TERRESTRIAL ECOLOGY OF JUVENILE AND ADULT GOPHER FROGS (*Rana capito*)

By

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Although many amphibians that breed in aquatic habitats spend the majority of their lives in surrounding upland habitats, the terrestrial ecology of amphibians is poorly understood. I used radio telemetry to study survival, movement patterns, and terrestrial habitat use of juvenile and adult gopher frogs (*Rana capito*). Both juvenile and adult frogs are capable of migrating long distances from breeding ponds. In my study, juveniles moved at least 691 m from ponds, and adults moved at least 396 m from ponds; however, other adult gopher frogs were observed up to 862 m from the nearest potential breeding pond at my sites. The final recorded locations of all surviving frogs that migrated from ponds were burrows excavated by gopher tortoises (*Gopherus polyphemus*) and small mammals (e.g., *Geomys pinetis*, *Podomys floridanus*), and both life stages exhibited strong site fidelity to these burrows.

Predation on juvenile gopher frogs was extremely high and only 9.4% of frogs survived their first month in the terrestrial environment. Although snakes were their major predators, frogs were also killed by mammals and birds, as well as vehicular traffic along unpaved roads. The use of underground refugia significantly increased a frog's probability of survival and reduced the risk of death to only 4% of the risk that frogs faced while in the open environment. Frogs that

survived to the end of the study located a burrow within their initial days in the terrestrial environment and remained there for the rest of the life of their transmitter.

Although my study ponds were located primarily in open-canopy longleaf pine (*Pinus palustris*) habitat, areas surrounding some of the ponds contained patches of closed-canopy habitat that had been invaded by hardwood trees (e.g., *Quercus* spp.) as a result of fire suppression. Emigrating frogs migrated nonrandomly at these ponds, moving through the center of the largest patch of open-canopy habitat, and thereby avoiding the edges where the closed-canopy habitat occurred. Patches of open-canopy habitat contained higher densities of burrows than closed-canopy patches, suggesting that frogs select open-canopy habitats because burrows are more abundant in those areas.

Conservation of gopher frogs requires protection of large areas of terrestrial habitats surrounding breeding ponds, as well as protection of populations of burrowing vertebrates. Terrestrial habitats must be managed appropriately, which includes using frequent prescribed fire in the uplands and burning all the way to the edges of ponds.

CHAPTER 1
INTRODUCTION

Human alteration of the earth has resulted in unprecedented losses in global biodiversity (e.g., Vitousek et al. 1997). Amphibians are declining more rapidly than all other groups of vertebrates and have the highest proportion of species threatened with extinction (Stuart et al. 2004, Beebee and Griffiths 2005). Although the causes are often complex and poorly understood, the loss and alteration of habitat is a major cause of population declines and extinctions for many species (Alford and Richards 1999, Semlitsch 2002). Most amphibians depend on aquatic and terrestrial habitats to complete their life cycle; therefore, the conservation of both of these habitats is essential to maintain viable populations (Semlitsch 2000).

The effects of anthropogenic disturbance are a major concern in areas that are experiencing rapid human population growth and contain a high density of small, isolated wetlands, such as the southeastern United States (Hefner and Brown 1985). Small, isolated wetlands are important breeding sites for many species of amphibians and play a critical role in sustaining biological diversity (Semlitsch and Bodie 1998, Russell et al. 2002), particularly in xeric ecosystems such as longleaf pine-wiregrass (*Pinus palustris-Aristida stricta*) sandhills (Dodd 1992) where most amphibians would not occur in their absence. More than 50% of original wetlands in the United States have been destroyed (Dahl 1990), and despite their biological importance, current federal regulations still do not protect small wetlands (< 4.0 ha) from destruction (Semlitsch 2000).

Although most amphibians depend on aquatic habitats for breeding and larval development, many spend the majority of their lives in the surrounding terrestrial habitats, often moving long distances from breeding ponds (Franz et al. 1988, Dodd 1996, Johnson 2003). Thus, protection of aquatic breeding sites may be of little conservation value if the surrounding terrestrial habitats are not also protected and managed appropriately. In the United States, widespread areas of native forests have been fragmented or cleared for agriculture, forest plantations, and urban development, and these changes have been linked to declines in amphibian populations and to changes in amphibian community composition (Delis et al. 1996, deMaynadier and Hunter 1998). Other less-intensive habitat alterations can also change the composition and structure of native forests, such as selective logging and fire suppression, and these changes also affect amphibian diversity and abundance (Mushinsky 1985, Harpole and Haas 1999).

Most amphibian research has focused on the aquatic ecology of amphibians, when individuals are congregated at breeding sites. Thus, much is known about the aquatic larval stage and the reproductive ecology of adults, while relatively little is known about the terrestrial juvenile and adult stages, even though many species spend a much greater proportion of their lives in the terrestrial habitat. Several population models have indicated that amphibian populations are most sensitive to mortality during the terrestrial stages (Taylor and Scott 1997, Biek et al. 2002), particularly juveniles (Hels and Nachman 2002, Vonesh and De la Cruz 2002). Thus, protection and appropriate management of terrestrial habitats for juveniles and adults is crucial for the persistence of populations. However, the migratory distances and terrestrial habitat requirements of most amphibians are unknown or poorly understood, and they may vary significantly by species, life stage, and habitat quality.

In addition to sustaining local populations, juvenile amphibians are also thought to be responsible for most interpond dispersal, thereby contributing to regional persistence and influencing metapopulation dynamics (Funk et al. 2005, Gill 1978, Breden 1987, Berven and Grudzien 1990). Despite the importance of the juvenile life stage in linking isolated populations, the most basic elements of juvenile amphibian ecology are virtually unknown for most species.

After emigrating from ponds following metamorphosis, juveniles generally remain in the uplands until maturity and are often not observed again until they are found at ponds as breeding adults (Semlitsch and Ryan 1999). Juvenile amphibians are difficult to study because of their small size, secretive behavior, and high mortality (Trenham et al. 2000, Altwegg and Reyer 2003, Rothermel and Semlitsch 2006); however, knowledge of terrestrial habitat use, levels and sources of mortality, and movement patterns in natural and disturbed habitats are necessary to increase our understanding of population dynamics and prevent further population declines.

Natural habitat has declined sharply in the southeastern United States, and this is especially true for the longleaf pine-wiregrass ecosystem, which has declined as much as 98% from its historic range and is considered one of the most endangered ecosystems in the nation (Noss 1989, Ware et al. 1993). Many of the remaining tracts of longleaf pine forest are in poor condition as a result of improper management—largely fire suppression (Noss 1989). Historically, frequent, low-intensity fire maintained a predominantly open, pine-dominated habitat, and the exclusion of fire has altered stand structure in many areas by permitting hardwood trees to invade the large gaps that were maintained by fire (Heyward 1939, Ware et al. 1993, Gilliam and Platt 1999). Many plants and animals that occur in the longleaf pine ecosystem have declined as a result of habitat loss and are further threatened by fragmentation and fire suppression in remaining habitat (Van Lear et al. 2005).

One species that has declined along with the loss of longleaf pine habitat is the gopher frog (*Rana capito*). Gopher frogs are imperiled throughout their range, which historically extended throughout the southeastern Coastal Plain from southeastern Alabama to North Carolina (Godley 1992, Jensen and Richter 2005). Gopher frogs breed in temporary or semi-permanent ponds that are shallow, have an open canopy and emergent vegetation, and lack predatory fishes (Godley

1992). They spend most of their lives in the terrestrial habitat and migrate to ponds to breed primarily in winter and early spring, although they have been documented breeding during other times of the year following heavy rains (Semlitsch et al. 1995, Palis 1998, Jensen and Richter 2005). While in the terrestrial habitat, gopher frogs use the burrows of other vertebrates for shelter, as well as stump holes and other crevices (Godley 1992). They are known to use the burrows of gopher tortoises (*Gopherus polyphemus*; Franz 1986), crayfishes (Phillips 1995), and several species of small mammals, including Florida mice (*Podomys floridanus*; Lee 1968), oldfield mice (*Peromyscus polionotus*; Gentry and Smith 1968), and southeastern pocket gophers, (*Geomys pinetis*; Blihovde 2006).

The greatest threat to gopher frogs is the loss and alteration of aquatic and terrestrial habitats due to urban development, silviculture, and fire suppression (Jensen and Richter 2005). Other threats include the introduction of predatory fishes to breeding ponds, road mortality, removal of tree stumps in forest plantations, and any factors that result in declines of populations of burrowing vertebrates, and therefore the availability of refugia near breeding ponds (Jensen and Richter 2005). Fire suppression is a major threat and decreases habitat quality in both aquatic and terrestrial environments (Jensen and Richter 2005). The exclusion of fire from ponds during dry periods encourages the growth of hardwood trees in and around ponds, and the resulting canopy closure has been linked to lower survival to metamorphosis and reduced size at metamorphosis in larvae of the closely related dusky gopher frog (*Rana sevosa*; Thurgate and Pechmann 2007). Fire suppression in the terrestrial habitat reduces habitat quality for burrowing vertebrates, such as gopher tortoises (Jones and Dorr 2004), which may limit the availability of refugia for gopher frogs in areas where populations of burrowing vertebrates decline, and may also increase the migratory distances that frogs must travel to locate suitable refugia.

Furthermore, the invasion of hardwoods may also act as barriers to movement and limit dispersal to other ponds.

A thorough understanding of the habitat requirements of all life stages is essential for the development of effective conservation plans to protect gopher frogs, but information is lacking on the terrestrial juvenile and adult life stages. My thesis focuses on the terrestrial ecology of juvenile and adult gopher frogs through the use of radio telemetry and is presented as three chapters that will be submitted as separate manuscripts for publication. In Chapter 2, I address survivorship of juvenile gopher frogs. Specifically, I identify sources of mortality, estimate an overall survival rate and survival rates for each pond, and determine which factors influence survivorship. In Chapter 3, I focus on the movement patterns and habitat use of juvenile gopher frogs. Here I quantify movements, examine the effects of canopy closure on burrow density and the orientation of frogs, and discuss appropriate habitat management for gopher frogs. In Chapter 4, I address the movement patterns, migration distances, habitat use, and site fidelity of adult gopher frogs. In Chapter 5, I examine the major conclusions of my research and implications of my findings on the conservation of gopher frogs.

CHAPTER 2
BURROW USE AND SURVIVAL OF JUVENILE GOPHER FROGS

Introduction

Both aquatic and terrestrial habitats are important for many species of reptiles and amphibians to carry out critical life-history processes (Semlitsch and Jensen 2001, Gibbons 2003, Semlitsch and Bodie 2003). For example, semi-aquatic species of turtles and snakes that occupy wetlands during most of the year also depend on terrestrial habitats for nesting, aestivating, and overwintering (Burke and Gibbons 1995, Buhlmann and Gibbons 2001, Roe et al. 2004). Although many species of salamanders and frogs depend on aquatic habitats for breeding and larval development, they forage, aestivate, and overwinter in terrestrial habitats (Semlitsch, 2003). Many species of pond-breeding amphibians spend the majority of their lives in the surrounding uplands and only return to ponds to reproduce (Dodd 1996, Johnson 2003, Greenberg and Tanner 2005).

Although much is known about the aquatic ecology of semi-aquatic species, much less is known about their use of terrestrial habitats. Individuals are more easily studied in aquatic habitats than in terrestrial habitats, where they are more secretive and difficult to locate. For amphibians, most studies have focused on the aquatic larval stage and on the reproductive ecology of adults, when individuals are congregated at breeding sites. Thus, information is lacking on the terrestrial juvenile and adult stages (Semlitsch 2003). Moreover, there is very little information on even the most basic elements of juvenile ecology. After emigrating from ponds following metamorphosis, juveniles generally remain in the uplands until maturity and are often not observed again until they are found at ponds as breeding adults (Semlitsch and Ryan 1999).

Although amphibian populations can be affected by mortality during the egg, larval, juvenile, and adult life stages, several population models indicate that amphibian populations are most sensitive to mortality during the terrestrial juvenile and adult stages (Taylor and Scott 1997, Biek et al. 2002), particularly juveniles (Hels and Nachman 2002, Vonesh and De la Cruz 2002). In addition to sustaining local populations, juvenile amphibians are thought to be responsible for most interpond dispersal, thereby contributing to regional persistence and influencing metapopulation dynamics (Funk et al. 2005, Gill 1978, Breden 1987, Berven and Grudzien 1990). The transition from the aquatic environment to terrestrial habitat is thought to be a period of high mortality for amphibians, and mortality appears to be highest immediately after metamorphosis (Trenham et al. 2000, Altwegg and Reyer 2003, Rothermel and Semlitsch 2006). Unlike adults, juveniles are unfamiliar with the locations of refuges in the surrounding uplands, plus their small body size puts them at a high risk of desiccation and predation (Arnold and Wassersug 1978, Newman and Dunham 1994). Factors thought to influence postmetamorphic survival of amphibians include predator densities, body size at metamorphosis (Berven and Gill 1983, Morey and Reznick 2001), lipid levels at metamorphosis (Scott et al. 2007), and habitat quality, which includes connectivity from breeding sites to suitable terrestrial habitat (Rothermel 2004, Rothermel and Semlitsch 2006), as well as the availability of refugia (Loredo et al. 1996, Seebacher and Alford 2002, Rothermel and Luhring 2005).

The gopher frog (*Rana capito*) is considered rare and imperiled throughout its range in the southeastern Coastal Plain of the United States (Godley 1992, Cox and Kautz 2000, Jensen and Richter 2005). Like many other pond-breeding amphibians, gopher frogs breed in temporary or semi-permanent ponds, but spend the vast majority of their lives in the surrounding terrestrial habitat. They can migrate long distances and have been found up to 2 km from breeding ponds (Franz et al. 1988). Gopher frogs are adapted to xeric habitats and adults seek shelter in underground refuges, such as the burrows of gopher tortoises (*Gopherus polyphemus*) and several species of small mammals (e.g., *Podomys floridana*.), as well as stump holes (Lee 1968, Franz 1986, Godley 1992).

I used radio telemetry to investigate survival and causes of mortality for newly metamorphosed gopher frogs at five ponds in north-central Florida. The primary goals of my study were to estimate survival rates of juvenile gopher frogs during their first month in upland habitats and to determine how survival is influenced by body size, underground refuge use, and distance from the pond of origin. I included distance from the pond of origin as a variable because many predators, such as snakes, are concentrated around ponds, particularly during periods of juvenile amphibian emigration (Arnold and Wassersug 1978). As a result, survival may increase as a function of distance from the pond, particularly for species known for long-distance migrations. Other objectives of my study were to compare variation in survival rates among ponds and to identify causes of mortality and predators of juvenile gopher frogs.

Methods

Study Area

My study took place at five small, isolated ponds and surrounding upland habitats at two sites in the Ocala National Forest, Marion and Putnam Counties, Florida, USA (Figure 2-1). Ponds 3, 5, and 6 are located approximately 9.5 km north of Ponds 7 and 8. The ponds range in size from 0.10 to 0.37 ha and all are located primarily within longleaf pine-wiregrass savannas, although hardwoods (e.g., *Quercus* spp.) had invaded areas around three of the ponds (Ponds 3, 7, and 8). These five ponds are part of an ongoing study of herpetofaunal use, and detailed descriptions of aquatic and terrestrial habitats at these sites are available in Greenberg (2001).

Radio Telemetry

Newly metamorphosed gopher frogs were captured at drift fences (7.6 m in length) placed at 7.6-m intervals to encircle 50% of each pond, except for one frog that was captured by hand in the uplands. Pitfall traps (1.9-L buckets) were positioned on the inside and outside of both ends of each fence (four per fence) so that I could detect the direction of travel. All pitfall traps were checked daily, and a sponge was placed in each trap and moistened daily to prevent desiccation of captured animals. Captured gopher frogs were measured (snout-urostyle length, SUL) to the nearest mm, and weighed to the nearest 0.5 g.

I fitted frogs with R1625 transmitters (Advanced Telemetry Systems, Isanti, MN), which weighed 0.6 g and had a maximum battery life of 33 d. I attached transmitters to frogs in the field using an external belt following the methods of Muths (2003). I threaded a piece of elastic through a prefabricated hole in the transmitter, strung small glass beads onto the elastic, and tied a knot in the elastic. I attached a transmitter to each frog by sliding the belt over the extended hind legs of the frog so that it rested on the frog's waist (Figure 2-2). Only the largest frogs were fitted with transmitters so that the combined mass of the transmitter and belt did not exceed the recommended maximum 10% transmitter-to-body-mass ratio for amphibians (Richards et al. 1994). I released frogs near their point of capture immediately after attaching the transmitter and observed each frog briefly after release to ensure that the movements of frogs were not obviously affected by the transmitter assembly. Any transmitters that were recovered from predators or frogs that shed their belts were redeployed on additional frogs when sufficient battery life remained.

I used a TRX-48S receiver (Wildlife Materials, Inc., Murphysboro, IL) and a hand-held 3-element Yagi directional antenna to track frogs. I located each frog daily until the frog died, the transmitter expired, or the frog shed the transmitter. When a frog was preyed upon, I made every effort to identify the predator by tracking and capturing the predator that had ingested the transmitter, or by examining the condition of the carcass and transmitter. Each time a frog was located, I recorded the date, time, behavioral observations, and habitat characteristics, including whether or not a frog was in a refuge. I defined refuges as burrows excavated by gopher tortoises or small mammals, as well as other underground retreats associated with stumps, roots, or coarse woody debris. I did not include leaf litter and clumps of grass as refuges for the purposes of my analyses, because these habitats offered little protection from predation. I recorded each location by averaging 50 consecutive position readings with a GeoXM Global Positioning System (GPS) unit (Trimble, Sunnyvale, CA), which had an accuracy of 1-3 m. I examined frogs every few days when possible, especially after a long-distance movement, to check for possible skin abrasions caused by the transmitter belt. When I found abrasions on a frog, I removed the transmitter and released the frog. Frogs that developed abrasions were omitted from all data analyses.

Data Analysis

The survival analysis was performed using SAS 9.1 (SAS Inštititute Inc., Cary, NC), and chi-square tests were performed using SYSTAT 10.2 (Systat Software Inc., San Jose, CA). All means are presented ± 1 SE, and alpha was set at 0.05, except where otherwise noted.

I used a Cox regression model (PROC PHREG in SAS) to estimate survival. I included in the analysis all frogs that were tracked until the transmitter or frog expired, as well as frogs that shed their transmitters after I obtained at least one location. In addition to a basic model (without covariates), I tested models with SUL at time of first capture, and Julian date of release as covariates. I also tested models that included two covariates that changed in value through time: for each day of observation, I included whether the frog was in a refuge, and the distance of a frog’s location from the pond of origin, which I measured in ArcGIS 9.2 (ESRI, Redlands, CA) as the distance between the GPS point and the center of the pond, respectively. I compared survival rates among ponds using multiple comparisons with a Bonferroni-corrected alpha (significance considered at $P < 0.008$) to minimize the possibility of Type I statistical error. I did not include Pond 5 in the comparisons because I only tracked one frog at that pond (see Results), and therefore could not compute a mean overall survival rate for that pond.

