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Terrestrial movements and habitat use of gopher frogs in longleaf pine forests: A comparative study of juveniles and adults

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ABSTRACT

Many animals exhibit changes in patterns of movement and habitat use as they age, and understanding such ontogenetic shifts is important for ensuring that habitat management is appropriate for all life stages. We used radiotelemetry to study movements and habitat use of juvenile and adult gopher frogs (*Rana capito*) as they migrated from the same ponds following metamorphosis or breeding. To supplement radiotelemetry data, we also captured adult gopher frogs at drift fences as they left ponds for the terrestrial environment. We directly compared patterns of movement, directional orientation, macrohabitat use (forest type), and microhabitat use (refugia) between the two life stages. Both juveniles and adults moved considerable distances from breeding ponds (up to 691 m) and selected fire-maintained longleaf pine (*Pinus palustris*) forest over fire-suppressed forest. However, fire-suppressed habitat appeared to be a greater barrier to juveniles than adults. Additionally, we found differences in microhabitat use; both juveniles and adults used underground refuges (e.g., burrows and stump holes) for shelter, but juveniles used such refuges less often than adults. Juveniles also took more time than adults to locate their first refuge after exiting ponds. These differences may reflect the juveniles' lack of experience in terrestrial habitats. Unlike juveniles, adults are likely more familiar with the locations of specific habitat features (e.g., burrows and ponds) and may take the shortest routes when moving among them, even if it requires moving through fire-suppressed habitat. Previous research has recommended that terrestrial habitats surrounding breeding ponds should be managed with frequent prescribed fire (i.e., 1–3-year intervals) in order to maintain suitable terrestrial habitat for juvenile gopher frogs, and our study suggests that these management practices are also likely beneficial to adults.

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1. Introduction

Movement patterns provide important insight into the habitat requirements of a species, including the type and amount of habitat necessary for survival and reproduction (White and Garrott, 1990; Kenward, 2001; Millspaugh and Marzluff, 2001). Knowledge of animal movement patterns can have important implications for management and conservation. For example, an understanding of the distances that amphibians move from wetlands into the surrounding terrestrial habitat can be used to determine the size of buffers necessary to protect and manage core terrestrial habitat (Dodd, 1996; Semlitsch and Bodie, 2003). Additionally, understanding how amphibians behave when they encounter disturbed or fragmented habitats may guide managers in maintaining or improving terrestrial habitat quality (Gibbs, 1998; Rittenhouse and Semlitsch, 2006; Graeter et al., 2008).

Many animals shift patterns of movement and habitat use as they age; these changes may reflect resource needs, life history strategies, intraspecific competition, or predator avoidance (Van Horne, 1982; Hart, 1983; Werner and Gilliam, 1984; Blouin-Demers et al., 2007). Understanding such ontogenetic shifts is critical to adequately protect and manage the areas where animals live at all stages of their lives. Many amphibian species exhibit an obvious shift in habitat use as aquatic larvae metamorphose and move into terrestrial habitat as juveniles (Semlitsch, 2003). However, there may also be subtle differences in habitat requirements of terrestrial stages, particularly between juveniles and adults. Just as aquatic and terrestrial habitats must be properly managed together to maintain viable populations of amphibians (Semlitsch, 2000), specific microhabitats must also be managed within the uplands to provide suitable habitat for all terrestrial life

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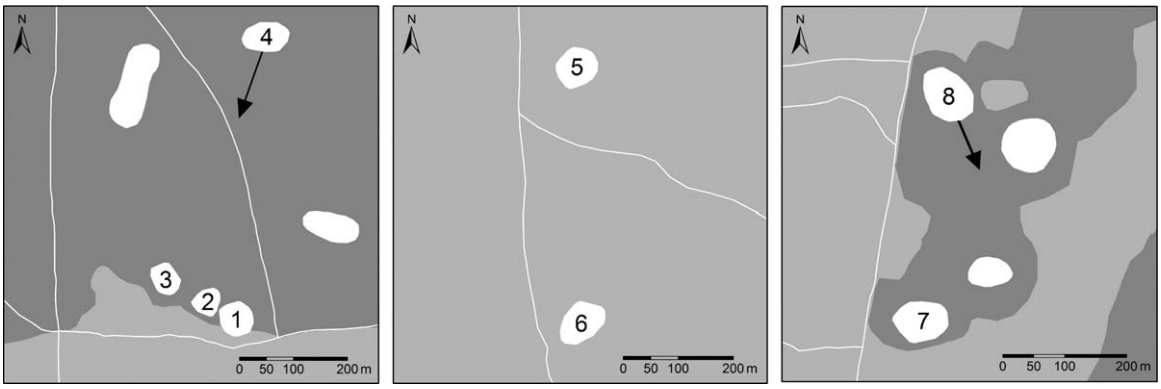

Fig. 1. Position of ponds (1–8) relative to other landscape features at our study sites. Ponds (white) were surrounded by fire-maintained longleaf pine forest (lightly shaded) and fire-suppressed longleaf pine forest (darkly shaded) and dirt roads (white lines). Also shown is the mean direction of movement (black arrows) by adult gopher frogs captured at drift fences where orientation was nonrandom. Note that ponds without labels were not studied.

