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Spatio-temporal Dynamics of Pond Use and Recruitment in Florida Gopher Frogs (*Rana cupito aesopus*)

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ABSTRACT.—This study examines spatio-temporal dynamics of Florida gopher frog (*Rana capito aesopus*) breeding and juvenile recruitment. Ponds were situated within a hardwood-invaded or a savanna-like longleaf pine-wiregrass upland matrix. Movement (*N* = 1444) was monitored using intermittent drift fences with pitfall and funnel traps at eight isolated, ephemeral ponds February 1994 to January 1999. Adult pond use was low but relatively constant among years and did not differ between habitat matrices. Juvenile recruitment was significantly higher in the savanna-like upland matrix. The number of adults using ponds was positively correlated with the number of next-year's recruits in only one year. Recruitment rates were relatively low (maximum 175 captured/pond/yr), but juveniles were produced from most ponds in three of five years. Recruitment was negligible in 1994 because of ponds drying and in 1997 for unknown reasons. Juvenile body size differed significantly among years and ponds. Body size was negatively correlated with the number of juveniles exiting ponds in only one year, suggesting that intraspecific competition is only one of many factors affecting juvenile body size. Most emigration by metamorphic juveniles occurred May through August and was unrelated to rainfall. Dates of first emergence and length of emigration periods varied. A high proportion of juveniles with tailbuds and similar tailbud lengths in most months suggest that metamorphosis occurred throughout the emigration period. High variability in juvenile recruitment success and significant differences in body size among years and ponds suggests that each is influenced by factors at both a landscape (e.g., rainfall and pond hydrology) and within-pond scale (e.g., competition and predation).

Gopher frogs (*Rana cupito*) historically occurred in the southeastern Gulf coastal plain from southeastern Louisiana to North Carolina, including most of Florida (Conant and Collins, 1991). The Florida subspecies (*Ratw capito aesopus*) occurs in southeastern Georgia and throughout most of Florida (Conant and Collins, 1991). Populations of *R. cupito* are thought to be declining throughout their range resulting from wetland habitat loss by drainage, filling, or stocking of fish, and upland habitat loss through development, fragmentation, and fire suppression (Bailey, 1991). In Florida, they are closely associated with gopher tortoise (*Gopherus polyphemus*) burrows (Franz, 1988), especially in xeric longleaf pine (*Pinus palustris*)-wiregrass (*Aristida beyrichiana*) uplands that are within about 1.7 km of suitable breeding ponds (Godley, 1992). *Rana cupito* breeds almost exclusively in isolated, ephemeral ponds, presumably because they do not support predatory fish and may have lower populations of predatory invertebrates (Moler and Franz, 1988).

Historically, frequent, low-intensity fire in the xeric longleaf pine-wiregrass ecosystem killed many young hardwood trees, thereby maintaining a predominantly open, pine-dominated habitat (Myers, 1990). During dry periods, fire maintained pond suitability by burning peat and vegetation in and around them. Wiregrass and herbaceous vegetation cover declines with increased shading from hardwoods that invade if fire is suppressed, thereby reducing habitat quality for G. *polyphemus.* The number of suitable upland refuges for *R. capito* could potentially decline as G. *polyphemus* numbers dwindle in such areas. High hardwood density also could change water chemistry and pond hydrology by increasing transpiration.

Little is known of the life history or ecology of *R. cupito.* Few studies report quantitatively on the species, and most include only a single season (Bailey, 1991; Palis, 1998), or multiple seasons at a single pond (e.g., Richter, 1998). Semlitsch et al. (1995) reported on breeding and recruitment of juveniles from several ponds and Carolina bays at the Savannah River Site in South Carolina over a 25-yr period. However, trapping was not continuous or concurrent at most of these sites, precluding a rigorous overview of spatial and temporal breeding and juvenile recruitment dynamics.

Larger body size of metamorphic juveniles could increase the likelihood of survival (Berven, 1990) and be an indicator of reproductive fitness at maturity (Berven and Gill, 1993). Body size also could serve as an indicator of pond conditions, including resource availability and competition (Wilbur, 1977). However, the spatial or temporal scope of most field studies of amphibians preclude comparisons of metamorphic body size among ponds and years.

