Canopy Closure and Emigration by Juvenile Gopher Frogs

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ABSTRACT Although studies have addressed effects of abrupt transitions in habitat type (e.g., forest–clear-cut or forest–field edges) on amphibian movements, little is known about effects of more subtle habitat transitions on patterns of migration and habitat use in amphibians. We used radiotelemetry to study movement patterns of juvenile gopher frogs (*Rana capito*) emigrating from ponds that were surrounded by longleaf pine (*Pinus palustris*) forest that varied in structure as a result of fire suppression. Our primary purpose was to determine if frogs emigrate directionally from their natal ponds and select habitat at random during their first month following metamorphosis. We found that frogs emigrated in nonrandom directions from ponds that were surrounded by heterogeneous habitat and selected fire-maintained habitat that was associated with an open canopy, few hardwood trees, small amounts of leaf litter, and large amounts of wiregrass (*Aristida beyrichiana*). Fire-maintained habitat contained higher densities of burrows excavated by gopher tortoises (*Gopherus polyphemus*) and small mammals, which are the primary refuge sites for both juvenile and adult gopher frogs. Frogs moved up to 691 m from their natal ponds, frequently crossed dirt roads, and even seemed to use these roads as migration corridors. To maintain suitable terrestrial habitat for gopher frogs, including habitat used by migrating individuals, it is important to apply frequent prescribed fire to uplands surrounding breeding ponds that lead all the way to the edges of breeding ponds, as well as through ponds during periodic droughts. (JOURNAL OF WILDLIFE MANAGEMENT 73(2):260–268; 2009)

For many species, breeding habitats are spatially separated from foraging and hibernation areas and individuals must seasonally migrate to and from these sites. Although this has been demonstrated for a broad range of taxa, including mammals (Ferguson and Elkie 2004), birds (O'Reilly and Wingfield 1995), fish (Dittman and Quinn 1996), reptiles (Schroeder et al. 2003), amphibians (Semlitsch 2008), and insects (Brower 1996), pond-breeding amphibians are a classic example because adults migrate from terrestrial habitats to aquatic sites to breed and subsequently migrate back into surrounding terrestrial habitat after breeding (Semlitsch 2008). Following metamorphosis, juvenile pond-breeding amphibians also move into terrestrial habitat, where they remain until sexual maturity (Semlitsch 2008). Although aquatic habitat is necessary for breeding and larval development, many pond-breeding amphibians spend a substantial portion of their lives in terrestrial habitat (Dodd 1996, Semlitsch and Bodie 2003). Thus, the terrestrial environment provides essential habitat during the non-breeding season and also serves as migration routes for juveniles and adults moving to and from breeding ponds.

Habitat type is one factor that affects migration patterns of pond-breeding amphibians. Studies have shown that pond-breeding frogs and salamanders that inhabit forests tend to avoid open fields and recent clear-cuts during migrations (deMaynadier and Hunter 1999, Rothermel and Semlitsch 2002, Marty et al. 2005, Rittenhouse and Semlitsch 2006). However, what happens when amphibians encounter variations in structure within the same habitat type? Although studies have addressed effects of abrupt transitions in habitat type on amphibian movements, little is known about effects of more subtle habitat variations on patterns of migration and habitat use in amphibians. One example of such habitat is a fire-dependent forest where one area has been regularly burned whereas an adjacent area has failed to burn or has had fire suppressed. The fire-suppressed area may be characterized by a higher density of trees and a more densely vegetated understory than the area that has been burned regularly, resulting in distinct structural differences (Heyward 1939, Gilliam and Platt 1999). Although 2 distinct habitat types may vary considerably in abiotic factors, such as temperature, moisture, and light (Saunders et al. 1991), subtle transitions in habitat type may also vary in these factors, and amphibians may subsequently detect and respond to them.

Understanding habitat preferences of pond-breeding amphibians is important because this information can be used to guide management activities that will improve nonbreeding habitat and upland migration routes. This is especially true for intensively managed ecosystems, such as the longleaf pine (*Pinus palustris*)–wiregrass (*Aristida beyrichiana*) ecosystem in the southeastern United States, which is maintained by frequent prescribed fire (Glitzenstein et al. 1995, Gilliam and Platt 1999). Distribution of the longleaf pine ecosystem has been reduced by as much as 98% and much of what remains is in poor condition, largely because of fire suppression (Noss 1989, Ware et al. 1993). Consequently, the longleaf pine ecosystem has been considered an endangered ecosystem (Noss 1989), and restoration and proper management of longleaf pine forests have thus become important conservation concerns. As a result of habitat loss and degradation, many wildlife species associated with longleaf pine forests have also declined (Van Lear et al. 2005), including the gopher frog (*Rana capito*; Jensen and Richter 2005).

