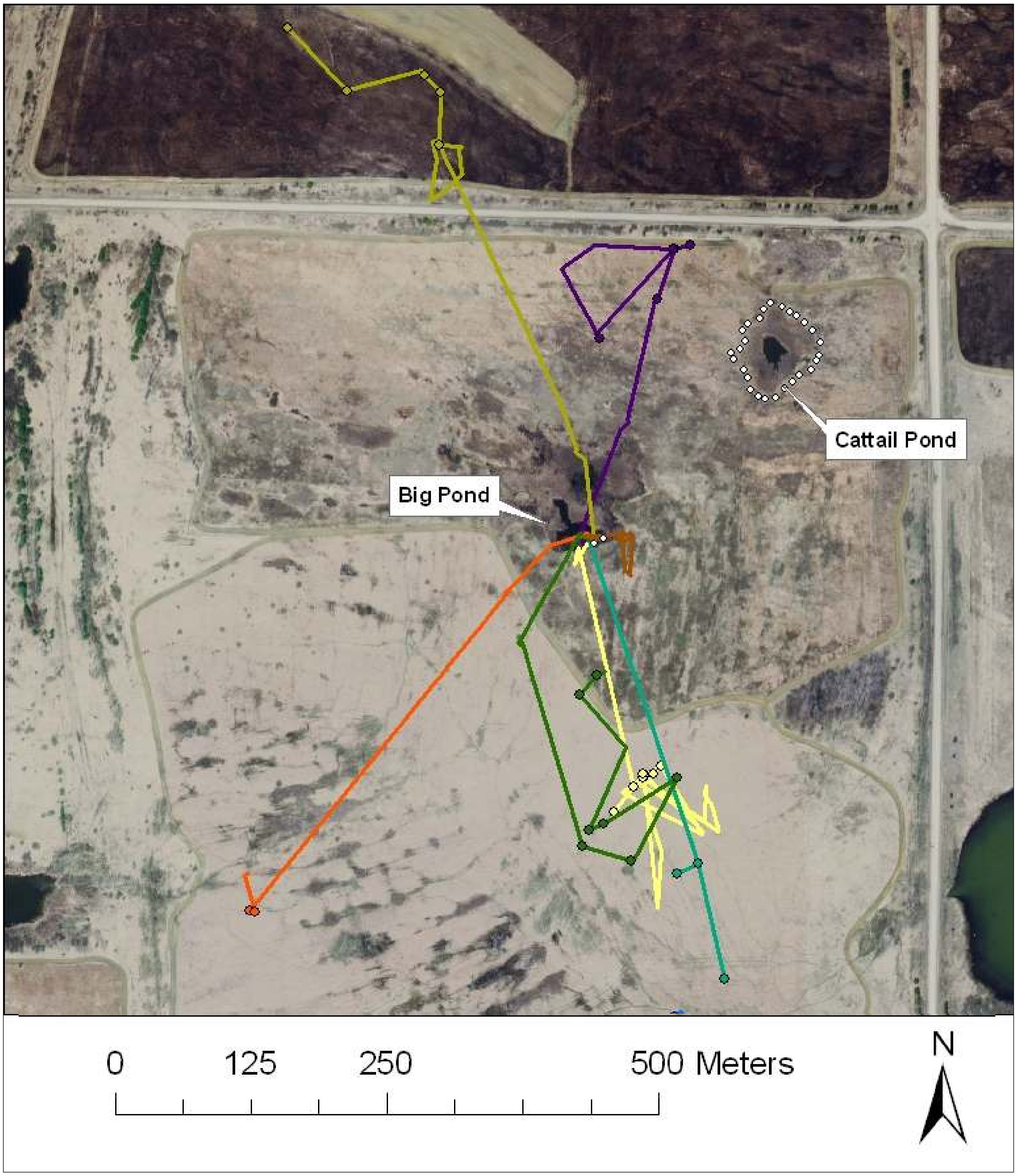


Figure 8. Movements of all frogs from all wetlands tracked pre-breeding in 2010 as they migrated into the wetland to breed. Pre-breeding migrations tended to be more direct and take less time than post-breeding migrations, although these differences were not statistically significant (see Fig 4).

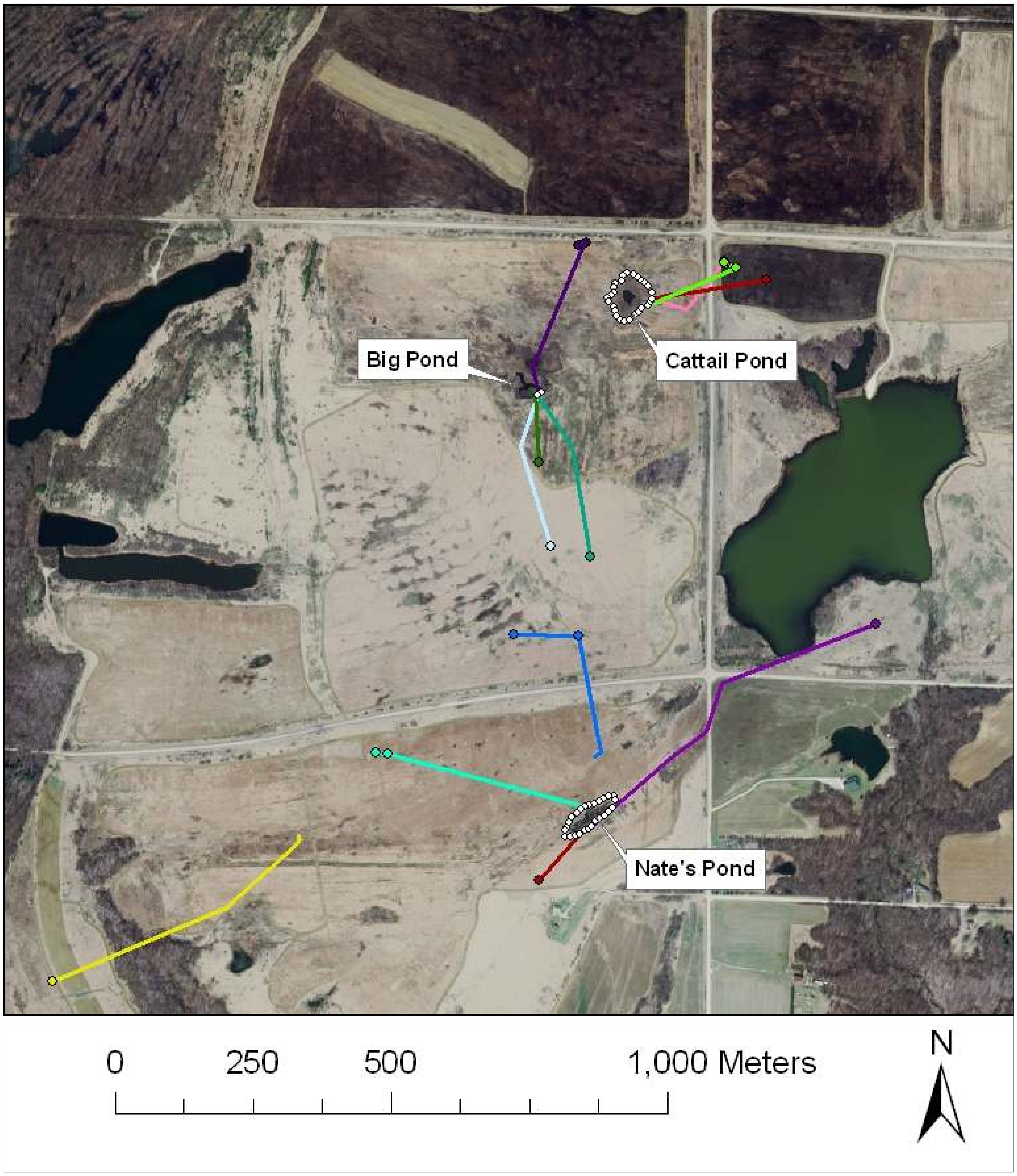


Figure 9. Movements of all frogs tracked post-breeding in 2010. Each color represents a different frog. Colored circles are sites where the frog was associated with a burrow. Minimum dist a frog moved was 28.1 m maximum distance frog moved was 1.187.8 m (Frog 52, burnt orange colored line). Eight frogs were also tracked post-breeding in 2009. Fourteen frogs crossed one road, and two frogs crossed two roads.

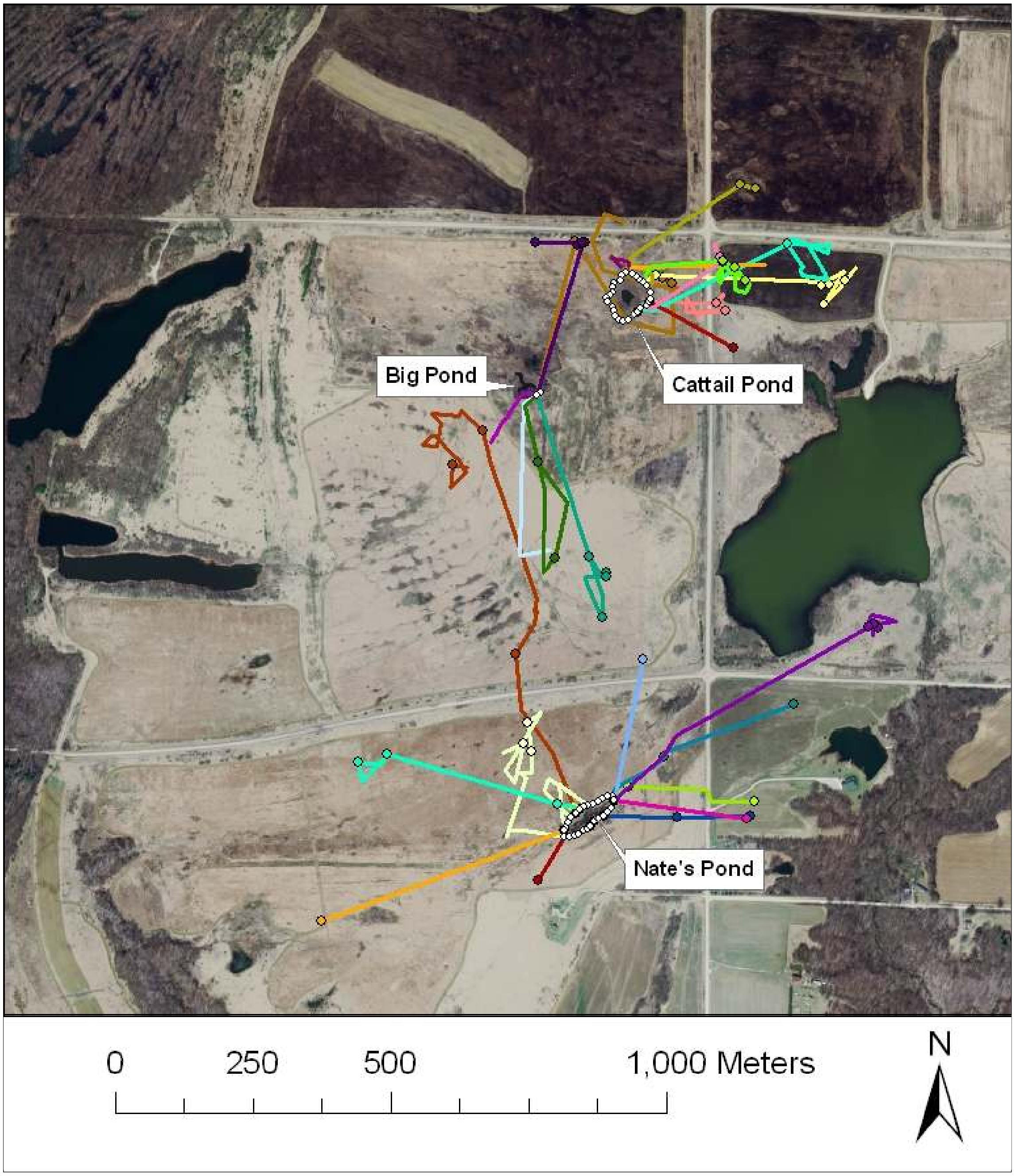


Figure 10. Movements of frogs tracked post-breeding in 2010 that exhibited movement Pattern 1. Movement Pattern 1 is defined as migrations in which animals migrated straight away from wetlands, did not reverse course, exhibited movements in the general direction of burrow, and turned at angles > 90 degrees. Minimum dist a frog moved was 91.4 m maximum distance frog moved was 469.8 m.

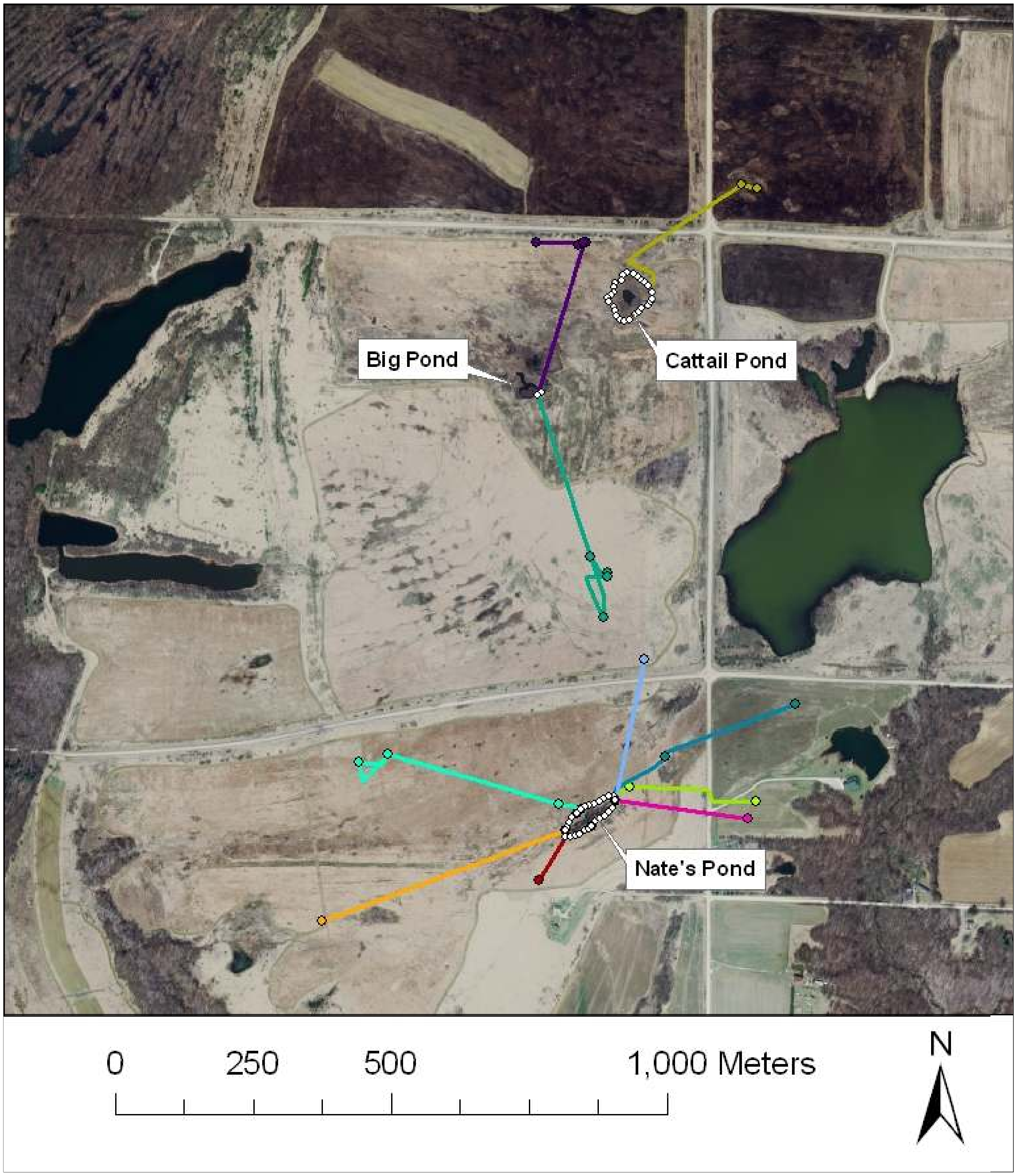


Figure 11. Movements of frogs tracked post-breeding in 2010 that exhibited movement Pattern 2. Movement Pattern 2 is defined as migrations in which animals reversed directions or made turns with angles < 90 degrees prior to burrowing. Minimum dist a frog moved was 76.0 m maximum distance frog moved was 1,187.8 m.

