

Burrow Use and Survival of Newly Metamorphosed Gopher Frogs (*Rana capito*)

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ABSTRACT.—The transition from aquatic to terrestrial habitat is thought to be a period of high mortality for amphibians. We used radio telemetry to estimate survival and study factors influencing survivorship of newly metamorphosed Gopher Frogs (*Rana capito*). Predation was very high and only 12.5% of frogs survived their first month in the terrestrial habitat. All documented predation occurred during the frogs' initial 12 days in the uplands, and snakes (*Coluber constrictor* and *Thamnophis sirtalis*) were the major predators. Also, frogs were preyed upon by mammals and birds and killed by vehicles along dirt roads. Survival rates varied among ponds, with the survival rate at one pond being significantly lower than survival rates at three other ponds. Survival of frogs was dependent on their use of underground refuges, particularly burrows excavated by Gopher Tortoises (*Gopherus polyphemus*) and small mammals. Using underground refuges reduced the risk of mortality to only 4% of that faced by frogs while in the open environment; in fact, all surviving frogs located a burrow within their initial eight days in the terrestrial habitat and remained there for the duration of tracking. Our results demonstrate the dependence of Gopher Frogs on underground refuges and suggest that the availability of burrows near breeding ponds influences survival of juveniles and, thus, the recruitment of adults.

Amphibian populations can be affected by mortality during the egg, larval, juvenile, and adult life stages. However, 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 (Breden, 1987; Berven and Grudzien, 1990; Funk et al., 2005). Despite the importance of juveniles to populations, information is lacking on many basic features of life history and demography of this life stage.

The transition from aquatic 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). Factors thought to directly influence postmetamorphic survival of amphibians include body size at metamorphosis (Berven, 1990; Morey and Reznick, 2001), lipid levels at metamorphosis (Scott et al., 2007), and habitat quality, which includes suitable

terrestrial habitat (Rothermel and Semlitsch, 2006), as well as the availability of refuges (Loredo et al., 1996; Rothermel and Luhring, 2005).

Refuges provide amphibians with protection from predation (Denton and Beebee, 1993; Spieler and Linsenmair, 1998) and minimize the effects of adverse weather conditions (Seebacher and Alford, 2002; Rothermel and Luhring, 2005). Newly metamorphosed amphibians are unfamiliar with the locations of refuges in the terrestrial habitat, which puts them at a high risk of predation and desiccation, which is exacerbated by their small body size (Thorson, 1955; Newman and Dunham, 1994). Thus, refuges are particularly important to juveniles, and locating and using suitable refuges may be an important correlate of juvenile survival. This may be true especially for species that use distinct, spatially discrete refuges, such as the Gopher Frog (*Rana capito*). Gopher Frogs breed in temporary or semipermanent ponds but spend the majority of their lives in the surrounding terrestrial habitat, where they seek shelter in underground refuges, such as the burrows of Gopher Tortoises (*Gopherus polyphemus*) and several species of small mammals, as well as stump holes (Lee, 1968; Franz, 1986; Jensen and Richter, 2005).

Because of their secretive nature, Gopher Frogs (*R. capito*) and the closely related Dusky Gopher Frog, *Rana sevosa* are very difficult to locate and capture in terrestrial habitats; thus,

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relatively little is known about their terrestrial ecology (but see Richter et al., 2001; Blihovde, 2006; Roznik and Johnson, 2009). Although Richter and Seigel (2002) studied adult survivorship of Dusky Gopher Frogs, virtually nothing is known about survivorship, sources of mortality, or factors influencing survival of immature Gopher Frogs. We used radio telemetry to investigate survival and causes of mortality for newly metamorphosed Gopher Frogs during their first month in the terrestrial habitat. We estimated survival rates for frogs dispersing from four ponds and compared variation in survival rates among ponds. We also determined how survival is influenced by underground refuge use, body size, timing of metamorphosis, and distance from natal pond.