stages. Furthermore, it is important to understand whether younger animals require more or less space than older animals so that these differences can also be considered when managing habitat. Although relatively little is known about terrestrial behaviors of pond-breeding amphibians, habitat quality is one factor known to affect patterns of movement and habitat use. For example, pond-breeding frogs and salamanders that inhabit uplands as adults may avoid disturbed areas, such as open fields and recent clearcuts (Vasconcelos and Calhoun, 2004; Rittenhouse and Semlitsch, 2006; Graeter et al., 2008). Amphibians also respond to natural variation within a single habitat type (Roznik and Johnson, 2009a). However, few studies have directly compared habitat selection between juveniles and adults at the same sites, particularly in species associated with open-canopy habitats, such as savannas.

Gopher frogs (*Rana capito*) occur in longleaf pine-wiregrass (*Pinus palustris–Aristida stricta* var. *beyrichiana*) savannas, which are maintained by frequent fire (i.e., 1–3-year intervals) and undergo succession to a mixed pine–hardwood forest in areas where fire is eliminated or suppressed. In the absence of natural fire regimes, active management with prescribed fire is the only way that these habitats are maintained (Glitzenstein et al., 1995; Gilliam and Platt, 1999). Our previous work has shown that juvenile gopher frogs move long distances from ponds, use underground refuges (e.g., burrows and stump holes) for shelter, and select fire-maintained open-canopy habitat, and we recommended that land managers apply frequent prescribed fire to maintain this type of habitat structure (Roznik, 2007; Roznik and Johnson, 2009a,b). Here we explore the extent to which adult gopher frogs move from ponds, use underground refuges, and select fire-maintained habitat by directly comparing novel adult behavioral data with data published on juveniles (Roznik and Johnson, 2009a). Thus, a major goal of this study was to determine the extent to which frequent prescribed fire benefits both juvenile and adult gopher frogs. To do this, we used radiotelemetry data to directly compare patterns of movement, directional orientation, macrohabitat use (i.e., forest type), and microhabitat use (i.e., refugia) between the two life stages when leaving breeding ponds. We also used an independent dataset from a long-term drift fence study at our sites to supplement our telemetry data and determine whether adult gopher frogs navigate towards fire-maintained habitat.

2. Materials and methods

2.1. Study area

Our study took place at eight ponds and the surrounding terrestrial habitat at two sites within the Ocala National Forest, Marion and Putnam Counties, FL, USA. Ponds 1–6 were located approximately 9.5 km north of Ponds 7 and 8. All ponds were located primarily within longleaf pine forest and prescribed burning was attempted at approximately 1–3-year intervals (Greenberg, 2001). Despite this active management, hardwoods (e.g., *Quercus* spp.) had invaded areas around some ponds, resulting in heterogeneous habitat with both fire-maintained (i.e., longleaf pine dominant) and fire-suppressed (i.e., mixed longleaf pine–hardwoods) habitats in close proximity (Fig. 1). We have shown that the structure of these two habitat types differs significantly at our sites; fire-maintained habitat is characterized by an open canopy, few hardwood trees, small amounts of leaf litter, and large amounts of wiregrass (Roznik and Johnson, 2009a).

Ponds 1–3 are close together with fire-suppressed habitat to the north, and fire-maintained habitat to the south (Fig. 1). Pond 4 is located within homogeneous fire-suppressed habitat and is approximately 500 m from the nearest fire-maintained habitat to the south (Fig. 1). Ponds 5 and 6 are surrounded by homogeneous fire-maintained habitat (Fig. 1). Ponds 7 and 8 are located primarily within fire-maintained habitat, although areas immediately surrounding the ponds are fire suppressed (Fig. 1). These eight ponds are part of an ongoing study of herpetofaunal use, and detailed descriptions of aquatic habitats at these sites are available in Greenberg (2001).

2.2. Movements

For our telemetry study, we captured juvenile gopher frogs following metamorphosis ($N = 31$) at drift fences surrounding five ponds (Ponds 3 and 5–8), except for one frog that we captured by hand in the uplands. We caught adult frogs ($N = 11$) at drift fences and by hand in breeding ponds at four ponds (Ponds 5–8). Drift fences (7.6 m in length) were placed at 7.6-m intervals to encircle 50% of each pond. We positioned pitfall traps (19-L buckets) on the inside and outside of both ends of each fence (four per fence). A single- or double-ended funnel trap was positioned at the midpoint of each fence on both sides (two funnel traps per fence). All traps were checked daily during the period when juveniles were tracked (May–August 2006) and three times each week during the remainder of the telemetry study period (September 2006–November 2007). A sponge placed in each trap was moistened at each trap check to prevent desiccation of captured animals. Adult males were distinguished from adult females by their enlarged thumbs and paired vocal sacs; sexes of juveniles were not determined because they are not sexually dimorphic based on external morphology.