Results

I outfitted a total of 49 newly metamorphosed gopher frogs with transmitters between 28 May and 19 July 2006. The average size of frogs in my study was 36.8 ± 0.3 mm SUL (range: 31-40 mm), and 7.4 ± 0.1 g (range: 7.0-10.0 g). Excluding Pond 5, where only one captured frog was large enough to carry a transmitter, I fitted a mean of 12 ± 2.9 frogs per pond (range: 7-18 frogs). All frogs were captured at the drift fences, except for one frog that was captured in the uplands, fitted with a transmitter, and released at that location. I assume that it originated from my nearest study pond, approximately 350 m away, although it may have come from one of several other ponds in the area that were not part of my study and are located farther away.

I tracked 32 of the 49 frogs (65.3%) for the life of the transmitter or until I confirmed the death of the frog. I recovered all of the transmitters from the non-surviving frogs ($N = 28$), and I attempted to determine cause of death by tracking the predator that had ingested the transmitter (i.e., snakes, birds) or by examining the remains of the frog and condition of the transmitter (e.g., broken belts, bite marks). I was able to determine cause of mortality for all but one of these frogs. The skeleton of this frog was found after 28 days in the uplands at the entrance to a small, shallow hole associated with vegetation that the frog had occupied for the previous five days. Since the frog was not visually observed in several days and because there were several ants on the carcass, it was unclear whether the frog was killed by ants, or if the frog had desiccated in the refuge and was dragged to the entrance by scavengers.

I was unable to successfully track 17 of the 49 frogs (34.7 %) that I outfitted with transmitters because I removed transmitters due to developing abrasions ($N = 3$), frogs shed their transmitters (*N* = 12), or I lost the signals and could not retrieve the transmitters (*N* = 2). Thus, I could not determine the survivorships or fates of these frogs. I presumed that frogs shed their transmitters when I found undamaged transmitter assemblies (without an associated carcass) near the previous daily location of the frog (< 10 m away) during the initial 1-2 days after release. Frogs probably shed their transmitters when the belts slipped from their waists over their extended hind legs while jumping. Five of the shed transmitters were found in pitfall traps, indicating that frogs most likely slipped through their belts before jumping out of the trap, although it is possible that they were preyed upon while in the traps. For two frogs, I was unable to detect a signal the day after the frogs were released or during the following days, and I never recovered these transmitters; I do not know whether the transmitters failed or the frogs were taken by avian predators.

Four frogs (12.5%) survived until the transmitters expired (mean: 24.8 ± 4.4 d; range: 12-32 d), but one transmitter expired early, so only three frogs (9.4%) are known to have survived for the first month of life in the terrestrial environment (Figure 2-3). Nearly all (*N* = 26, 92.6%) of the non-surviving frogs died during the initial 12 days following release, and all known predation occurred during this period. The mean survival time from release to death was 6.3 ± 1.2 d (range: 1-28 d). The known causes of mortality were predation by mammals, birds, and snakes (common gartersnakes, *Thamnophis sirtalis*; and eastern racers, *Coluber constrictor*), and vehicle mortality (Table 2-1). Snake predation was the largest source of mortality (67.9%; $\chi^2 = 40.571$, df = 4, $P < 0.001$), and frogs were preyed upon equally by common gartersnakes and eastern racers ($\chi^2 = 1.316$, df = 1, $P = 0.251$). Vehicles were responsible for the deaths of three frogs that were run over at various distances from the ponds (98-691 m) on unpaved roads that were used as firebreaks by the U.S. Forest Service, access roads for residents in forest inholdings, and trails for off-road vehicle recreation.

There was no significant effect of SUL at capture ($P = 0.604$), Julian date of release ($P = 0.280$), or distance from pond ($P = 0.539$) on survival ($N = 32$). Frogs with larger and smaller body sizes experienced equal survival probabilities, and frogs that metamorphosed later in the year were just as likely to survive as frogs that metamorphosed earlier in the year. Frogs were preyed upon near the pond edges and in the uplands, at a mean distance of 157 ± 30.1 m (range: 7-691 m) from the ponds, and the probability of survival did not change with increasing distance from the pond. The survival rate for Pond 6 was lower than the survival rates at the other three ponds for which comparisons could be made (Bonferroni-corrected probability, all $P < 0.008$, Figure 2-4) and survival rates among the other three ponds did not differ (Bonferroni-corrected probability, all $P > 0.008$). Predation of frogs by snakes occurred after a mean of 2.6 ± 0.5 d (range: 1-4 d). When compared with Pond 6, the hazard ratios for Ponds 3, 7, and 8 are 0.118, 0.146, and 0.213, respectively, which can each be interpreted as the ratio of the estimated hazard for frogs at that pond to the estimated hazard for frogs at Pond 6 (Allison 1995). Simply put, the likelihood of mortality for frogs at other ponds is 11.8 – 21.3% of the likelihood of mortality for frogs at Pond 6. Because of low sample sizes, I was unable to compare predator composition among ponds.

Underground refuge use was the only factor that significantly influenced survival of juvenile gopher frogs ($P = 0.002$, Figure 2-5). The estimated likelihood of mortality for a frog occupying a refuge was 4.0% of the likelihood of mortality for a frog not occupying a refuge. Only two deaths occurred while frogs were occupying refuges, and circumstantial evidence indicates that predation occurred at the entrances to the refuges, rather than inside the actual cavities. A total of ten frogs occupied at least one burrow or other subterranean refuge, and all refuges were used for three or more consecutive days. The final locations of all surviving frogs were burrows created by gopher tortoises ($N = 3$) or small mammals ($N = 1$). Surviving frogs entered their first refuge within the first five days in the terrestrial environment, and they occupied their final refuge within an additional three days, where they remained until the transmitters expired. Although none of the final locations of surviving frogs were associated with stumps, roots, or coarse woody debris, frogs used these underground refugia between movements to other locations. When not underground, frogs sought refuge in leaf litter or clumps of wiregrass. Frogs were often located in self-constructed shallow depressions in bare soil, cleared of vegetation, and then covered in leaf litter or shaded by vegetation.

Discussion

I found that predation pressure on newly metamorphosed gopher frogs was very high during my study. All known predation occurred within the first two weeks in the terrestrial environment, and only 9.4% of frogs survived their first month following metamorphosis. Snakes of two species were the major predators, although frogs were also preyed upon by mammals and birds. My study supports the findings of other studies that postmetamorphic mortality appears to be highest immediately after metamorphosis, and that the first few months in the uplands is a critical period for terrestrial amphibians that directly affects survival to first reproduction (Trenham et al. 2000, Altwegg and Reyer 2003, Rothermel and Semlitsch 2006).

The use of refuges significantly increased a frog's probability of survival in my study and reduced the risk of death to only 4% of the risk that frogs faced while in the open environment. Frogs that survived to the end of my study located a burrow within the initial days in the terrestrial environment and remained there for the remainder of the life of their transmitter. Frogs that were unable to find suitable refuges and spent more time in the open were more vulnerable to predation. The final refuges occupied by surviving frogs were burrows created by gopher tortoises or small mammals. Although some frogs temporarily sought shelter in underground refuges associated with stumps, roots, and coarse woody debris, they eventually left these locations and either found a burrow or were soon preyed upon.

Although most mortality was attributed to predator-prey interactions, I found that vehicular traffic was also a significant source of mortality of frogs at my sites (Table 2-1). Vehicles were responsible for the deaths of 9.4% of the frogs I tracked. Because all of my study ponds are located less than 100 m from the nearest unpaved road, many frogs were vulnerable to road mortality, especially the longest-living frogs, which moved the longest distances and crossed the most roads (this study, Chapter 3). Of the three frogs killed by vehicles in my study, one had one of the highest survivorships of all frogs at the time of death (25 d), and another had migrated the farthest distance from the pond of all the frogs I tracked (691 m; this study, Chapter 3). Thus, traffic mortality of juvenile gopher frogs has the potential to reduce recruitment of juveniles and to reduce population connectivity, which is primarily achieved through juvenile dispersal (Funk et al. 2005, Gill 1978, Breden 1987, Berven and Grudzien 1990). If the deaths of these two frogs had not occurred, 15.6% of frogs I tracked may have survived for the duration of my study, which would have been a 6.1% increase in my observed survival rate.

Although predators may be concentrated near ponds because they provide a water source as well abundant food sources during periods of amphibian metamorphosis, predation occurred at various distances from the pond and the probability of survival did not decrease with increasing distance from the pond. Predation pressure was extremely high immediately after release and likely occurred before most frogs began to experience significant thermal and osmotic stress. This may partially explain why there was no effect of body size on survival, even though I would expect smaller frogs to experience greater rates of evaporative loss (Thorson 1955, Ray 1958) and have reduced locomotor ability (John-Alder and Morin 1990), which could result in the inability to locate refuges quickly. An absence of body size effect may also be due to the narrow range in body size of frogs within my sample, because I chose only the largest juveniles to carry transmitters.

The survival rate of juveniles was significantly lower at one pond than at three other ponds for which comparisons could be made, and the likelihood of mortality was 78.7-88.2% higher at this pond than at the other ponds. Snakes preyed upon all of the frogs I tracked there within the first week, and none of the frogs were able to successfully locate a burrow or any other refuge. There are several possible explanations for this variation in survival among sites. Local snake densities may have been higher near this pond, so predators may have been able to prey upon more frogs before they were able to locate burrows or other refuges to protect them from predation. Another possibility is that there were fewer burrows available near that pond, so frogs were more vulnerable to predation by spending more time in the open environment while searching for a suitable refuge. Finally, some combination of higher snake densities and lower burrow densities may have been acting simultaneously at this pond to cause low survival rates. Predator densities are dynamic and may change over time, so ponds with lower survival rates of juvenile frogs may be population sinks during one year, but may experience higher rates of survival in other years when predator densities are lower. Thus, longer-term patterns of variability in the production of individual ponds are necessary to understand the population dynamics of species using both aquatic and terrestrial environments.

The commensal relationship between gopher frogs and burrowing vertebrates, particularly gopher tortoises, has long been acknowledged (Test 1893, Carr 1940, Franz 1988, Blihovde

2006), and my results further demonstrate the dependence of gopher frogs on existing burrows. Although observations of adult frogs at burrows have frequently been reported, much less is known about the habitat use and movement patterns of juveniles. During the first month in the terrestrial environment, the survival of newly metamorphosed frogs appears to be dependent on their ability to locate suitable refuges that will protect them from predators and extreme environmental conditions. While predation was the most immediate threat at my sites, desiccation is also a major risk in the xeric habitats where gopher frogs occur. Unlike adults, juveniles are unfamiliar with the locations of burrows, so the availability of burrows appears to be important for the successful recruitment of juveniles into populations.

There are important conservation implications of the commensal relationships between gopher frogs and vertebrate burrow excavators, because several of these burrowing species are imperiled. Perhaps most important is the gopher tortoise, which is imperiled throughout its range and declining in many areas, largely due to habitat loss, degradation, and fragmentation (Auffenberg and Franz 1982, Hermann et al. 2002, McCoy et al. 2006). Any factors that result in declines or extirpations of populations of mammalian and reptilian burrow excavators have the potential to affect both juvenile and adult gopher frogs as well as other commensal species by altering the availability of burrows. Due to the high predation rates of newly metamorphosed gopher frogs and their dependence on burrows for survival during their first month in the terrestrial environment, the density and spatial arrangement of burrows near breeding ponds may be important factors that play a role in the population dynamics of gopher frogs. Conservation decisions should be based on an understanding of all of the life stages and associated habitats of a species to ensure adequate protection, and protection of both breeding ponds and the surrounding uplands is essential for the conservation of amphibian populations. For gopher frogs, an understanding of important microhabitat features (i.e., burrows), as well as information on the amount and spatial orientation of terrestrial habitat used by all terrestrial stages, is necessary to establish protected areas around breeding ponds and properly manage them for both gopher frogs and the burrowing species on which they depend.

Table 2-1. Fates of newly metamorphosed gopher frogs during their first month in the terrestrial habitat. I determined cause of death by tracking and capturing the predator that had ingested the transmitter, or by examining the condition of the carcass and transmitter. Only frogs that could be confirmed dead or that survived until the transmitter expired are included in this summary. Fates could not be determined for the remaining frogs outfitted with transmitters because I removed transmitters due to developing abrasions ($N = 3$), frogs shed their transmitters ($N = 12$), or the lost the signals and I could not retrieve the transmitters ($N = 2$).

Fate	*N* (%)
Survived	4 (12.5)
Preyed upon by snake	
Common gartersnake, *Thamnophis sirtalis*	7 (21.9)
Eastern racer, *Coluber constrictor*	12 (37.5)
Preyed upon by mammal	3 (9.4)
Preyed upon by bird	2 (6.3)
Killed by vehicular traffic	3 (9.4)
Unknown (desiccated or preyed upon)	1 (3.1)
Total	32 (100)

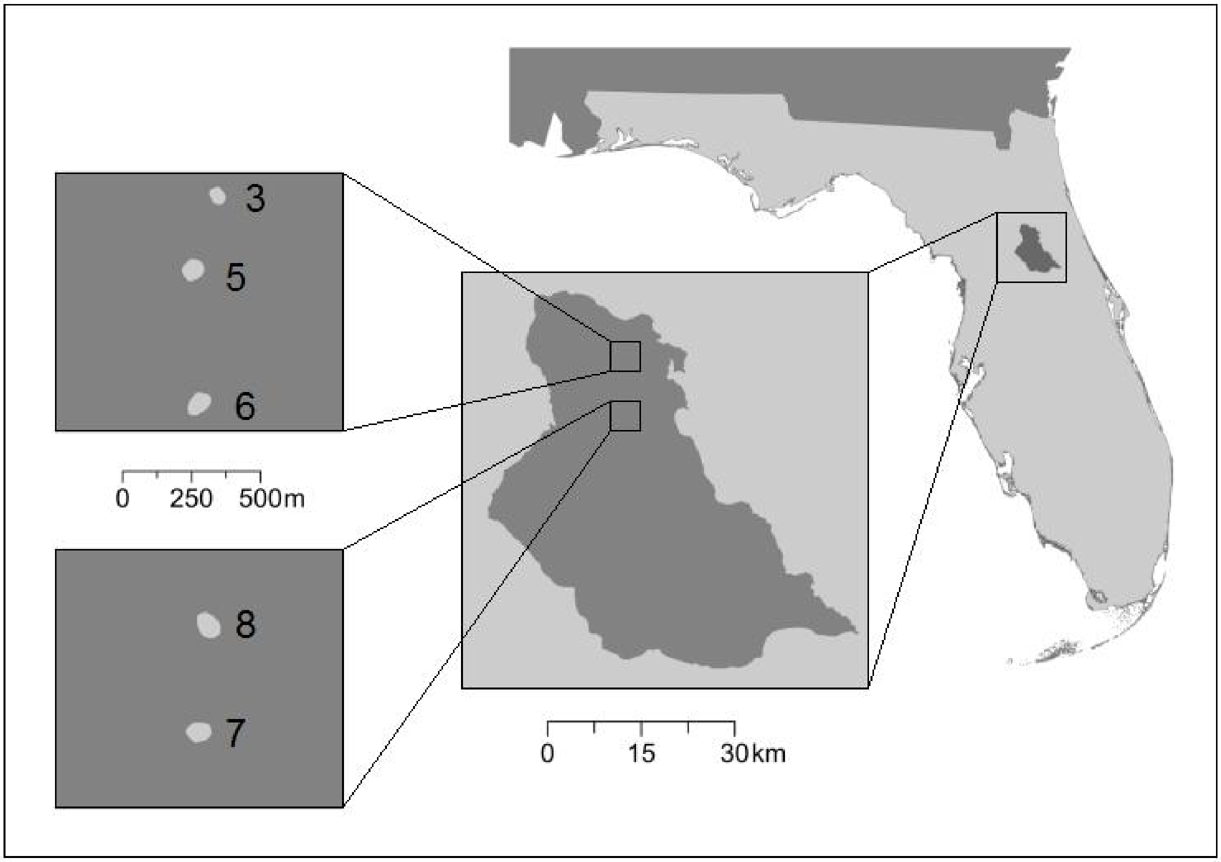

Figure 2-1. Study area. My study took place at five ponds and the surrounding upland habitats at two sites in the Ocala National Forest, Florida. Ponds 3, 5, and 6 are located approximately 9.5 km north of Ponds 7 and 8.

Figure 2-2. Gopher frog wearing a transmitter belt. Belts were made of elastic thread and small, glass beads, and were threaded through a prefabricated hole in the transmitter. The assembly was attached to the frog by sliding the belt over the extended hind limbs of the frog so that it rested on the frog's waist.

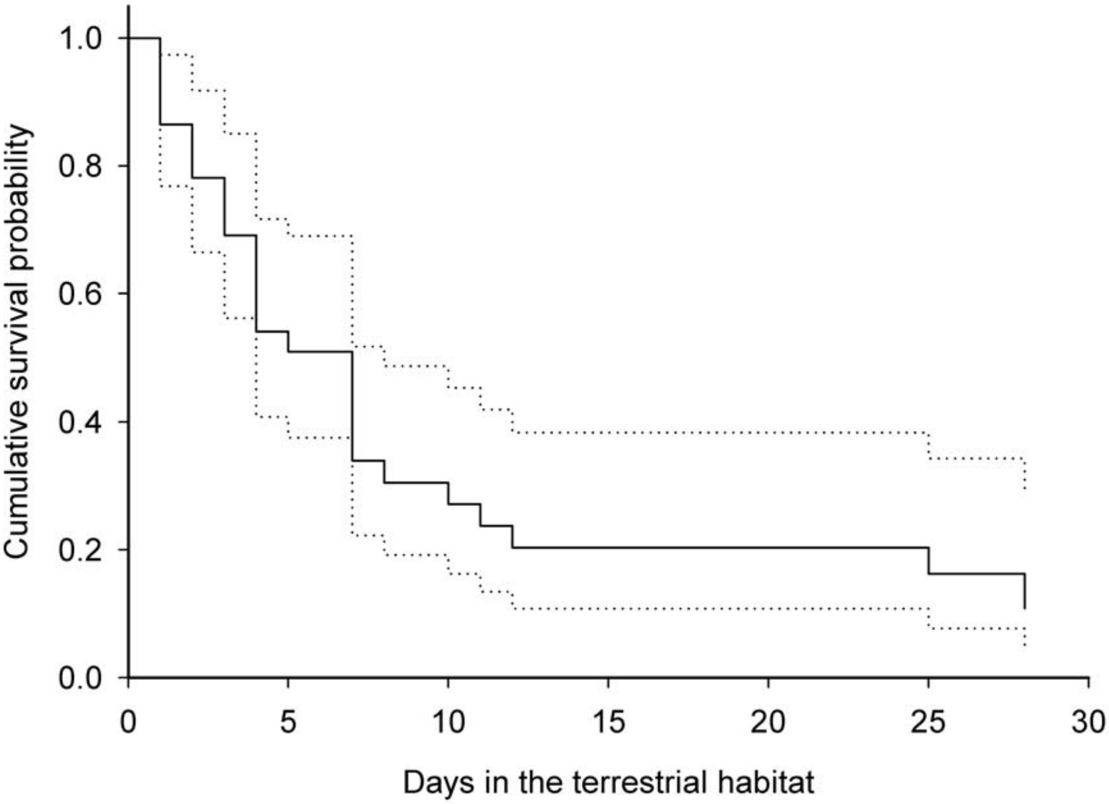

Figure 2-3. Overall cumulative survival probability (solid line) with the 95% confidence interval (dotted lines) for newly metamorphosed gopher frogs during their first month in the terrestrial habitat after emigrating from five ponds.