MATERIALS AND METHODS

Study Site.—Our study took place from May through August 2006 at five ponds and the surrounding upland habitat at two sites within the Ocala National Forest, Marion and Putnam Counties, Florida. 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-wiregrass (*Pinus palustris-Aristida beyrichiana*) savannas, and prescribed burning was attempted at approximately 1–3-yr intervals (Greenberg, 2001). Despite this active management, 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 in close proximity to the ponds (Roznik and Johnson, 2009). Habitat surrounding Ponds 5 and 6 was homogenous fire-maintained habitat. The five ponds we studied are part of an ongoing study of herpetofaunal use, and detailed descriptions of aquatic 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. We positioned pitfall traps (19-liter buckets) on the inside and outside of both ends of each fence (four per fence), and we used frogs captured on both sides of the fences in our study. 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, Minnesota), which weighed 0.6 g and had a maximum battery life of 33 days. Immediately after removing frogs from pitfall

traps, we attached transmitters using an external belt made of elastic thread and small glass beads (Muths, 2003). Only the largest captured frogs were fitted with transmitters such 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 we 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 (with new belts) on additional frogs when sufficient battery life remained.

We used a TRX-48S receiver (Wildlife Materials, Inc., Murphysboro, IL) 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. We presumed that frogs shed their transmitters when we found an undamaged transmitter assembly (without an associated carcass) near the previous daily location of the frog (<10 m away) during the initial 1–2 days after release. When a frog was preyed upon, we 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 we located a frog, we recorded the date, time, behavioral observations, and habitat characteristics, including whether or not the frog was in an underground refuge. We defined such refuges as burrows excavated by a Gopher Tortoise or small mammal (e.g., *Geomys pinetis*), as well as other underground retreats associated with stumps and roots. While frogs were in refuges, their transmitter signals periodically moved toward the entrances or deeper underground, which we used as evidence that frogs were still alive, along with the presence of distinctive nocturnal resting areas beside burrows (Richter et al., 2001; Roznik, 2007). We recorded each location with a GeoXM GPS unit (Trimble, Sunnyvale, CA), and we used ArcGIS 9.2 (ESRI, Redlands, CA) to measure the distance between GPS locations and frogs' natal ponds. 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. Frogs that developed abrasions were omitted from all data analyses.

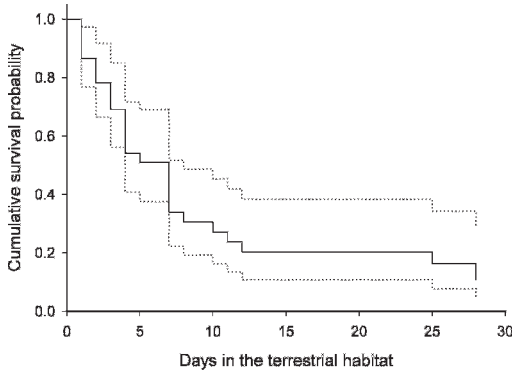


FIG. 1. Overall cumulative survival probability (solid line) with the 95% confidence interval (dotted lines), for newly metamorphosed Gopher Frogs (*Rana capito*) during their first month in the terrestrial habitat after dispersing from five ponds in the Ocala National Forest, Florida.

Data Analysis.—Survival analyses were performed using SAS 9.1, and all other statistical analyses were performed using SYSTAT 10.2. All means are presented ± 1 SE, and alpha was set at 0.05, except where otherwise noted. We used a Cox regression model (PROC PHREG) to estimate survival. We included in the analysis all frogs that were tracked until the transmitter expired or the frog died, as well as frogs that shed their transmitters after we obtained at least one location. In addition to a basic model (without covariates), we tested models with body mass at capture, snout–urostyle length at capture, and Julian date of release. We also tested models that included two covariates that changed in value through time: For each day of observation, we included whether the frog was in an underground refuge, and the distance of the frog's location from its natal pond. We 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. We did not include Pond 5 in the comparisons because of inadequate sample size. All frogs that survived until their transmitters expired had been fitted with new transmitters; hence, we did not have to account for remaining battery life (and thus the maximum days a frog could “survive”) in the survival analyses for frogs fitted with used transmitters.

RESULTS

We outfitted a total of 49 newly metamorphosed Gopher Frogs with transmitters between 28 May and 19 July 2006. Mean body

TABLE 1. Fates of newly metamorphosed Gopher Frogs (*Rana capito*) during their first month in the terrestrial habitat. Only frogs that could be confirmed dead or surviving until their transmitters expired are included in this summary.