We fitted juvenile frogs with R1625 transmitters (0.6 g) and adult frogs with R1655 transmitters (1.2 g; both models manufactured

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by Advanced Telemetry Systems, Isanti, MN, USA). Although battery life was longer for adult transmitters than for juvenile transmitters (115 and 33 days, respectively), no adults changed locations after 33 days, which allowed us to make direct comparisons of movements between the two life stages. Immediately after capturing frogs or removing them from pitfall traps we attached transmitters using an external belt following the methods of Muths (2003). Transmitter assemblies did not exceed the recommended maximum 10% transmitter to body mass ratio for amphibians (Richards et al., 1994). We released frogs near their point of capture immediately after attaching the transmitter and observed each frog briefly after release to ensure that movements were not noticeably affected by the transmitter assembly. Any transmitters that were recovered from predators or from frogs that shed their belts were redeployed on additional frogs when sufficient battery life remained.

We used a TRX-48S receiver (Wildlife Materials, Inc., Murphysboro, IL, USA) and a hand-held 3-element Yagi directional antenna to track frogs. We located each frog daily until its transmitter expired, the frog died, the frog shed the transmitter assembly, or the signal was lost. When adult frogs did not change locations after 3 weeks, we tracked them three times per week instead of daily. We recorded each location with a GeoXM GPS unit (Trimble, Sunnyvale, CA, USA). When we located frogs in the open (i.e., not in burrows or leaf litter), we examined them for possible skin abrasions caused by the transmitter belt. When we found abrasions on a frog, we immediately removed the transmitter and released the frog. Frogs that developed abrasions were omitted from all data analyses.

We used ArcGIS 9.2 (ESRI, Redlands, CA, USA) to measure distances between daily locations and from the frogs' pond of origin, and we used these values to determine six movement metrics for each frog: mean daily distance, maximum daily distance, range of daily distances, coefficient of variation of daily distances, farthest straight-line distance from the pond center, and total distance moved during the study period. We compared these measures of movement between juveniles and adults using a MANOVA (factor: life stage; dependent variables: the six movement metrics listed above) in addition to testing for differences in each individual movement metric using separate one-way ANOVAs. Data for the farthest-distance-from-pond analysis were log-transformed prior to analysis to satisfy the assumptions of parametric statistical tests, but mean values using raw data are presented for ease of interpretation. We used SYSTAT 11.0 (Systat Software, Inc., San Jose, CA, USA) to perform all statistical tests, except where otherwise noted. Alpha was set at 0.05 for significance testing, and all means presented are ± 1 SE.

To qualitatively determine whether the average distance between daily locations for juveniles and adults was similar to the average distance between underground refuges in the landscape (i.e., whether movements are limited by refuge availability), we attempted to locate all refuges (e.g., burrows and stump holes) within 100 m of Ponds 3 and 6–8. We recorded the refuge locations with a GPS and used ArcGIS 9.2 to measure the distance between successive refuges. We pooled data from all ponds to compute an overall mean distance between refuges at our study sites.

2.3. Orientation

2.3.1. Telemetry

We determined the directional orientation of movements of transmitter-equipped adult frogs from the ponds to their final locations in the uplands. We used ArcGIS 9.2 to determine the azimuth from the last known location of each frog (before death, or transmitter loss or expiration) to the center of its breeding pond. For frogs that returned to their pond and were subsequently preyed upon or shed their transmitters near the pond, we used the farthest recorded location from the pond for this analysis. We analyzed orientation data using Rayleigh tests (ORIANA 2.0, Kovach Computing Services, Anglesey, UK), which test whether the captures are uniformly distributed around the pond, and we compared mean directions moved by juveniles and adults at ponds where orientation was directional using a Watson–Williams test (ORIANA 2.0). The factor was life stage, and the dependent variable was azimuth. Although we previously performed such orientation analyses for juvenile frogs at four ponds (Ponds 3 and 6–8; Roznik and Johnson, 2009a), we were only able to perform the same analyses for adults at two ponds (Ponds 6 and 8) because of small sample sizes at the other ponds.

2.3.2. Drift fences

To augment our telemetry data, we used drift fences and pitfall traps surrounding ponds to capture adult gopher frogs and infer their habitat use and migration routes (e.g., Todd et al., 2009). Although we captured both juveniles and adults at all ponds, we only performed directional orientation analyses for adults. Our earlier radiotelemetry work showed that at our study ponds juveniles often change their direction of movement once they pass beyond the drift fence, such that the direction that an individual was found in the drift fence was not indicative of its later movements at ponds surrounded by heterogeneous habitat (Roznik and Johnson, 2009a). Therefore, captures of juveniles at drift fences at our sites are not useful in determining direction of migration, and thus for inferring habitat use. However, individual adult gopher frogs tend to migrate to and from ponds in the same directions (Palis, 1998; Roznik, 2007), suggesting that the orientation of captured frogs towards the drift fences is indicative of their orientation into the terrestrial habitat.