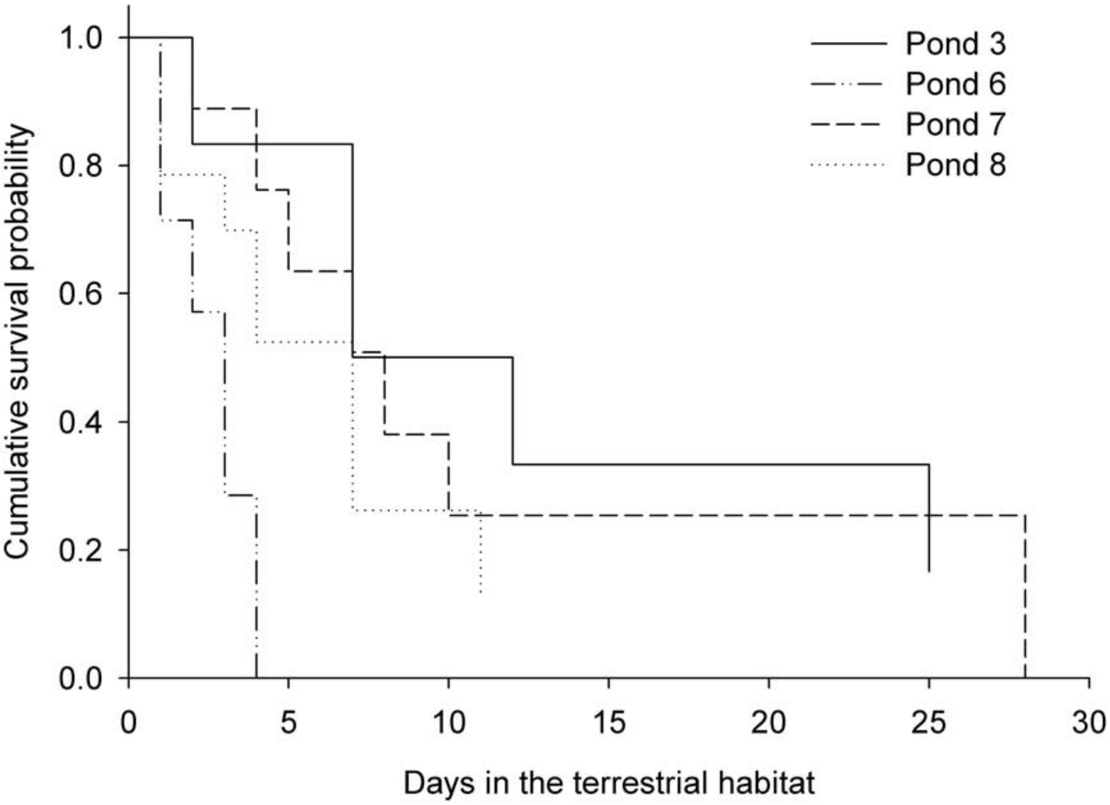

Figure 2-4. Cumulative survival probabilities for newly metamorphosed gopher frogs originating from four ponds. The survival rate for Pond 6 is significantly lower than the survival rates for the other ponds, which do not differ from one another. The other pond I studied (Pond 5) is not shown because I only obtained survival data on one frog there and therefore could not compute a cumulative survival probability.

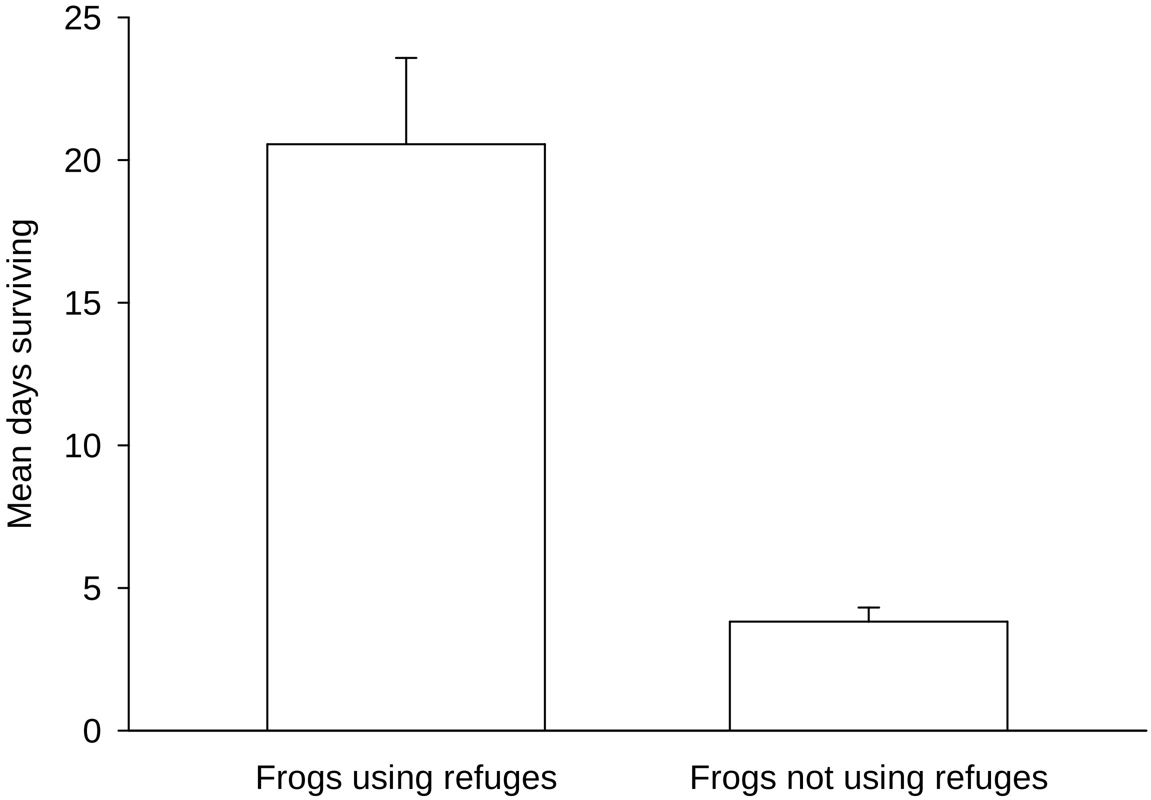

Figure 2-5. Mean survival for newly metamorphosed gopher frogs that used and did not use refuges (+ 1 SE, *N* = 31). Refuges are defined as burrows and other underground retreats associated with stumps, roots, and coarse woody debris, and do not include leaf litter or clumps of grass. Frogs that used at least one refuge were included as using refuges. Mean days surviving refers to the mean of the number of known days that a frog survived or lived until the transmitters expired (*N* = 4). The longest a transmitter lasted, and thus the longest that a frog could "live" was 32 days.

CHAPTER 3
CANOPY CLOSURE AND EMIGRATION BY JUVENILE GOPHER FROGS

Introduction

Human alteration of Earth has been dramatic, resulting in unprecedented losses in global biodiversity (Vitousek et al. 1997, Dirzo and Raven 2003). Although many factors have been implicated, habitat alteration and destruction are thought to be major causes of declines and extinctions worldwide (Vitousek et al. 1997, Semlitsch 2002). Human-mediated habitat disturbances often result in loss of contiguous habitat that serves as movement corridors, especially for species distributed in metapopulations. Pond-breeding amphibians are a classic example of this because populations in breeding ponds become extinct and are recolonized by individuals dispersing from nearby ponds (Hanski and Gilpin 1991, Marsh and Trenham 2001); however, disturbed habitats may become barriers to dispersal and lead to population declines increased local extinctions and decreased recolonization rates (Fahrig and Merriam 1994, Gibbs 1998).

The effects of anthropogenic disturbance are a major concern in areas that are experiencing rapid human population growth and also contain a high density of small, isolated wetlands, such as the southeastern United States (Hefner and Brown 1985). The longleaf pine-wiregrass (*Pinus palustris-Aristida stricta*) ecosystem has declined as much as 98% from its historic range throughout the southeastern United States and many of the remaining tracts of longleaf pine forest are in poor condition as a result of improper management, largely due to fire suppression (Ware et al. 1993, Noss 1989). Historically, frequent, low-intensity fire maintained a predominantly open, pine-dominated habitat, and the exclusion of fire has altered stand structure in many areas by permitting hardwood trees to invade the large gaps that were maintained by fire (Heyward 1939, Ware et al. 1993, Gilliam and Platt 1999). Many plant and animal species that occur in longleaf pine forests have declined as a result of habitat loss and are further threatened by fire suppression in remaining habitat (Van Lear et al. 2005). One such species is the gopher tortoise (*Gopherus polyphemus*), which is associated with open-canopy habitat and is considered a keystone species because tortoises excavate burrows that are used by hundreds of commensal species (Jackson and Milstrey 1989, Boglioli et al. 2000); prominent among these is the gopher frog (*Rana capito*).

Gopher frogs occur primarily within the longleaf pine-wiregrass ecosystem and breed in temporary or semi-permanent ponds, but spend the majority of their life in the terrestrial environment, seeking refuge in the burrows of gopher tortoises and several species of small mammals (e.g., *Podomys floridanus*), as well as stump holes (Lee 1968, Franz 1986, Godley 1992). The gopher frog is considered rare and imperiled throughout its range (Jensen and Richter 2005), and is threatened by loss and alteration of both upland and wetland habitats. Fire suppression is a major threat and degrades habitat quality in both environments (Jensen and Richter 2005). Exclusion of fire from ponds during dry periods encourages growth of trees in and around ponds, and the resulting canopy closure has been linked with lower survival to metamorphosis and reduced size at metamorphosis in larvae of the closely related dusky gopher frog (*Rana sevosa*; Thurgate and Pechmann 2007). Fire suppression in the terrestrial habitat reduces habitat quality for gopher tortoises and burrowing mammal species (Jones and Dorr 2004), which may limit the availability of refuges for gopher frogs in areas where populations of burrowing vertebrates decline. Emigrating frogs may also perceive stands of hardwoods as barriers, which could limit dispersal among breeding ponds. In amphibians, juveniles are thought to be responsible for most interpond dispersal (Gill 1978, Breden 1987, Berven and Grudzien 1990). Despite their importance in linking otherwise isolated populations, information on the habitat preferences and sensitivity to disturbance of newly metamorphosed amphibians is limited, particularly for amphibians associated with open-canopy habitats, such as grasslands and savannas. However, recent studies have found that forest-associated amphibians prefer closed-canopy forest and avoid fields and recent clear-cut areas (deMaynadier and Hunter 1999, Rothermel and Semlitsch 2002, Vasconcelos and Calhoun 2004, Rittenhouse and Semlitsch 2006).

I used radio telemetry to quantify movement patterns of newly metamorphosed gopher frogs emigrating from five small, isolated ponds in the Ocala National Forest, Florida, USA that varied in the amount and distribution of open-canopy longleaf pine habitat and closed-canopy, hardwood-invaded habitat. My objectives were to determine the extent of habitat used by frogs during their first month in the terrestrial habitat and to compare the movements of frogs in relation to habitat characteristics. Because gopher frogs depend on burrows for shelter, I expected frogs to move into areas with high burrow densities and avoid areas where burrows are spare. Thus, my third objective was to examine burrow density in relation to habitat characteristics and the movement patterns of frogs.

Methods

Study Area

My study took place at five small, isolated ponds and the surrounding upland habitats at two sites in the Ocala National Forest, Marion and Putnam Counties, Florida, USA (Figure 3-1). Ponds 3, 5, and 6 are located approximately 9.5 km north of Ponds 7 and 8. The ponds range in size from 0.10 to 0.37 ha and all are located primarily within longleaf pine-wiregrass savannas, although hardwoods (e.g., *Quercus* spp.) have invaded areas around some of the ponds. These five ponds are part of an ongoing study of herpetofaunal use, and detailed descriptions of aquatic habitats at these sites are available in Greenberg (2001).

Movements

I captured newly metamorphosed gopher frogs at drift fences (7.6 m in length) placed at 7.6-m intervals to encircle 50% of each pond, except for one frog that was captured by hand in the uplands. I positioned pitfall traps (1.9-L buckets) on the inside and outside of both ends of each fence (four per fence) so that I could detect the direction of travel. All pitfall traps were checked daily and a sponge placed in each trap was moistened daily to prevent desiccation of captured animals. Captured gopher frogs were measured (snout-urostyle length) to the nearest mm and weighed to the nearest 0.5 g.

I fitted 49 frogs with transmitters and tracked them for varying periods of time between 29 May and 16 August 2006. I used R1625 transmitters (Advanced Telemetry Systems, Isanti, MN), which weighed 0.6 g and had a maximum battery life of 33 days. I attached transmitters to frogs in the field using an external belt following the methods of Muths (2003), which entailed threading a piece of elastic through a prefabricated hole in the transmitter, stringing small glass seed beads onto the elastic, and tying a knot in the elastic. I attached a transmitter assembly to each frog by sliding the belt over the extended hind legs of the frog so that it rested on the frog's waist (Figure 3-2). Only the largest frogs were fitted with transmitters so that the combined mass of the transmitter and belt did not exceed the recommended maximum 10% transmitter-to-body-mass ratio for amphibians (Richards et al. 1994). I released frogs near their point of capture immediately after attaching the transmitter and observed each frog briefly after release to ensure that the movements of frogs were not obviously affected by the transmitter assembly. Any transmitters that were recovered from predators or frogs that shed their belts were redeployed on additional frogs when sufficient battery life remained.

I used a TRX-48S receiver (Wildlife Materials, Inc., Murphysboro, IL) and a hand-held 3-element Yagi directional antenna to track frogs. I located each frog daily until its transmitter expired, the frog died, the frog shed the transmitter assembly, or until the signal was lost. I recorded each location by averaging 50 consecutive position readings with a GeoXM Global Positioning System (GPS) unit (Trimble, Sunnyvale, CA), which had an accuracy of 1-3 m. I used ArcGIS 9.2 (ESRI, Redlands, CA) to measure the distance between successive locations and from the pond of origin. I examined frogs every few days when possible, especially after long-distance movements, to check for possible skin abrasions caused by the transmitter belt. When I found abrasions on a frog, I removed the transmitter and released the frog. Frogs that developed abrasions were removed from all data analyses. Although I used all frogs tracked at all ponds to summarize overall movement patterns, all other sampling and analyses took place at only four of my five ponds because I only captured and tracked one frog at Pond 5.

Orientation

I determined the orientation of frog movements into the uplands at two spatial scales at each pond: (1) from the pond into pitfall traps and (2) from the pond to their final locations in the uplands. All newly metamorphosed gopher frogs captured in pitfall traps were used at the first scale, whereas only transmitter-equipped frogs were used at the second scale. I determined the azimuths of pitfall traps by standing at each pair of pitfall traps and using a compass to determine the direction to the center of the pond, which was marked with a pipe driven into the sediment. I used ArcGIS 9.2 to determine the azimuth from the last known locations of the frogs (before death, or transmitter loss or expiration) to the center of their pond of origin. For frogs that returned to their ponds and were preyed upon or shed their transmitters near the ponds, I used the farthest location from the pond for this analysis.

Upland Habitat Characteristics

To describe upland habitat characteristics I sampled vegetation at 50-m intervals (50, 100, 150, 200, and 250 m from the pond) along four transects at each pond. At the ponds where frogs exhibited directional movement to their final locations, one transect represented habitat that the frogs selected to move through, and three transects represented random habitat. The transect representing selected habitat was determined by averaging the azimuths of all frogs at that pond, and the other three transects representing random habitat were chosen at 90°, 180°, and 270° to the mean azimuth. At the pond where frogs oriented randomly into the uplands, I sampled vegetation at plots along transects following the four cardinal directions. At each plot I sampled the basal area of longleaf pines and hardwoods or sand pine (*Pinus clausa*) using a 10 Basal Area Factor (BAF) wedge prism, and I visually estimated the percent cover of wiregrass, herbaceous vegetation, shrub (< 2.5-cm diameter at breast height), leaf litter, coarse woody debris (≥ 12.5-cm diameter), and bare ground in circular 12-m^2 plots. I also measured the proportion of overstory cover in each plot using a spherical densiometer (Lemmon 1956).

Burrow Density

I located all gopher tortoise burrows and attempted to find all small mammal burrows (e.g., *Geomys pinetus* and *Podomys floridanus*) within 100 m of ponds by surveying adjoining 2-m wide transects encircling each pond. I recorded the GPS location of each burrow and determined the percentage of canopy cover above each burrow entrance using a spherical densiometer. Using ArcGIS 9.2, I buffered each pond by 100 m and split each buffered area into two polygons: the area selected by frogs, and the random area. I designated the selected area as the polygon encompassing the range of azimuths representing the final locations of frogs, and the random area as the remaining area within the buffer (Figure 3-3). At the pond where frogs exhibited random orientation, I divided the buffered pond into three polygons based on the final location of each of the three frogs that I located at least once, and designated those polygons as selected habitat for the analyses.

Statistical Analysis

I analyzed data using ORIANA 2.0 (Kovach Computing Services, Anglesey, UK) for analyses involving circular data, and SYSTAT 10.2 (Systat Software Inc., San Jose, CA) for all other statistical analyses. Alpha was set at 0.05 for significance testing, and all means presented are ± 1 SE. I assumed that any deviance from normality in raw datasets did not affect my results, and therefore used parametric tests in all analyses, even when transformations failed to correct these problems (Johnson 1995).