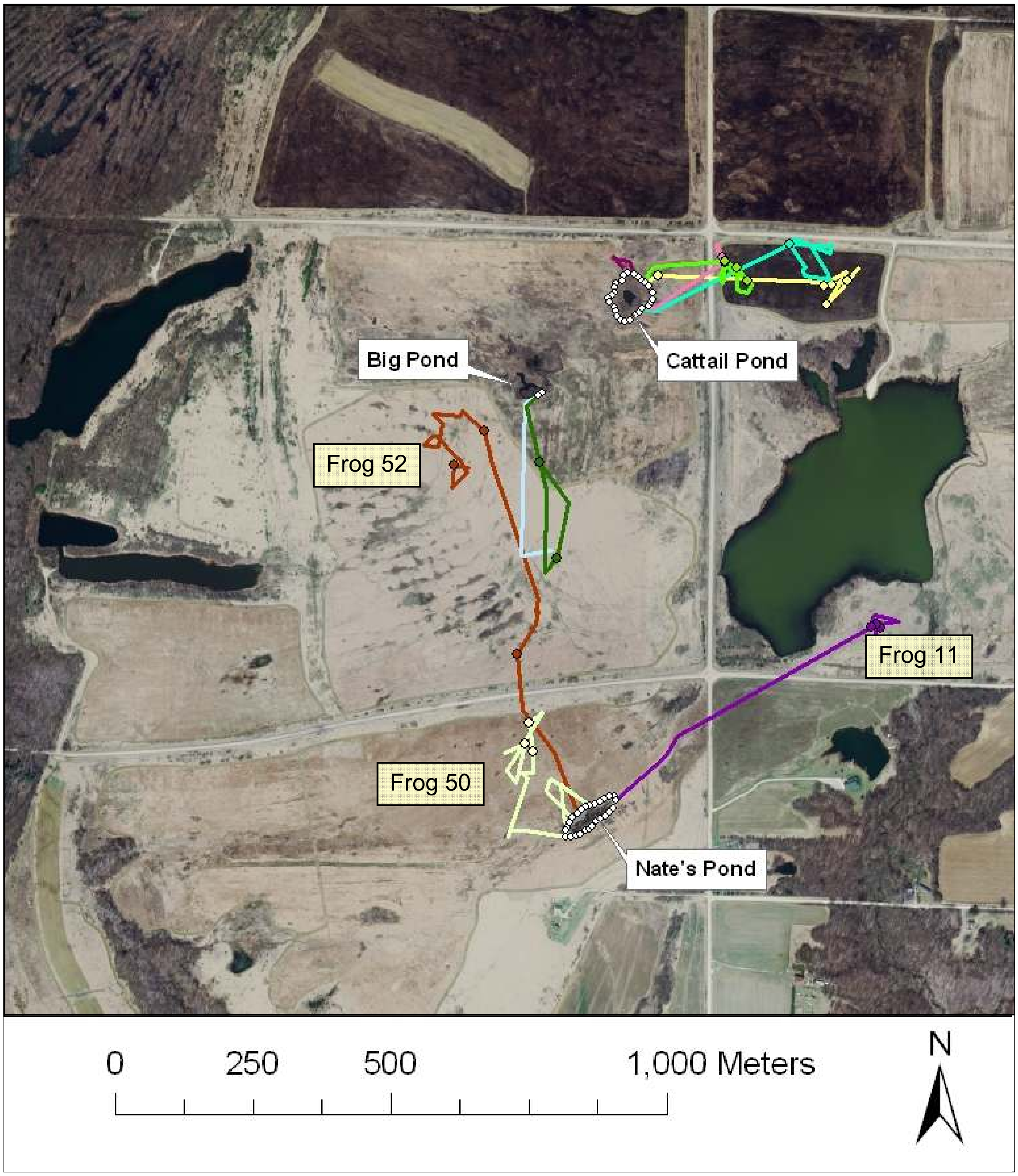


Figure 12. Movements of frogs tracked post-breeding in 2010 from Nate's Pond. As in 2009, frogs moved every direction except southeast. Distances traveled ranged from 28.1–1,187.8 m.

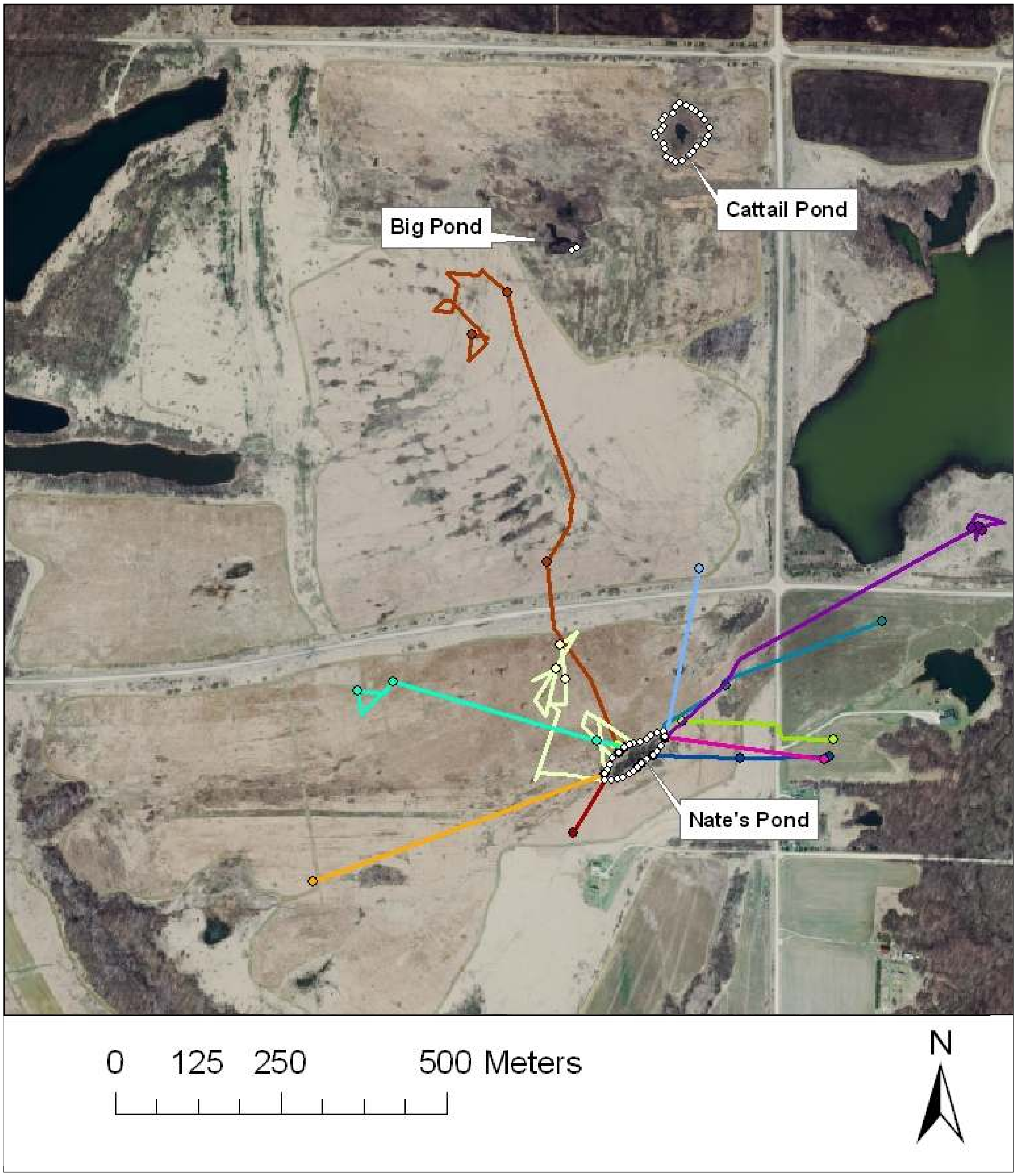


Figure 13. Movements of frogs tracked post-breeding in 2010 from Cattail Pond. As in 2009, frogs generally moved northeast. Distances traveled ranged from 86.8 –709.5 m.

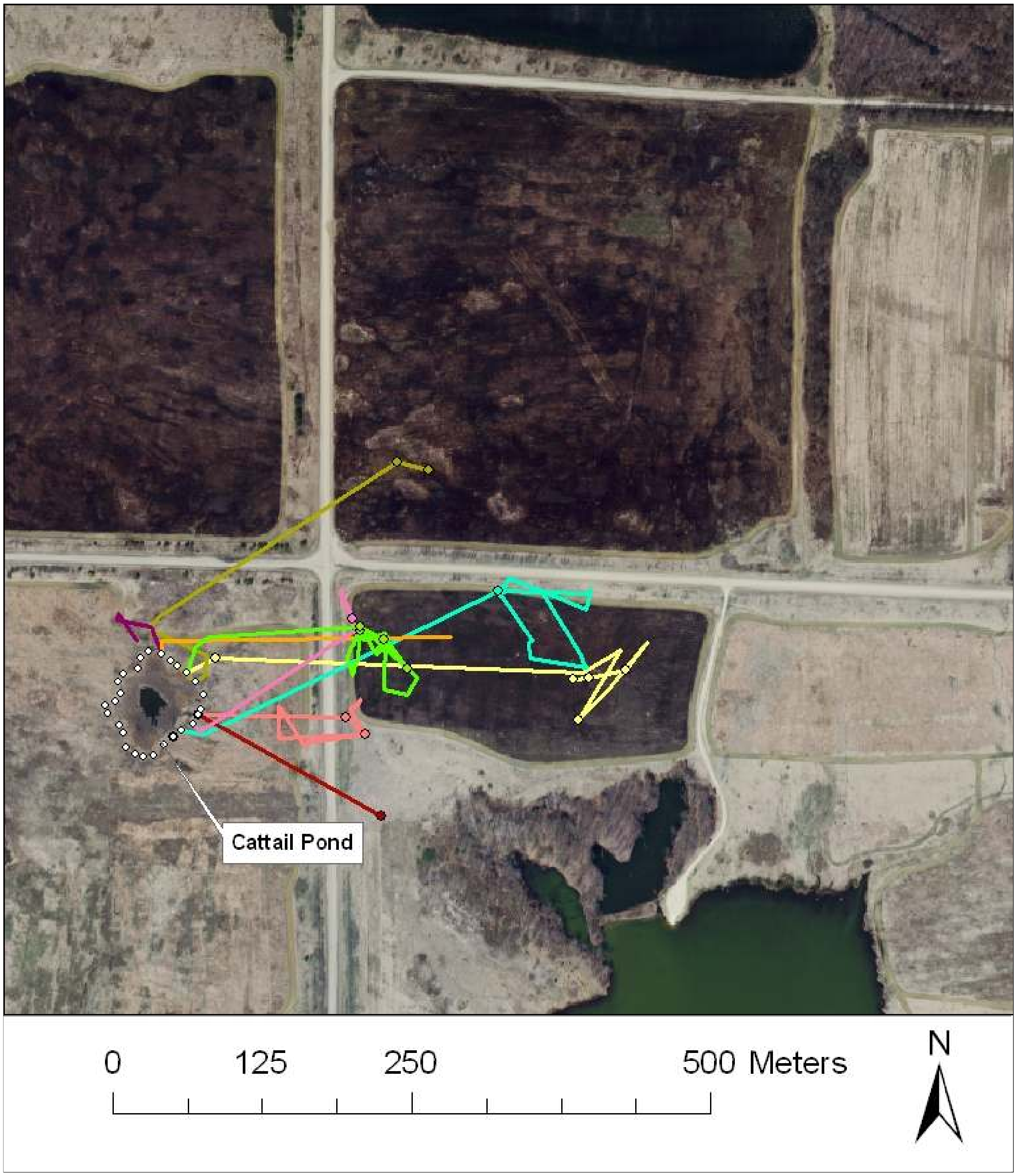


Figure 14. Movements of frogs tracked post-breeding in 2010 from Big Pond. As in 2009, frogs generally moved either north or south. Distances traveled ranged from 76.0–1,000.1 m.

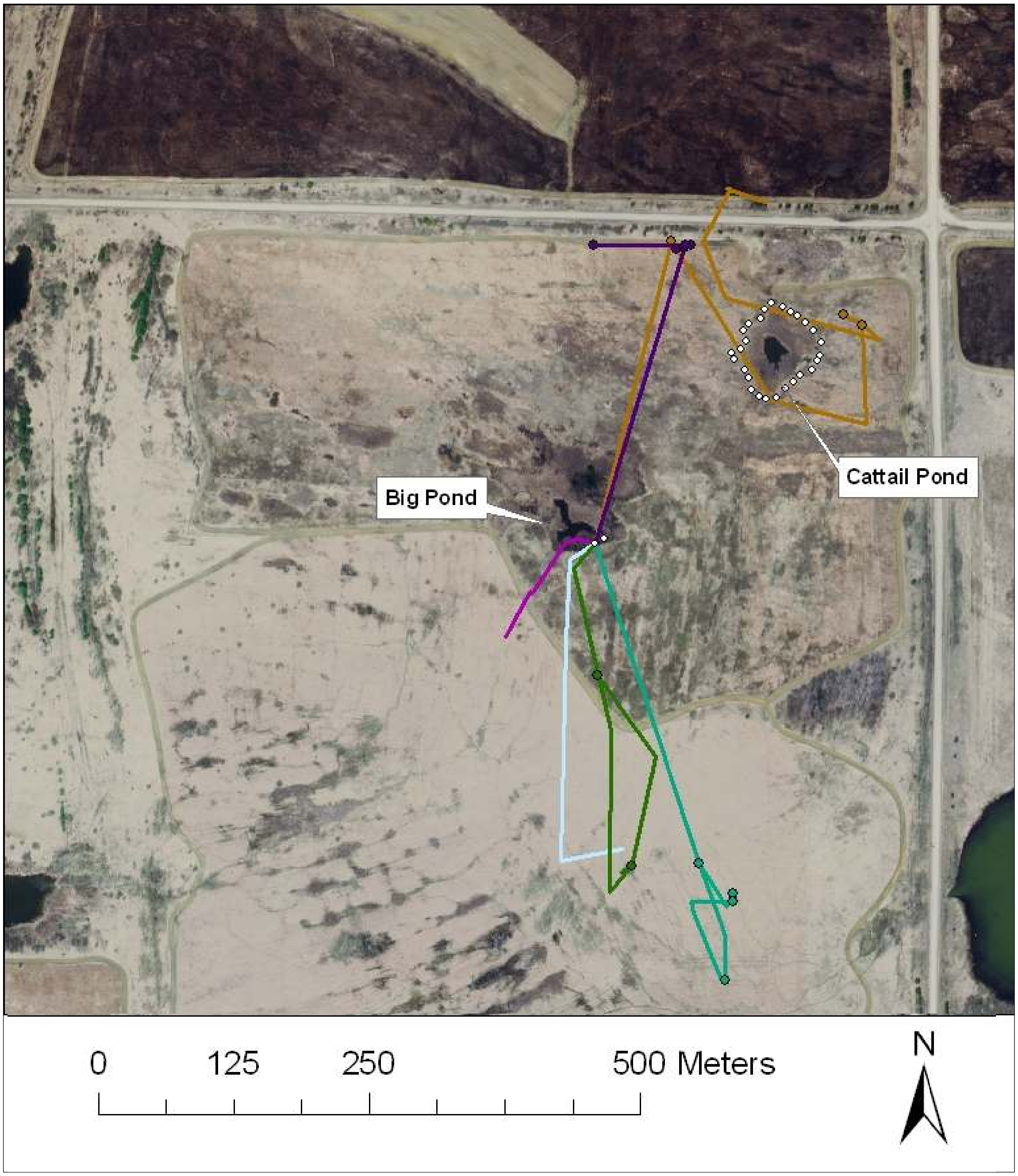


Figure 15.  Daily total of rain verses the average daily distance (2009 A & 2010 B) and verses daily number of frogs that moved (2009 C & 2010 D) throughout the study period.  The stippled region indicates the movements that occurred post-breeding, and the shading indicates the movements that occurred pre-breeding.