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We used radiotelemetry to study movement patterns of juvenile gopher frogs emigrating from ponds that were surrounded by fire-maintained and fire-suppressed habitat within contiguous longleaf pine forest. Gopher frogs breed in temporary or semipermanent ponds but spend most of their lives in surrounding uplands, where they seek shelter in stump holes and burrows of gopher tortoises (*Gopherus polyphemus*) and small mammals (Lee 1968, Franz 1986, Jensen and Richter 2005). Our primary purpose was to determine if juvenile gopher frogs emigrate directionally from their natal ponds and whether they select upland habitat at random. Because migration exposes amphibians to mortality risks (e.g., predation, desiccation; Spieler and Linsenmair 1998, Roznik and Johnson 2009), presence of refugia along migration routes is important, particularly for gopher frogs because both juveniles and adults depend on burrows of other vertebrates for shelter (Jensen and Richter 2005, Roznik 2007). Because these burrow-excavating species are generally associated with fire-maintained habitat (Funderburg and Lee 1968, Boglioli et al. 2000), we also examined burrow density in relation to habitat type and migration patterns of juvenile gopher frogs.

STUDY AREA

Our study took place at 5 ponds and the surrounding upland habitat at 2 sites in the Ocala National Forest, Marion and Putnam counties, Florida, USA. Ponds 3, 5, and 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). However, hardwoods (e.g., *Quercus* spp.) invaded areas around ponds 3, 7, and 8, resulting in heterogeneous upland habitat with fire-maintained (i.e., longleaf pine dominant) and fire-suppressed (i.e., mixed longleaf pine–hardwoods) areas largely clumped together (Figs. 1, 2). Habitat surrounding ponds 5 and 6 was homogenous fire-maintained habitat. The 5 ponds we used are part of an ongoing study of herpetofaunal use, and detailed descriptions of aquatic habitats at these sites are available in Greenberg (2001).

METHODS

Movements

We captured recently metamorphosed gopher frogs at drift fences (7.6 m long) placed at 7.6-m intervals to encircle 50% of each pond, except for one frog that we captured by hand in the uplands. All drift fences were located in fire-suppressed habitat at ponds 3, 7, and 8 and in fire-maintained habitat at ponds 5 and 6. We positioned pitfall traps (19-L buckets) on the inside and outside of both ends of each fence (4 per fence) so that we could detect the direction of travel. We checked all pitfall traps daily and placed a moistened sponge in each trap daily to prevent desiccation of captured animals.

We fitted frogs with R1625 transmitters (Advanced Telemetry Systems, Isanti, MN), which weighed 0.6 g and had a maximum battery life of 33 days. Immediately after
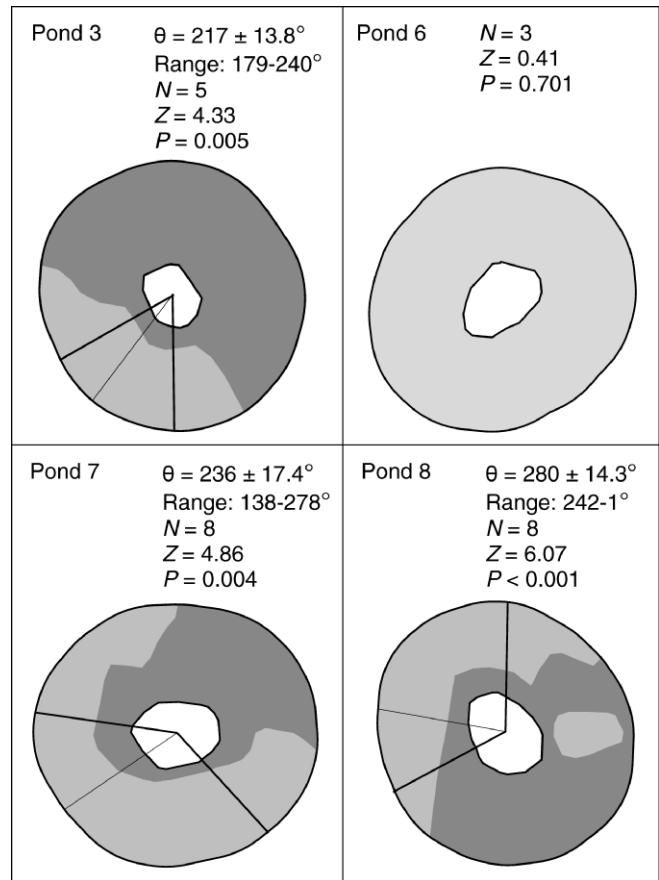

Figure 1. Orientation of juvenile gopher frogs emigrating from 4 ponds surrounded by fire-maintained longleaf pine forest (lightly shaded) and fire-suppressed longleaf pine forest (darkly shaded) within 100 m of ponds in the Ocala National Forest, Florida, USA, May–August 2006. At ponds where orientation was directional, thick lines indicate the range in azimuths moved by frogs from the center of the pond to their final locations in the uplands, and a thin line represents mean azimuth. We show sample size (N), Rayleigh test statistic (Z), and significance value (P) for each pond, and we show mean azimuth (θ) and range of azimuths for ponds where orientation was directional.

removing frogs from pitfall traps we attached transmitters using an external belt following methods of Muths (2003). We fitted all captured frogs ≥ 7.0 g 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). 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 obviously affected by the transmitter assembly. We redeployed any transmitters that we recovered from predators or from frogs that shed their belts on additional frogs when sufficient battery life remained.