Results

Movements

The maximum distance that frogs were located from breeding ponds was 691 m (mean: 168.9 ± 30 m; $N = 31$), and the final locations of surviving frogs were located a mean distance of 269.7 ± 126.2 m from ponds (range: 110.3-640.7 m; $N = 4$). The mean total distance moved by frogs, determined by summing the straight-line distances between successive locations, was 221.0 ± 33.6 m (range: 30.7 – 725.7 m; $N = 31$). The maximum distance from the ponds did not differ between surviving and non-surviving frogs ($t = -1.309$, df = 29, $P = 0.201$), nor did the total distance moved ($t = -1.031$, df = 29, $P = 0.311$).

The mean total distance moved was significantly greater than the farthest straight-line distance from the pond (paired *t*-test, $t = 4.683$, df = 30, $P < 0.001$), indicating that frogs did not move along straight paths while emigrating from ponds. While frogs generally continued to move away from ponds with successive movements, some frogs (22.6%) returned to the ponds from up to 116.5 m away and made a second emigration attempt (Figure 3-13).

There are many unpaved roads near my study ponds, which are used as firebreaks by the U.S. Forest Service, access roads for residents in forest inholdings, and trails for off-road vehicle recreation (Figures 3-9, 3-10, 3-11, 3-12, 3-13). All of my study ponds are located less than 100 m from the nearest unpaved road; therefore, frogs frequently crossed roads. Of the frogs that I located at least once ($N = 29$), 58.6% crossed roads, and for frogs that I located at least twice ($N = 20$), 85.0% had crossed roads. Thus, dirt roads did not seem to be barriers by the frogs, and in fact, it appears that several frogs used them as migration corridors. For example, at Pond 8, a road was located perpendicular to the pond in an east-west direction, and several frogs were found in successive locations along the road (Figure 3-13).

Even though the mean distance between successive daily locations was 62.0 ± 7.8 m (range: 1.4-324.7 m; $N = 118$), frogs often moved large distances over short periods of time, with 17.9% of movements greater than 100 m, and 7.1% greater than 200 m. Although I only tracked frogs during the day, frogs appeared inactive and were found in very sheltered locations (e.g., in burrows, buried in soil, or deep under leaf litter), except occasionally during rainy days, indicating that most movements occurred at night. Some movements (37.2%) were associated with rainfall events during the previous 24 h, including 46.7% of long-distance movements greater than 100 m ($N = 15$).

Orientation

Frogs moved randomly from the pond into the pitfall traps at all ponds (Rayleigh test, all $P > 0.05$), and transmitter-equipped frogs exhibited significantly nonrandom orientation into the uplands at three ponds (Ponds 3, 7, and 8; Figure 3-3), and random orientation into the uplands at one pond (Pond 6; $Z = 0.411$, $P = 0.701$). Frogs moved from Pond 3 in an arc ranging south to southwest (Figures 3-3, 3-9). At Pond 7, frogs moved in an arc ranging from southeast to west (Figures 3-3, 3-12), and frogs emigrated from Pond 8 in an arc ranging from southwest to north (Figures 3-3, 3-13).

Upland Habitat Characteristics

Frogs selected upland habitats that supported a lower basal area of hardwoods and sand pine (Figure 3-4), lower percentage of canopy cover (i.e., more open canopies; Figure 3-5), higher percent cover of wiregrass (Figure 3-6), and lower percent cover of leaf litter (Figure 3-7) when compared with random areas (repeated-measures analysis of variance [ANOVA] with habitat [selected or random] as the factor and distance from pond as the repeated measure; Table 3-1). Selected and random habitats did not differ in basal area of longleaf pines and snags, or percent cover of herbaceous plants, bare ground, and coarse woody debris (Table 3-1). With increasing distance from ponds, percent cover of wiregrass increased (Table 1; Figure 3-6) and there was a trend toward decreasing basal area of hardwoods and sand pine ($P = 0.065$, Table 3-1; Figure 3-4). There was no interaction between habitat (selected or random) and distance from pond for any habitat variable (Table 3-1).

Burrow Density

I located 33 gopher tortoise burrows and 14 small mammal burrows within 100-m buffers around the four ponds. There was an average of 2.4 ± 0.4 burrows per ha within a 100-m buffer around each pond, and burrow density did not vary between selected and random habitats (two-way analysis of covariance [ANCOVA] with direction and burrow type [gopher tortoise or mammal] as factors and habitat area as the covariate; $F_{1,13} = 0.066$, $P = 0.802$). Burrows were located in areas with relatively open canopies, and gopher tortoise burrows were located in areas with significantly lower proportions of canopy cover of light than mammal burrows ($t = -3.714$, df = 45, $P = 0.001$). Gopher tortoise burrows were located in areas with an average of 48.3 ± 2.4 % canopy cover (range: 16-72 % canopy cover), and mammal burrows were located in areas with an average of 66.1 ± 4.9 % canopy cover (range: 41-100 % canopy cover).

Upland habitats surrounding Ponds 3, 7, and 8, were patchy, and although the open-canopy patches of habitat were located primarily within the selected habitat, these patches often extended from the selected habitat into the random habitat. Although burrow densities were similar in selected and random habitats, I predicted that burrow density would be higher in the open-canopy habitat. These habitat patches can be easily distinguished on aerial photographs, so using ArcGIS 9.2 I delineated all patches of open-canopy habitat (1-2 patches per pond) within the 100-m buffers of ponds, and determined the densities of burrows in all open-canopy and closed-canopy habitat patches. I then compared the densities of burrows between these habitats using a two-way ANCOVA with habitat type (open- or closed-canopy) and burrow type as factors and area as the covariate. I found that there were significantly higher densities of burrows in the open-canopy habitats ($F_{1,15} = 16.430$, $P = 0.001$; Figure 3-8). There was a significant habitat type × burrow type interaction, revealing that the difference in burrow density between habitat type was much greater for gopher tortoise burrows than for mammal burrows ($F_{1,15} = 14.117$, $P = 0.018$; Figure 3-8).

After I delineated the open-canopy patches and overlaid selected areas, it was apparent that the areas that frogs selected to move through were located at the center of the largest patch of open habitat at each pond (Figure 3-3). Frogs avoided moving through the edges of the open-canopy habitat, where the forest stand structure changed into a more closed-canopy habitat invaded by hardwoods and sand pine. The movement paths of individual frogs further support this finding; all of the frogs that I tracked began moving towards the open-canopy habitat with their first movement, sometimes even moving around the pond before migrating toward the open habitat and away from the pond (Figures 3-9, 3-12, 3-13). The one exception is the frog at Pond 3 that moved 140 m into the closed-canopy habitat and then reversed its direction, moving in a straight line into the open-canopy habitat in the direction that the other frogs had taken (Figure 3-9).

Discussion

Newly metamorphosed gopher frogs are capable of moving long distances immediately after exiting ponds. The maximum distance that frogs migrated from a pond during their first month in the terrestrial environment was 691 m. Despite a high mortality rate (87.5%; this study, Chapter 2) and the limited temporal scope of my study, I documented many long-distance movements over 24 hr and also long distances covered over longer periods of time. For example, one frog moved a total of 665 m in a series of three movements over seven days before entering a small mammal burrow, where it remained for the next 25 days. Given the difficulty in detecting long-distance movements in amphibians (Marsh and Trenham 2001), I am undoubtedly underestimating the dispersal abilities of juvenile gopher frogs. Furthermore, adult gopher frogs have been found up to 2 km from breeding ponds (Franz et al. 1988), and juvenile amphibians are thought to be responsible for most long-distance dispersal (Breden 1987, Funk et al. 2005). Regardless of migratory capability, these are the first reported movements of juvenile gopher frogs, which support the growing consensus that large areas of terrestrial habitat surrounding aquatic habitats are necessary for gopher frogs and other semi-aquatic species (Richter et al. 2001, Semlitsch and Bodie 2003, Blihovde 2006).

Unpaved roads did not seem to be barriers for the frogs; many frogs crossed the numerous roads near my study ponds (Fig. 2), and it also appears that several frogs used them as migration corridors. For example, several frogs were found in successive locations along a road leading away from Pond 8 (Fig. 2B). Migrating along roads may allow frogs to migrate more rapidly than would be possible through vegetated areas. Brown et al. (2006) observed the use of roads as dispersal corridors for cane toads (*Bufo marinus*), and found that toads were able to move more rapidly along roads than in more densely vegetated habitats. Vehicle mortality has been found to be a significant source of mortality for juvenile gopher frogs (this study, Chapter 2), and may potentially reduce connectivity of populations by limiting long-distance dispersal to nearby ponds.

Frogs oriented randomly into the pitfall traps after exiting the ponds, but following release from the traps, frogs exhibited directional movement into the uplands at three of four ponds (Figure 3-3). Greenberg (2001) found that juvenile gopher frogs returning to ponds at my sites were distributed nonrandomly in pitfall traps at Ponds 7 and 8 each year from 1995 to 1998. Frogs returned from a west-southwest direction to Pond 7, the same general direction that frogs moved in my study, although frogs returned from the east to Pond 8, while frogs in my study moved towards the west.

The direction that frogs moved from the pond is likely a reflection of the distribution of favorable terrestrial habitat, which has been shown to influence movement patterns in other amphibians (Dodd and Cade 1998, deMaynadier and Hunter 1999, Rothermel and Semlitsch 2002, Vasconcelos and Calhoun 2004, Rittenhouse and Semlitsch 2006). Although all of my study ponds are located primarily within longleaf pine-wiregrass uplands, the terrestrial habitat at the three ponds where I observed directional movement was patchy and contained closed-canopy areas that had been invaded by hardwoods, whereas the habitat surrounding the pond where frogs emigrated randomly was contiguous longleaf pine-wiregrass habitat. Where movement was directional, frogs moved through the center of the largest open-canopy patches, avoiding the edges where the hardwoods began to encroach (Figure 3-3). My habitat selection data confirm this observation. Frogs moved into habitats that had open canopies and were characterized by few hardwood trees, high percent cover of wiregrass, and low percent ground cover of leaf litter (Table 3-1; Figures 3-4, 3-5, 3-6, 3-7).

I found that the densities of gopher tortoise and small mammal burrows at my sites were much higher in the patches of open-canopy habitat than in the more closed-canopy patches associated with hardwoods (Figure 3-8). These results support the conclusions of other studies that canopy closure is one of the main factors influencing the distribution of gopher tortoise burrows (Boglioli et al. 2000, Hermann et al. 2002, Jones and Dorr 2004). Canopy closure reduces foraging and nesting conditions for tortoises and is positively related to the occurrence of abandoned burrows (Jones and Dorr 2004). Therefore, the number of suitable refuges for gopher frogs could decline in areas where canopy closure increases and populations of gopher tortoises and other burrowing vertebrates decline.

Because gopher frogs are dependent on the burrows of gopher tortoises and small mammals for shelter, frogs are most likely choosing to move into open-canopy habitats because burrows are more abundant in those areas. Thurgate (2006) found that the number of burrows in the terrestrial habitat was significantly higher in habitats where dusky gopher frogs were present as compared to where they were absent. Thus, burrows abundance is important for gopher frogs, and by selecting areas with high burrow densities, frogs will be able to locate a burrow more quickly. Unlike adult gopher frogs, which are familiar with their surroundings and are able to home back to specific burrows after breeding or translocation (Richter et al. 2001, Blihovde 2006), juveniles are unfamiliar with the landscape and the locations of burrows. Finding a suitable refuge quickly is extremely important for newly metamorphosed gopher frogs because their small body size makes them particularly susceptible to desiccation (Newman and Dunham

1994) and predation, which has been observed to be extremely high with most mortality occurring within the first week in the terrestrial environment (this study, Chapter 2).

Ponds situated within large tracts of hardwood-invaded longleaf-pine forest may be population sinks due to high mortality of newly metamorphosed gopher frogs. The ability of amphibians to orient towards habitat features has been shown to decrease with distance (Mazerolle and Vos 2006), so if frogs cannot detect the direction of favorable habitat, they may never locate these areas and the associated burrows, and will eventually succumb to desiccation or predation. I documented several frogs reversing their direction of migration from the pond, presumably because they were unable to locate suitable microhabitats or refugia (Figure 3-13). This behavior has also been observed in other amphibians in fragmented landscapes (Rothermel and Semlitsch 2002, Rothermel 2004, Rittenhouse and Semlitsch 2006). All of the frogs that I tracked migrated towards open-canopy habitat except for one frog that moved 140 m into closed-canopy habitat and then reversed its direction and moved into open-canopy habitat (Figure 3-9). Similarly, several frogs returned to the ponds (Figure 3-13), the only known landmark to newly metamorphosed frogs after their initial dispersal, presumably because they were unable to locate suitable habitat or refuges and began to experience stress from water loss.

The quality of terrestrial habitats surrounding breeding ponds may affect regional population dynamics in addition to local demography. Pond-breeding amphibians are often represented as metapopulation models in which populations in breeding ponds become extinct and are recolonized by individuals originating from nearby ponds (Marsh and Trenham 2001, Smith and Green 2005). My results suggest that extinction rates may be higher and recolonization rates may be lower for gopher frog populations at ponds located in closed-canopy habitat. Populations may experience more frequent extinctions if survival to maturity is low in fire-suppressed habitat, resulting in small populations, which can become increasingly susceptible to stochastic extinction processes (Pimm et al. 1988). Recolonization rates may also be lower in large tracts of fire-suppressed habitat because closed-canopy areas are barriers to frogs. Frogs that disperse from other ponds will move though open-canopy habitat and avoid closed-canopy habitat that contains potential breeding ponds or that may lead to high quality terrestrial and aquatic habitat beyond their perception (e.g., Figure 3-3). Thus, pond occupancy is controlled by the spatial configuration of breeding ponds and terrestrial habitats (Marsh and Trenham 2001), and both must be protected and managed appropriately to protect gopher frogs and other pond-breeding amphibians associated with longleaf pine forests.

Management Implications

Terrestrial habitats surrounding wetlands are important habitats for many semi-aquatic species and must be protected (Semlitsch and Bodie 2003). Because juvenile gopher frogs use roads as migration corridors and because vehicular traffic is a significant source of mortality (this study, Chapter 2), all roads near breeding ponds should be closed permanently or at least during periods of metamorphosis (May-July in central Florida; Greenberg 2001). My results indicate that terrestrial habitats must not simply be protected from destruction and alteration, but must also be actively managed to maintain high habitat quality. Juvenile gopher frogs avoid closed-canopy habitats and prefer open-canopy habitats, which contain higher densities of burrows, an important determinant of post-metamorphic survival (this study, Chapter 2). Thus, gopher frog populations will benefit from maintaining open-canopy longleaf pine forests and restoring habitat that has been invaded by hardwoods as a result of fire suppression.

Because natural fires no longer maintain longleaf pine forests, land managers must use prescribed fire to mimic the historical fire regime. Managers should apply an appropriate fire regime (Means et al. 2004) to maintain open-canopy habitat surrounding breeding ponds that continues all the way to the pond edge in order to maintain connectivity between ponds and the surrounding uplands, which will facilitate emigration by juvenile gopher frogs. Habitat should also be restored at historically open-canopy ponds where canopy closure has occurred. In heavily fire-suppressed areas where fire alone cannot successfully remove trees, restoration may involve the application of prescribed fire in conjunction with other restoration practices, such as the careful removal of trees using mechanical practices or herbicides (Brockway and Outcalt 2000).

Table 3-1: Habitat characteristics (mean values ± SE) and basal area (BA) of trees in random habitat and habitat selected by juvenile gopher frogs while emigrating from four ponds. Habitat characteristics were sampled along transects at 50-m intervals (50, 100, 150, 200, and 250 m from the pond) and statistical results are presented for a repeated-measures ANOVA with habitat (selected or random) as the factor and distance from pond as the repeated measure. Degrees of freedom were 1 for the treatment, 4 for the error, and 4 for the interaction term.

	Habitat				
Habitat characteristic	Selected	Random	Habitat *P*	Distance *P*	Habitat × distance *P*
Wiregrass (% cover)	27.7 ± 3.9	0.8 ± 0.4	0.009	0.001	0.547
Herbaceous (% cover)	13.9 ± 3.5	0.8 ± 0.4	0.445	0.207	1.000
Leaf litter (% cover)	28.2 ± 3.7	71.1 ± 17.9	0.010	0.853	0.796
Bare ground (% cover)	4.6 ± 1.5	7.0 ± 2.2	0.393	0.275	0.986
Coarse woody debris ≥ 12.5 cm (% cover)	0.8 ± 0.3	3.7 ± 1.1	0.091	0.112	0.379
Shrub (% cover)	25.9 ± 4.2	19.0 ± 3.3	0.389	0.229	0.075
Canopy cover (%)	38.2 ± 3.3	67.3 ± 4.8	0.006	0.243	0.630
Longleaf pine BA (m^2)	3.9 ± 0.4	3.1 ± 0.4	0.362	0.333	0.322
Hardwoods and sand pine BA (m^2)	0.7 ± 0.3	3.5 ± 0.6	0.034	0.065	0.322
Snag BA (m^2)	0.8 ± 0.4	0.2 ± 0.1	0.429	0.276	0.871

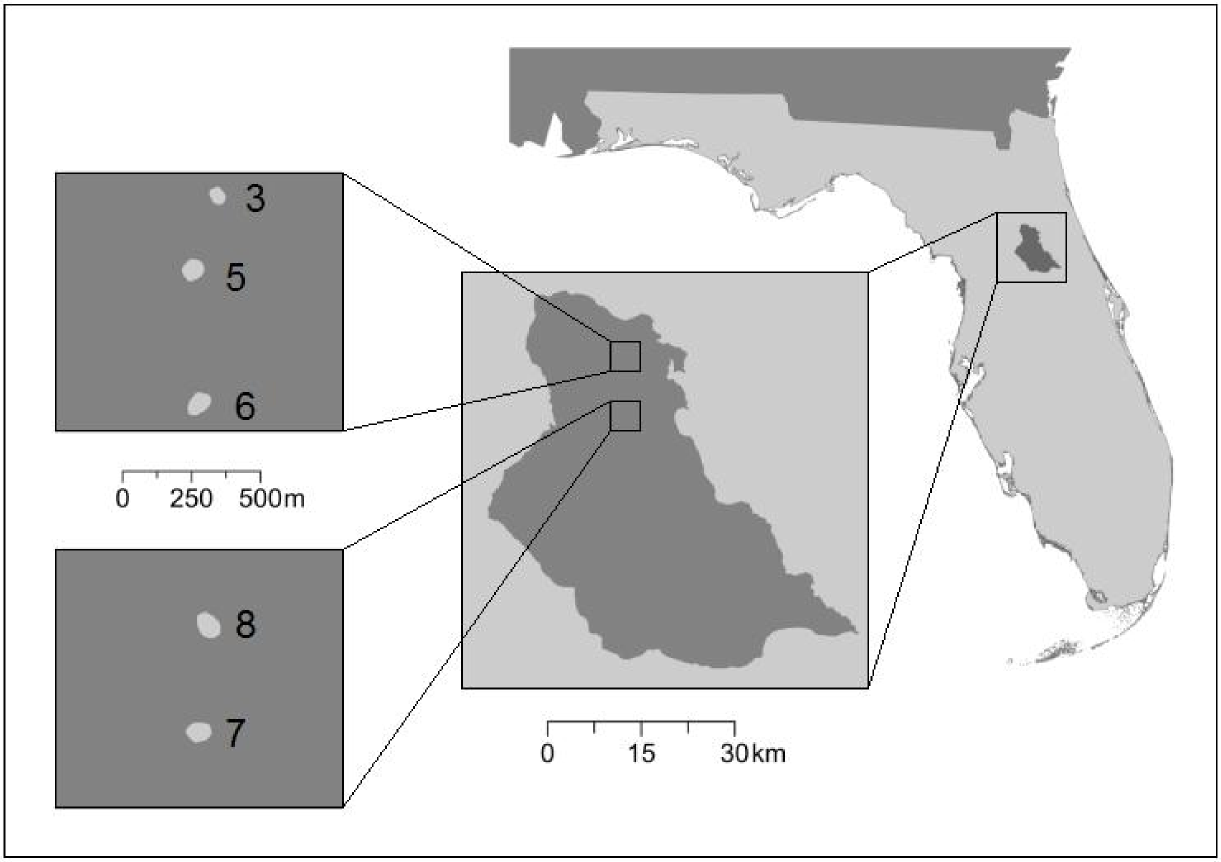

Figure 3-1. Study area. My study took place at five ponds and the surrounding upland habitats at two sites in the Ocala National Forest, Florida. Ponds 3, 5, and 6 are located approximately 9.5 km north of Ponds 7 and 8.