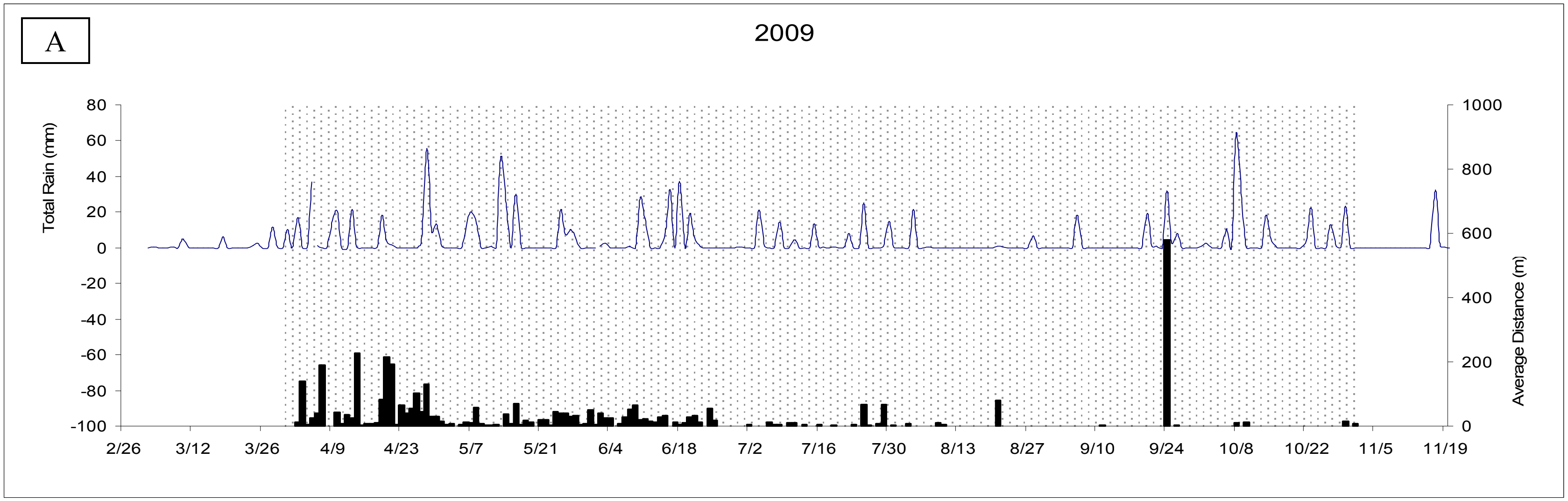
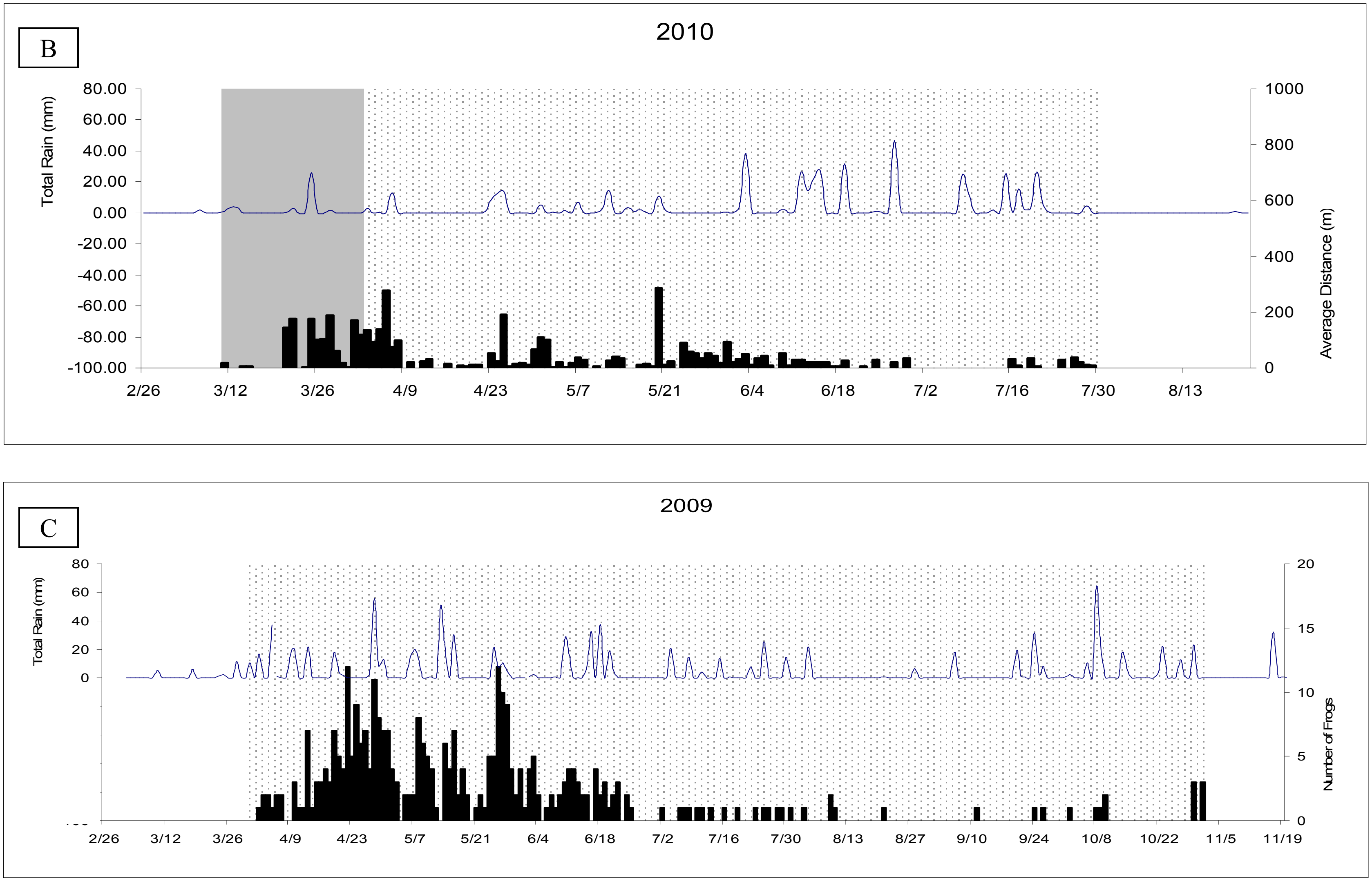


Figure15.  (Continued)



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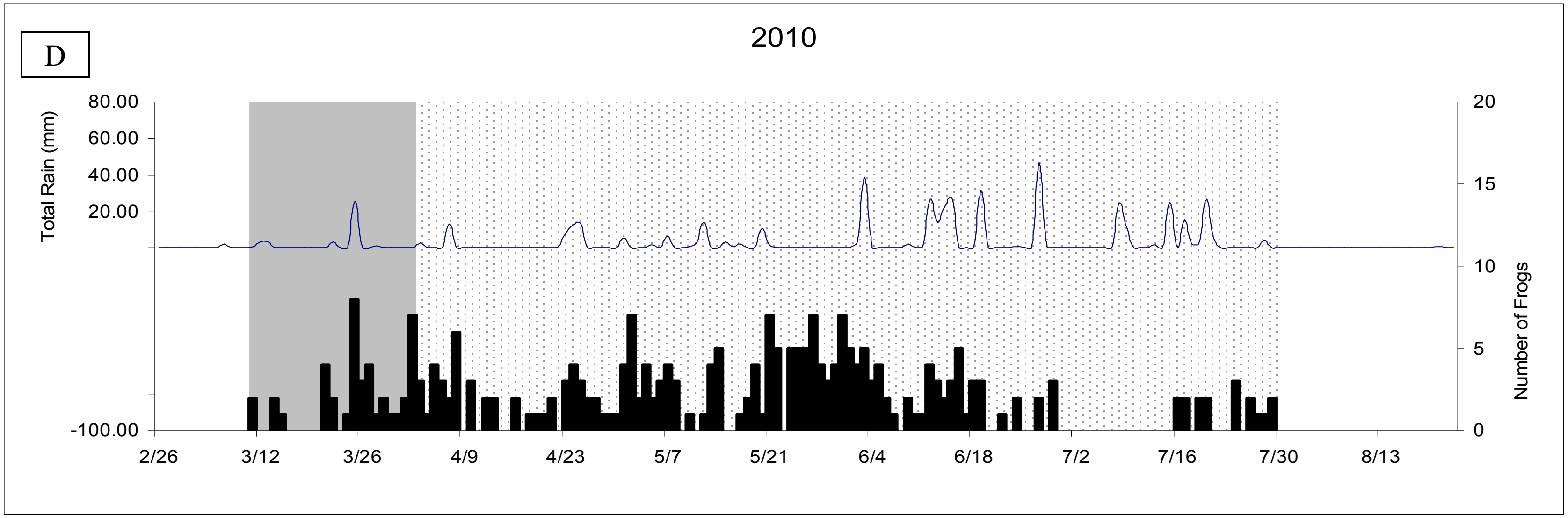


# CHAPTER 2

# OBLIGATE CRAYFISH BURROW USE BY ADULT CRAWFISH FROGS (*LITHOBATES AREOLATUS*): HABITAT CONSTRAINTS IN A SPECIES OF CONSERVATION CONCERN

## INTRODUCTION

Habitat can be generally defined as the area in which an animal lives and where it can meet its needs, including finding food and water, avoiding temperature extremes, and perhaps finding protection from predators (Morrison et al. 2006). Habitat is often but not always defined by either vegetation (e.g., prairies and old growth forest) or by physical factors (e.g., semi-permanent wetlands and tide pools). Habitat needs for any particular species can be broad (e.g., forest understory) or narrow (e.g., deep sea thermal vents), and among species with narrow needs, can be highly specific. Among the most specialized habitats are those where one species relies exclusively on another for its habitat (parasites such as fleas and lice come to mind), or to create its habitat. One of the best examples involves burrow use.

While many species of amphibians, reptiles, mammals, and invertebrates, even some birds, utilize subterranean burrows as habitat, only a few of these species dig their own burrows. Species that construct burrows include mammals such as moles, muskrats, ground squirrels, and other small rodents (Rodentia), amphibians such as spadefoot toads

(Pelobatidae), and reptiles such as some tortoises (Testudinidae). Besides the original resident, many other species use burrows as habitat. Examples include Burrowing Owls inhabiting ground squirrel burrows (Thomsen 1971; Winchell 1994), frogs, snakes, lizards and rodents inhabiting tortoise burrows (Franz 1986; Jones and Franz 1990; Pike & Grosse 2006), and frogs, snakes, salamanders, and invertebrates inhabiting crayfish burrows (Thompson 1915; Neil 1951; Kingsbury & Coppola 2000; Minton 2001; Jensen & Richter 2005; Parris & Redmer 2005; Richter & Jensen 2005; Thoma & Armitage 2008). Some non-burrowing species have such narrow habitat requirements that they have come to obligately depend on the burrows of particular species for their habitat. Moreover, when dependent species become a focus of conservation concern, the relationship between these habitat specialists and their hosts must be fully understood.

The *Nenirana* subgenus of Hillis and Wilcox (2005) is the only clade of North America anurans that is dependent upon burrows created by other species for their upland habitat. The *Nenirana* clade is composed of four species: Crawfish Frogs (*Lithobates areolatus*), Gopher Frogs (*L. capito*), Dusky Gopher Frogs (*L. sevosus*), and Pickerel Frogs (*L. palustris*). Crawfish Frogs are the sister species to the two Gopher Frog species; Pickerel Frogs represent the sister species to the Gopher Frog/Crawfish Frog clade (Young & Crother 2001).

Both Gopher Frog species and Crawfish Frogs rely on other species to excavate the burrows that become their upland habitat. Gopher Frogs typically, but not exclusively, occupy Gopher Tortoise (*Gopherus polyphemus*) burrows (Jensen & Richter 2005). Gopher Frogs and Dusky Gopher Frogs will also occupy stump holes, crayfish burrows, and other types of underground retreats (Carr 1940; Richter et al. 2001; Jensen

& Richter 2005; Richter & Jensen 2005; Blihovde 2006). Crawfish Frogs are frequently associated with crayfish burrows (Thompson 1915), and derive their common name from this tendency. Crawfish Frogs have also been reported to occupy mammal burrows, sewer pipes/manholes, sinkholes, and scrapes (Blatchley 1900; Goin & Netting 1940; Wright and Wright 1949; Smith 1961; Dundee & Rossman 1989; Parris & Redmer 2005; Collins et al. 2010).

All three Gopher and Crawfish Frog species are in decline and are of conservation concern. Dusky Gopher Frogs are listed as a Federally Endangered Species (US FWS 2001). Fewer than 20 populations of Gopher Frogs are known in any state in which they occur, except Florida and they are being considered for federal protection (Jensen & Richter 2005; SEPARC 2010). Crawfish Frogs are a state endangered species in Indiana and Iowa (where they have not been seen since 1942 [Christiansen & Bailey 1991]). Declines in these species have been attributed to breeding wetland loss resulting from stocking of predatory fish, or draining; as well as destruction of upland habitat resulting from development, agricultural and silvicultural fragmentation, and fire suppression (Thompson 1915; Wright & Wright 1949; Busby & Brecheisen 1997; Greenberg 2001; Jensen & Richter 2005; Parris & Redmer 2005; Richter & Jensen 2005). What is also known is that threats to host species (e.g., the western population segment of Gopher Tortoises is listed as federally threatened [US FWS 1987] and the eastern population is under review for federal listing as well [US FWS 2010*a*]) in turn threaten dependent species.