We captured adult gopher frogs at drift fences (see Section 2.2 above) at all eight ponds from February 1994 to February 2008. Traps were checked three times each week, except during periods of flooding when traps were underwater. Frogs were given a cohort toe clip representing pond number and year of capture. We determined the azimuths of pitfall traps from the center of the pond by standing at each pair of pitfall traps and using a compass to determine the direction to the center of the pond, which we marked with a pipe driven into the sediment. We then determined the directional orientation of movements towards and away from ponds using Rayleigh tests (ORIANA 2.0). Because individual adult gopher frogs tend to emigrate from ponds in the same direction as they immigrate (Palis, 1998; Roznik, 2007), we pooled data from both sides of the drift fences for analysis to increase sample sizes.

2.4. Terrestrial habitat use

We used aerial photographs and ArcGIS 9.2 to determine whether transmitter-equipped adult frogs used habitat types (fire-maintained and fire-suppressed longleaf pine forests) in proportion to their availability. For adults, we buffered each pond by 400 m, which included the farthest distances traveled by all adult frogs. We then used aerial photographs to delineate fire-maintained and fire-suppressed areas within the buffers, and generated random points in each buffer equal to the number of frog locations at that pond. To determine whether frogs used habitat types in proportion to availability, we evaluated the number of frog locations and random points in fire-maintained and fire-suppressed habitats using a contingency table analysis. For this analysis, we used location type (frog or random) and habitat type (fire-maintained or fire-suppressed forest) as the independent variables and the number of locations in each category as the dependent variable. This method is similar to the approach we used for juveniles in an earlier study in which we buffered each

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Table 1
Mean values (±SE) and ranges of body sizes and six movement metrics for juvenile ($N = 31$) and adult ($N = 11$) gopher frogs tracked using radiotelemetry. The six metrics are mean daily distance, maximum daily distance, range in daily distances, coefficient of variation in daily distances, farthest straight-line distance located from pond center, and total distance moved during the study period. Also shown are results from separate statistical tests comparing these metrics between the two life stages (see text for details). Statistically significant results are shown in bold font. Because of high mortality in juvenile frogs, sample sizes differ among analyses when data were insufficient to calculate movement metrics.

Variable	Juvenile		Adult		*F*	df	*P*
	Mean ± SE	Range	Mean ± SE	Range			
Body mass (g)	7.4 ± 0.2	7.0–10.0	57.8 ± 3.6	45.5–85.0	581.260	1, 40	**<0.0001**
Snout-urostyle length (mm)	36.8 ± 0.4	31–40	73.3 ± 1.3	67–82	1209.640	1, 40	**<0.0001**
Mean distance (m)	60.4 ± 8.5	6.2–200.8	91.3 ± 23.3	17–274	2.442	1, 39	0.126
Maximum distance (m)	106.6 ± 16.5	6–325	143.5 ± 35.8	36–355	1.132	1, 39	0.294
Range (m)	112.6 ± 19.4	2–277	112.1 ± 44.5	4–331	<0.0001	1, 27	0.990
Coefficient of variation	0.84 ± 0.09	0.07–1.5	0.64 ± 0.12	0.07–1.00	1.575	1, 27	0.220
Farthest distance (m)	173.0 ± 30.7	24–691	180.3 ± 39.8	35–396	0.187	1, 39	0.668
Total distance (m)	215.1 ± 30.1	31–665	279.4 ± 63.3	63–730	2.378	1, 37	0.132

pond by 250 m, which included the farthest distances traveled from ponds by over 80% of the frogs and only excluded outliers (Roznik and Johnson, 2009a). Although we previously performed this analysis at three ponds for juveniles (Ponds 3, 7, and 8; Roznik and Johnson, 2009a), we were only able to analyze data from one pond (Pond 8) for adults because of small sample sizes or homogeneous habitat at the other ponds.

To determine whether juveniles used habitat types differently than adults at Pond 8, we used a contingency table analysis to test for differences in the number of frog locations by habitat type and life stage, using the total number of locations in each habitat type, irrespective of individual. We used habitat type and life stage as the independent variables, and number of frog locations in each category as the dependent variable. To control for individual variation in frog behavior, we also calculated the proportion of locations in fire-maintained habitat for each frog and used an ANOVA to determine whether juveniles used fire-maintained habitat more or less often than adults. For this analysis, the factor was life stage, and the dependent variable was the proportion of locations in fire-maintained habitat.

2.5. Refuge use

We performed four slightly different analyses to determine whether juveniles and adults used underground refuges equally. Each time we located a transmitter-equipped frog, we recorded whether the frog was in an underground refuge (e.g., tortoise or mammal burrow and stump hole) or whether it was sheltering aboveground (e.g., under leaf litter or vegetation). We summed the total number of underground and aboveground locations (irrespective of individual) and used a contingency table analysis to test for differences in refuge use. We used life stage and refuge type (underground or aboveground) as the independent variables and number of frog locations in each category as the dependent variable. To control for individual variation in microhabitat preference, we also calculated the proportion of underground locations for each individual frog and used an ANOVA to determine whether juveniles used underground refuges more or less often than adults. For this analysis, the factor was life stage, and the dependent variable was proportion of locations. Because juvenile mortality was high during our study (Roznik and Johnson, 2009b), many juveniles were preyed upon before they were able to locate a burrow. Therefore, we also re-ran this analysis to compare refuge use between adults and only those juveniles that used at least one underground refuge. Finally, to determine whether juveniles took longer to locate their first refuge than adults, we used an ANOVA to compare the number of days that juveniles (those that used at least one underground refuge) and adults sheltered aboveground before using their first refuge after exiting ponds. For this analysis, the factor was life stage, and the dependent variable was the number of days aboveground.