Fate	N (%)
Survived	4 (12.5)
Preyed upon by snake	
Eastern Racer (<i>Coluber constrictor</i>)	12 (37.5)
Common Gartersnake (<i>Thamnophis sirtalis</i>)	7 (21.9)
Preyed upon by mammal	3 (9.4)
Preyed upon by bird	2 (6.3)
Killed by vehicle	3 (9.4)
Unknown (desiccated or preyed upon)	1 (3.1)
Total	32 (100)

mass of tracked frogs was 7.4 ± 0.2 g (range: 7.0–10.0 g) and mean snout–urostyle length was 36.8 ± 0.4 mm (range: 31–40 mm). We tracked 32 of the 49 frogs (65.3%) for the life of the transmitter ($N = 4$) or until we confirmed the death of the frog ($N = 28$). We were unable to determine survivorship or fate for the remaining 17 frogs (34.7%) because frogs shed their transmitters ($N = 12$), we removed transmitters because of developing abrasions ($N = 3$), or the transmitter signals were lost ($N = 2$).

Predation on newly metamorphosed Gopher Frogs was common during our study (Fig. 1). Four frogs (12.5%) survived until their transmitters expired (mean: 24.8 ± 4.4 days; range: 12–32 days), and nearly all ($N = 26$, 92.6%) of the nonsurviving frogs died during the initial 12 days following release. The mean survival time from release to death was 6.3 ± 1.2 days (range: 1–28 days). Known causes of mortality were predation by snakes, mammals, and birds, as well as vehicle mortality (Table 1). Snake predation accounted for the majority of mortality (67.9%; $\chi_1^2 = 40.571$, $P < 0.0001$), and frogs were preyed upon equally by Eastern Racers (*Coluber constrictor*) and Common Gartersnakes (*Thamnophis sirtalis*; $\chi_1^2 = 1.316$, $P = 0.251$). Although the species of mammal and bird predators are unknown, they were likely raccoons (*Procyon lotor*) and owls, which were observed at our study sites and are primarily nocturnal like Gopher Frogs.

The survival rate for Pond 6 was lower than the survival rates at the other three ponds for which comparisons could be made (Ponds 3, 7, and 8; Bonferroni-corrected probability, all $P < 0.008$; Fig. 2), and survival rates among the other three ponds did not differ (Bonferroni-corrected probability, all $P > 0.008$). When compared with Pond 6, the hazard ratios for Ponds 3, 7, and 8 are 0.118, 0.146, and 0.213,

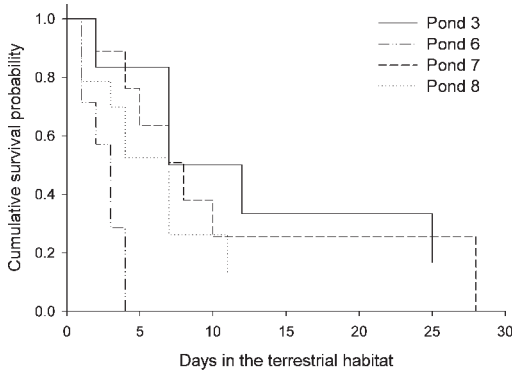


FIG. 2. Cumulative survival probabilities for newly metamorphosed Gopher Frogs dispersing from four ponds. The survival rate for Pond 6 is significantly lower than the survival rates for the other ponds, which do not differ from one another. Pond 5 is not shown because of inadequate sample size.

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 small sample sizes, we were unable to compare predator composition among ponds.

There was no significant effect of body mass at capture ($\chi_1^2 = 0.001$, $P = 0.982$), snout-urostyle length at capture ($\chi_1^2 = 0.270$, $P = 0.604$), Julian date of release ($\chi_1^2 = 1.167$, $P = 0.280$), or distance from natal pond ($\chi_1^2 = 0.378$, $P = 0.539$) on survival. 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. Mortality occurred near the pond edges as well as in the uplands at a mean distance of 157 ± 30.1 m (range: 7–691 m) from ponds.