Of the three Crawfish and Gopher Frog species, Crawfish Frogs are the most understudied. Adults are unusually secretive (Smith 1950), spend the majority of their lives at upland burrow sites (Chapter 1), and rarely leave their burrows except to breed. Because of their dependence on upland burrows, it is important to further understand the relationship between Crawfish Frogs and their burrow habitat. I posed the following questions in order to describe Crawfish Frog burrow use: 1) What burrow types are used? 2) Where are Crawfish Frog burrows situated on the landscape? 3) What are the physical characteristics and habitat associations of Crawfish Frog burrows? and 4) What behaviors do Crawfish Frogs exhibit at these burrows? With this latter question, I build off my previous work (Hoffman et al. 2010) by examining upland calling, and burrow sharing with other species. I conclude by considering the conservation implications of these findings, and by making management recommendations for critical habitat designations.

## METHODS

### *Field Site*

My study site is located on the 729 hectares of Hillenbrand Fish and Wildlife Area-West (HFWA-W), located approximately 5 km south of Jasonville, in Green County, Indiana (39.120275°N, 87.222187°W). HFWA-W is the only portion of the larger Hillenbrand Fish and Wildlife complex that supports Crawfish Frogs. From 1976–1982, HFWA-W was surface mined for coal (Lannoo et al. 2009). Afterwards, the site was re-contoured and seeded to non-native vegetation. In 1988, the Indiana Department of Natural Resources (IDNR) purchased the land and began the process of converting the vegetation to native prairie species using seedings and regular controlled burns. The site is maintained for hunting and fishing, and food plots are scattered through the property. To maintain the prairie ecosystem, plots ranging from 2–40 ha are burned in the spring or fall. Two species of large burrowing crayfish occur in this area—the Painted-hand Mudbug (*Cambarus* [*Tubericamberus*] *polychromatus*) and the Digger Crayfish (*Fallicambarus* [*Creaserinus*] *fodiens*; Thoma & Armitage 2008).

### ***Burrow Location***

**Telemetry.** I used radiotelemetry to track post-breeding Crawfish Frogs to upland burrows. Frogs were caught either at drift fences encircling two ponds—Nate's Pond and Cattail Pond (V.C. Kinney *unpubl. data*)—or in minnow traps at a third pond, Big Pond (Fig. 16). I used implanted or external radio transmitters (3.8 g, PD-2T temperature-sensitive transmitters with internal helical antennae; Holohil, Ontario, Canada; see Heemeyer et al. 2010*a* and Chapter 1). Frogs were tracked using an R-1000 receiver (Communication Specialists, Orange, CA) and a Yagi unidirectional antenna. Frogs were tracked daily throughout the warm seasons of 2009 and 2010, every other day during the fall seasons of both years, and once a week during winter (from late November to mid February). Each time an individual was located, weather metrics were measured and recorded at the site using a handheld Kestrel 4000© weather meter. Frog locations were recorded using a Garmin® GPSMAP 76CSx, and the location data were then plotted using Geographic Information System (GIS) software (ArcMap 9.3©). At each burrow I noted any changes or unusual features such as flooding or attempts to excavate the burrow, animals present, animal tracks (especially in the snow but also in the mud), as well as activity at the burrow entrance since the last visit (I placed Big Bluestem stem sections in an "X" pattern across the entrance of each burrow during each visit and noted at the next visit whether they had moved during the intervening time period).

**Other Techniques.** While tracking, incidental encounters of Crawfish Frog burrows were recorded. Crawfish Frog burrows were also identified by searching the ground left bare following prescribed burns, and by locating upland calling males.

### *Burrow Characteristics*

**Physical Features.** To visualize Crawfish Frog burrow conditions without destroying the burrow I used a Visual Optics © VS72-10WD Digital Video Borescope. Nighttime conditions were best to see the scope screen clearly; dry conditions were best to keep the scope end from becoming obstructed with mud and other debris. On 10 September 2009, I scoped four occupied frog burrows; on 19 November 2010, I scoped six occupied frog burrows.

**Habitat Characteristics.** In late July 2009, habitat measurements were taken at 18 known Crawfish Frog burrows and at 54 randomly generated (using Excel, Microsoft Office 2003) locations throughout HFWA-W. I excluded points that were in lakes, heavily wooded areas, on roadways or railways, and sites that were plowed—places where Crawfish Frogs would not occupy burrows. At each site, vegetation height, vegetation weight (using a Robel pole; Robel et. al. 1970), and percent cover (using the categories “forbes,” “woody,” “grass,” and “bare,” with a visual estimation of percent coverage of each within a 1-$m^2$ plot, and the percent of each species present) were measured or estimated.

**Burrow Distribution.** To obtain information on the location, characteristics, and spatial distribution of all burrow types at HFWA-W, I surveyed the bare ground of areas burned in the fall of 2009 and in the spring of 2010. On 19 September 2009, Indiana Department of Natural Resources land managers burned two sections (here termed the north burn and the south burn) of HFWA-W, totaling 8.5 ha (1.9 ha in the north burn, 6.6 ha in the south burn). These fall burns eliminated nearly all of the overlying vegetation, which had senesced, exposing bare ground, and making burrow openings clearly visible. I used this opportunity to survey for all burrows, and from among all burrows for Crawfish Frog burrows (medium-to-large-bore holes associated with a small area of compacted soil characterizing feeding platforms). I recorded the location of every burrow in 5.6 ha of the total 8.5 ha (all of the north burn and a portion of the south burn) using a Garmin® GPSMAP 76CSx. I measured the diameter of every burrow, and, when chimneys were present, measured their height. The 2010 spring burn covered approximately 40.5 ha and was much less complete (due to wetter combustible material and higher relative humidity) than the 2009 fall burns, and thus could not be systematically searched for burrows.

Based on the burrow descriptions of Hurter (1911) and Thompson (1915), as well as personal observations, I identified possible Crawfish Frog burrows as those that: 1) did not have a crayfish chimney; 2) were between 40 and 150 mm in diameter; 3) had an oval opening, and 4) had a cleared, compacted feeding platform outside the burrow entrance (Hurter 1911; Thompson 1915; Stevenson & Dyer 2002). All other burrows were classified by the type of animal that made them. Mammal burrows were in complexes with multiple openings and tunnels, had burrows that were shallow and leveled out into horizontal passages, and were associated with lighter colored soils which are drier because of the aeration provided by the underlying burrows). Turtle forms were large in diameter but shallow. Crayfish burrows were variably sized, deep, often had chimneys, and had circular openings. Smooth burrow walls, oval openings, and the presence of a feeding platform identified possible Crawfish Frog burrows. Burrow occupancy of possible Crawfish Frog burrows was then established (Heemeyer & Lannoo 2010); if a frog was present it was extracted (Heemeyer & Lannoo 2010), weighed, measured, scanned for a pit tag number (Christy 1996; animals were tagged the first time they were encountered; if they lacked a pit tag one was implanted [V. C. Kinney *unpubl. data*]), and released back into the burrow. One frog found in the south burn was extracted and implanted with a radio transmitter (using methods detailed in Chapter 1).

### *Behavior*

**Activity.** In addition to monitoring burrow entrance activity using crossed plant stems placed over burrow openings, when approaching each burrow I moved slowly and attempted to see the resident frog, which, if out, usually dove into its burrow when I approached. I placed Cuddeback® time-lapse digital wildlife cameras (Non Typical Inc. Park Falls, WI) at burrow entrances to monitor activity, and when I had questions about the health or status of the resident frog (Hoffman et al. 2010). Cameras were programmed to take digital photographs at 1-hr intervals (the minimum time allowed by the design). At any given time, 1–6 cameras were deployed, with the exception of the opening week of hunting season in the fall, when cameras were removed.

**Upland Calling.** While tracking Crawfish Frogs throughout the summer and early fall, males would occasionally call from their burrows. Calling in non-breeding upland Crawfish Frogs was first documented in 1948 (Smith et al. 1948), and has been observed in both Gopher Frog species (S.A. Johnson, L. Smith, & S. C. Richter *pers. com.*). I was able to take advantage of these vocalizations to pinpoint the location of one occupied Crawfish Frog burrow. In addition, I deployed frogloggers (Songmeters©

[Wildlife Acoustics, Concord, MA]) at known frog burrows to record calls and used Songscope Bioacoustic$^{©}$ software to plot them (Wildlife Acoustics, Concord, MA). Upland calling in two males (one male twice) was filmed (M. Lannoo, unpubl. data), which offered insights into where males call and triggers to calling.

**Burrow Sharing.** Using Cuddeback$^{®}$ time-lapse cameras (Hoffman et al. 2010) oriented to view burrow entrances, as well as personal observations while tracking, I was able to document burrow sharing between Crawfish Frogs and other animals.

### *Critical Habitat*

I measured the straight-line distances of each known Crawfish Frog's primary burrow from the centroid of the occupant's breeding wetland using tools available on GIS software (ArcMap 9.3$^{©}$). There was not a significant difference in straight-line distance between years ($p = 0.14$) so measurements were grouped to estimate core habitat and buffer. Based on these grouped distances, I calculated core habitat and buffer intervals around each breeding wetland that would encompass given percentages of the known frog burrows.

### *Analyses*

All statistical analyses were performed using program R. I used a Kruskal-Wallis test to compare numbers of burrows used by males and females, within and between years. I performed Wilcoxon rank-sum tests with continuity correction to test for differences between habitat characteristics of the selected sites and random sites. In this test, habitat measurements that were taken as percentage of the total ground cover within a given plot area were arcsine transformed to ensure that the variance was independent of the mean (Wheater & Cook 2000). I also used Wilcoxon rank-sum tests with continuity correction to test for differences in straight-line distance of burrows per year, and to test for differences in the vegetation characteristics of known burrow locations, or selected sites, and the vegetation characteristics of random locations throughout HFWA-W. I used a Spearman rank correlation matrix to determine relationships between number of burrows used and straight-line distance, SVL of each frog, mass of each frog, and number of movements each frog made; as well as to determine correlation of habitat variables to each other and the number of burrows used. As grass and forbes were highly correlated (Rho = -0.97; see results) I removed forbes from the model analysis. I fit a set of generalized linear models (GLMs), with binomially distributed errors, to the burrow selection data as a result of habitat parameters (Table 6). Then, I compared the relative fits of these models using Akaike's information criterion (AICc). I compared the $AIC_C$ scores of the GLMs to determine the model that best described the variation in burrow selection, as denoted by the model with the lowest $AIC_C$ score and the highest Akaike weight (w) based on the $\Delta$ $AIC_C$ (Anderson et al. 2001).

## RESULTS

### *Burrow Location*

I tracked 34 frogs from their breeding wetlands to their upland burrows (see Chapter 1). Later, I discovered an additional seven frogs occupying upland burrows; three were found during post-burn surveys, three were found while tracking other frogs, and one male was located when heard calling from upland burrows. In total, I located 41 upland burrows in which adult Crawfish Frogs spent the summer/winter (Fig. 16).

I estimate that I walked ~2 km per day when tracking Crawfish Frogs. Therefore, I covered approximately 1,000 km during the course of this study, and only incidentally encountered four inhabited burrows, reinforcing Smith's (1950) notion that this species represents the most secretive ranid in the United States.

**Burrow Use.** By radio tracking multiple Crawfish Frogs during several migrations, I was able to distinguish two types of burrows based on usage: 1) Primary burrow—the burrow in which an individual frog would spend the majority of its time, typically the entire summer, fall, and winter; 2) Secondary burrow—burrows that were used by an individual while migrating to and from the wetland or while ranging from the primary burrow. Primary and secondary burrows were used for noticeably different lengths of time; primary burrows were used for 260–334 d; secondary burrows were usually used for periods of only a few days. Frogs were regarded as inhabiting their primary burrows if they did not move burrow locations for at least two weeks.

The 34 frogs that we tracked to their individual primary burrows used a range of 1–11 burrows per migration ($\bar{x}$ = 3.4, SD = 2.6), including the primary burrow. There was no difference in the number of burrows used by frogs between years ($p = 0.0688$), or in the number of burrows used by males and females between or within years ($p = 0.567$). The number of burrows that frogs used during both the 2009 and 2010 post-breeding seasons was positively correlated with the number of moves the frog made during each migration (Rho = 0.47, $p = 0.070$) and negatively correlated with the straight distance from the pond center to the burrow (Rho = -0.26, $p = 1.000$), though neither is significant ($\alpha = 0.01$).

All burrows used by frogs were dug by crayfish, with the exception of one frog that in 2010 made a shallow scrape in the loose soil in between movements into the wetland (Frog 33; Engbrecht et al. 2011). Frogs often used the same burrows multiple times both within years, during pre- and post-breeding migrations and after ranging movements (Chapter 1), and between years, after breeding. Of the 34 frogs tracked to primary burrows, eight were tracked during consecutive 2009 and 2010 post-breeding migrations, where they re-used an average of 6.3 burrows (SD = 3.4, range = 0–10). All eight frogs returned to the vicinity of their 2009 primary burrows; six to their original burrows and one to a nearby burrow (within a few meters; Chapter 1), and one frog was preyed upon as it approached its former burrow.

### *Burrow Characteristics*

**Physical Features.** All burrows (both primary and secondary) that Crawfish Frogs occupied were crayfish burrows (Fig. 16). These burrows ranged from 40–140 mm in entrance diameter and could be best distinguished from burrows not supporting Crawfish Frogs by the presence of a roughly 100–200 mm diameter feeding platform situated at the entrance of the burrow.

Using the burrow scope, I observed that the shape of individual burrows varied; some maintained a constant diameter while others opened up into a larger tunnel. Some burrows had sharp turns while others were straight. I did not observe any side chambers or evidence of multiple tunnels, though some occupied burrows that were not scoped did have second entrances. Slopes of the burrows were generally greater than 45 degrees. Within burrows, I often saw insect remains (especially beetle carapaces) embedded into the walls. I occasionally saw live invertebrates, for example millipedes, isopods, and spiders; in one active Crawfish Frog burrow I saw a clump of grass that may have been a rodent nest (based on Cuddeback® photographs of a small mammal, as well as tunnels in the snow [Murie & Elbroch 2005]).

Three burrows were < 1 m in depth (79, 89, and 92 cm). In other burrows, the scope traveled as far as 122 cm and did not reach bottom. Burrow walls were smooth, often punctuated with cracks or protruding roots and rocks. With the scope, three frogs were observed in burrows. In 2009, I observed one female sitting in the water pooled at the bottom of a straight burrow. In 2010, burrows were dry and I saw one female sitting at the end of her burrow with her head facing the entrance. A male was observed at the bottom of his burrow, where it was flat and wide enough for him to sit horizontally.

Comparing frog temperatures to air temperatures, I found little difference during the summer months (Figs. 17 & 18). However, during winter conditions—from 1 November 2009 to 24 February 2010—frog temperatures were on average 5.4 ºC warmer than air temperatures. Winter frog temperatures also remained relatively constant, until they warmed again in the spring (Figs. 17 & 18).