3. Results

3.1. Movements

We tracked 31 juvenile frogs at five ponds (Ponds 3 and 5–8) and 11 adult frogs (2 females and 9 males) at four ponds (Ponds 5–8). Adult frogs were much larger than juvenile frogs, both in body mass and snout-urostyle length (Table 1). Based on multivariate analysis, there were no statistically significant differences between the measures of movement we examined for juveniles and adults (MANOVA, $F_{6,22} = 1.009$, $P = 0.445$). Mean daily distance, maximum daily distance, farthest straight-line distance from the pond center, and total distance moved during the study period were greater for adults than juveniles, but these differences were not statistically significant (Table 1). Additionally, the average distance between successive underground refuges at our sites (32.0 ± 2.4 m; $N = 73$) was much shorter than the average daily distance traveled by both juveniles and adults (60.4 and 91.3 m, respectively).

3.2. Orientation

3.2.1. Telemetry

Based on their final locations in the uplands, adult frogs oriented in random directions from Pond 6 ($Z = 1.608$, $P = 0.210$; $N = 4$), where habitat was homogenous fire-maintained forest, but moved directionally from Pond 8, where habitat was heterogeneous. Adult frogs moved from Pond 8 towards the largest patch of fire-maintained habitat at a mean azimuth of 270 ± 14.6° (range: 244–298°; $Z = 4.263$, $P = 0.006$; $N = 5$; Fig. 2). Juvenile frogs also moved directionally from Pond 8 ($N = 8$; Roznik and Johnson, 2009a), and we found that the mean direction of movement was similar between juveniles and adults at this pond ($F_{1,11} = 0.331$, $P = 0.576$; Fig. 2).

3.2.2. Drift fences

We captured 233 adult gopher frogs between 1994 and 2008, and successful reproduction occurred (i.e., metamorphosing juveniles were captured) on a per-pond basis during an average of 70.8 ± 4.6% of years (range: 50.0–85.7% of years), although the number of captures was low (≤5 juveniles) in 24.0% of pond-year combinations. Seventeen adult frogs were recaptured; two of these frogs were recaptured in the subsequent year, one of which was recaptured at another study pond 300 m away. At ponds surrounded by homogeneous fire-maintained habitat (Ponds 5 and 6), adult frogs moved to and from ponds in random directions (Table 2). At the pond surrounded by homogeneous fire-suppressed habitat (Pond 4), adult frogs moved directionally in the direction of the nearest fire-maintained habitat (Table 2; Fig. 1). At ponds surrounded by heterogeneous habitat, adult frogs moved randomly at Ponds 1, 2, and 7, but directionally (away from

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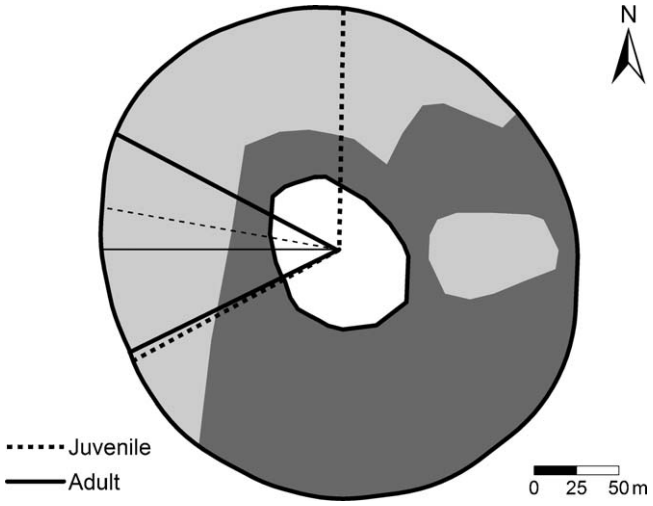

Fig. 2. Orientation of transmitter-equipped juvenile and adult gopher frogs migrating from a breeding pond (Pond 8) surrounded by longleaf pine forest that was fire-maintained (lightly shaded) and fire-suppressed (darkly shaded). The pond (white) is in the center and is buffered by a distance of 100 m. Thick lines indicate the range in azimuths moved by frogs from the center of the pond to their final locations in the uplands, and thin lines represent the mean azimuths.

Table 2
Results from separate orientation analyses testing for directionality of movements towards and away from breeding ponds by adult gopher frogs. The sample size (*N*), Rayleigh test statistic (*Z*), and significance value (*P*) are given for each pond. Pond 3 is not shown because of a small sample size (*N* = 1), and statistically significant results are shown in bold.