Figure 3-2. Gopher frog wearing a transmitter belt. Belts were made of elastic thread and small, glass beads, and were threaded through a prefabricated hole in the transmitter. The assembly was attached to the frog by sliding the belt over the extended hind limbs of the frog so that it rested on the frog's waist.

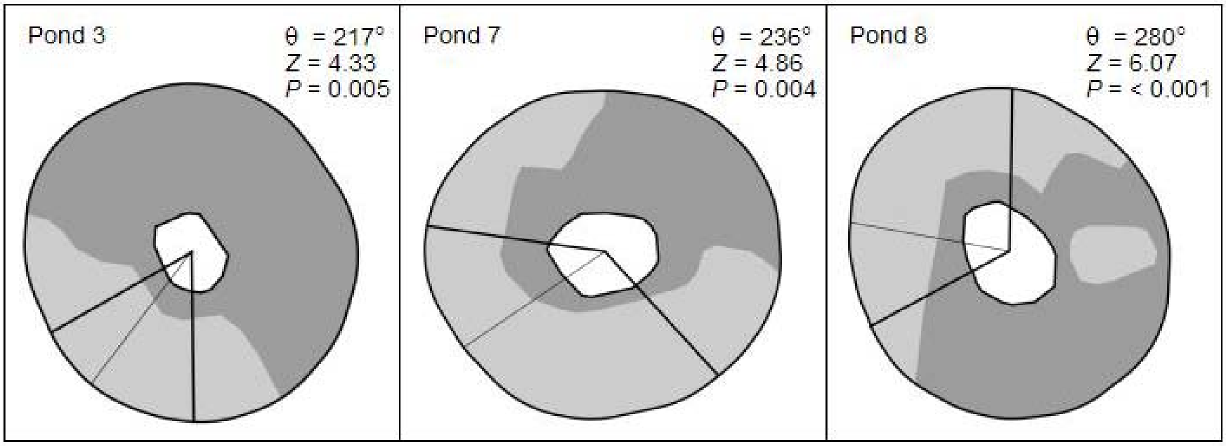

Figure 3-3. Directional orientation of juvenile gopher frogs emigrating from three ponds. Thick lines indicate the range in azimuths moved by frogs from the center of the pond to their final location in the uplands, determined through radio telemetry, and a thin line represents the mean azimuth. The mean azimuth (θ), Rayleigh test statistic (*Z*), and significance value (*P*) are given for each pond. Frogs moved through the largest patch of open-canopy habitat (lightly shaded) at each pond and avoided the closed-canopy habitat (darkly shaded) within a 100-m buffer of each pond.

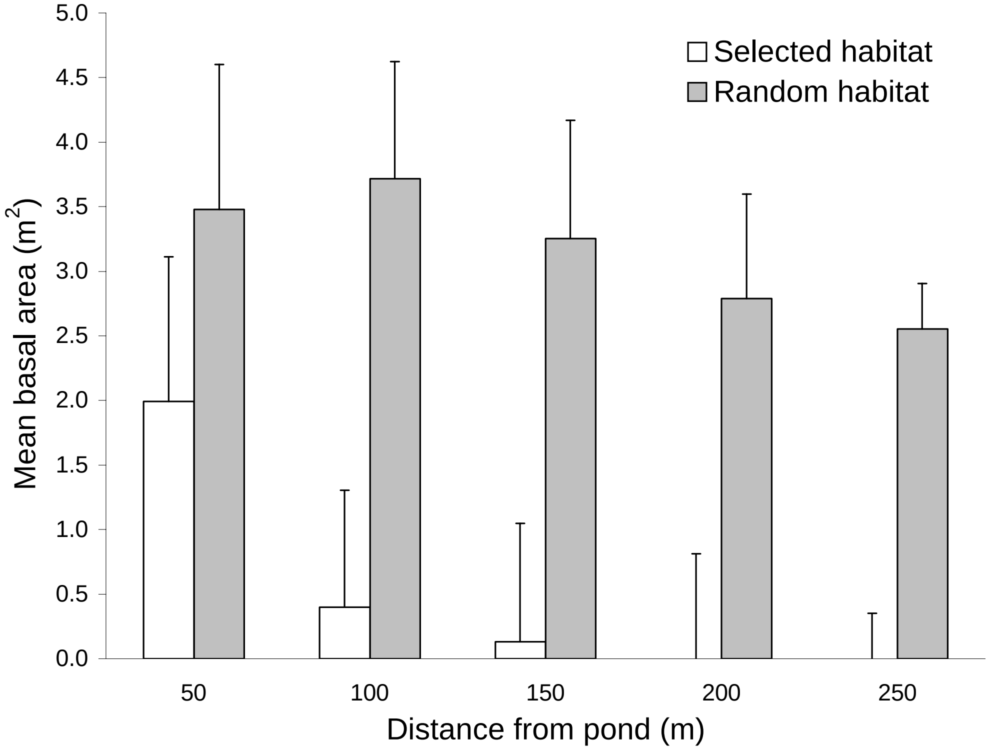

Figure 3-4. Mean basal area (+ SE) of hardwoods (e.g., *Quercus* spp.) and sand pine (*Pinus clausa*) at various distances from ponds in habitat selected by juvenile gopher frogs while emigrating from four ponds and random habitat.

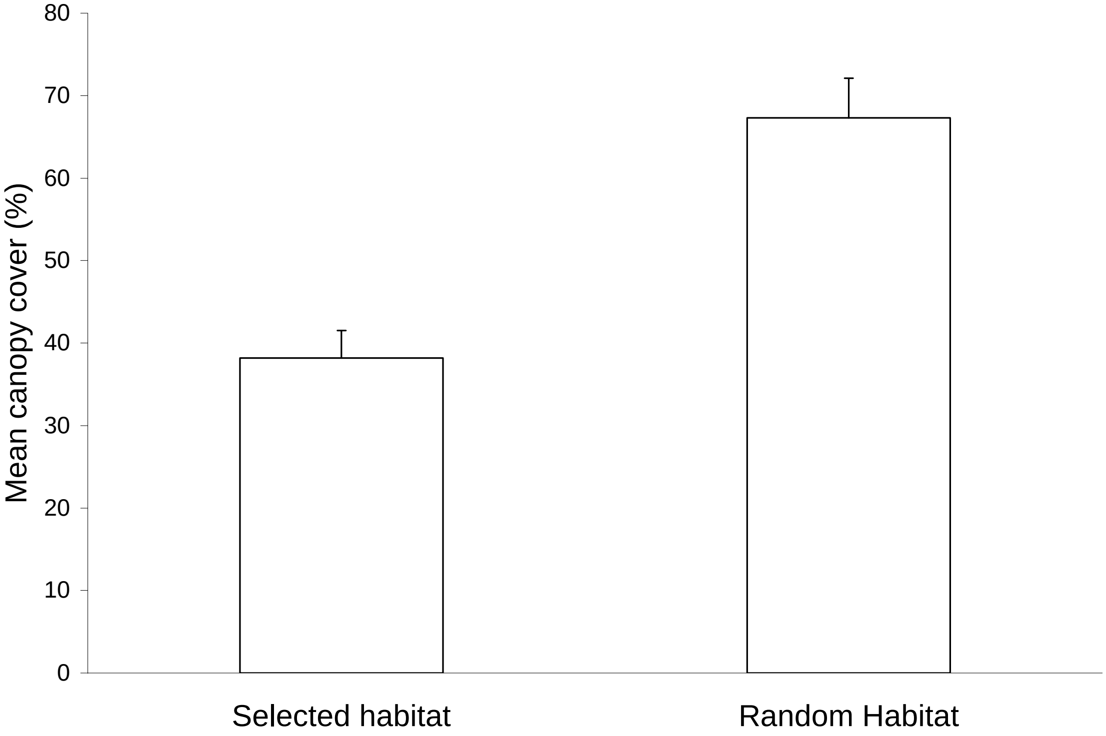

Figure 3-5. Mean percentage of canopy cover (+ SE) in habitat selected by juvenile gopher frogs while emigrating from four ponds and random habitat.

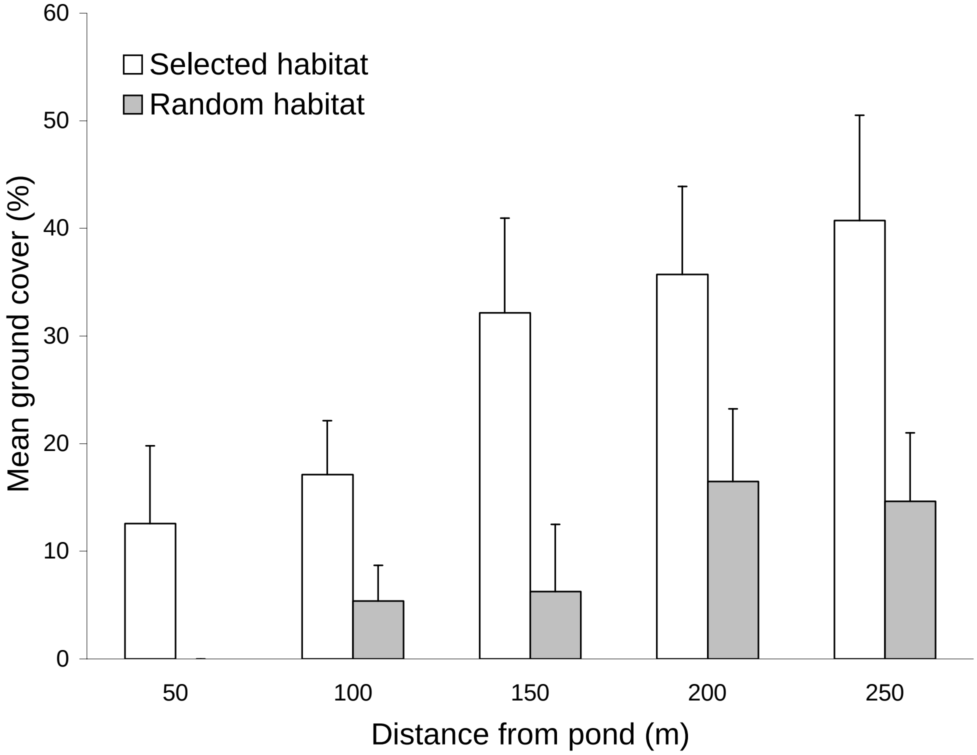

Figure 3-6. Mean percent cover (+ SE) of wiregrass (*Aristida stricta*) at various distances from ponds in habitat selected by juvenile gopher frogs while emigrating from four ponds and random habitat.

Figure 3-7. Mean percent cover of leaf litter in habitat selected by juvenile gopher frogs while emigrating from four ponds and random habitat.

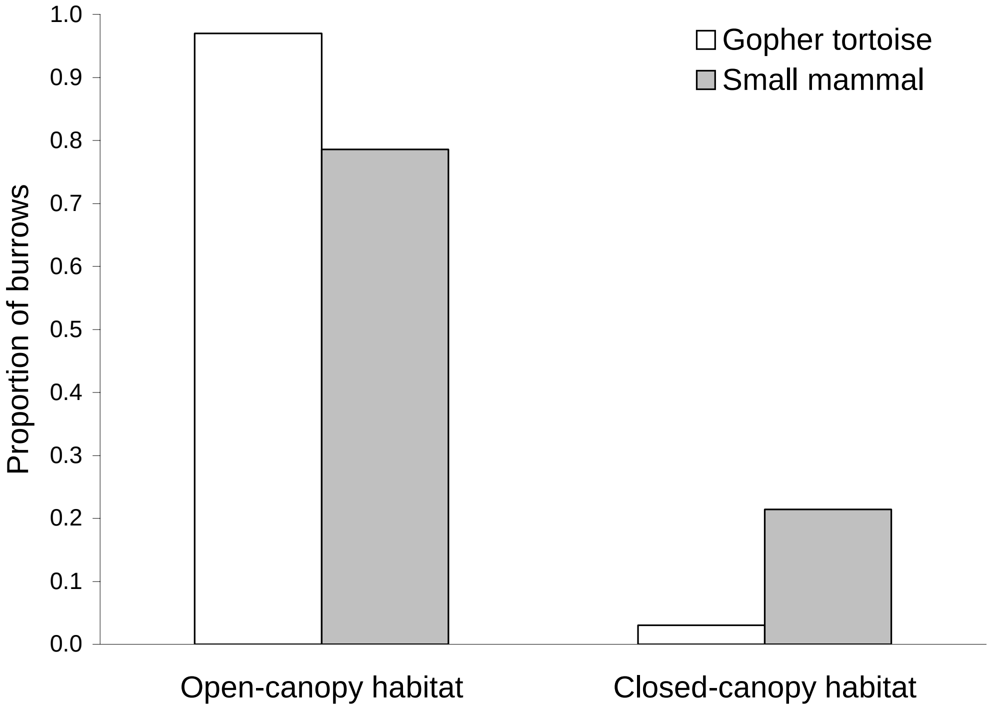

Figure 3-8. Proportion of gopher tortoise (*Gopherus polyphemus*; *N* = 33) and small mammal (e.g., *Geomys pinetis*; *N* = 14) burrows in open-canopy and closed-canopy habitats within 100 m of four ponds.

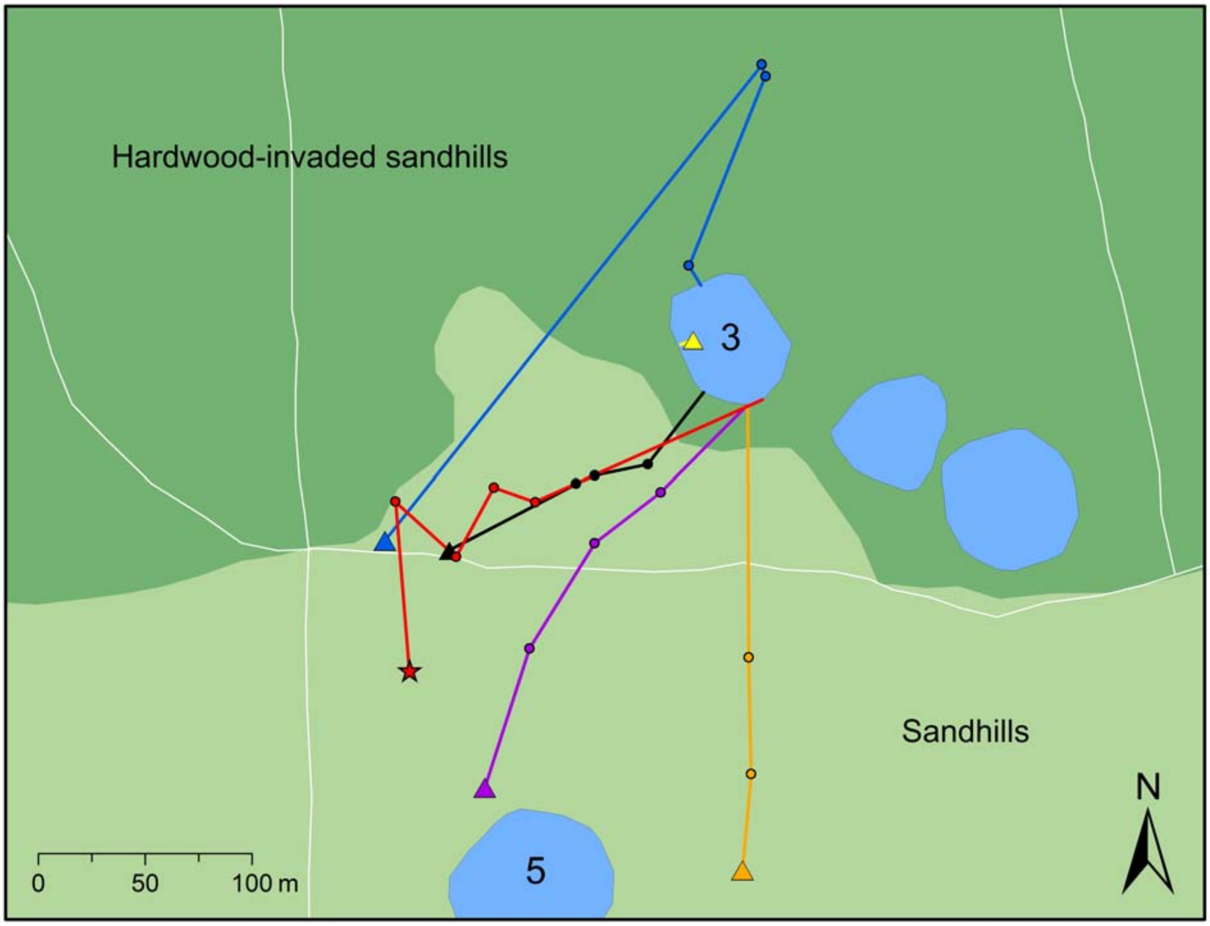

Figure 3-9. Movement paths of juvenile gopher frogs emigrating from Pond 3. The surrounding terrestrial habitats are sandhills (light green) and hardwood-invaded sandhills (dark green). The different colored paths represent different frogs. Paths were created by drawing straight lines between daily locations. A star represents the last known location of a surviving frog, and triangles represent that last known locations of frogs before predation or death by vehicular traffic. The thin, white lines represent unpaved roads. Other nearby ponds are also shown, including Pond 5, another pond used in this study.