**Habitat Characteristics.** Within grassland habitats, I found little difference between the vegetation of random sites and the vegetation of known frog burrow locations. In particular, vegetation height, vegetation weight, and the percent cover of forbes, dead woody vegetation, grass, and live woody vegetation did not significantly differ between random and known sites ($p > 0.01$; Table 6). One variable was significantly different—the amount of bare ground at known frog sites was significantly greater than at the random sites ($p = 0.008$; Table 6). Bare ground was positively correlated (Rho = 0.37; $p = 0.035$), percent dead woody debris was positively correlated (Rho = 0.20; $p = 1.000$), and vegetation height was negatively correlated (Rho = -0.22; $p = 1.000$) with known burrow sites. Grass and forbes were highly negatively correlated (Rho = -0.97; $p < 0.001$). I created and compared 23 $AIC_C$ models. The model that had the lowest $AIC_C$ score, and thus explained the most variation, was a complex model that included vegetation weight, vegetation height, percent bare ground, percent dead woody debris, percent grass, and interactions between these variables (model 1; Table 7). This model indicates that there may be complicated habitat interactions that result in burrow site selection.

**Burrow Distribution.** Within the two areas burned in September 2009, I measured and identified 432 burrows (Fig. 19), as follows: 381 crayfish burrows, 47 mammal burrows, and 4 turtle forms. The entrances of 39 of these burrows in the north burn, and 57 in the south burn were $\geq$ 40 mm in diameter, and from among these, I identified 12 (4 in the north burn, 8 in the south) as possible Crawfish Frog burrows. I flooded these burrows (Heemeyer & Lannoo 2010) and found three frogs: a female in the north burn, one frog of undetermined sex in the south burn, and a male in the south burn. The undetermined frog was observed, but left its burrow (after a no-till drill collapsed the burrow entrance) prior to being captured. In addition, during the fall burns in 2009, one known frog that was tracked to her location (Frog 29) was burned over in her burrow. During the spring burns in 2010, two frog burrows (Frogs 3 and 7) were also burned over and not harmed.

### *Behavior*

**Activity.** Following post-breeding migrations, Crawfish Frogs typically settled into a single primary burrow, where they spent their summer active period and overwintered. Between returning from breeding in the late spring of 2009 and leaving to breed in 2010, frogs in this study occupied the same primary burrow—approximately the same 0.05 m$^2$ area that encompasses the burrow and feeding platform—for up to 334 d (Chapter 1).

While at burrows, frogs were active throughout most of the year (Hoffman et al 2010). Images showed the frogs constantly on their feeding platform throughout the day, sitting and waiting for prey. When migrating or ranging and not in crayfish burrows, Crawfish Frogs took temporary cover under large bunch grasses such as Big Bluestem and Indian Grass, occasionally for periods of days while migrating.

A subset of Crawfish Frogs exhibited ranging behaviors, and a small subset changed burrows prior to overwintering (Chapter 1). In general, these movements occurred following rains or when burrows flooded. The data suggest that normal rainfall is permissive for movements, burrow flooding promotes movements, and drought restricts movements. In 2009, 10 frogs made ranging movements throughout the summer. When I scoped burrows in September 2009, they had standing water at the bottom. Following torrential rains in mid-October, burrows flooded, and three frogs moved to new overwintering burrows. Later that winter, one frog that did not switch burrows in the fall died in a burrow that flooded and subsequently froze over (Heemeyer & Lannoo *submitted*). In 2010, eight frogs made ranging movements during the early-midsummer, but no frogs moved after 29 July, when the region experienced a severe drought. When I scoped burrows in November 2010, the bottoms of the burrows were dry.

**Upland Calling.** Male Crawfish Frogs inhabiting burrows were heard/recorded vocalizing on nearly 100 separate occasions both before and after the breeding season. Calling prior to breeding was heard at dusk, two days before breeding migrations to the wetlands had begun, and at night during breeding. Calling from upland burrows after breeding was heard both day and night, as early as 8 July and as late as 1 October.

Video and audio recordings suggest that upland calling occurred in association with or in response to calling by other Crawfish Frogs, thunder, rain, airplane noise, 2-cycle engine noise, non-functioning automobile mufflers, human conversation, and the white noise generated by my radiotelemetry receiver. Braswell (*pers. com.*) commented that non-breeding calling of a captive Gopher Frog seemed to be stimulated by drilling on the concrete structure of the building as well as thunder, and was more likely to occur during wet weather. Males will call either while on their feeding platform, at their burrow entrance, or in their burrow. When calling, usually both vocal sacs inflate. Video recordings showed that on 30 August 2009 Frog 6 called from within his burrow entrance using both vocal sacs; he was recorded calling again on 6 September from his feeding platform using only one vocal sac. Upland burrow calls and breeding calls have noticeably different sound pressure and frequency (Fig. 20).

**Burrow Sharing.** Wildlife cameras revealed that at different times throughout the year, burrows known to host Crawfish Frogs were also visited or occupied by crayfish, snakes, and rodents. In addition, by tracking frogs, I was also able to confirm burrow sharing between Crawfish Frogs (Chapter 1). The same burrow system (one burrow with two entrances) was shared between a Crawfish Frog and a crayfish (species undetermined; Fig. 21). We have evidence that a frog (presence determined by radiotelemetry) inhabited a burrow with a Painted-hand Mudbug (*C. polychromatus*; seen at the burrow entrance). Common Gartersnakes (*Thamnophis sirtalis*; a known Crawfish Frog predator; Chapter 1) were observed entering and exiting the burrow of Frog 11 (Fig.

22) on four separate occasions when the frog was known to inhabit the burrow. It is not clear whether these sightings were of the same or different snakes; however, all observations were of small- medium-sized snakes (too small to prey upon the frog, and too big to be preyed upon by the frog). Cameras also captured images of rodents (either *Peromyscus* sp. or *Microtus* sp.) at the entrance to the same burrow (Frog 11). When I scoped this burrow, I saw a tangle of grass that may have been a mammal nest. In Chapter 1, I detailed burrow sharing between two Crawfish Frogs, both of which were implanted with transmitters. In total, I observed Crawfish Frogs sharing a burrow for four days (eight telemetered frog days since both frogs were implanted with transmitters) out of the 7,898 telemetered frog days comprising this study, a ratio of about 1/1000.

### *Critical Habitat*

Based on the straight-line distances from the centroid of the respective breeding wetland to the primary burrows, I calculated that a radius of 350 m from each wetland encompassed 55% of the total known Crawfish Frog burrows, a radius of 500 m encompassed 83% of known burrows, a radius of 750 m encompassed 95% of known burrows, and a radius of 1,020 m encompassed 100% of known burrows (Fig. 23).

## DISCUSSION

### *Burrow Use and Function*

I recorded burrow use in 34 frogs tracked from their breeding wetlands to their upland burrows, and incidentally found another seven frogs at their upland burrows. Crawfish Frogs occupied burrows dug only by crayfish. Crayfish burrows have at least two advantages for Crawfish Frogs: 1) they extend to the water table during years with near-normal rainfall amounts, and 2) they extend below the frost line.

I classified Crawfish Frog burrows as either primary burrows, where frogs spent the majority of their time, or as secondary burrows, which were used as refuges during migration and ranging behaviors for periods spanning days to a couple weeks. On average, Crawfish Frogs spent about 10.5 months of each year in upland burrows, the remaining time was spent breeding, and migrating to and from breeding wetlands (Chapter 1).

There has been confusion about the type of burrows inhabited by Crawfish Frogs. Thompson (1915; see also Wright and Wright, 1949) writes (p. 6): "Professor LaRue found the frogs in the mammal burrows along the shores of the ponds, as well as in crayfish holes, but it is probable that they were only temporarily occupying the former during the spawning season for we were unable to discover any mammal burrows, either in the vicinity of ponds or elsewhere, inhabited by frogs." It seems likely that if burrow types other than crayfish burrows are used, it is when Crawfish Frogs are migrating to and from breeding sites and ranging. I have only observed Crawfish Frogs using crayfish burrows as secondary burrows, but they will also hide temporarily in vegetation. On one occasion, a frog dug a shallow scrape in an open area near a breeding wetland, even though these frogs possess no morphological specializations for digging (Engbrecht et al. 2011). Observations by others (Goin & Netting 1940; Dundee & Rossman 1989; Parris & Redmer 2005; Collins et al. 2010) of Crawfish Frogs using other burrow types may have occurred during their breeding migrations, when only temporary retreats are required and Crawfish Frogs have less access to crayfish burrows. On the other hand, my study site is near the northern extreme of the current distribution of this species. It is possible that frogs in southern populations, where the frost line is negligible and the relative humidity is high, may not need the protection from freezing and desiccation that northern populations require, and therefore regularly use other burrow types as upland retreat sites.

To avoid temperature extremes and dehydration, many terrestrial amphibians seek refuge during the day (Cohen & Alford 1996; Schwarzkopf & Alford 1996; Seebacher & Alford 1999; Seebacher & Alford 2002). Burrows offer excellent refugia; Schwarzkopf & Alford (1996) found that burrows significantly reduced water loss during the dry season. In my study, Crawfish Frogs were seen at their burrow entrance hourly through the hottest portion of the hottest days of the year (Hoffman et al. 2010). The microclimate and proximity of their burrow allows them to escape the heat and hydrate as needed. Amphibians also commonly use refugia to avoid freezing temperatures (Costranzo & Lee 1994). Crayfish burrows buffered Crawfish Frogs from cold winter temperatures; frogs were an average of 5.4 ºC warmer than the air temperature (Figs. 17 & 18). Crayfish burrows also provide Crawfish Frogs with a moist, cool environment during the summer. Crayfish burrows occupied by Crawfish Frogs had water at their base during times of average rainfall; but during prolonged droughts, their bases were dry, though still moist and humid. I observed Crawfish Frogs sitting at the base of burrows in water, or on land when conditions are dry. Burrows provide access to a cool, moist environment and prevent excessive water loss from summer exposure (Rothermel & Luhring 2005; Rittenhouse et al. 2008). Unlike other ranids (Southern Leopard Frogs [*L. sphenocephala*], Green Frogs [*L. clamitans*], and Bullfrogs [*L. catesbeiana*]) Crawfish Frogs will drown if submerged for a prolonged period (Heemeyer & Lannoo *submitted*). During periods of heavy rain burrows often flooded; when this occurred

Crawfish Frogs likely remained closer to the burrow entrance, where they could breathe. Intentionally flooding burrows typically caused Crawfish Frogs to surface to breathe every 30–45 min (Heemeyer & Lannoo 2010), although I observed that frogs stay submerged longer when temperatures are colder.

In addition to hydration and thermoregulation, crayfish burrows provide protection from predators. Crawfish Frog burrows are oval shaped in cross section—similar to Crawfish Frogs—and they are only slightly larger bore than the frogs themselves. When frightened, Crawfish Frogs will lower their heads and inflate their bodies, much like toads (Smith 1961; Altig 1972). Inflating and lowering their heads while in a burrow allows Crawfish Frogs to wedge themselves against the burrow walls (Smith 1961; Heemeyer & Lannoo 2010) making them nearly impossible for me, or potential predators (snakes, raccoons, etc.), to pry from burrows.

Crawfish Frogs in crayfish burrows were 12 times less likely to be preyed upon than when undertaking migratory or ranging behaviors (Chapter 1). At HFWA-W, over the 20 mo of this study I know of only two frogs that died while inhabiting burrows; one was eaten by a Hog-nosed Snake (Engbrecht & Heemeyer 2010), the other was winterkilled (Heemeyer & Lannoo *submitted*).

Crayfish burrows also provide Crawfish Frogs protection from the direct effects of prairie fires. Three burrows inhabited by frogs implanted with transmitters were burned over, one in the fall of 2009 (Frog 29), two in the spring of 2010 (Frogs 3 & 7). These frogs survived without injury. However, the indirect effects of these burns may have had more severe consequences. After burns, vegetative cover is reduced and exposure is increased. About 1.5 months after the burn, when the ground was still bare, coyotes attempted to dig out Frog 29's burrow, as well as a nearby (60 m) burrow of another Crawfish Frog. I saw no other excavations in the burned areas—only Crawfish Frog burrows appeared targeted, and neither frog was harmed. However, Frog 29 later died while migrating through the burned area. I did not have the opportunity to observe how the indirect effects of fires impact frogs remaining at their burrows.

Exposure during breeding migrations and ranging movements is also increased. Of the three known Crawfish Frogs occupying burrows at the times of the burn, Frog 29, as mentioned above, was killed but not eaten in a burned area within 100 m of her breeding wetland during her pre-breeding migration; Frog 3 bred after the burn and then returned to his previous primary burrow; Frog 7 also returned to her previous primary burrow after successfully breeding but then went missing (possible transmitter failure). The fates of the three frogs that were found during post-burn burrow searches are unknown. One frog left after a no-till drill wrecked its burrow entrance; the transmitter of a second frog was found on the ground 2 m away from its burrow with no viscera or other frog remains associated. This frog may have been killed or it may have shed its transmitter (Weick et al. 2005; Tracy et al. 2011). The status of the third frog, a female, is also unknown; she left her burrow and was not seen again after being discovered.

Despite these data suggesting prescribed burns have negative effects on Crawfish Frogs, I have evidence that Crawfish Frogs do not alter migration routes or burrow selection to avoid burned areas. Four frogs that migrated through burned areas in 2010 used the same routes and burrows that they used in 2009, when these routes were heavily vegetated. I also have evidence that Crawfish Frogs occupy burrows in burned areas following breeding migrations. For example, I began following Frog 7 in 2009. In the spring of 2010, her burrow was burned over; she migrated through the burned area to the wetland to breed. Then she followed the same post-breeding migration path as in 2009 and returned to her previous primary burrow.

From measurements of surface areas of feeding platforms and burrow entrances, I calculated Crawfish Frog home range sizes of about 0.05 $m^2$. Millspaugh and Marzluff (2001) point out that home range is a concept, not an entity, and that an appropriate definition of home range is the "extent of area with a defined probability of occurrence of an animal during a specified time period." Based on the biology of Crawfish Frogs, one definition of home range includes the feeding platform and burrow entrance of the primary burrows that Crawfish Frogs inhabit for 8–11 months of the year. A second definition of home range could include ranging behaviors after Crawfish frogs have established their primary burrows, although not all frogs exhibited ranging movements (Chapter 1). A third definition for home range could include all frog movements, including time at their burrow, the distance to and from breeding wetlands, and breeding wetlands. Given the unusual biology of Crawfish Frogs, I feel that the 0.05 $m^2$ area that an animal occupies for the majority of the year is the best approximation of home range size. It has also occurred to me that a more accurate way to describe home range in Crawfish Frogs is to use volume, not area. Because they occupy upright tunnels, Crawfish Frogs, and perhaps both Gopher Frog species, may be the only ranid frogs that move more in a vertical direction than they do horizontally. The volume of a crayfish burrow can be approximated by the volume of a cylinder. The crayfish burrows occupied by Crawfish Frogs are only slightly larger (bore) than the frogs themselves, and frogs use the entire length. If the average Crawfish Frog burrow is 50 mm in diameter and 1 m deep, the volume would be ($\pi * r^2 *$ length = 3.14 * 2,500 $mm^2$ *1,000 mm) 7,850,00 $mm^3$ or about 0.01 $m^3$. Using either an area or a volume, it is apparent that Crawfish Frog home ranges are miniscule, especially when compared to the distances frogs will migrate to breed (Chapter 1).