Pond	*N*	*Z*	*P*
1	42	0.083	0.921
2	24	1.426	0.243
4	22	4.328	**0.012**
5	23	2.045	0.129
6	35	0.008	0.992
7	14	1.830	0.161
8	63	3.940	**0.019**

fire-maintained habitat) at Pond 8 (Table 2; Fig. 1). We were unable to perform orientation analyses at Pond 3 because of a small sample size ($N = 1$).

3.3. Terrestrial habitat use

When we compared all adult frog locations ($N = 16$ locations, determined by radiotelemetry) to an equal number of random points at a pond surrounded by heterogeneous habitat (Pond 8), we found that adult frogs used fire-maintained habitat disproportionately more often than fire-suppressed habitat (Fishers exact test: $P = 0.015$; Fig. 3). Because this pattern was also observed in juvenile frogs (Roznik and Johnson, 2009a), we were able to directly compare the use of fire-maintained habitat between the two life stages at ponds in heterogeneous habitat. We found that both life stages used fire-maintained habitat and fire-suppressed habitat equally when considering the total number of locations (juveniles: $N = 69$ locations from 31 frogs; adults: $N = 16$ locations from 11 frogs) in each habitat type, irrespective of individual (Fishers exact test: $P = 0.284$), and also when controlling for individual variation by using the proportion of locations in fire-maintained habitat for each frog ($F_{1,27} = 2.262$, $P = 0.144$). The average percentage of locations in fire-maintained habitat was 68.8 ± 9.0% (range: 0–100%) for juveniles and 95.8 ± 4.2% (range: 75–100%) for adults.

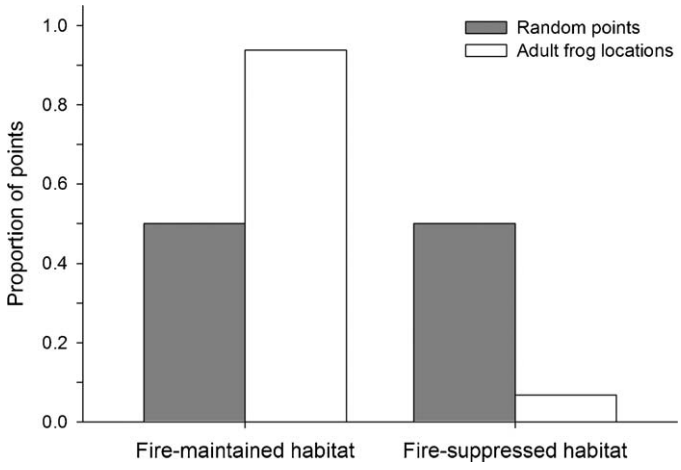

Fig. 3. Proportion of adult gopher frog locations ($N = 16$) and an equal number of random points in fire-maintained and fire-suppressed longleaf pine forests at Pond 8. Random points were generated within a 400-m buffer around the pond. Frog locations occurred in fire-maintained habitat more often than they occurred in fire-suppressed habitat based on availability.

3.4. Refuge use

Of all locations for juveniles, 11.3 ± 0.04% (range: 0–100%; $N = 29$ locations) were underground refuges (e.g., burrows and stump holes). Of those juvenile frogs that used at least one refuge (a subset of all juveniles; $N = 8$), 41.0 ± 0.09% of locations (range: 20.0–100%) were underground. Of all locations for adults, 74.9 ± 0.08% of locations (range: 40.0–100%) were associated with underground refuges. The proportion of underground locations was significantly greater for adults as compared to juveniles ($\chi^2 = 22.016$, df = 1, $P < 0.0001$). We obtained the same result when we controlled for individual variation by analyzing data for frogs individually. This was consistent whether we included all juveniles ($F_{1,38} = 58.946$, $P < 0.0001$) or if we truncated the data to only include those juveniles that used at least one underground refuge ($F_{1,17} = 8.188$, $P = 0.011$). We also found that juvenile frogs took significantly longer than adults to locate their first refuge ($F_{1,17} = 5.626$, $P = 0.030$; Fig. 4). On average, juveniles spent 2.8 ± 0.5 days aboveground before locating their first refuge, whereas adults found their first refuge after only 1.5 ± 0.3 days (Fig. 4).

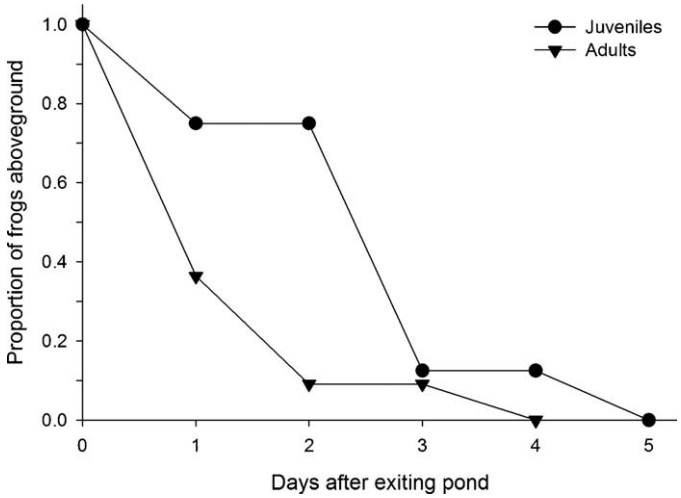

Fig. 4. Proportion of juvenile ($N = 8$) and adult ($N = 11$) gopher frogs aboveground (i.e., not in burrows or stump holes) during the first 5 days after migrating from breeding ponds following metamorphosis or breeding, respectively. Only juvenile frogs that survived until they located at least one underground refuge are included. Juveniles took longer than adults to locate their first refuge.