We used a TRX-48S receiver (Wildlife Materials, Inc., Murphysboro, IL) and a handheld 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. We recorded each location with a Global Positioning System (GPS) unit and used ArcGIS 9.2 to measure distances between
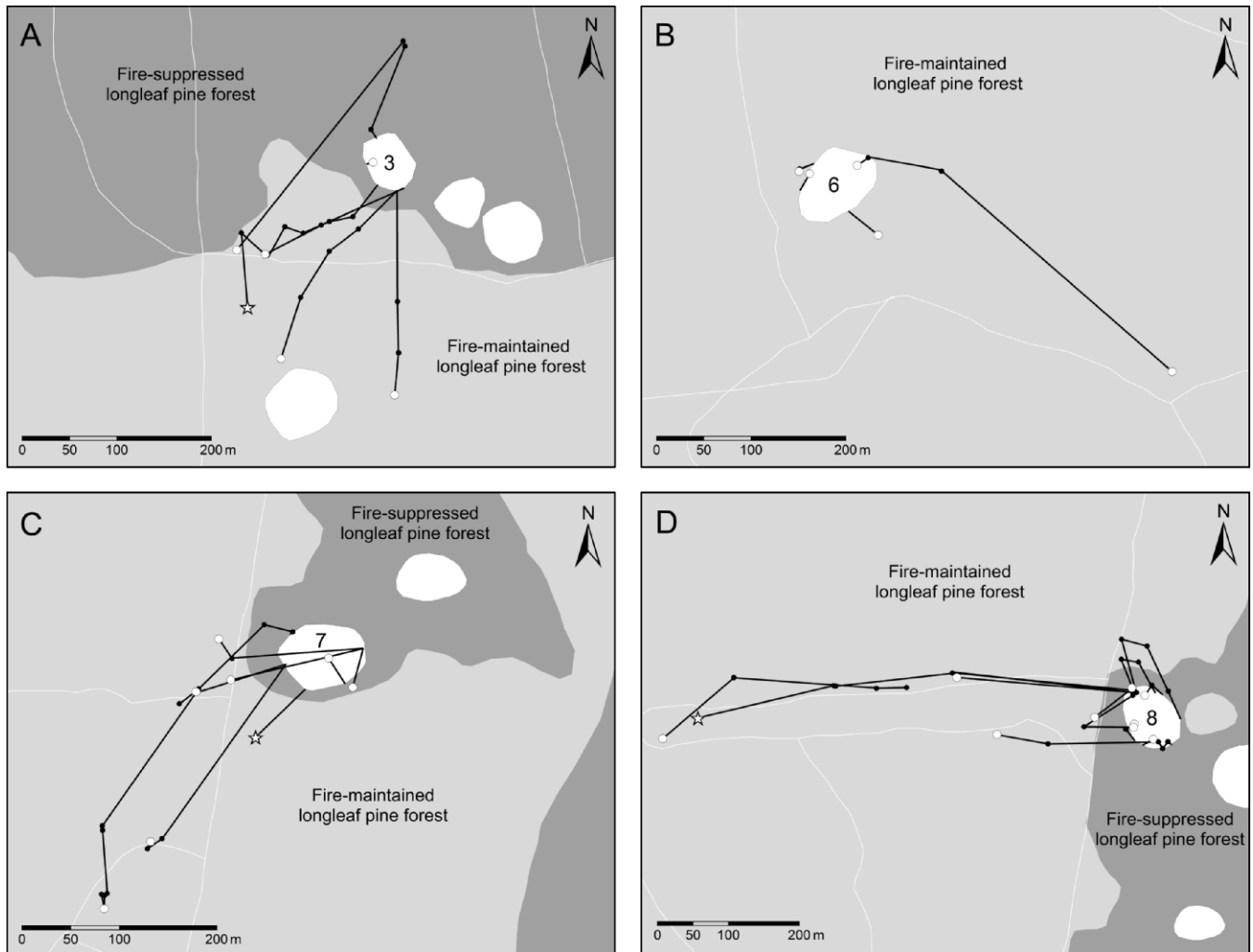
Figure 2. Movement paths of juvenile gopher frogs emigrating from (A) pond 3, (B) pond 6, (C) pond 7, and (D) pond 8 in the Ocala National Forest, Florida, USA, May–August 2006. Surrounding terrestrial habitat was fire-maintained longleaf pine forest (lightly shaded) and fire-suppressed longleaf pine forest (darkly shaded). We created paths by drawing straight lines between daily radiotelemetry locations (closed circles). Stars represent the last known locations of surviving frogs, and open circles represent that last known locations of frogs before death. Thin white lines represent dirt roads, and we also show other nearby ponds (white).