### ***Burrow Distribution***

One of the questions that arise when habitats for one species are created by the actions of another is "Is the rarity of the host contributing to the rarity of the dependent species?" For Crawfish Frogs, this question becomes "Is the availability of crayfish burrows limiting population sizes in Crawfish Frogs?" I cannot definitively answer this question with the data I have collected, but I can speculate on two possible explanations.

**Evidence that burrows are not limiting.** During the post-burn burrow survey, I assessed the occupancy of 12 burrows that appeared to be actively inhabited by Crawfish frogs (had large-bores, oval entrances, smooth sides, and what appeared to be a feeding platform); I only found three frogs. The remaining burrows appeared to be uninhabited, but could have held crayfish. If they were uninhabited, this would suggest that not all potentially suitable burrows were being used, and that burrow numbers are not limiting.

In fact, the landscape at HFWA-W appears to support a high density of crayfish burrows. I counted 381 crayfish burrows/5.6 ha, which equals 68 burrows/ha (68 burrows/1,000 m), which equals one crayfish burrow every 15 $m^2$. Of these crayfish burrows, 96 were at least 40 mm in diameter (57 in the south burn, 39 in the north burn)—large enough to accommodate an adult Crawfish Frog. Using the same burrow density (96 burrows/5.6 ha), I estimate HFWA-W (729 ha) has 12,393 potential Crawfish Frog burrows. Only four (of 96) burrows in the burned areas were known to be inhabited by Crawfish Frogs. At this rate, crayfish burrows at HFWA-W would offer capacity for 516 Crawfish Frogs. Either number (12,393 [potential burrows], or 516 [potential burrows * occupancy rate]), is several times higher than the current Crawfish Frog population estimate at HFWA-W (164 known adult frogs at HFWA-W [V.C. Kinney *unpubl. data*], estimated total population ranges from 100–200 [N. J. Engbrecht *submitted*]). From these data, there is little evidence to support that burrows are limiting. However, if burrows are not limiting then why would frogs share burrows?

**Evidence that burrows are limiting—Burrow sharing.** Although burrow sharing between Crawfish Frogs was observed, it was rare, occurring only 8 days out of ~ 8,000 telemetered frog days (0.001% of the time). However, burrow sharing with other species such as crayfish, gartersnakes, and rodents occurs routinely. What is curious about this is that Crawfish Frogs will eat crayfish (Smith 1961; Altig 1972), and gartersnakes will eat Crawfish Frogs (Chapter 1). In order for Crawfish Frogs to share burrows with potential prey and potential predators, size must be important—i.e., the crayfish mush be relatively large and the gartersnakes must be relatively small. One occupied Crawfish Frog burrow hosted both a gartersnake and rodents (identified by pictures and tracks in the snow; Murie & Elbroch 2005). A second issue is physical: how do all of these animals occupy a single, straight burrow?

**Upland calling.** Reasons underlying upland calling remain a mystery. I observed and recorded male upland burrow calling over 100 times—it is common. However, calling is an inherently risky behavior and I wonder why males would waste energy and potentially expose their location to predators in order to call outside of the breeding season. Perhaps it is used to advertise territories; perhaps to inform other frogs (especially juveniles) that there is suitable burrow availability within the area of the calling frog; perhaps it results from fluctuating male hormones; or perhaps it is a remnant behavior from a species that is likely to have arisen in the south, where, like Dusky Gopher Frogs, they have more variable breeding seasons when weather conditions are favorable (following a hurricane [Richter 2002]).

### ***Critical Habitat and Buffer Zones***

When measuring the habitat characteristics of crawfish frog burrows it is important to understand that because crawfish frogs are dependent on crayfish burrows for their upland habitat, aside from choosing burrows, crawfish frogs may have little say in selecting their upland habitat. That is, burrowing crayfish may be selecting the habitat and crawfish frogs are simply choosing from among the burrows. Due to the amount of time that Crawfish Frogs spend in upland burrows, and the survival advantages that burrows appear to offer, burrow habitat is a key ecological feature in this species. However, until recently, amphibian habitat use outside of breeding has gone largely understudied (but see Semlitsch & Jensen 2001; Rittenhouse & Semlitsch 2007; Rittenhouse et al. 2009). Wetlands are not islands (Semlitsch 2006), and as such, when preserving wetlands, the terrestrial habitat that surrounds them must be taken into account. Semlitsch and Bodie (2003) proposed a stratified wetland buffer system to protect the surrounding terrestrial habitat. This system of buffer classification involves levels of zones around the core wetland with the aquatic buffer being part of the core habitat, which is the most protected, and the outside terrestrial buffer being the most available to human use (Semlitsch & Jensen 2001; Semlitsch & Bodie 2003). This method takes into account all species of amphibians that use the wetland and allows for protection of the terrestrial habitat surrounding the wetland as well as space to prevent edge effects.

Gopher Frogs and Dusky Gopher Frogs have also been found to spend a large portion of time in upland terrestrial habitat (Richter et al. 2001; Blihovde 2006; Roznik et al. 2009). A buffer of 1,000 m was recommended for the protection of Dusky Gopher Frogs ([Richter et al. 2001] although this has been interpreted as 350 m; US FWS 2010*b*). In this study, the average straight-line distance of Crawfish Frog upland burrows from breeding wetlands was 370 m; the longest straight-line distance observed in this study was 1,020 m. My data suggest at least a 1.1 km radius of core habitat be implemented around each wetland, in which plowing and human use is limited, and traffic and burning are restricted from March–May. I therefore, suggest at least a 1.1 km radius of core habitat around each breeding crawfish frog wetland. In addition, we propose adding an additional 100 m, which would act as the outer terrestrial buffer, preventing edge effects from affecting the most distant burrows. Within the 1,070 m buffer, I propose that the critical core area of 1,020 m, which contained 100% of the known Crawfish Frog primary burrows, be the critical habitat that is strictly off limits to plowing, or otherwise churning up the soil. As movement of the soil will destroy the Crawfish Frog burrows and may lead to direct frog injury or death (Thompson 1915). This 1,020 m core would ensure protection of all known Crawfish frog burrows as well as connect the three wetlands at HFWA-W that compose my field site (Fig. 23). Preserving the connectivity between wetlands is important to maintain amphibian population viability (Pilliod et al. 2002; Bartelt et al. 2004; Baldwin et al. 2006) and it is necessary for Crawfish Frogs because males occasionally breed in different wetlands between years (Chapter 1). The 1,020 m (or an additional 50 m added to the critical habitat) would act as the outer terrestrial buffer. Managing areas in order to preserve the crayfish burrows in the terrestrial habitat around breeding wetlands would benefit Crawfish Frogs, as well as Gopher Frogs and Dusky Gopher Frogs (Richter et al. 2001; Blihovde 2006; Roznik et al. 2009).

## ***Summary and Conclusions***

In this study, Crawfish Frogs exclusively occupied crayfish burrows, which they used as both their primary burrows (which they occupy for between 8 and 11 mo of the year) and their secondary burrows (temporary retreats occupied while exhibiting migration or ranging behaviors). On one occasion a female frog occupied a scrape she dug herself. Occupied burrows were wide bore (from 40–140 mm in entrance diameter) and extended ≥ 79 cm deep. All burrows had feeding platforms (100–200 mm diameter) that had been cleared by the frog. Burrow walls were smooth sided and were littered with embedded insect remains. Burrow sites had more bare ground and lower vegetation height than random sites; this may be a function of the presence of feeding platforms and the trampling of vegetation due to the daily monitoring of burrows.

Crawfish Frog burrows were located at distances up to 1,020 m from the breeding wetlands HFWA-W. To protect these animals, and other Crawfish Frog populations, I recommend a core habitat of 1,020 m, and a terrestrial buffer of another 50 m, for a total buffer radius of 1,070 m. This critical habitat would conserve 100% of the known burrows and the additional 50 m terrestrial buffer would minimize edge effects and reduce human impact by curtailing disturbance.

In summary, these data show that Crawfish Frogs inhabit a single, pinpoint spot ($0.05\ m^2$; $0.01\ m^3$) on the landscape—composed of a crayfish burrow and a feeding platform—for most of the year. This tiny site provides hydration, thermal buffering, protection from predators, and access to food. When not at this site (i.e., when migrating or ranging), Crawfish Frogs are 12 times more likely to be preyed upon (Chapter 1). Further, Crawfish Frogs will return to this spot, even if it means a migration distance of > 1 km. If the data here can be generalized, Crawfish Frogs are obligate crayfish burrow dwellers, and are therefore the only North American amphibian that relies exclusively on another species group for its upland habitat, habitat it will occupy for up to 11 months of the year.

Given this, in order to conserve Crawfish Frog populations, there must be at least three critical elements present in their habitat: 1) an adequate number of large upland crayfish burrows; 2) no landscape turnover (i.e., temporal autocorrelation must be maintained) of the sort that would destroy crayfish burrow entrances; and 3) landscape connectivity such that Crawfish Frog migration routes from burrows to breeding wetlands and vice-versa (the same route) are maintained without unnecessarily reducing the probability of survival.

Table 6. Mean habitat values (± SD) for known Crawfish Frog burrow sites and randomly generated sites. P-values are from Wilcoxon signed rank tests comparing known frog burrow sites to random sites.

| | Known | Random | P-value |
|---|---|---|---|
| N | 18 | 55 | - |
| Vegetation Height | 65.2 ± 15.2 | 75.3 ± 23.8 | 0.068 |
| Percent Forbes (arcsine) | 32.3 ± 23.0 | 37.9 ± 28.8 | 0.078 |
| Percent Grass (arcsine) | 53.2 ± 25.1 | 48.4 ± 29.3 | 0.139 |
| Percent Bare (arcsine) | 7.9 ± 8.6 | 2.4 ± 6.9 | 0.008 |
| Robel Pole Vegetation Weight | 4786.0 ± 1575.7 | 5197.3 ± 1582.9 | 0.898 |
| Percent Dead Woody (arcsine) | 2.0 ± 6.0 | 2.0 ± 10.2 | 0.917 |
| Percent Woody (arcsine) | 0.0 ± 0.0 | 0.5 ± 2.4 | 0.096 |

Table 7. General linear model $AIC_C$ analysis of burrow site (y) as a result of the measured habitat variables: vegetation height (VH), vegetation weight (VW), and percent cover of woody (W), grass (G), bare (B), and percent dead woody debris (DW). Shown are the 10 lowest scoring $AIC_C$ models.

| # | Model | K | $AIC_C$ | $\Delta$ $AIC_C$ | w |
|---|---|---|---|---|---|
| 1 | y=VW*B*VH+VW*B+VW*DW+B*DW+VW*G+B*G+VW*VH+B*VH+G*VH | 15 | 76.20 | 0.00 | 0.583 |
| 2 | y=VW*B+B*G+B*VH | 8 | 79.20 | 3.00 | 0.130 |
| 3 | y=VW*B+VW*G+B*G+B*VH | 9 | 79.41 | 3.21 | 0.117 |
| 4 | y=VW*B+DW+B*G+B*VH | 9 | 81.76 | 5.56 | 0.036 |
| 5 | y=VW*B+DW+VW*G+B*G+B*VH | 10 | 81.91 | 5.71 | 0.034 |
| 6 | y=VW*B*VH+VW*B+VW*DW+B*DW+VW*G+B*G+VW*VH+B*VH+G*VH+VW*W | 17 | 82.03 | 5.82 | 0.032 |
| 7 | y=VW*B+VW*DW+VW*G+B*G+VW*VH+B*VH+G*VH | 13 | 83.09 | 6.89 | 0.019 |
| 8 | y=VW*B+DW+B*G+B*VH+W | 10 | 83.60 | 7.39 | 0.014 |
| 9 | y=VW*B+DW+VW*G+B*G+B*VH+W | 11 | 83.81 | 7.60 | 0.013 |
| 10 | y=VW*B+VW*DW+VW*G+B*G+VW*VH+B*VH+G*VH+W | 14 | 85.23 | 9.03 | 0.006 |

Figure 16. All known primary burrows of Crawfish Frogs that were tracked and found throughout 2009 and 2010 at HFWA-W (N = 41).

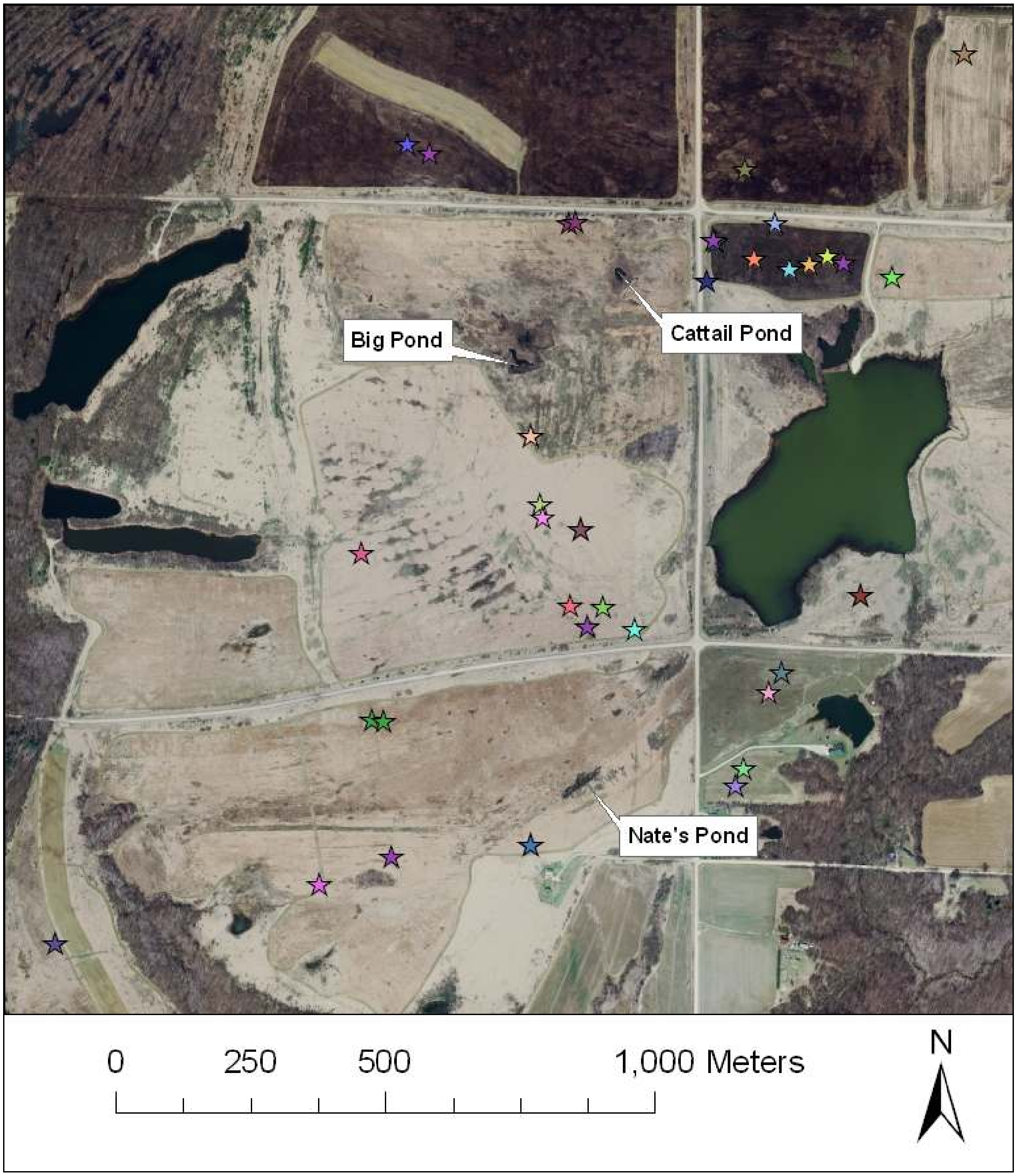


Figure 17. Individual temperature graphs from three frogs (Frogs 7, 8, and 11) spanning the duration that each frog was tracked, from 4 April 09 to 11 June 2010, 21 June 2010, and 19 November 2010 respectively. Blue lines represent frog temperature and gray lines are the corresponding air temperature at the time that the measurement was taken. Note that frog temperatures correspond to air temperatures throughout the year except during the winter.