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4. Discussion

An understanding of the distances that juvenile and adult amphibians move from ponds can be used to determine the minimum area of terrestrial habitat that must be protected and properly managed for pond-breeding amphibians. We found that both life stages of gopher frogs moved considerable distances from breeding ponds (up to 691 m; Table 1). Despite the large difference in body size between juveniles and adults (Table 1), juveniles traveled on average just as far from ponds as adults, and daily movements of juveniles were as consistent as those of adults (Table 1). Furthermore, the farthest movement we recorded (691 m) was by a juvenile, and this was 57% farther than the longest adult movement (Table 1). Although both life stages exhibited high variability in movements, the mean daily distance moved was 50% farther in adult frogs (Table 1), suggesting that a statistically significant difference may be detected with larger sample sizes. Gopher frogs have been consistently reported to move long distances from breeding ponds (up to 2 km; Table 3), and our values fall within the general ranges reported for this and other species of gopher frogs (Table 3). Unfortunately, direct comparisons between our data and other studies are precluded by differences in study design, including where frogs were captured (i.e., at ponds or in uplands), study duration, and a lack of consistency in the movement data reported.

Gopher frogs are closely associated with underground refuges, particularly burrows excavated by gopher tortoises (*Gopherus polyphemus*), small mammals (e.g., *Geomys pinetis*), and crayfish (Phillips, 1995; Jensen and Richter, 2005; Blihovde, 2006). Gopher frogs are rarely observed aboveground where they are susceptible to predation and desiccation (Blihovde, 2006; Roznik, 2007; Roznik and Johnson, 2009b); therefore, we would expect frogs to minimize time aboveground and thus move directly between burrows. However, daily movements did not appear to be constrained by the distance between underground refuges in the landscape, suggesting that suitable refuges were not limiting in these habitats. On an average day, juvenile and adult frogs moved two to three times farther than the average distance between refuges at our sites. This disparity could be caused by a difficulty in locating refuges, because not all refuges are suitable (e.g., Bulova, 2002), or because some refuges are already occupied by another frog. Adult gopher frogs have been observed sharing burrows for multiple days, refuting the latter hypothesis (Roznik and Johnson, 2009c), although whether juveniles also display this behavior is unknown. Future studies on burrow selection by juvenile and adult gopher frogs would be worthwhile to understand how burrows are selected, and whether the number of burrows in the landscape may limit population sizes.

Because both juvenile and adult gopher frogs depend on burrows for shelter (Phillips, 1995; Blihovde, 2006; Roznik, 2007), we would expect the two life stages to use such underground refuges equally. However, we found that adults used refuges more often than juveniles and began using them more quickly after leaving a pond (Fig. 4). One explanation for this is that adults, unlike juveniles, have previous experience in the terrestrial environment and are familiar with the locations of specific refuges surrounding breeding ponds. Adults then may be deliberately moving among refuges. This hypothesis is supported by studies showing that individual adult gopher frogs tend to emigrate and immigrate to and from ponds in the same direction (Palis, 1998), and that individuals can return to specific refuges they have used in the past (Richter et al., 2001; Blihovde, 2006; Roznik, 2007). Thus, it appears that adults can easily navigate among known habitat features, whereas recently metamorphosed frogs must learn the spatial locations of refuges by exploring their habitat (e.g., Pike, 2005). This learning process is critical for juveniles because using underground refuges appears to be important for their survival (Roznik and Johnson, 2009b).

Although the cues that gopher frogs use to select terrestrial habitat are unknown (e.g., temperature, moisture, light, chemical, etc.), it is clear that radio-tracked juveniles and adults selected fire-maintained forest over habitat that was fire suppressed; however, the two life stages may use these forest types slightly differently. After exiting ponds surrounded by heterogeneous habitat (fire-maintained and fire-suppressed areas), juveniles moved into the closest patch of fire-maintained habitat (Roznik and Johnson, 2009a). Although the adults that we radio-tracked showed this same pattern (Fig. 2), long-term drift fence data suggest that adults tend to move into or out of ponds in all directions, irrespective of the distance to the nearest fire-maintained habitat when such habitat is less than 500 m away (Fig. 1). If the orientation of adult frogs captured at ponds accurately indicates the direction of migration into the terrestrial habitat, then fire-suppressed habitat does not appear to be a major barrier to movements of adult frogs. An alternative hypothesis is that adults move around unpredictably during the breeding season and therefore drift fence captures do not indicate the ultimate direction of migration from ponds. For example, frogs may move among ponds in close proximity during the breeding season, which has been observed in other pond-breeding amphibians (Semlitsch, 2008). Many of our ponds are located in clusters (Fig. 1), and we found some support for this hypothesis. For example, at Pond 8 orientation of adult frogs was directed towards three other breeding ponds within 300 m (Fig. 1), and one adult frog captured at one of the ponds in this cluster was recaptured at another nearby pond during the subsequent year. Regardless of whether frogs use multiple ponds for breeding, it is clear that adults will move relatively long distances through fire-suppressed habitat during migrations to and from breeding ponds. For example, at the pond surrounded by homogenous fire-suppressed habitat (Pond 4), adult captures were directed towards the nearest fire-maintained habitat, which was located