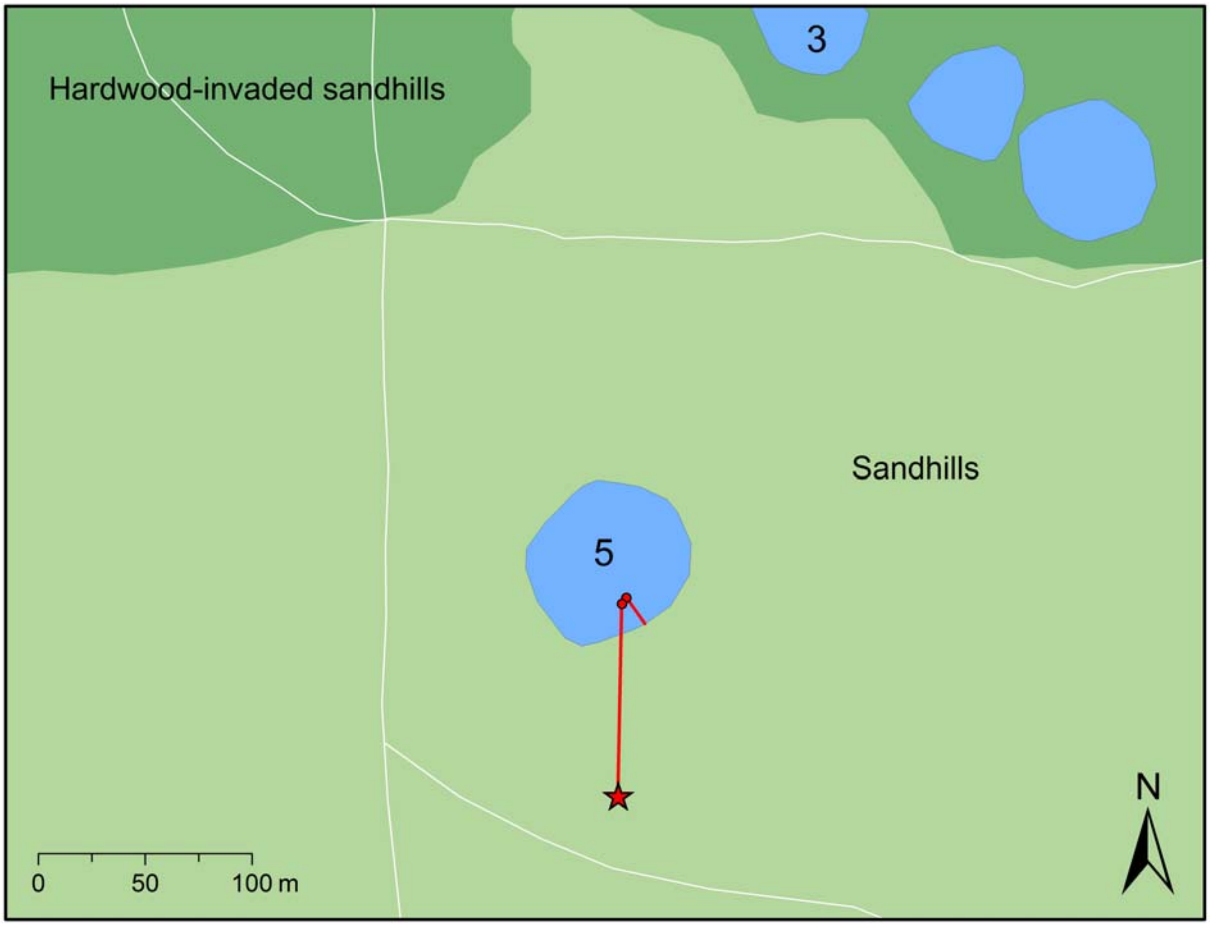

Figure 3-10. Movement path of a surviving juvenile gopher frog emigrating from Pond 5. The pond is surrounded by sandhill habitat (light green), with hardwood-invaded sandhill habitat (dark green) more than 180 m away. A star represents the last known location of the frog, and the thin, white lines represent unpaved roads. Other nearby ponds are also shown, including Pond 3, another pond used in this study.

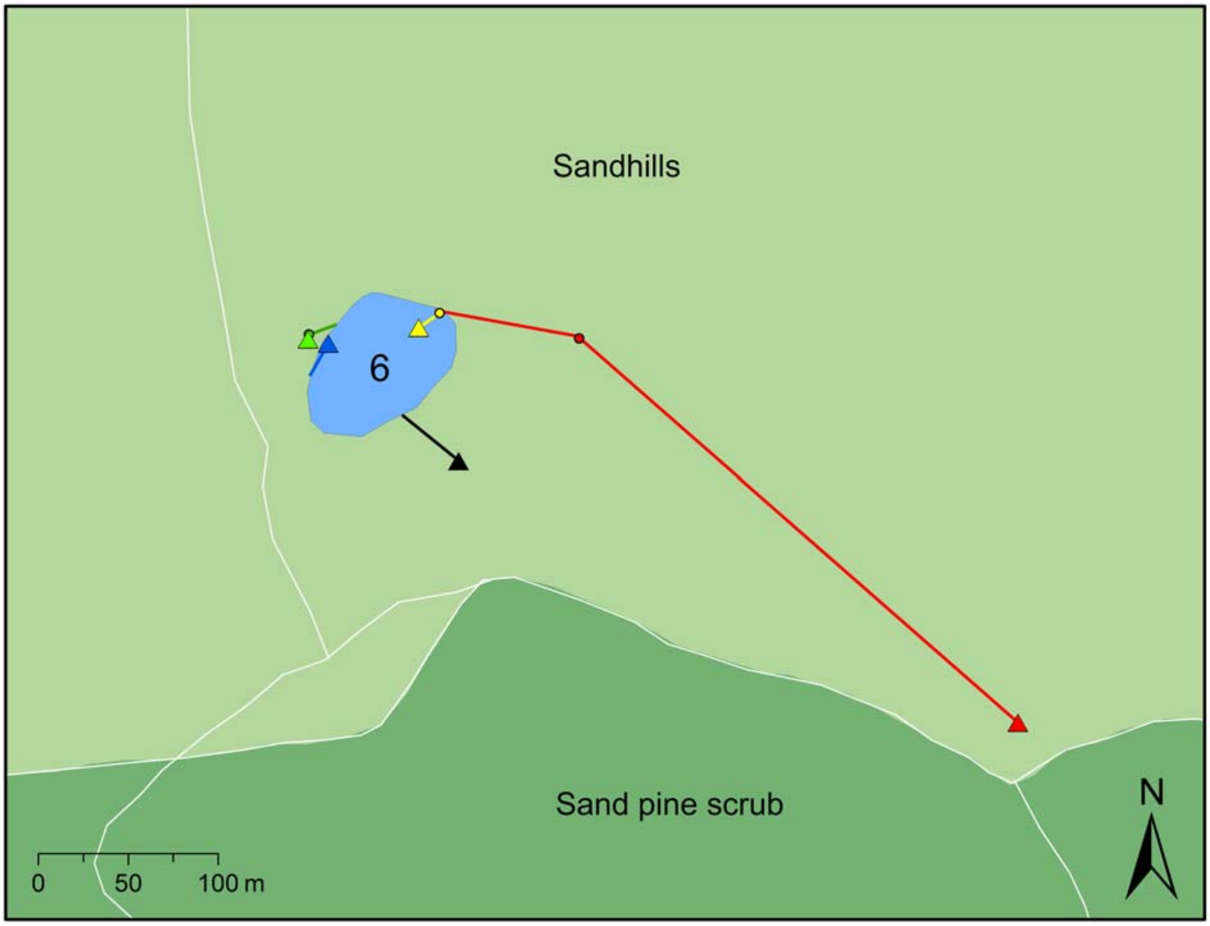

Figure 3-11. Movement paths of juvenile gopher frogs emigrating from Pond 6. The pond is surrounded by sandhill habitat (light green), with sand pine scrub habitat (dark green) more than 142 m away. The different colored paths represent different frogs. Paths were created by drawing straight lines between daily locations. Triangles represent that last known locations of frogs before predation.

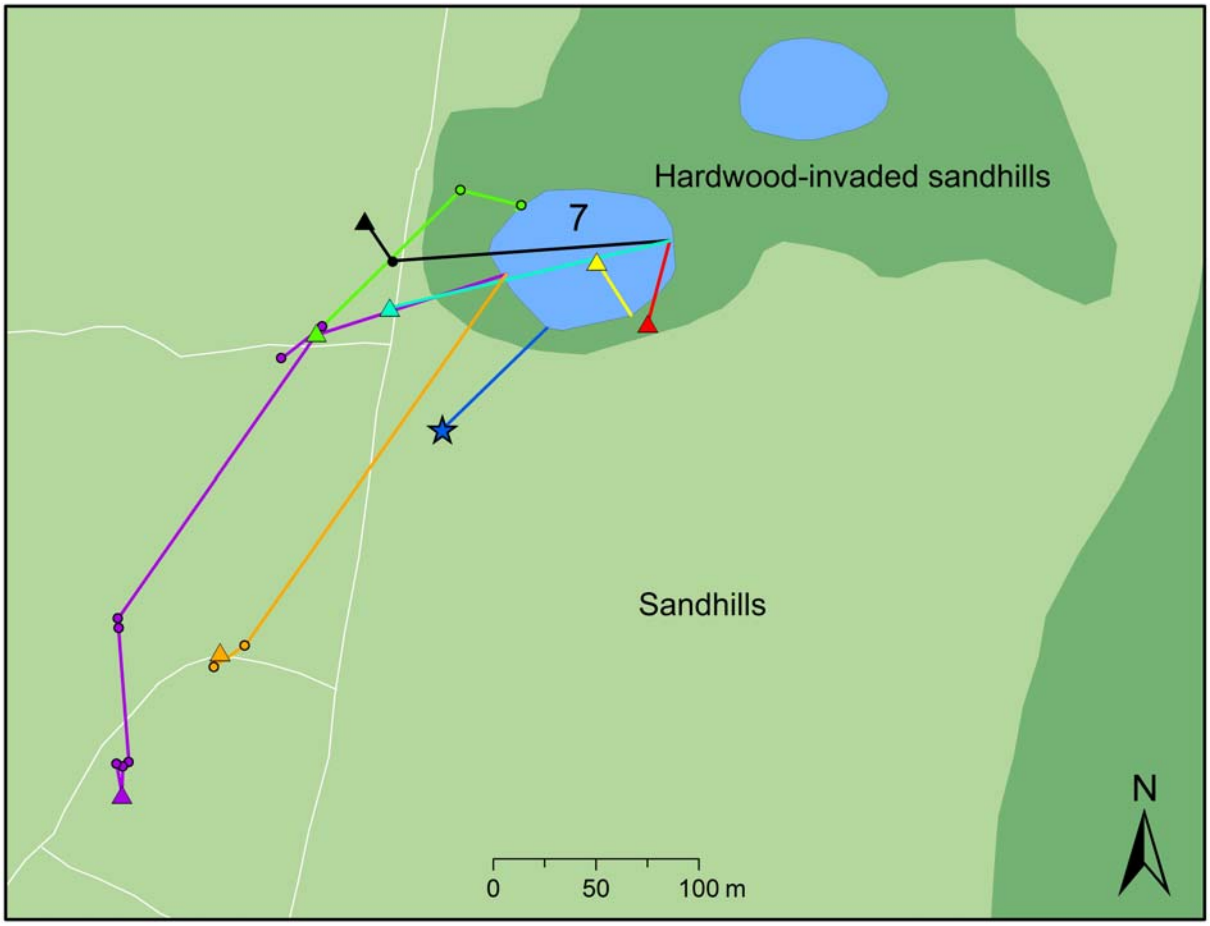

Figure 3-12. Movement paths of juvenile gopher frogs emigrating from Pond 7. The surrounding terrestrial habitats are sandhills (light green) and hardwood-invaded sandhills (dark green). The different colored paths represent different frogs. Paths were created by drawing straight lines between daily locations. A star represents the last known location of a surviving frog, and triangles represent that last known locations of frogs before predation or death by vehicular traffic. The thin, white lines represent unpaved roads, and another nearby pond is also shown.

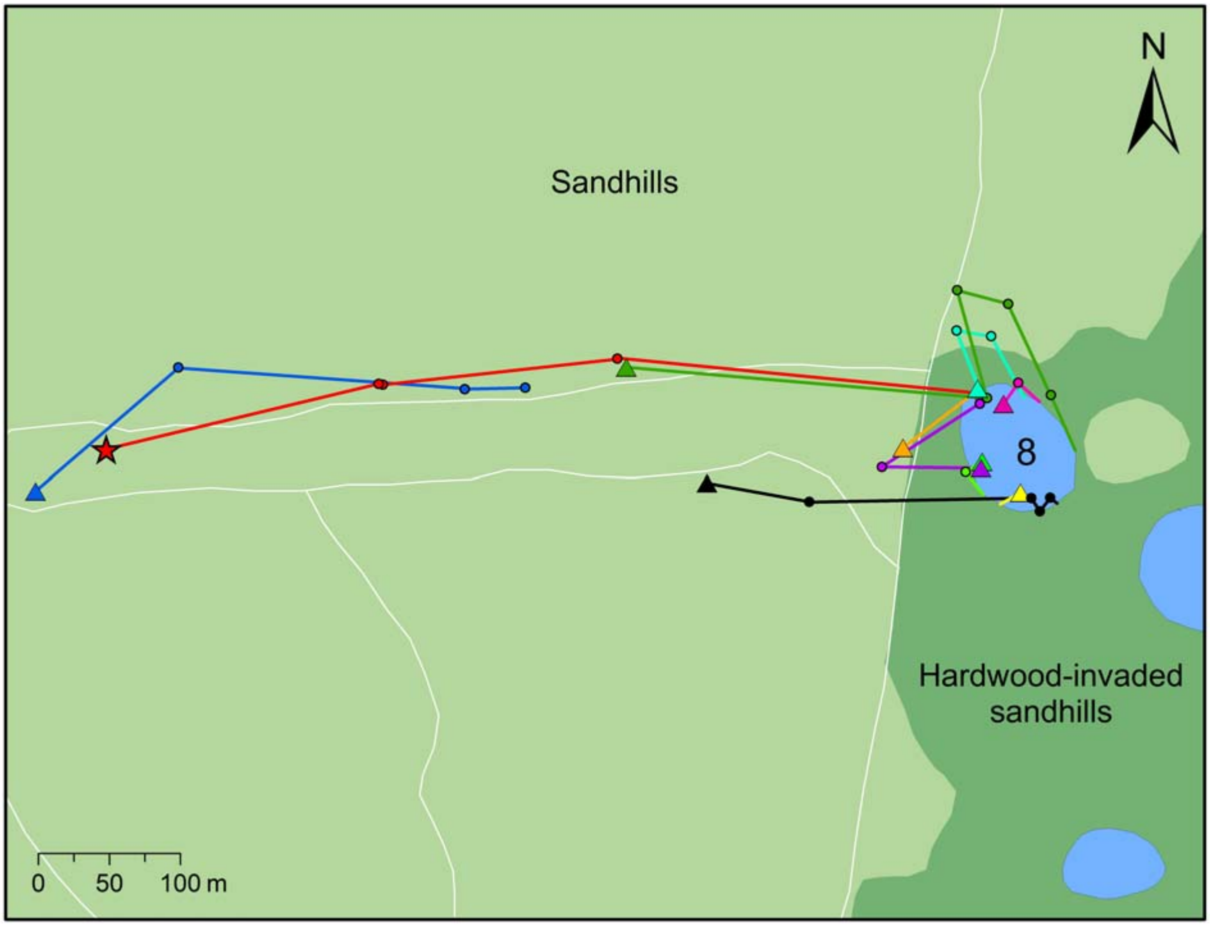

Figure 3-13. Movement paths of juvenile gopher frogs emigrating from Pond 8. The surrounding terrestrial habitats are sandhills (light green) and hardwood-invaded sandhills (dark green). The different colored paths represent different frogs. Paths were created by drawing straight lines between daily locations. A star represents the last known location of a surviving frog, and triangles represent that last known locations of frogs before depredation, transmitter loss, or death by vehicular traffic. The thin, white lines represent unpaved roads, and other nearby ponds are also shown.

CHAPTER 4
MOVEMENT PATTERNS AND TERRESTRIAL HABITAT USE OF ADULT GOPHER FROGS

Introduction

Although amphibians are vulnerable to numerous threats, the loss and alteration of aquatic and terrestrial habitats are major causes of population declines and extinctions for many species (Semlitsch 2002). The effects of anthropogenic disturbances are a major concern in areas that are experiencing rapid human population growth and urban development, particularly in areas that contain a high density of small, isolated wetlands. In the southeastern United States widespread areas of native forests have been fragmented or cleared for agriculture, forest plantations, and urban development (Ware et al. 2003), and many of the small, isolated wetlands that characterize this region have also been destroyed (Hefner and Brown 1985).

Most amphibians depend on aquatic habitats for breeding and larval development, but many also spend the majority of their lives in surrounding terrestrial habitats, often moving long distances from breeding ponds (Franz et al. 1988, Dodd 1996, Johnson 2003). Thus, direct protection of aquatic breeding sites may be of little conservation value if the surrounding terrestrial habitats are not also protected and managed appropriately. Due to the difficulty of locating amphibians in terrestrial habitats and studying movement patterns of amphibians, the migratory distances and terrestrial habitat use are unknown or poorly understood for most species (Dodd 1996). However, a comprehensive understanding of their terrestrial habitat requirements is essential for the development of conservation plans to protect species that breed in small, isolated wetlands.

Gopher frogs (*Rana capito*) are rare and imperiled throughout their range in the southeastern Coastal Plain of the United States (Godley 1992, Jensen and Richter 2005). A very closely related species, the dusky gopher frog (*R. sevosa*), which is known to occur only at a single pond in Mississippi (Richter et al. 2001), has recently been listed as federally endangered (U.S. Fish and Wildlife Service 2001) following a study by Young and Crother (2001), which determined that it is genetically distinct from other gopher frog populations. The greatest threats to gopher frogs (both *R. capito* and *R. sevosa*) are the loss and alteration of aquatic and terrestrial habitats due to urban development, silviculture, and fire suppression (Jensen and Richter 2005, Thurgate and Pechmann 2007). The destruction of terrestrial habitat is particularly threatening to gopher frogs because they spend the vast majority of their lives in terrestrial habitats and move long distances from breeding ponds (up to 2 km; Franz et al. 1988).