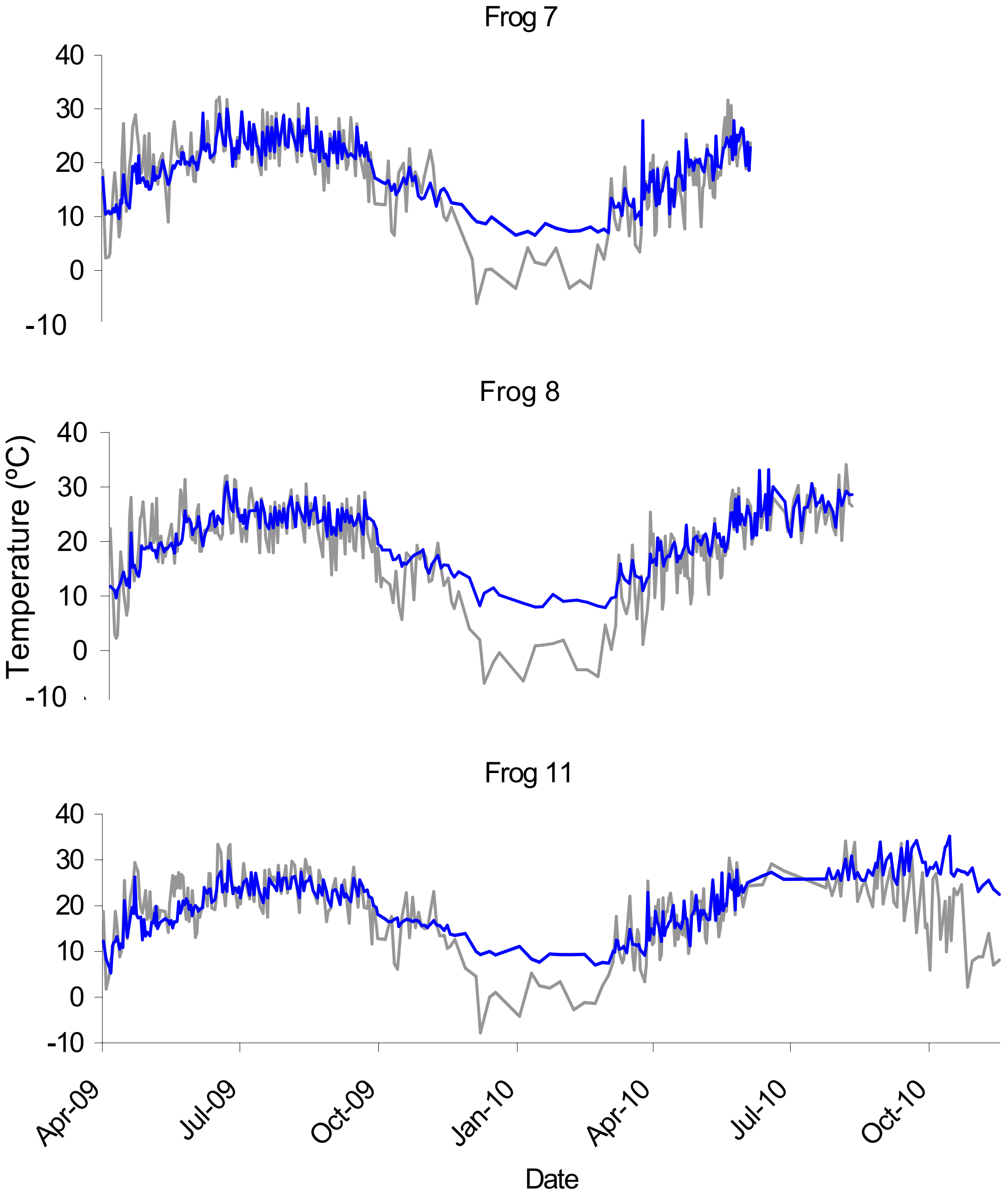


Figure 18. The daily average difference of frog temperature minus air temperature (the black line). The gray line is the daily average of the corresponding air temperature measured at the time of tracking. Throughout the summer months, the difference oscillates around zero, indicating that there is little or no difference between frog temperature and air temperature. The difference peaks in the winter months, which indicates that frog temperatures were warmer than air temperatures.

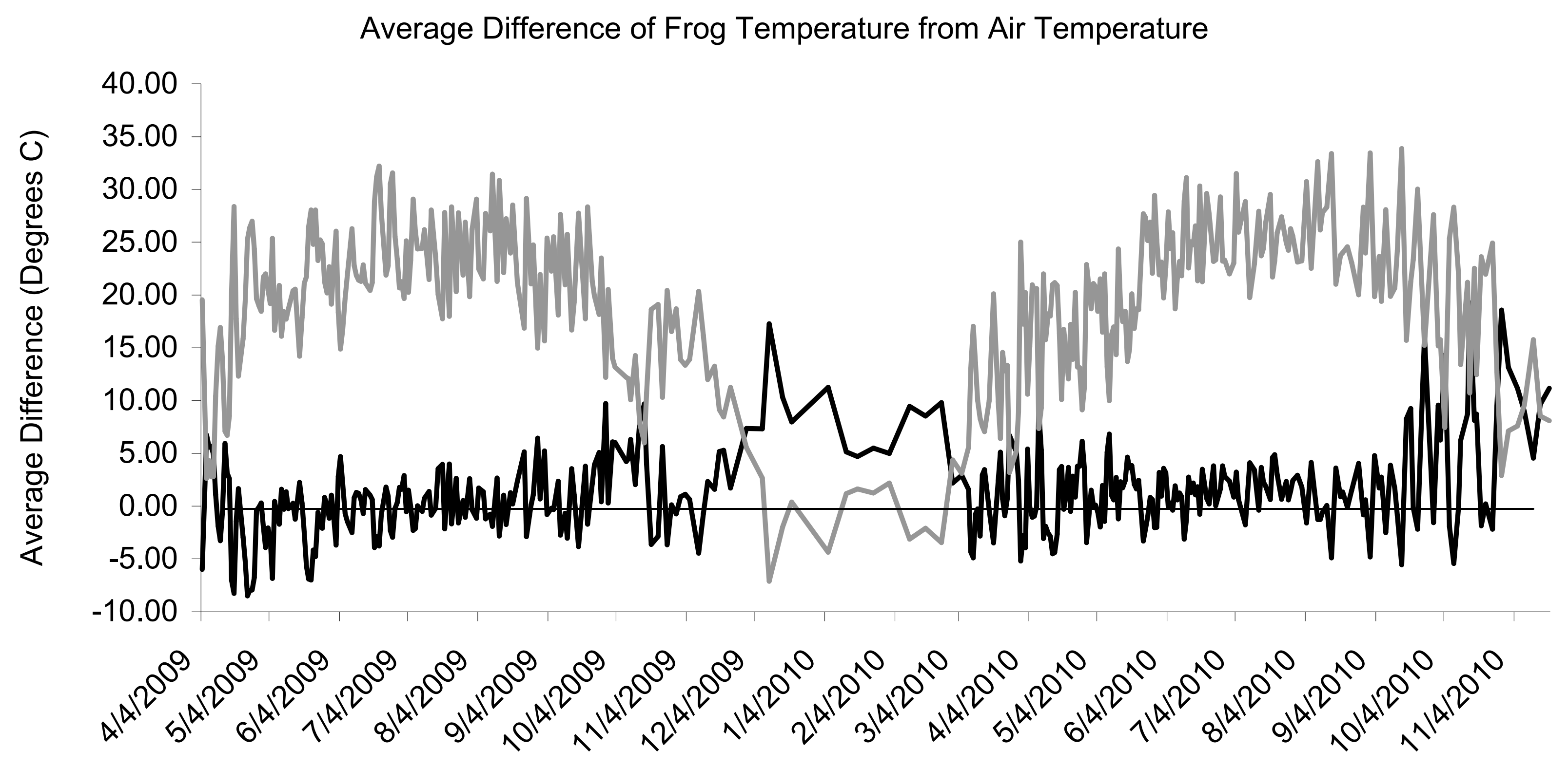


Figure 19. The north and south areas that were burned 19 September 2009. Red dots indicate individual crayfish burrows that were located and measured.

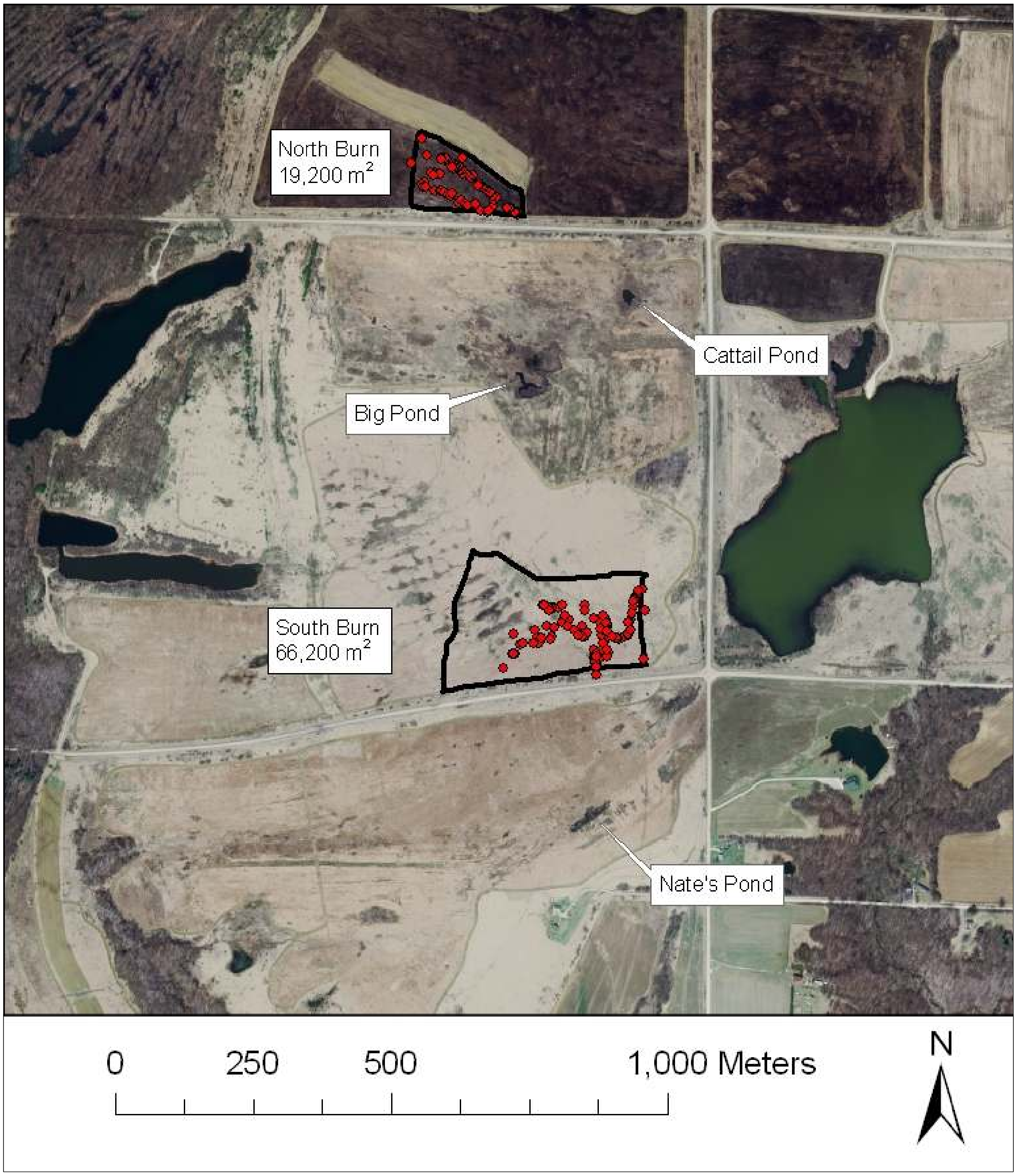


Figure 20. The waveform (top) and spectrogram (bottom) plots of breeding versus upland burrow calls of male Crawfish Frogs. The waveform plots show the sound pressure (on a scale relative to the 16-bit audio stream) as it varies over time and the spectrograms illustrate changes in frequency over time (Songscope Bioacoustic©, Wildlife Acoustics, Concord, MA). Note the differences between sound pressure and frequency between the two calls.