successive locations and from the frogs' natal pond. We examined frogs every few days when possible, especially after long-distance movements, to check 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. We omitted frogs that developed abrasions from all data analyses. We handled animals under protocols approved by the Institutional Animal Care and Use Committee of the University of Florida (permit no. E485). Although we used data from frogs tracked at all ponds to summarize overall movement patterns, all other sampling and analyses took place for only 4 of our 5 study ponds because we only captured and tracked one frog at pond 5.

Orientation

We determined the directional orientation of frog movements into the uplands at 2 spatial scales at each pond: 1) from the pond into pitfall traps and 2) from the pond to their final locations in the uplands. At the first scale, we performed 2 tests, one using all frogs captured in pitfall traps during the study period and one including only frogs that we radiotracked. At the second scale we used only radiotracked frogs. 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 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 natal pond. For frogs that returned to their ponds and were preyed upon or shed their transmitters near the ponds, we used the farthest known location from the pond for this analysis. We analyzed orientation data using Rayleigh tests in ORIANA 2.0 (Kovach Computing Services, Anglesey, United Kingdom).

Upland Habitat Use

We used a combination of Geographic Information System (GIS) and field-based methods to describe upland habitat

use by frogs. Fire-maintained and fire-suppressed areas are easily distinguished on aerial photographs, so we used GIS to characterize habitat use at a coarse scale. We buffered each pond by 250 m, which included the farthest distances traveled from ponds by >80% of frogs, and we delineated fire-maintained and fire-suppressed areas within the buffers. We then generated a number of random points in each buffer that was equal to the number of points representing frog locations at that pond. To determine whether frogs used habitat types in proportion to their availability, we evaluated expected and observed numbers of frog locations and random points in fire-maintained and fire-suppressed habitat using a contingency table analysis. We used SYSTAT 11.0 (Systat Software Inc., San Jose, CA) to perform statistical tests. We set $\alpha = 0.05$ for all significance testing; all means are ± 1 standard error.

We also sampled upland habitat characteristics at each pond. Frogs emigrated from ponds along linear paths and in nonrandom directions at ponds where surrounding habitat was heterogeneous (see Results); therefore, we chose to sample habitat characteristics at plots along transects. To describe upland habitat characteristics, we sampled vegetation at 50-m intervals (50 m, 100 m, 150 m, 200 m, and 250 m from the pond) along 4 transects at each pond. At ponds where frogs exhibited directional movement to their final locations, one transect represented habitat that the frogs used, and 3 transects represented available habitat. We determined the transect representing used habitat by averaging azimuths of all frogs at that pond, and we chose the other 3 transects representing available habitat at 90°, 180°, and 270° angles to the mean azimuth. If frogs oriented randomly into terrestrial habitat at the ponds, we sampled vegetation at plots along transects following the 4 compass directions and used these transects to represent habitat used by frogs.

At each 50-m interval we sampled the basal area of longleaf pines, hardwoods, and snags using a 10 basal area factor wedge prism, and we visually estimated percentage of cover of wiregrass, herbaceous vegetation, shrub (<2.5 cm dbh), leaf litter, coarse woody debris (≥12.5 cm diam), bare ground, and canopy within circular 12-m^2 plots (Greenberg 2001). We measured percentage of canopy cover at the center point of each plot by averaging 4 readings (one in each compass direction) taken with a spherical densiometer (Lemmon 1956). We removed 4 habitat characteristics (i.e., basal area of snags, percentage of cover of coarse woody debris, herbaceous vegetation, and shrubs) from analyses because of very little variation among plots (i.e., most plots were devoid of each variable).

We sampled habitat characteristics along 16 transects (9 available, 7 used) at 80 plots (45 available, 35 used). We pooled habitat data from all 4 ponds into 2 categories (available and used) for statistical analysis. We used a principal-components analysis to combine the 6 remaining habitat variables into fewer factors that weighted variables according to their importance. This generated principal components (PCs) with a given loading value for each habitat variable, which designated its importance to the PC (ranging from −1.0 to +1.0). To determine whether used and available habitat differed and whether habitat structure varied with distance from pond, we then used each PC with an eigenvalue <1 (Quinn and Keough 2002) in an analysis of covariance (ANCOVA) with habitat type (available or used) as the factor and distance from pond as the covariate.