Underground refuge use was the only factor we studied that influenced survival of newly metamorphosed Gopher Frogs ($\chi_1^2 = 9.549$, $P = 0.002$; Fig. 3). The estimated likelihood of mortality for a frog occupying an underground refuge was only 4.0% of the likelihood of mortality for a frog not occupying an underground refuge. Only two deaths occurred while frogs were in underground refuges, and circumstantial evidence indicates that predation occurred at the entrances to the refuges, rather than inside the actual cavities. Eight frogs used at least one underground refuge during our study, and these frogs used an average of 1.6 ± 0.5 underground refuges (range: 1–5 refuges). Surviving frogs entered their first underground refuge within the first five days in the terrestrial habitat, and they occupied their final under-

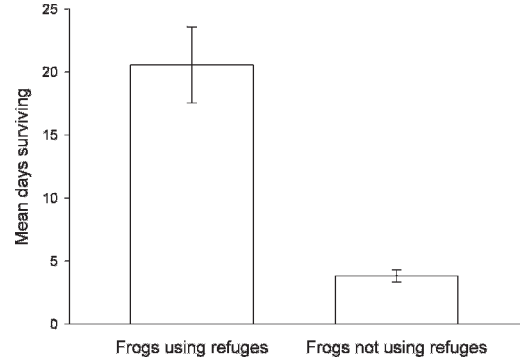


FIG. 3. Mean survival (+ 1 SE) for newly metamorphosed Gopher Frogs that used and did not use underground refuges. Refuges are defined as burrows excavated by Gopher Tortoises (*Gopherus polyphemus*) and small mammals, as well as other underground retreats associated with stumps and roots. Frogs that used at least one refuge were included as using refuges. Mean days surviving refers to the average of the number of days that frogs survived until death or until their transmitters expired. The longest a transmitter lasted; thus, the longest that a frog could “live” was 32 days.

ground refuge within an additional three days, where they remained until their transmitters expired. Frogs used Gopher Tortoise ($N = 6$) and small mammal ($N = 3$) burrows, as well as stump and root holes ($N = 4$) during dispersal, although the final recorded locations of surviving frogs were tortoise or mammal burrows. When frogs were located aboveground, they were found sheltering in leaf litter, in clumps of grass, or under coarse woody debris.

DISCUSSION

Predation on newly metamorphosed Gopher Frogs occurred often during our study, and only 12.5% of frogs survived their first month in the terrestrial habitat (Table 1; Fig. 1). One possible explanation for the high rate of mortality is that transmitters affected the movements or behavior of frogs and, thus, caused them to be more vulnerable to predators. However, we found no support for this hypothesis. If transmitters increased mortality by affecting the vagility of frogs, we would expect smaller frogs to be more burdened by this extra mass and, thus, be more susceptible to predation; however, the survival model showed that there was no relationship between body size and longevity in our study. Furthermore, frogs appeared to move normally; they moved long distances from their natal ponds (up to 691 m; Roznik and Johnson, 2009), and successfully located burrows. Additionally, the timing of predatory events does not support the supposition that transmitters biased our

results. If transmitters caused increased predation, this should be most pronounced when frogs were moving (mainly at night), rather than when they were sedentary (during the day). However, snakes of two species (*C. constrictor* and *T. sirtalis*) were the major predators of frogs in our study, and both species are primarily diurnal, active foragers (Fitch, 1963; Rossman et al., 1996). Therefore, frogs were likely preyed on during the day, while they were in diurnal shelter sites; thus, the transmitters could not have directly affected the ability of frogs to avoid predation.

We should expect low survival rates for immature Gopher Frogs given the life history of this species. Although little information is available on the numbers of metamorphosing amphibians that survive to sexual maturity, species that produce large numbers of eggs can tolerate low survival and still maintain stable populations (Duellman and Trueb, 1986). For a population to be stable, the lifetime reproductive output of an average female must yield one male and one female offspring that survive to breed. Because Gopher Frogs have large egg masses that contain an average of 2,210 eggs (Palis, 1998), populations should experience high levels of mortality, which was exactly what we found in newly metamorphosed Gopher Frogs during their first month in the terrestrial habitat. Because Gopher Frogs have a long period between metamorphosis and first reproduction (1.5–2 yr; Jensen and Richter, 2005), future studies that are longer in duration would enhance our understanding of survival during the juvenile life stage.

Although most mortality in our study was attributed to predator-prey interactions, we found that vehicular traffic was also a source of mortality, accounting for the deaths of 9.4% of the frogs we tracked (Table 1). All of these mortality events occurred on dirt roads used for firebreaks, access roads to forest inholdings, and off-road-vehicle recreation trails. Because there were numerous dirt roads near our study ponds, frogs frequently crossed these roads and even seemed to move along these roads (Roznik and Johnson, 2009). Therefore, many frogs were vulnerable to road mortality, particularly the longest living frogs, which moved the longest distances and crossed the most roads (Roznik and Johnson, 2009). Our results suggest that roads may negatively affect populations of Gopher Frogs, even on dirt roads in protected areas. Where traffic intensity is high, these effects are likely to be more pronounced (Fahrig et al., 1995).