Gopher frogs spend the majority of their time in the burrows of gopher tortoises (*Gopherus polyphemus*), crayfishes, and several species of small mammals (e.g., *Geomys pinetis*, *Podomys floridanus, Peromyscus polionotus*), as well as in holes associated with tree stumps and roots (Lee 1968, Franz 1986, Jensen and Richter 2005). Thus, gopher frogs are very difficult to locate and study outside of the breeding season. Nonetheless, several researchers have used radio telemetry to study the terrestrial ecology of gopher frogs. Phillips (1995) studied postbreeding movements of Carolina gopher frogs (*Rana capito capito*) in Georgia; Richter et al. (2001) studied postbreeding movements of dusky gopher frogs (*R. sevosa*) in Mississippi; and Blihovde (2006) studied terrestrial movement patterns of Florida gopher frogs (*R. c. aesopus*) in central Florida. I used radio telemetry to study postbreeding movement patterns and terrestrial habitat use of Florida gopher frogs at five ponds in north-central Florida. I use my data and the findings of the three studies cited above to summarize the published information on movement patterns and terrestrial habitat use of gopher frogs.

Methods

Study Area

My study took place at eight isolated ponds and surrounding upland habitats at two sites in the Ocala National Forest, Marion and Putnam Counties, Florida, USA (Figure 4-1). However, gopher frogs were captured and tracked at only five of the eight ponds (see Results). Ponds 1-6 are located approximately 9.5 km north of Ponds 7 and 8. The ponds range in size from 0.10 to 0.37 ha and all are located primarily within longleaf pine-wiregrass savannas, although hardwoods (e.g., *Quercus* spp.) have invaded areas around six of the ponds (Pond 1-4,7,8). These ponds are part of an ongoing study of herpetofaunal use, and detailed descriptions of aquatic and terrestrial habitats at these sites are available in Greenberg (2001).

Radio Telemetry

I captured adult gopher frogs by hand in ponds during breeding events and at drift fences during breeding migrations. Drift fences (7.6 m in length) were placed at 7.6-m intervals to encircle 50% of each pond. I positioned pitfall traps (1.9-L buckets) on the inside and outside of both ends of each fence (four per fence) so that I could detect the direction of travel, and I placed double- or single-ended funnel traps at the midpoint of each fence on both sides (two funnel traps per fence). Captured frogs were measured (snout-urostyle length) to the nearest mm and weighed to the nearest g. Males were distinguished from females by their enlarged thumbs and paired vocal sacs. All pitfall traps were checked three times per week and a sponge was placed in each trap and moistened at each trap check to prevent desiccation of captured animals.

I fitted frogs with R1655 transmitters (Advanced Telemetry Systems, Isanti, MN), which weighed 1.2 g and had a maximum battery life of 115 d. I attached transmitters to frogs in the field using an external belt following the methods of Muths (2003), which entailed threading a piece of elastic through a prefabricated hole in the transmitter, stringing small glass beads onto the elastic, and tying a knot in the elastic. I attached a transmitter assembly to each frog by sliding the belt over the extended hind legs of the frog so that it rested on the frog's waist (Figure 4-2). The combined mass of the transmitter and belt was 1-4% of the body mass of the frogs, which is well below the recommended maximum 10% transmitter-to-body-mass ratio for amphibians (Richards et al. 1994). I released frogs near their point of capture immediately after attaching the transmitter and observed each frog briefly after release to ensure that the movements of frogs were not obviously affected by the transmitter assembly.

I used a TRX-48S receiver (Wildlife Materials, Inc., Murphysboro, IL) and a hand-held 3-element Yagi directional antenna to track frogs. I located each frog at least three times per week until the transmitter expired, the signal was lost, or the frog was preyed upon. I recorded each location by averaging 50 consecutive position readings with a GeoXM Global Positioning System (GPS) unit (Trimble, Sunnyvale, CA), which had an accuracy of 1-3 m. I used ArcGIS 9.2 (ESRI, Redlands, CA) to measure the distances between successive locations and from the center of the pond of origin.

Results

Predation

I tracked 14 adult gopher frogs at five of the eight study ponds (Ponds 1, 5, 6, 7, and 8) between 3 October 2006 and 5 November 2007. The transmitter signals for two frogs were lost before the frogs were documented emigrating from the ponds, which could be due to predation, transmitter failure, or long-distance movements beyond detection. I determined that two additional frogs were preyed upon by avian predators because the signals originated from the tree canopy and the transmitters were found on the ground below on the next day of tracking. One of these frogs was preyed upon immediately after emigrating from the pond before I located it for the first time, and the other frog was preyed upon after returning to the pond after leaving a small crevice 42 m from the pond. I was not able to identify specific predators. Frogs surviving past the first day of tracking were followed for an average of 41.5 ± 8.2 days (range: 9-99 days; Table 1).

Movement patterns

Of the 10 frogs that were known to survive until the end of the study and migrate from the ponds, one frog remained in a stump hole near the pond edge for the life of its transmitter (23 d) after migrating to the pond from uplands beyond the drift fences, and nine frogs emigrated from ponds into the surrounding uplands. Frogs that migrated into the uplands moved an average of 211.9 ± 41.7 m (range: 63-397 m) from ponds (Table 1; Figures 4-3 and 4-4); however, I observed gopher frogs at burrows located up to 862 m from the nearest potential breeding pond at my sites. Frogs moved an average of 123.2 ± 19.6 m (range: 18-284 m) between successive locations, and they moved farther from ponds with successive movements, except for frogs that returned to the ponds after a prescribed fire or to breed another time. Several frogs appeared to move along the same paths when migrating to and from ponds. Two frogs were located in the same underground refugia just before entering a pond and immediately after exiting a pond. Similarly, frogs that were captured in the pitfall traps emigrated from ponds in the same directions from which they originated.

Refugia

I recorded 1-5 locations for frogs during the study, which were associated with a variety of refugia. During migration between ponds and upland habitats, frogs sought refuge in burrows excavated by gopher tortoises and small mammals, as well as in leaf litter and holes associated with stumps and roots. All of the final recorded locations of frogs that migrated into the uplands were burrows excavated by gopher tortoises or small mammals. Frogs moved frequently during migrations, but when sufficient transmitter battery life remained, I found that they eventually became sedentary and settled into one burrow for the remainder of the study. Frogs were often observed sitting beside their burrows on distinctive patches of soil cleared of vegetation for up to 200 days after their transmitters expired.

Burrow cohabitation

I documented several instances of frogs sharing burrows and occupying adjoining burrows. I observed a transmitter-equipped frog and another frog at the entrance to a gopher tortoise burrow one night, and the next night I found two transmitter-equipped frogs in the same burrow, including one frog from the previous night. This indicates that at least two, and possibly three, adult frogs occupied that burrow at the same time. The two transmitter-equipped frogs shared the burrow for 11 days until one frog left the burrow. I also located another pair of frogs in close proximity to one another; two entered pocket gopher (*Geomys pinetis*) burrows with entrances located 1.5 m apart and perhaps leading into the same burrow. They remained in these locations for five days until one frog left its burrow. Two other frogs entered adjoining burrows; one frog occupied a gopher tortoise burrow whereas the other occupied a Florida mouse (*Podomys floridanus*) burrow that adjoined the gopher tortoise burrow. These frogs remained in these locations for at least 68 days when one frog's transmitter expired.

Direct effects of prescribed fire

On 11 October 2007, the U.S. Forest Service conducted a prescribed fire during my study as a normal management activity to maintain suitable habitat for gopher frogs and other species that occur in longleaf pine habitats. Three transmitter-equipped frogs were present in the burn area during the fire. During the previous day two frogs were located in leaf litter and the other frog was located in a gopher tortoise burrow. During the night of the fire I found that one frog remained in the gopher tortoise burrow and another transmitter-equipped frog had moved 20 m and entered that same burrow, as described above in "Burrow cohabitation." The third frog moved 52 m towards the pond and was located approximately 3 cm under leaf litter. The fire had passed directly over the frog and the frog survived and moved back to the pond within the next 24 hr.

Discussion

I documented migratory distances of 63-396 m from breeding ponds, which are similar to postbreeding migration distances documented during other radio telemetry studies of adult gopher frogs (Phillips 1995, Richter et al. 2001; Table 2). Phillips (1995) documented migratory distances of up to 102 m, and Richter et al. (2001) documented migratory distances of up to 299 m. Although these migratory distances are relatively short, adult gopher frogs have been observed at much greater distances from breeding ponds. Franz et al. (1988) observed an adult gopher frog 2 km from the pond at which it was marked, and Carr (1940) observed an adult gopher frog 1.6 km from the nearest potential breeding pond. Additionally, I observed adult gopher frogs up to 862 m from the nearest potential breeding pond at my sites. The results from these radio telemetry studies suggest that long-distance migrations (> 1 km) appear to be uncommon in adult gopher frogs, although long-distance dispersal is difficult to detect and typically underestimated by radio telemetry and mark-recapture studies involving relatively small sample sizes (Marsh and Trenham 2001). Furthermore, the transmitter signals for four frogs in my study were lost abruptly following nights of heavy rainfall, and I suspect that those frogs may have moved long distances beyond detection, which may have led to an underestimation of migratory distances in my study.

Several frogs used the same underground refugia, or migrated in the same directions, while migrating to and from the ponds, providing evidence that adult frogs are familiar with their environment and with the locations of ponds and underground refugia and can easily navigate among them. Richter et al. (2001) also documented one frog migrating 236 m to a breeding pond and then back to its original burrow, and Blihovde (2006) captured two frogs at burrows and found that they homed back to their original burrows after he released them 10 m away from those burrows.

Gopher frogs moved infrequently outside of the breeding season. I recorded 1-5 moves per frog and, when sufficient transmitter battery life remained, I found that all frogs eventually settled into a burrow and stayed there for the remainder of the study. These results support the findings of other studies; for example, Richter et al. (2001) recorded 1-5 moves per frog, Blihovde (2006) recorded frogs using 1-4 refugia, and although Phillips (1995) recorded numerous movements, they were all short distances (< 13 m).

Although adult gopher frogs have rarely been observed sharing burrows with conspecifics (Wright and Wright 1949, Jensen and Richter 2005), I documented two, and possibly three, frogs sharing a gopher tortoise burrow. Later in the study, I also documented two other pairs of frogs living in close proximity to one another. Two entered pocket gopher burrows with entrances located 1.5 m apart and perhaps leading into the same burrow, and two other frogs entered adjoining burrows; one frog occupied a gopher tortoise burrow whereas the other occupied a Florida mouse burrow that adjoined the gopher tortoise burrow. Although frogs have not been previously reported to cohabit burrows, they may only share them temporarily during migrations or fires, or cohabitation may be more common than previously thought, but rarely observed due to the difficulty in monitoring gopher frogs at burrows.

Sources of mortality for adult gopher frogs are unknown, except for several observations of predation by banded water snakes (*Nerodia fasciata*; Jensen 2000). I documented predation of two frogs by avian predators during migrations from ponds, and although I was not able to identify the species, they were likely owls, since gopher frogs are active primarily at night. The majority of mortality for adult gopher frogs probably occurs during migrations when frogs are more exposed to predators and lack the protection of a nearby burrow.

Although prescribed fire is essential for maintaining habitats for gopher frogs and other species that occur in longleaf pine habitats, little is known about the effects of prescribed fire on amphibians (Russell et al. 1999, Lanford et al. 2007). Three frogs were present during a prescribed fire at one of my sites, and all three survived and made subsequent movements within several days after the fire. Other studies have reported the survival of adult (Richter et al. 2001) and juvenile (this study, Appendix) gopher frogs during prescribed fires, also suggesting that gopher frogs are not highly vulnerable to fire. Frogs survived the fire in gopher tortoise burrows or beneath leaf litter, which emphasizes the importance of burrows and frequent, low-intensity prescribed fire (Means et al. 2004).

Gopher frogs are threatened by the loss and alteration of both terrestrial and aquatic habitats (Godley 1992, Jensen and Richter 2005). My study, together with the other published studies of gopher frog movements, demonstrates the importance of large areas of intact habitat surrounding breeding ponds for gopher frogs, as well as the dependence of gopher frogs on the burrows of gopher tortoises and small mammals. Conservation plans for gopher frogs should focus on protection of both terrestrial and aquatic habitats and protecting local populations of burrowing vertebrates. Furthermore, despite the apparent rarity of long-distance migrations from breeding ponds, such movements do occur and should be considered when developing conservation plans for gopher frogs.

Table 4-1. Movement distances and morphometric data for adult gopher frogs monitored through radio telemetry at four breeding ponds in the Ocala National Forest, Florida.

Frog	Pond	Sex	Mass (g)	SUL (mm)	Distance from pond center (m)	Tracking period (d)	Dates monitored
732	5	F	51.5	77	35	23	3 Oct – 26 Oct 06
102	6	M	68.0	71	218	76	6 Feb – 23 Apr 07
131	6	M	65.0	75	63	99	6 Feb – 16 May 07
192	6	M	85.0	77	63	68	8 Feb – 17 Apr 07
221[1]	6	M	47.0	68	42	33	22 Feb – 27 Mar 07
251[1]	1	F	67.0	81	-	3	5 Mar – 8 March 07
281	7	F	63.5	82	188	9	24 Sept – 3 Oct 07
311[2]	7	M	87.0	78	-	9	24 Sept – 3 Oct 07
401[2]	8	M	65.0	75	-	15	3 Oct – 18 Oct 07
672	8	M	46.0	70	396	22	3 Oct – 25 Oct 07
761	8	M	54.0	74	127	27	3 Oct – 30 Oct 07
461	8	M	54.0	71	397	33	3 Oct – 5 Nov 07
371	8	M	56.5	74	182	33	3 Oct – 5 Nov 07
731	8	M	45.5	67	273	33	3 Oct – 5 Nov 07

[1] Indicates frogs that were preyed upon during the study. The distance from pond center could not be determined for one frog because it was preyed upon before the first day of tracking.

[2] Indicates frogs that were last located at the ponds before their transmitter signals were lost.

Table 4-2. Maximum distances that adult gopher frogs have been found from breeding ponds.

Species	Maximum distance from pond (m)	Method	*N*	Source
Rana capito aesopus	396	Radio telemetry	11	This study
Rana capito aesopus	862	Observation	1	This study
Rana capito aesopus	1609	Observation	1	Carr 1940
Rana capito aesopus	2000	Observation	1	Franz et al. 1988
Rana capito aesopus	460*	Observation/Radio telemetry	9	Blihovde 2006
Rana capito capito	102	Radio telemetry	2	Phillips 1995
Rana sevosa	299	Radio telemetry	12	Richter et al. 2001

* This value indicates the approximate distance between a potential breeding pond and the center of a 1-ha study plot containing burrows where frogs were captured for the radio telemetry study.

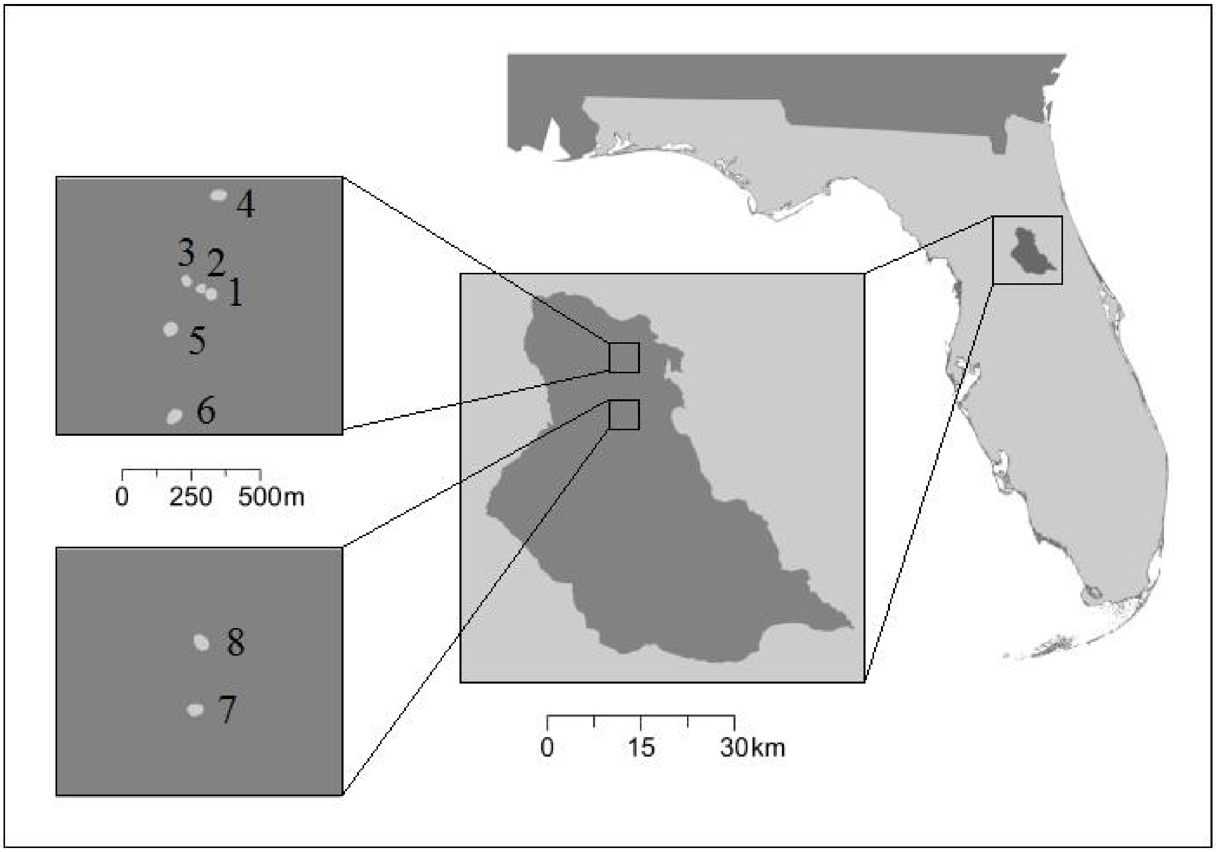

Figure 4-1. Study area. My study took place at eight ponds and the surrounding upland habitats at two sites in the Ocala National Forest, Florida. Ponds 1-6 are located approximately 9.5 km north of Ponds 7 and 8.

Figure 4-2. Gopher frog wearing a transmitter belt. Belts were made of elastic thread and small, glass beads, and were threaded through a prefabricated hole in the transmitter. The assembly was attached to the frog by sliding the belt over the extended hind limbs of the frog so that it rested on the frog's waist.