Burrow Density

We attempted to locate all gopher tortoise and small mammal (e.g., southeastern pocket gopher, *Geomys pinetis*) burrows by surveying adjoining 2-m-wide transects encircling each pond. Because we wanted to survey habitat thoroughly and thus increase the likelihood of locating all burrows, we limited our search to a 100-m radius of ponds. We used a GPS unit to record the location of each burrow, and we measured percentage of canopy cover over each burrow entrance by averaging 4 readings (one in each compass direction) taken with a spherical densiometer (Lemmon 1956). We used aerial photographs and ArcGIS 9.2 to calculate the area of each habitat type (fire-maintained and fire-suppressed) within the 100-m radius of each pond. We reported densities as number of burrows observed per hectare in each of the 2 habitat types. We compared burrow densities with a 2-way ANCOVA with habitat type (fire-maintained or fire-suppressed) and burrow type (tortoise, mammal) as factors and habitat area as the covariate.

RESULTS

Movements

Of 105 juvenile gopher frogs that we captured at 5 ponds between 28 May and 16 August 2006, we fit 49 with transmitters and tracked them daily for varying periods of time during the study period. We obtained 286 relocations and 90 unique locations from 31 frogs. We did not obtain movement data from the other 18 frogs due to immediate predation ($N = 4$), slipped transmitter belts ($N = 9$), lost signals ($N = 2$), and frogs removed from analyses because of transmitter-related abrasions ($N = 3$; Roznik and Johnson 2009). Because of high mortality (Roznik and Johnson 2009) and variation in frog behavior, sample sizes vary and appear in parentheses following the results from each analysis.

Maximum straight-line movement distance for an individual frog from its natal pond was 691 m ($\bar{x}$: 173.0 ± 30.7 m; $N = 31$), and final locations of surviving frogs occurred at a mean distance of 269.7 ± 126.2 m from ponds (range: 110.3–640.7 m; $N = 4$). Mean total distance moved by individual frogs, determined by summing straight-line distances between successive locations, was 215.1 ± 30.1 m (range: 31–665 m; $N = 31$). Although frogs generally moved from ponds along linear paths (Fig. 2), some frogs ($N = 7$ of 31; 23%) returned to ponds from up to 117 m away and made a second emigration attempt (Fig. 2D). Excluding these movements back to the ponds, only one frog reversed its direction of travel; after moving 141 m into fire-suppressed habitat, it turned 198° and moved 285 m toward fire-maintained habitat (Fig. 2A).
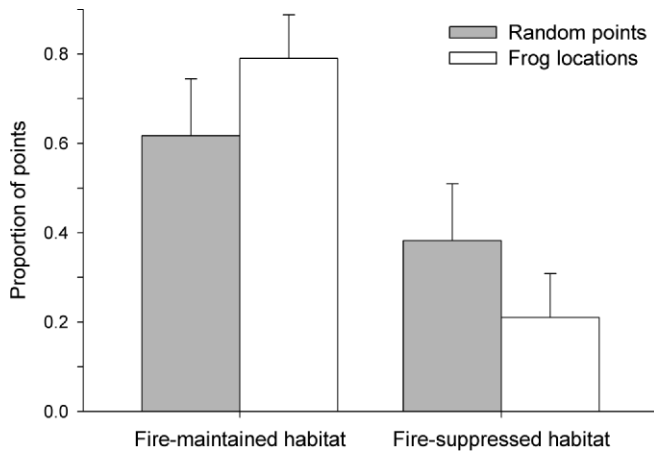
Figure 3. Proportion of locations of juvenile gopher frogs and an equal number of random points in fire-maintained and fire-suppressed longleaf pine forest in the Ocala National Forest, Florida, USA, May–August 2006. Frog locations occurred in fire-maintained habitat more often than in fire-suppressed habitat based on availability.

Even though mean distance between successive moves was 60.4 ± 8.5 m (range: 6–201 m; $N = 90$), frogs sometimes moved long distances over short periods of time, with 17% ($N = 15$) of 24-hour movements >100 m and 7% ($N = 6$) >200 m. All of our study ponds were located <100 m from the nearest dirt road, and frogs frequently crossed these roads (Fig. 2). Of frogs located at least once outside of the area enclosed by the drift fences, 59% ($N = 17$ of 29) crossed roads, and for frogs for which we recorded ≥ 2 unique locations, 85% ($N = 17$ of 20) crossed roads.

Orientation
All captured frogs moved randomly from the pond into pitfall traps at each pond (Rayleigh test, all $P > 0.091$). Frogs large enough to outfit with transmitters (a subset of all captured frogs) also moved randomly into traps at all ponds (all $P > 0.241$) but exhibited directional movement from traps to their final locations at 3 ponds where habitat was heterogeneous (ponds 3, 7, and 8; Fig. 1) and random orientation into the uplands at one pond where habitat was homogenous (pond 6; $Z = 0.411$, $P = 0.701$).