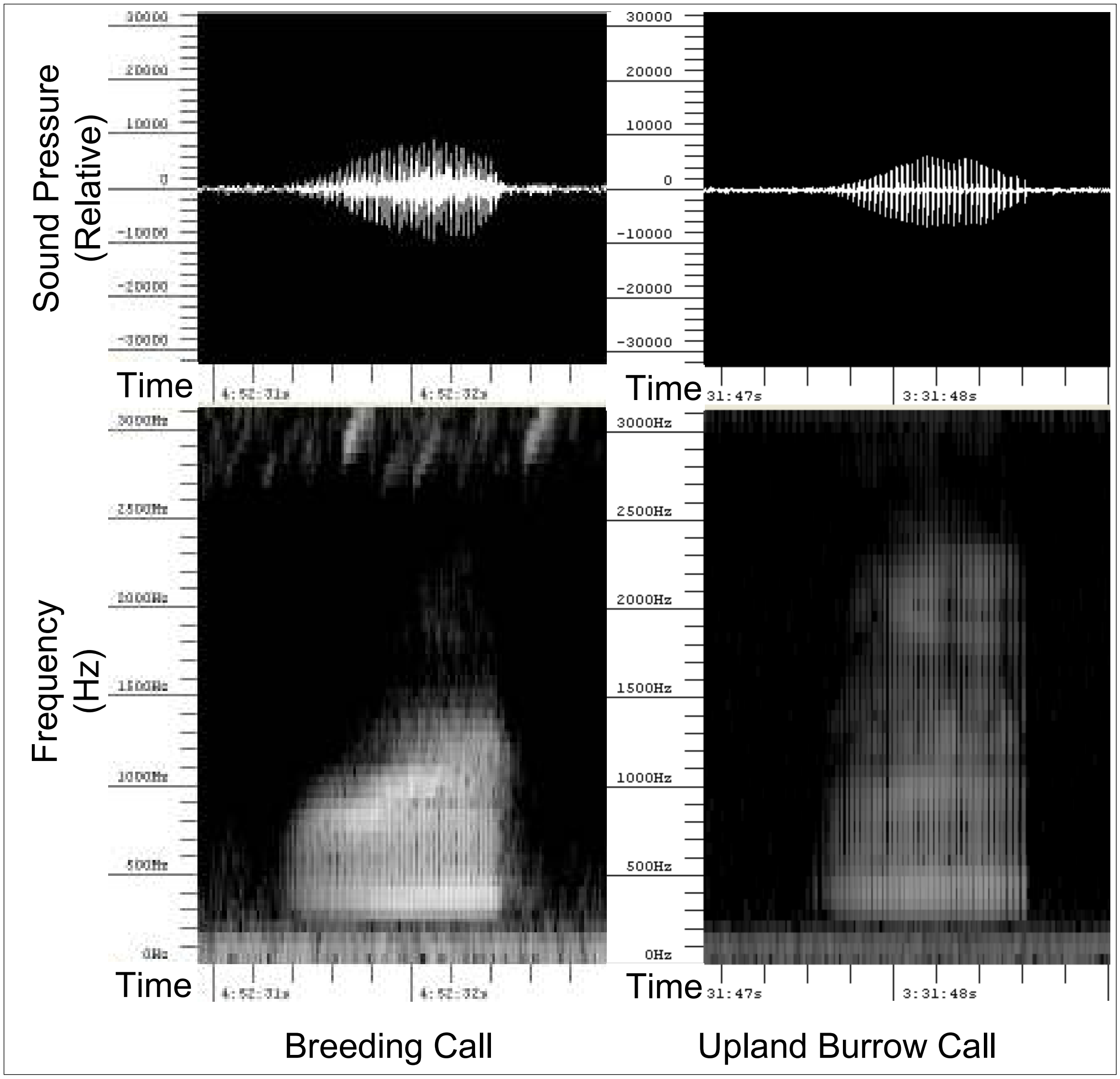
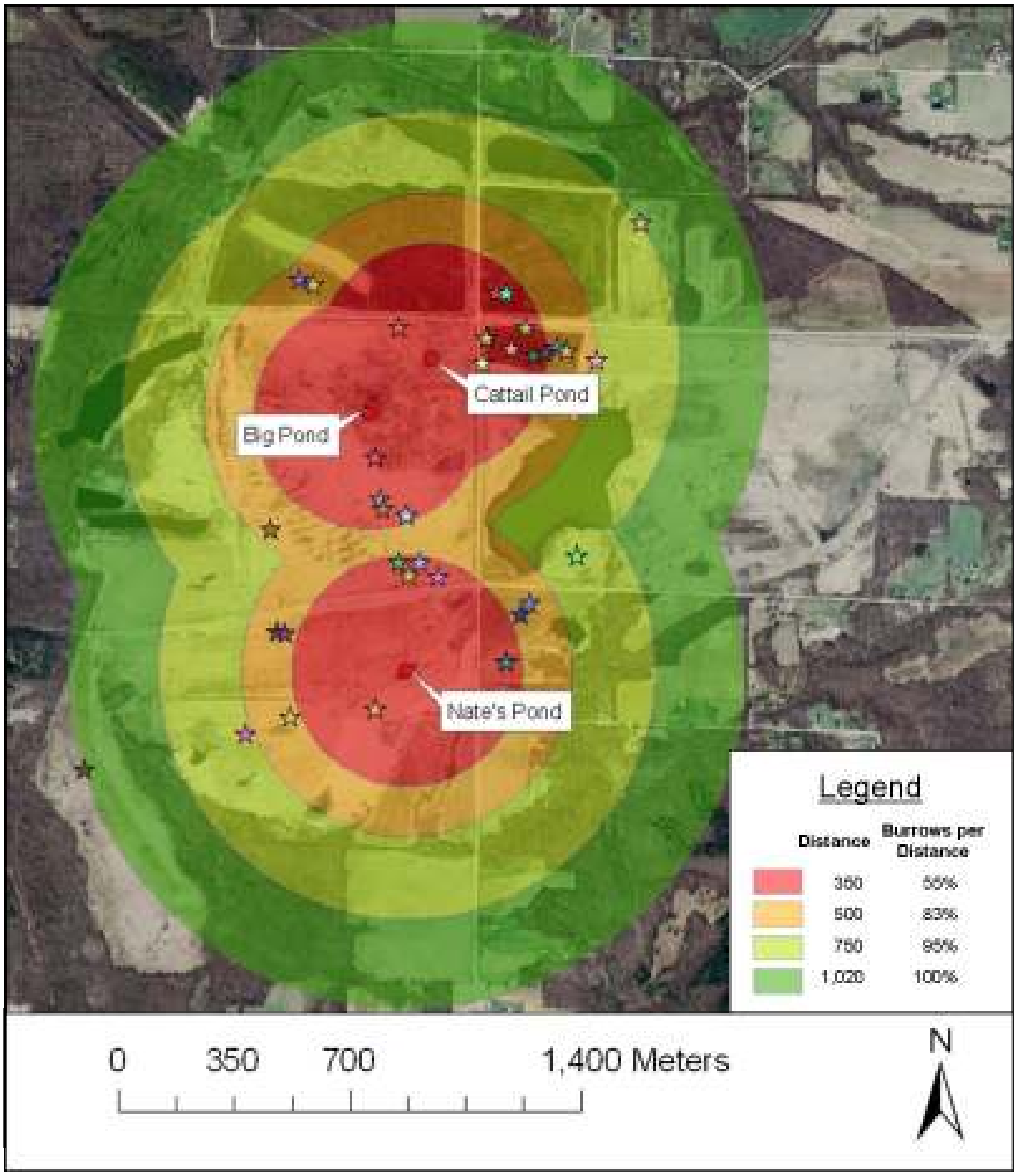


Figure 21. Cuddeback® wildlife camera image of a Crawfish Frog (Frog 16; male) and a crayfish (species unknown) sharing the same burrow, which has two entrances. This image is at the only secondary burrow that this frog used during 2010, which he inhabited on two separate occasions for periods of 12 and 8 days.

Figure 22. Cuddeback® wildlife camera image of a Crawfish Frog (Frog 16; male); at his primary burrow and a Common Gartersnake (*T. sirtalis*) sharing a burrow. Note this is the same frog as in Fig. 6, but this picture was taken at the frog’s primary burrow where he was located for at least 124 days (after which I can no longer verify his presence because his transmitter failed).


3/10/10 8:00 AM

Figure 23. Circles around each breeding wetland that encompassed a percentage of known Crawfish Frog burrows. A circle with a radius of 350 m (red) from each wetland encompassed 55% of the total known Crawfish Frog burrows, a radius of 500 m (orange) encompassed 83% of known burrows, a radius of 750 m encompassed 95% (yellow) of known burrows, and a radius of 1,020 m (green) encompassed 100% of known burrows. Based on this, I recommend implementing a core habitat of 1,020 m and an additional 50 m terrestrial buffer.



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# APPENDIX 1

## A summary of all frogs used in this study.

Transmitters in red are implants and blue are belt harnesses.

| Frog | Date Caught | Sex | Pond | Transmitter | Ended Tracking | Date of Death | Fate | # Days Tracked | # Seasons Tracked | # Surgeries |
|---|---|---|---|---|---|---|---|---|---|---|
| 1 | 3/19/09 | F | Nate's | 150.020 | n/a | 4/15/09–4/23/09 | died from unk causes | 27 | 1 | 1 |
| 2 | 3/19/09 | M | Nate's | 150.040 | 4/16/09 | n/a | trans removed | 28 | 1 | 2 |
| 3 | 3/24/09 | M | Nate's | 150.060 | 7/24/10 | n/a | missing, presumably alive | 487 | 3 | 2 |
| 4 | 3/29/09 | M | Cattail | 150.101 | n/a | 4/17/09 | hernia | 19 | 1 | 2 |
| 5 | 3/29/09 | M | Cattail | 150.080<br>150.080 | 8/13/10 | n/a | trans died | 502 | 1 | 2 |
| 6 | 4/1/09 | M | Big | 150.139<br>150.660 | 6/27/10 | n/a | alive, still being tracked | 452 | 3 | 2 |
| 7 | 4/1/09 | F | Nate's | 150.121 | 6/12/10 | n/a | missing, presumably alive | 437 | 3 | 1 |
| 8 | 4/1/09 | F | Big | 150.160<br>150.520 | n/a | 8/11/10 | eaten by garter snake | 497 | 3 | 2 |
| 9 | 4/1/09 | M | Big | 150.182 | n/a | 4/6/09 | winterkill (Heemeyer & Lannoo *submitted*) | 5 | 1 | 1 |
| 10 | 4/3/09 | F | Nate's | 150.200 | n/a | 5/2/09 | chytrid (Kinney et al. *in press*) | 29 | 1 | 1 |
| 11 | 4/3/09 | F | Nate's | 150.580<br>150.200 | 10/28/10 | n/a | alive, still being tracked | 573 | 3 | 2 |
| 12 | 4/3/09 | M | Nate's | 150.560<br>150.799 | 8/12/09 | n/a | trans died | 131 | 1 | 2 |
| 13 | 4/4/09 | M | Big | --- | n/a | 4/4/09 | bled out | 0 | 0 | 1 |
| 14 | 4/6/09 | M | Big | 150.401 | n/a | 5/2/09 | hernia | 26 | 1 | 2 |
| 15 | 4/6/09 | M | Big | --- | n/a | n/a | stopped surgery | 0 | 0 | 2 |
| 16 | 4/7/09 | M | Big | 150.460 | 7/28/10 | n/a | trans died | 477 | 3 | 1 |
| 17 | 4/7/09 | F | Big | 150.440 | 8/21/09 | n/a | trans died | 136 | 1 | 1 |
| 18 | 4/10/09 | M | Nate's | --- | n/a | n/a | stopped surgery | 0 | 0 | 1 |
| 19 | 4/10/09 | F | Big | 150.420 | n/a | 5/26/09 | unk, skin stitches were unhealed | 46 | 1 | 1 |
| 20 | 4/10/09 | F | Cattail | 150.520 | n/a | 5/14/09 | eaten by hog-nosed snake (Engbrecht & Heemeyer 2010) | 34 | 1 | 1 |
| 21 | 4/14/09 | M | Nate's | 150.501<br>150.780 | n/a | 4/2/10 | eaten by raccoon (Heemeyer et al. 2010*b*) | 353 | 2 | 2 |
| 22 | 4/17/09 | F | Cattail | 150.480<br>150.780 | 8/10/09 | n/a | trans removed | 115 | 1 | 3 |

| | | | | | | | | | | |
|---|---|---|---|---|---|---|---|---|---|---|
| 23 | 4/17/09 | M | Nate's | 150.040 | 4/18/09 | n/a | missing, presumably alive | 1 | 0 | 1 |
| 24 | 4/20/09 | M | Cattail | 150.220<br>150.501 | 3/7/10 | n/a | trans died | 321 | 1 | 2 |
| 25 | 4/20/09 | F | Cattail | 150.359<br>150.660 | 8/11/09 | n/a | trans removed | 113 | 1 | 2 |
| 26 | 4/20/09 | M | Cattail | 150.279<br>149.129<br>150.220 | 10/28/10 | n/a | alive, still being tracked | 556 | 3 | 3 |
| 27 | 4/20/09 | M | Cattail | 150.379<br>150.821 | 3/29/10 | n/a | found trans | 343 | 2 | 2 |
| 28 | 4/20/09 | F | Cattail | 150.101 | n/a | 4/20/09 | anesthesia | 0 | 0 | 1 |
| 29 | 5/6/09 | F | Nate's | 150.538 | n/a | 4/6/10 | alive, still being tracked | 335 | 2 | 1 |
| 30 | 5/14/09 | M | Nate's | 150.401<br>149.029<br>150.239 | n/a | 4/10/10 | eaten by garter snake | 331 | 3 | 2 |
| 31 | 5/15/09 | F | Nate's | 150.101 | n/a | 5/20/09 | preyed upon by unk | 5 | 1 | 1 |
| 32 | 10/1/09 | M | Cattail | 150.301 | 3/12/10 | n/a | found trans | 162 | 1 | 1 |
| 33 | 3/10/10 | F | Cattail | 149.069<br>150.440 | 6/16/10 | n/a | trans died | 98 | 2 | 1 |
| 34 | 3/22/10 | M | Nate's | 149.090 | n/a | 4/1/10 | chytrid (Kinney et al. *submitted*) | 10 | 0 | 0 |
| 35 | 3/25/10 | M | Big | 149.049 | 4/6/10 | n/a | found trans | 12 | 1 | 0 |
| 36 | 3/26/10 | F | Big | 150.200 | 3/26/10 | n/a | found trans | 0 | 0 | 0 |
| 37 | 4/1/10 | F | Nate's | 150.079 | 4/16/10 | n/a | trans removed | 15 | 1 | 0 |
| 38 | 4/1/10 | F | Big | 149.069 | 4/1/10 | n/a | found trans | 0 | 0 | 0 |
| 39 | 4/1/10 | M | Cattail | 149.110 | 4/14/10 | n/a | missing, presumably alive | 13 | 1 | 0 |
| 40 | 4/1/10 | F | Nate's | 150.480 | 7/31/10 | n/a | trans died | 121 | 1 | 1 |
| 41 | 4/2/10 | F | Cattail | 150.560 | 4/6/10 | n/a | found trans | 4 | 1 | 1 |
| 42 | 4/3/10 | M | Nate's | --- | n/a | n/a | stopped surgery | 0 | 0 | 1 |
| 43 | 4/5/10 | M | Cattail | 150.101 | 5/2/10 | n/a | trans removed | 27 | 1 | 0 |
| 44 | 4/6/10 | M | Nate's | 150.279 | 10/28/10 | n/a | alive, still being tracked | 205 | 1 | 1 |
| 45 | 4/8/10 | F | Cattail | 150.440 | n/a | 4/23/10 | preyed upon unk | 15 | 1 | 1 |
| 46 | 4/8/10 | M | Nate's | 150.780 | 4/21/10 | n/a | missing, presumably alive | 13 | 1 | 1 |
| 47 | 4/8/10 | M | Cattail | 150.139 | 10/28/10 | n/a | alive, still being tracked | 203 | 1 | 1 |
| 48 | 4/11/10 | F | Nate's | 149.090 | 4/16/10 | n/a | found trans | 5 | 1 | 0 |
| 49 | 4/13/10 | M | Nate's | 149.029 | 4/26/10 | 5/12/10 | trans removed, found dead at burrow-chytrid (Kinney et al. *submitted*) | 29 | 1 | 0 |
| 50 | 5/2/10 | M | Nate's | 149.069<br>150.200 | n/a | 6/5/10 | eaten by black racer | 34 | 1 | 1 |
| 51 | 4/23/10 | F | Cattail | 150.520 | n/a | 6/6/10 | preyed upon unk | 44 | 1 | 1 |
| 52 | 4/25/10 | M | Nate's | 150.420 | 8/4/10 | n/a | missing, presumably alive | 101 | 1 | 1 |
| 53 | 5/2/10 | F | Nate's | 150.020 | 10/28/10 | n/a | alive, still being tracked | 179 | 1 | 1 |
| 54 | 5/2/10 | M | Nate's | --- | n/a | n/a | stopped surgery | 0 | 0 | 1 |
| 55 | 5/25/10 | M | Nate's | 149.129<br>150.079 | 10/28/10 | n/a | alive, still being tracked | 156 | 1 | 1 |