It is clear that underground refuges played an important role in survival of newly metamorphosed Gopher Frogs (Fig. 3). Frogs that survived to the end of our study entered a burrow excavated by a Gopher Tortoise or small

mammal within their initial eight days in the terrestrial habitat and remained there for the duration of tracking. The use of underground refuges reduced the risk of mortality to only 4% of the risk that frogs faced while in the open environment and likely provided several benefits to frogs, including protection from predation (Denton and Beebee, 1993; Spieler and Linsenmair, 1998) and adverse weather conditions (Seebacher and Alford, 2002; Rothermel and Luhring, 2005). Although predation was the most immediate threat during our study, desiccation is also a major threat in the xeric habitats where Gopher Frogs occur, particularly for newly metamorphosed frogs because of their small body size (Thorson, 1955; Newman and Dunham, 1994). Additionally, because hundreds of invertebrate species are associated with Gopher Tortoise burrows (Jackson and Milstrey, 1989), burrows may also provide an abundant food source for Gopher Frogs.

We found that the survival rate was lower at one pond (Pond 6) than at three other ponds; the likelihood of mortality was 78.7–88.2% higher at Pond 6 than at the other ponds (Fig. 2). Survival rates of newly metamorphosed Gopher Frogs at individual ponds are likely influenced by various factors in the terrestrial habitat, such as local predator abundance or the density and spatial arrangement of burrows, and likely vary among years. Differences in surrounding habitat type may have indirectly contributed to the high mortality rate at Pond 6; this pond was completely surrounded by fire-maintained habitat (i.e., longleaf pine dominant), whereas the other three ponds were surrounded by heterogeneous habitat with fire-maintained and fire-suppressed (i.e., mixed longleaf pine-hardwoods) areas. We previously found that fire-maintained habitat contained higher burrow densities than fire-suppressed areas at our sites (Roznik and Johnson, 2009). Thus, low burrow density in the surrounding terrestrial habitat likely did not contribute to the high mortality at Pond 6, but other differences related to habitat type may have played a role. For example, if predators of Gopher Frogs prefer habitat that has been regularly burned to habitat that has been fire suppressed, local predator densities may be higher near Pond 6 than at the other ponds. Regardless of the causes of the variation in mortality during our one-year study, longer-term studies of patterns of variability in survival as well as the production of metamorphs at individual ponds are necessary to fully understand the population dynamics of Gopher Frogs.

The commensal relationship between Gopher Frogs and burrowing vertebrates, particularly Gopher Tortoises, has long been acknowledged (Test, 1893; Carr, 1940; Franz, 1986). Although

many other species have been reported to use tortoise burrows for shelter (Jackson and Milstrey, 1989; Lips, 1991), the Gopher Frog is one of the most frequently cited commensal species and is particularly reliant on burrows because of its moisture requirements. Our results further demonstrate the dependence of Gopher Frogs on existing burrows; during their first month in the terrestrial habitat, the survival of newly metamorphosed frogs appears to be dependent on their ability to quickly locate burrows. This dependence on burrows may be one explanation for why newly metamorphosed Gopher Frogs select open-canopy (i.e., fire-maintained) habitat (Roznik and Johnson, 2009), which is also preferred by Gopher Tortoises and small mammals (e.g., *Geomys* spp.) and, thus, contains higher densities of burrows than habitat with a more closed canopy (Funderburg and Lee, 1968; Hermann et al., 2002; Roznik and Johnson, 2009).

Fire suppression of habitat and other factors that result in declines of populations of Gopher Tortoises and burrowing mammals (e.g., disease, urban development; Auffenberg and Franz, 1982) have the potential to negatively affect juvenile recruitment of Gopher Frogs by altering the availability of burrows. The density and spatial arrangement of burrows near breeding ponds appear to be important factors that influence population dynamics of Gopher Frogs. Because juvenile and adult Gopher Frogs rely heavily on burrows for shelter, creating artificial burrows (e.g., Souter et al., 2004) near breeding ponds is one potential management tool that could enhance juvenile survival and populations of Gopher Frogs. Closing forest roads near breeding ponds during dispersal periods of Gopher Frog metamorphs would also likely be an effective management strategy.

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