Upland Habitat Use
When we compared points representing frog locations ($N = 53$) to an equal number of random points, we found that frogs used fire-maintained habitat disproportionately more often than fire-suppressed habitat based on availability ($\chi^2 = 5.40$, df $= 1$, $P = 0.020$; Fig. 3). A factorial analysis incorporating 6 habitat variables resulted in 3 PCs that together explained 84.7% of variation among habitat characteristics (Table 1). For PC1, gopher frogs were negatively associated with percentage of canopy cover, basal area of hardwoods, and percentage of cover of leaf litter and were positively associated with basal area of longleaf pines, percentage of cover of wiregrass, and bare ground. Used and available habitat was different in PC1 ($F_{1,73} = 27.31$, $P < 0.001$) and habitat structure varied with distance from pond ($F_{1,73} = 8.80$, $P = 0.004$; Fig. 4). For PC2, there was no

Table 1. Eigenvalues and loading values from a principal-components analysis for upland habitat characteristics at 4 ponds in the Ocala National Forest, Florida, USA, August 2006. This analysis resulted in 3 principal components (PC), which together explained 84.7% of the variation among habitat characteristics.

Eigenvalues and loading values	PC1	PC2	PC3
Eigenvalue	3.010	1.248	0.824
Variation explained (%)	50.16	20.80	13.74
Loading values			
Canopy cover (%)	−0.891	0.228	0.017
Hardwood (basal area)	−0.847	−0.241	0.197
Leaf litter (% cover)	−0.839	0.061	−0.173
Wiregrass (% cover)	0.714	0.214	0.551
Bare ground (% cover)	0.414	−0.720	−0.483
Longleaf pine (basal area)	0.335	0.775	−0.467

difference between used and available habitat ($F_{1,73} = 2.026$, $P = 0.159$), and habitat structure did not vary with distance from pond ($F_{1,73} = 1.816$, $P = 0.182$). Because PC3 had an eigenvalue <1, we did not retain it for further analysis (Quinn and Keough 2002).

Burrow Density
Fire-maintained habitat had higher burrow densities than did fire-suppressed habitat ($F_{1,15} = 16.430$, $P = 0.001$; Fig. 5). Burrow densities were 80% higher in fire-maintained habitat, with an average of 3.7 ± 0.6 burrows/ha in fire-maintained habitat and an average of 0.4 ± 0.1 burrows/ha in fire-suppressed habitat. The difference in burrow density between habitat types was 18% greater for gopher tortoise burrows than for mammal burrows ($F_{1,15} = 14.117$, $P = 0.018$; Fig. 5). Gopher tortoise burrows were located in areas with less canopy cover than were mammal burrows ($t = -3.714$, df $= 45$, $P = 0.001$). Gopher tortoise burrows were located in areas with an average of $48.3 \pm 2.4\%$ canopy cover (range: 16–72% canopy cover) and mammal burrows were located in areas with an average of $66.1 \pm 4.9\%$ canopy cover (range: 41–100% canopy cover).
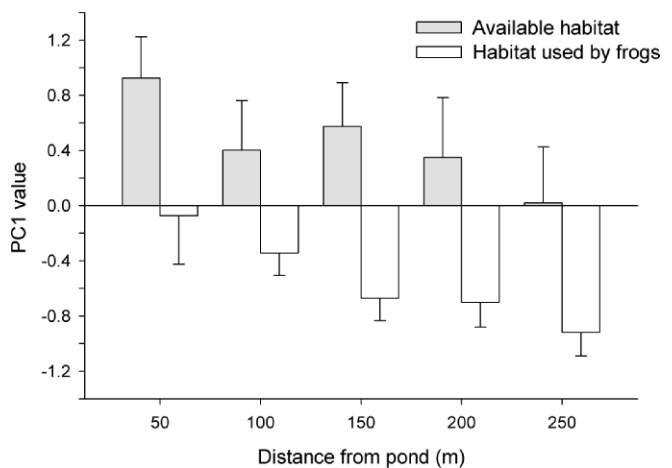

Figure 4. Values from a principal components (PC) analysis for PC1 ($+$ SE) in habitat available to and used by juvenile gopher frogs at 50-m intervals from 4 ponds in the Ocala National Forest, Florida, USA, August 2006. Habitat variables included in PC1 and their loading values are available in Table 1. Habitat structure varied with distance from ponds in habitat available to and used by frogs.
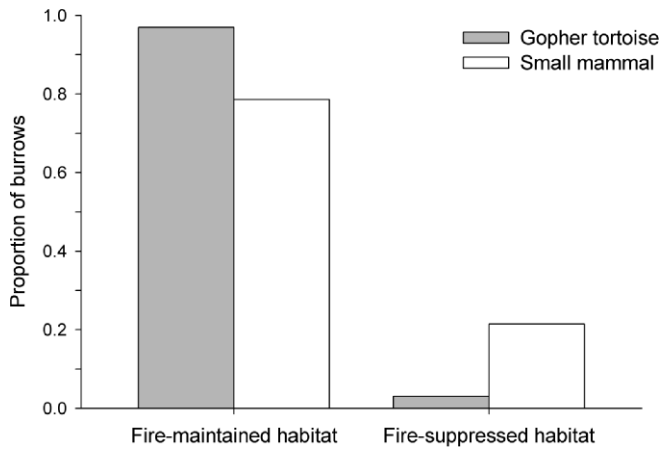
Figure 5. Proportion of gopher tortoise burrows and small-mammal burrows in fire-maintained and fire-suppressed longleaf pine forest within 100 m of 4 ponds in the Ocala National Forest, Florida, USA, August 2006.