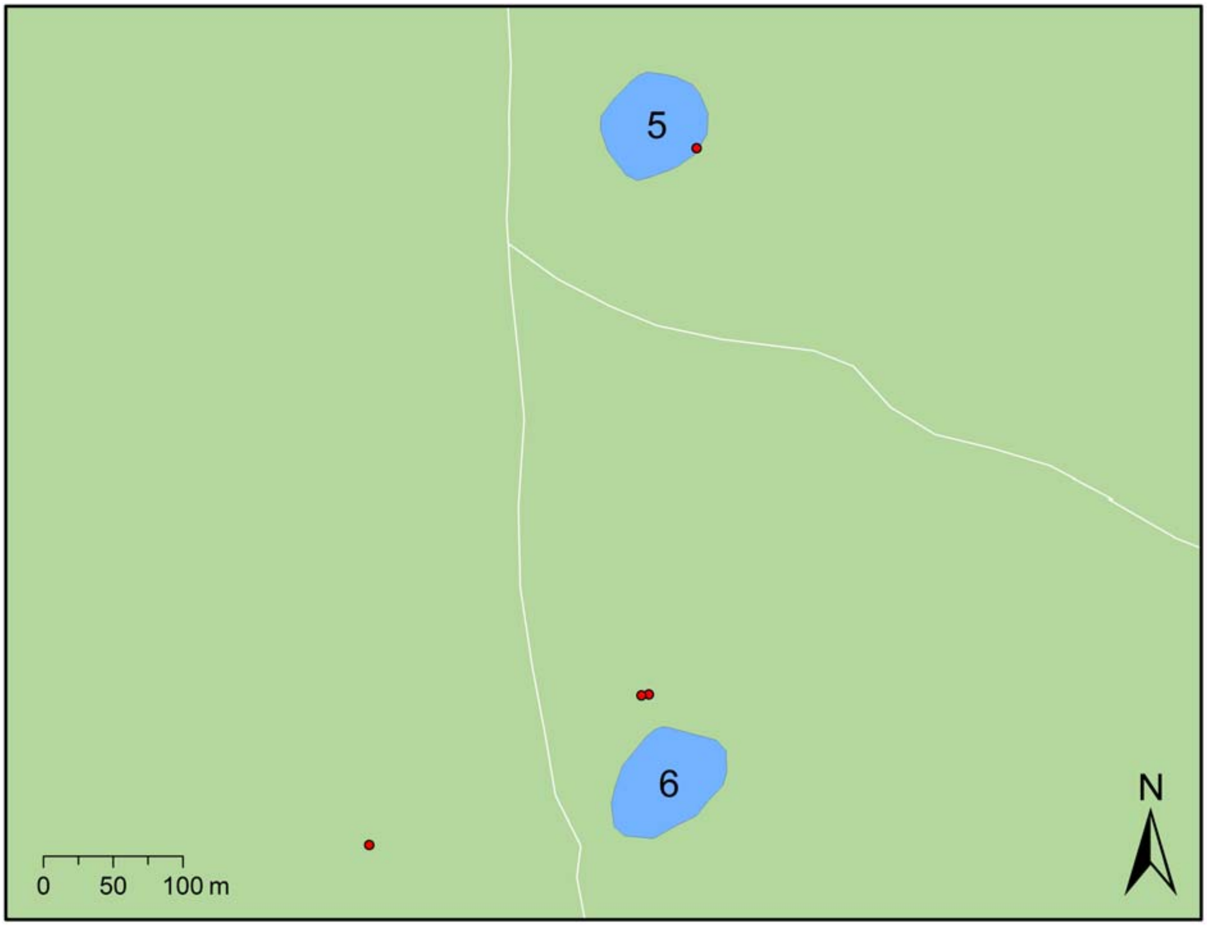

Figure 4-3. Last known locations of adult gopher frogs emigrating from Ponds 5 and 6. Both ponds are completely surrounded by sandhill habitat. The thin, white lines represent unpaved roads.

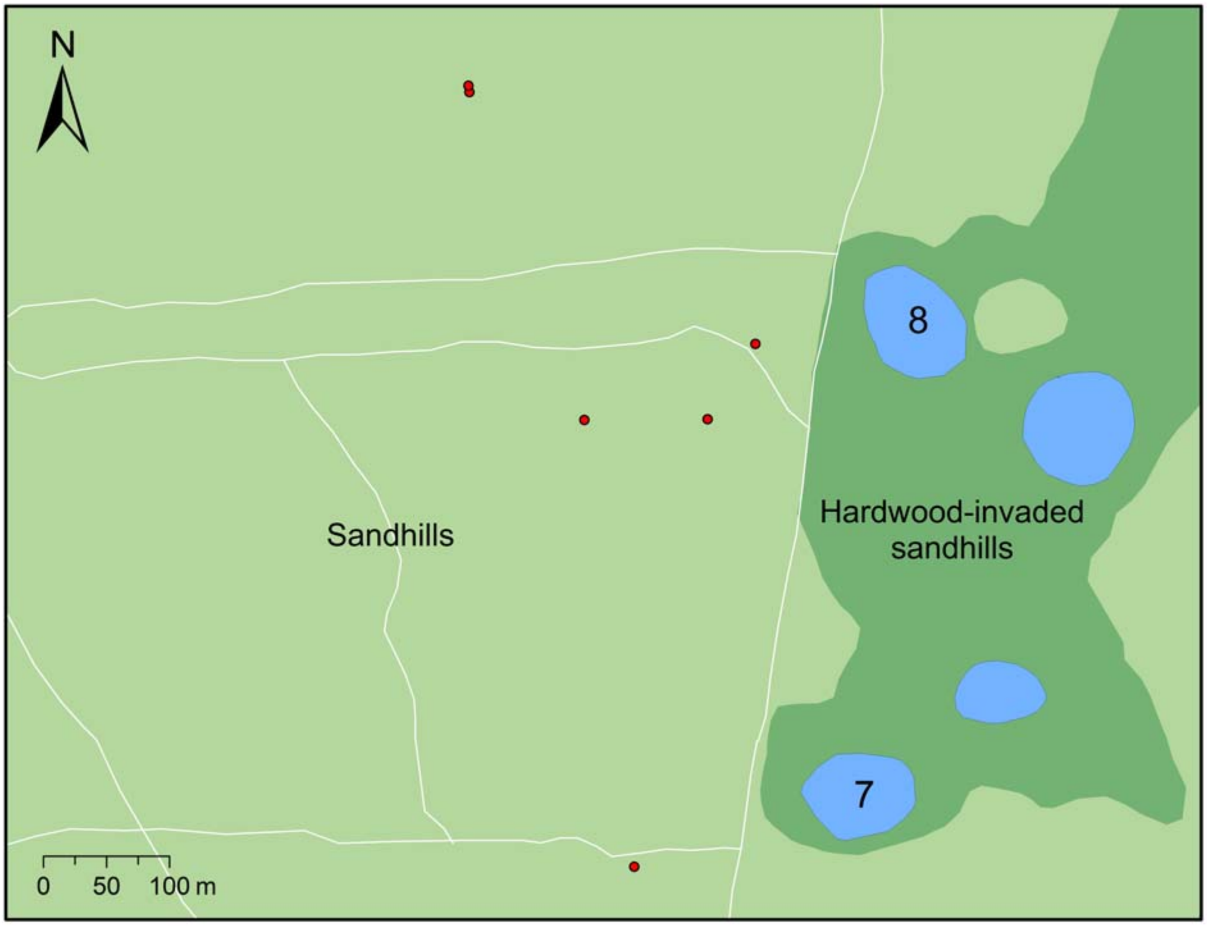

Figure 4-4. Last known locations of adult gopher frogs emigrating from Ponds 7 and 8. The surrounding terrestrial habitats are sandhills (light green) and hardwood-invaded sandhills (dark green). The thin, white lines represent unpaved roads, and other nearby ponds are also shown.

CHAPTER 5
CONCLUSIONS

My research demonstrates the importance of large areas of well-managed habitat surrounding breeding ponds for gopher frogs (*Rana capito*), as well as the dependence of gopher frogs on the burrows of gopher tortoises (*Gopherus polyphemus*) and small mammals (e.g., *Geomys pinetis*, *Podomys floridanus*). Both juvenile and adult frogs are capable of migrating long distances from breeding ponds. I documented juveniles moving at least 691 m from ponds, and adults moving at least 396 m from ponds. Although adult gopher frogs have been observed 1.6 km and 2 km from breeding ponds (Carr 1940, Franz et al. 1988), and up to 862 m from the nearest breeding pond at my sites, the results from my study and other radio telemetry studies suggest that such long-distance migrations (> 1 km) are rare in gopher frogs (Phillips 1995, Richter et al. 2001, Blihovde 2006). However, juveniles in my study moved more than twice the maximum distance of postbreeding migrations of transmitter-equipped adult frogs, suggesting that juveniles may require more terrestrial habitat than adults. Although juvenile and adult gopher frogs used many types of refugia during migrations, the final locations of all surviving frogs that migrated from ponds were burrows excavated by gopher tortoises and small mammals. Both life stages exhibited strong site fidelity to burrows; frogs changed locations very infrequently after entering a burrow, and evidence from my study and others (Richter et al. 2001, Blihovde 2006) indicates that adults are able to home back to specific burrows.

The transition from aquatic to terrestrial habitat is thought to be a period of high mortality for newly metamorphosed amphibians (Trenham et al. 2000, Altwegg and Reyer 2003, Rothermel and Semlitsch 2006), and I found that this is true for gopher frogs. Only 9.4% of frogs survived their first month in the terrestrial habitat and all documented predation occurred within the initial 12 days in the uplands. Although snakes were their major predators, frogs were also preyed upon by mammals and birds, and killed by vehicular traffic along unpaved roads. Road mortality has not been previously documented as a cause of mortality for gopher frogs, but my results indicate that it may be a significant source of mortality for juveniles, particularly since they appear to use roads as migration corridors. Vehicles were responsible for the deaths of 9.4% of the frogs I tracked, and those most vulnerable were among the frogs that survived longest and migrated farthest from the ponds. Thus, road mortality of juvenile gopher frogs has the potential to affect populations by reducing recruitment of juveniles and also by reducing connectivity of populations through dispersal to nearby ponds. Permanent or seasonal closure of paved and unpaved roads near breeding ponds to vehicle traffic would reduce the likelihood of traffic mortality during periods of juvenile emigration.

The use of underground refugia significantly increased a juvenile frog’s probability of survival in my study and reduced the risk of death to only 4% of the risk that frogs faced while in the open environment. Juvenile frogs that survived to the end of the study located a burrow within their initial days in the terrestrial environment and stayed there for the remainder of the life of their transmitter. Frogs that were unable to find suitable refugia and spent more time in the open were more vulnerable to predation. The final recorded refugia occupied by surviving frogs were burrows created by gopher tortoises or small mammals. Although some juvenile frogs temporarily sought shelter in small crevices and other underground refugia associated with stumps and coarse woody debris, they eventually left these locations and either found a burrow or were soon preyed upon. Due to high predation rates of juvenile gopher frogs and their dependence on burrows for survival, the density and spatial configuration of burrows near breeding ponds may be important factors that play a role in the population dynamics of gopher frogs. Habitat should be managed appropriately to maintain or increase populations of burrowing vertebrates, because any factors that result in declines in populations of gopher tortoises or other burrowing vertebrates may affect populations of gopher frogs by altering the availability of burrows.

Although all of my study ponds were located primarily in longleaf pine-wiregrass (*Pinus palustris-Aristida stricta*) sandhills, areas surrounding some of the ponds contained patches of closed-canopy habitat that had been invaded by hardwood trees (e.g., *Quercus* spp.) as a result of fire suppression. I found that emigrating juvenile frogs oriented in random directions at the one pond completely surrounded by homogenous open-canopy habitat, whereas frogs oriented nonrandomly at ponds where upland habitats varied in the amount of canopy cover. Where orientation was nonrandom, frogs migrated through the center of the largest patch of open-canopy habitat, avoiding the edges where the closed-canopy hardwoods began to encroach. My habitat selection data confirm this observation; frogs moved into habitats that had a high percentage of light penetrating through the canopy and were characterized by few hardwood trees, high percent cover of wiregrass, and low percent ground cover of leaf litter.

A survey of burrow density in relation to canopy closure revealed that patches of open-canopy habitat contained significantly higher densities of burrows than closed-canopy patches. Canopy closure reduces habitat quality for gopher tortoises and has been found to be one of the main factors influencing the distribution of burrows (Boglioli et al. 2000, Hermann et al. 2002, Jones and Dorr 2004). Because juvenile and adult gopher frogs are dependent on the burrows of gopher tortoises and small mammals for shelter, it is likely that frogs select open-canopy habitats because burrows are more abundant in those areas. Locating a burrow quickly is especially important for juvenile gopher frogs because predation is very high and their small body size makes them particularly susceptible to desiccation (Newman and Dunham 1994).

Canopy closure could affect population dynamics of gopher frogs in several ways. There is evidence that dusky gopher frog (*Rana sevosa*) larvae in closed-canopy ponds experience decreased survival to metamorphosis (Thurgate and Pechmann 2007). In addition, ponds occurring within large tracts of hardwood-invaded longleaf-pine forest may be population sinks due to high juvenile mortality if frogs cannot detect the direction of favorable habitat and the associated burrows. Because closed-canopy habitats are barriers to juvenile frogs, ponds in closed-canopy habitat may also experience less frequent colonizations by juveniles dispersing from other ponds. Gopher frog populations will benefit from maintaining open-canopy longleaf pine forests and restoring habitat that has been invaded by hardwoods as a result of fire suppression. Gopher frogs require large areas of protected upland habitat, and this protected habitat must be actively managed. Because natural fires no longer maintain longleaf pine forests, land managers must use prescribed fire to mimic historical fire regimes. Land managers should apply an appropriate fire regime to maintain open-canopy habitat surrounding breeding ponds that continues all the way to the pond edges in order to maintain connectivity between ponds and upland habitat, which will facilitate juvenile emigration into the surrounding uplands.

To prevent further population declines and to facilitate the recovery of gopher frog populations, we must first understand their habitat requirements and identify potential threats. Prior to my research, information on juvenile gopher frogs was limited to data collected from newly metamorphosed frogs captured at drift fences encircling breeding ponds (Semlitsch et al. 1995, Palis 1998, Greenberg 2001), and juveniles were assumed to require the same terrestrial habitats as adults (Jensen and Richer 2005). Several other radio telemetry studies have addressed the terrestrial ecology of adult gopher frogs in other parts of their range (Phillips 1995, Richter et al. 2001, Blihovde 2006), and my data add to the collective knowledge of this life stage. Despite these studies, there are many untested assumptions and remaining gaps in our knowledge of gopher frog ecology. Frogs have been tracked for relatively short periods of time (i.e., a maximum of four months and usually much less) during radio telemetry studies of gopher frogs, so future research should focus on monitoring frogs throughout the entire year between breeding seasons. This information will greatly enhance our understanding of the terrestrial habitat use of gopher frogs during the nonbreeding season. Although populations of pond-breeding amphibians are often assumed to exist as metapopulations, this paradigm has rarely been tested (Smith and Green 2005). Future studies should address gene flow in gopher frog populations and determine whether populations are indeed structured as metapopulations. This information will help managers successfully balance management at local and regional scales.

Gopher frogs may soon colonize unoccupied ponds following restoration of the surrounding terrestrial habitats; however, translocating frogs may be a useful strategy to augment dwindling populations and reestablish populations at ponds where populations have become extirpated. Future research should assess the response of frogs to restored habitats (uplands and wetlands), as well as the success of translocations through long-term monitoring. The probability of successful translocations of a species depends on habitat quality (Semlitsch 2002), so for gopher frogs, open-canopy habitats and high burrow densities are essential. Excavating artificial burrows is one potential management strategy that could be used near occupied ponds as well as translocation sites. By increasing the availability of underground refugia, managers may be able to increase juvenile survival and also provide habitat for larger populations of frogs. Although gopher frogs are most frequently cited using gopher tortoise burrows, they also use a variety of other subterranean refugia; therefore, an understanding of their dependence on various types of burrows would also provide important information for conservation planning. Gopher frogs are rare and imperiled throughout their range and there is concern about their status in each state in which they occur (Jensen and Richter 2005). By studying the habitat use of juveniles and adults, we can begin to understand the terrestrial ecology of gopher frogs and use that information to make wise conservation and management decisions.

Based on the findings of my research, I recommend the following practices to manage terrestrial habitats for gopher frogs:

- Terrestrial habitats surrounding breeding ponds should be protected from destruction and managed with prescribed fire. Fire should be used to maintain open-canopy habitat that continues all the way to the pond edge and burns through the pond basin during dry years.
- Populations of burrowing vertebrates (gopher tortoises and small mammals) near breeding ponds should be protected and monitored. Where populations are small or declining, managers should attempt to increase populations.
- Tree stumps near breeding ponds should not be removed.
- All roads (paved and unpaved) near breeding ponds should be closed permanently or at least during periods of gopher frog metamorphosis, which is typically May through July in central Florida (Greenberg 2001).

APPENDIX
JUVENILE GOPHER FROG REFUGE DURING FIRE

Most animals have adaptive behaviors that help them escape from fire, but little is known about how amphibians survive fires in fire-maintained ecosystems. During a radio telemetry study that I was conducting on gopher frogs (*Rana capito*) in the Ocala National Forest, Marion and Putnam Counties, Florida, USA, the U.S. Forest Service conducted a prescribed fire on 20 July 2006 as a normal management activity to maintain suitable habitat for gopher frogs and other species that occur in the longleaf pine (*Pinus palustris*) ecosystem. Two newly metamorphosed juveniles equipped with transmitters were present in the burn area during the fire. They were both captured at drift fences surrounding ephemeral ponds and outfitted with external transmitters at ca. 1100 h on 19 July 2006. Immediately following transmitter attachment I released the frogs near the drift fences where they were captured. I located the frogs immediately after the fire at ca. 2000 h on 20 July 2006. One frog moved 71m from the drift fence into an abandoned burrow excavated by an adult gopher tortoise (*Gopherus polyphemus*) The second frog moved 43 m from the drift fence into an unburned patch of wiregrass (*Aristida stricta*). Because I did not locate frogs immediately before the fire, I do not know whether these frogs moved to refuges in response to the fire or sometime during the previous day and before the fire.

These observations indicate that gopher frogs are able to survive fires in underground refuges and in areas that do not burn when the fire passes. There was no evidence of mortality, as we might expect for a species that evolved in a fire-maintained ecosystem. Richter et al. (2001) reported the survival of three adult dusky gopher frogs (*Rana sevosa*) during a prescribed fire, also suggesting that gopher frogs are not highly vulnerable to fire. These observations highlight the importance of burrows and heterogeneous fire, which allows animals to take shelter in unburned areas when no other refugia are available.

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BIOGRAPHICAL SKETCH

Elizabeth “Betsy” Roznik grew up in Green Bay, Wisconsin, and graduated from high school at Notre Dame Academy in 2001. She attended the University of Wisconsin—Stevens Point and graduated in 2005 with a Bachelor of Science in wildlife ecology, with a minor in scientific and technical writing. Betsy’s continued interests in the ecology and conservation of wildlife, particularly amphibians and reptiles, soon brought her to the University of Florida, where she received a Master of Science in wildlife ecology and conservation in 2007.