Table 3
Summary of maximum distances that gopher frogs (Florida gopher frogs, *Rana capito aesopus*; Carolina gopher frogs, *R. c. capito*; and dusky gopher frogs, *R. sevosa*) have been found from breeding ponds.

Species	Life stage	Maximum distance from pond (m)	Method	*N*	Source
Rana capito aesopus	Adult	396	Radiotelemetry	11	This study
Rana capito aesopus	Adult	1609	Observation	1	Carr (1940)
Rana capito aesopus	Adult	2000	Observation	1	Franz et al. (1988)
Rana capito aesopus	Adult	460[a]	Radiotelemetry	9	Blihovde (2006)
Rana capito aesopus	Adult	862	Observation	1	Roznik (2007)
Rana capito aesopus	Juvenile	691	Radiotelemetry	31	Roznik and Johnson (2009a)
Rana capito capito	Adult	102	Radiotelemetry	2	Phillips (1995)
Rana sevosa	Adult	299	Radiotelemetry	12	Richter et al. (2001)

[a] Approximate distance between a potential breeding pond and the center of a 1-ha study plot containing burrows where frogs were captured for the study.

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approximately 500 m away (Fig. 1). Although gopher frogs will move through fire-suppressed habitat and may inhabit it for some period of time, there may be costs associated with occupying poor habitat, such as increased mortality and lower growth (Todd and Rothermel, 2006).

Although juveniles and adults preferred fire-maintained longleaf pine forest over fire-suppressed forest, juveniles appear to be more selective of regularly burned habitat. One reason for this may be their unfamiliarity with the habitat and their need to locate a burrow quickly after exiting ponds. Newly metamorphosed gopher frogs have high rates of mortality, and survival is positively correlated with refuge use (Roznik and Johnson, 2009b). Because burrowing vertebrates prefer habitat that has been regularly burned over habitat that has been fire-suppressed (Funderburg and Lee, 1968; Boglioli et al., 2000), and fire-maintained habitat therefore contains higher densities of burrows (both tortoise and mammal; Roznik and Johnson, 2009a), juveniles may be more likely to encounter a suitable refuge and survive in fire-maintained habitat. Conversely, adults are more familiar with the locations of breeding ponds and refuges in surrounding terrestrial habitat, and they may take the shortest route when moving among them, even if it means moving through fire-suppressed areas.

5. Management implications

Land managers must use prescribed fire to maintain the species composition and structure of longleaf pine savannas that were historically maintained by natural fire. High quality terrestrial habitat is especially important to gopher frogs because of high annual variation in reproductive effort and success (Richter et al., 2003; this study) and also because of high juvenile mortality rates (Roznik and Johnson, 2009b). We previously recommended that large areas of longleaf pine forest surrounding breeding ponds should be managed with frequent prescribed fire in order to maintain suitable terrestrial habitat for juvenile gopher frogs, and that habitat should be burned all the way to the edges of breeding ponds, as well as through ponds during periodic droughts (Roznik and Johnson, 2009a). Our present study suggests that these management practices should also benefit adult gopher frogs because of the similarity in behavior between juveniles and adults. The purpose of our study was not to determine which fire regime (i.e., season or return interval) is best for gopher frogs, but growing-season (i.e., April–July) fires with a fire-return interval of 1–3 years adequately maintain the natural vegetative characteristics of longleaf pine forest similar to that selected by frogs at our sites (e.g., Wahlenberg, 1946; Robbins and Myers, 1992; Means et al., 2004; Bishop and Haas, 2005). Both juveniles and adults moved long distances from breeding ponds, used gopher tortoise and mammal burrows for shelter, and selected fire-maintained habitat over habitat that was fire suppressed. However, our study suggests that fire-suppressed habitat may be a greater barrier to juveniles than adults. Therefore, applying frequent prescribed fire to terrestrial habitat immediately surrounding ponds is essential to maintain suitable habitat for juveniles, and this management practice is also likely beneficial to adults. Importantly, fire is also beneficial to the burrowing animals (e.g., tortoises and mammals) that juvenile and adult gopher frogs depend on for shelter (Funderburg and Lee, 1968; Boglioli et al., 2000).

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Disclosure

All animals were handled under protocols approved by the Institutional Animal Care and Use Committee of the University of Florida (permit no. E485).

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