DISCUSSION

We found that although juvenile gopher frogs randomly exited ponds, they ultimately migrated in nonrandom directions from ponds that were surrounded by heterogeneous habitat, selected fire-maintained habitat, and avoided habitat that had been invaded by hardwoods as a result of fire suppression. We also found that fire-maintained habitat contained a higher density of gopher tortoise and small mammal burrows, which are the primary refuge sites for both juvenile and adult gopher frogs (Jensen and Richter 2005, Roznik 2007).

Juvenile gopher frogs are capable of moving long distances during their first month in the terrestrial environment. The maximum distance that an individual frog migrated from its natal pond was 691 m. Frogs generally migrated from ponds along linear paths (Fig. 2), although one frog reversed its initial direction (Fig. 2A) and several frogs returned to ponds before making a second emigration attempt (Fig. 2D). Other juvenile amphibians have been observed returning to their natal ponds (Johnson 2002, Rothermel 2004, Rittenhouse and Semlitsch 2006), and these observations suggest that individuals that are unable to locate suitable habitat sometimes return to their natal pond, which is their only known refuge from harsh environmental conditions.

Numerous dirt roads near our study ponds were used for firebreaks, access roads to forest inholdings, and off-road vehicle recreation (Fig. 2). Frogs frequently crossed these roads and it also appears that 4 frogs traveled along roads (Fig. 2D). Invasive cane toads (*Bufo marinus*) have also been observed moving along roads (Seabrook and Dettmann 1996, Brown et al. 2006). Cane toads, like gopher frogs, are associated with open habitats (Seabrook and Dettmann 1996, Brown et al. 2006). Thus, for species that prefer open habitats to more densely vegetated areas, using roads as movement corridors may be a common behavior, particularly along unpaved roads. Although moving along roads may allow individuals to move more rapidly than would be possible through vegetated areas, we found that 3 frogs were run over by vehicles along roads (Roznik and Johnson 2009), indicating that roads also have negative direct effects on gopher frogs.

Frogs were distributed randomly in the pitfall traps around all ponds but moved directionally from 3 of 4 ponds once we released them from traps. Terrestrial habitat at these 3 ponds was heterogeneous (i.e., fire-maintained and fire-suppressed habitat), whereas habitat was homogeneous (i.e., fire-maintained habitat) at the other pond (Figs. 1, 2). Where orientation was directional, frogs moved though the center of the largest patch of fire-maintained habitat, thereby avoiding fire-suppressed habitat and the transitional edges between the 2 habitat types (Fig. 1). Although other drift fence studies have detected patterns in orientation of amphibians emigrating from ponds with respect to habitat type (e.g., Vasconcelos and Calhoun 2004, Marty et al. 2005, Rittenhouse and Semlitsch 2006), there was no evidence of directional orientation at our sites until frogs migrated beyond drift fences, which indicates that juvenile frogs did not respond to differences in habitat structure while in ponds but instead began to respond to these terrestrial cues after they had exited ponds.

Because adult gopher frogs are familiar with the landscape, their movements would likely be more directed. Palis (1998) found that adult gopher frogs tended to emigrate from ponds in the direction of immigration, and several radio-telemetry studies have documented adult gopher frogs returning to terrestrial refuges that they had previously used (Richter et al. 2001, Blihovde 2006, Roznik 2007). In our study, drift fence data failed to reveal directional orientation of juvenile gopher frogs in response to habitat type when patterns actually did exist over longer timescales, which may be true for other drift fence studies of juvenile amphibians. Using concentric drift fences placed at multiple distances from ponds (e.g., Johnson 2003, Vasconcelos and Calhoun 2004) or using drift fences in conjunction with other techniques (e.g., radiotelemetry; Rittenhouse and Semlitsch 2006, this study) may be more effective than using only drift fences at ponds to determine ultimate patterns of orientation.

Evidence from a coarse-scale analysis of habitat use (based on aerial photographs) indicated that juvenile gopher frogs selected open-canopy habitat that had been maintained by fire and avoided closed-canopy habitat that had been invaded by hardwoods as a result of fire suppression (Fig. 3). A principal-components analysis of habitat structure revealed a similar pattern; frogs selected habitat that was significantly associated with an open canopy, few hardwood trees, small amounts of leaf litter, and large amounts of wiregrass (PC1; Table 1). Although there was no difference between used and available habitat in PC2, we do not consider this component to be biologically relevant because it loads high on 2 characteristics (many longleaf pines and large amounts of bare ground; Table 1) that are not representative of the major structural differences between the habitat types we sampled (Heyward 1939, Gilliam and

Platt 1999). For example, mean basal area of longleaf pines in used and available habitat at our sites were similar (Roznik 2007), and furthermore, we would not expect them to differ because fire suppression alters stand structure in longleaf pine forests by permitting hardwood trees to invade gaps among pines that were historically maintained by fire, and not by decreasing basal area of longleaf pine (Heyward 1939, Gilliam and Platt 1999). Additionally, contribution of bare ground did not differ between used and available habitat (Roznik 2007), and it is presumably correlated with basal area of hardwoods and percentage of canopy cover and is thus is not a good indicator of habitat type alone. In sum, these 2 analyses at different scales demonstrate that migrating juvenile gopher frogs selected fire-maintained longleaf pine forest. Several drift fence studies on gopher frogs found that juveniles and adults migrated directionally toward a recent clear-cut and an open field, further supporting the assertion that gopher frogs prefer open habitats (Palis 1998, Richter and Seigel 2002).

Habitat structure changed with distance from ponds from a closed-canopy habitat that was invaded by hardwoods to a more open-canopy habitat that was dominated by longleaf pines and wiregrass (Figs. 2, 4). Therefore, fire-suppressed areas were concentrated near ponds and habitat quality improved for frogs as they migrated farther from ponds. Although most frogs immediately moved toward fire-maintained habitat, one frog initially moved into fire-suppressed habitat but eventually reversed its direction (Fig. 2A). At ponds located within large tracts of fire-suppressed forests, juvenile gopher frogs could exhibit such altered migration patterns, which may increase risk of mortality. Ponds that have become shaded as a result of fire suppression can also potentially reduce the growth, survival, and size at metamorphosis of larvae that are dependent on open-canopy ponds (Werner and Glennmeier 1999, Skelly et al. 2002, Thurgate and Pechmann 2007). A 5-year study conducted at our study sites found that juvenile gopher frog recruitment was significantly higher in ponds primarily surrounded by fire-maintained habitat than in ponds located in fire-suppressed habitat (Greenberg 2001), further supporting this assertion.

We found that densities of gopher tortoise and small-mammal burrows at our sites were higher in fire-maintained habitat than in fire-suppressed habitat (Fig. 4). Both tortoises (Boglioli et al. 2000, Jones and Dorr 2004) and several species of small mammals (e.g., *Geomys* spp.; Funderburg and Lee 1968, Himes et al. 2006) that occur in longleaf pine forests prefer open-canopy habitat, where foraging conditions are more favorable. Gopher frogs depend on burrows for shelter, and short-term data suggest that these refuges are important to juvenile survival (Roznik and Johnson 2009). Therefore, juveniles may select fire-maintained habitat to increase the likelihood of locating a burrow quickly, which may increase probability of survival. However, in the absence of long-term growth and survival data, it is currently unknown whether fire-maintained habitat benefits gopher frogs. Adult gopher frogs are also associated with fire-maintained habitat types (Jensen and Richter 2005), and although it has not yet been directly tested, adults are also thought to prefer fire-maintained longleaf pine forest (Roznik 2007). Regardless, in areas where canopy cover increases as a result of fire suppression, the number of refuges available to juvenile and adult gopher frogs may decline. All burrows used by juvenile frogs in our study were located in fire-maintained habitat, which may reflect preference of frogs or distribution of burrows in the landscape.

MANAGEMENT IMPLICATIONS

Because natural fires no longer occur at a scale and frequency to maintain species composition and structure of longleaf pine forests, land managers must use prescribed fire to mimic historical fire regimes. Burning terrestrial habitat all the way to the edges of breeding ponds, as well as through ponds during periodic droughts, is important for maintaining suitable habitat for juvenile gopher frogs and the burrowing vertebrates on which gopher frogs depend for shelter. Where increases in canopy cover have occurred, land managers should attempt to restore the habitat. In areas where fire alone cannot effectively remove hardwoods, restoration could involve application of prescribed fire in conjunction with other restoration practices, such as careful removal of trees using mechanical practices (Provencher et al. 2001) or selective application of herbicides (Brockway and Outcalt 2000). 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., Apr–Jul) 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). Importantly, such fire regimes are unlikely to directly cause mortality of juvenile or adult gopher frogs, even when they are sheltering above ground (Richter et al. 2001, Roznik 2007, Roznik and Johnson 2007).

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