This paper presents data on R. *capito* from the first five years of an ongoing study of herpetofaunal use of eight isolated, ephemeral ponds in the Ocala National Forest, Florida. My objectives in this study were to (1) quantify use of and juvenile recruitment from small, isolated, ephemeral ponds situated within hardwood-invaded versus savanna-like, upland sandhill matrices, and (2) gather spatio-temporal data on breeding biology and juvenile recruitment at a landscape level.

MATERIALS AND METHODS

Study Area.-This ongoing study was conducted at eight isolated, ephemeral ponds in longleaf pine-wiregrass sandhills of the Ocala National Forest, Marion and Putnam Counties, Florida. Hydrological characteristics of ponds are described in the Results section. Ponds 14 are located within fire-suppressed sandhills having high densities of laurel oak (*Quercus hemisphaerica),* other hardwood species, and sand pine (*Pinus clausa*). Ponds 1-3 are closely spaced. They are surrounded by hardwood-invaded sandhills on three sides and are separated from adjacent, savanna-like sandhills by a sand road on the fourth side. Ponds 5-8 are located within regularly burned, savanna-like, longleaf pine-wiregrass sandhills. Ponds 7 and 8 are approximately 9.5 km south of the other six. Prescribed burning is attempted at approximately 1-3 yr intervals, but fire is successfully carried by wiregrass only in the savanna-like sandhills.

All study ponds are of sinkhole origin, ranging from 0.10–0.37 ha in size. Pond basins contain *Andropogon* spp. and wetland vegetation including maidencane *(Panicum hemitomum), Rhexia* spp., blood root (*Lachnanthes caroliniana),* and white waterlily *(Nymphaea oa'orata).* Buttonbush *(Cephalanthus occidentalis*) sparsely encroaches some of the ponds.

Upland Matrix Sampling.-Uplands surrounding ponds were sampled in 1997. Tree basal area (BA) was sampled using Bitterlich prism plots (10-BAF prism factor) in 13-14 plots per treatment. Wiregrass, herbaceous vegetation, shrub ($<$ 2.5-cm diameter at breast height), leaf litter, coarse woody debris ($\geq$ 12.5-cm diameter), and bare ground cover were ocularly estimated in circular 12-m^2 subplots. Percentage of light was measured using a spherical densiometer in each plot.

Drift Fence Sampling.-Drift fences (7.6 m in length) were placed at 7.6-m intervals to encircle 50% of each pond. Pitfall traps (19-liter buckets) were positioned on the inside and outside of both ends of each fence (4 per fence) to detect directional movement to and from ponds. A sponge was placed in each pitfall trap and moistened at each trap check to reduce the likelihood of desiccation. A single- or double-ended funnel trap was positioned at the midpoint of each fence on both sides (two funnel traps per fence).

Traps were checked three times weekly from February 1994 through January 1999. Upon initial capture, frogs were measured (snout-vent length (SVL), and tailbud base to tip for metamorphic juveniles with remnant tailbuds) to the nearest millimeter, weighed to the nearest 0.1 g using a hand-held Pesola spring scale, sexed when possible (vocal sacs and nuptial excrescences on thumbs are apparent in breeding males), and given a cohort toe clip representing pond number and year of capture. Recaptured frogs were not measured. Animals were released on the opposite side of the fence from which they were captured. Water depths were measured weekly. Maximum and minimum air temperatures and rainfall were measured daily with a max-min thermometer and rain gauge.

Statistical Analysis-The number of drift fences and traps varied among different-sized ponds, and some traps were closed during periods of flooding. Therefore, capture data were standardized for comparison by converting to number of individuals captured per 100 trapnights (one open pitfall or funnel trap for 100 nights = 100 trapnights), and square-root arcsine transformed for comparisons of pond use and juvenile recruitment between habitat matrix quality, and among ponds and years. Percentage data for upland matrix measurements also were square-root arcsine transformed for statistical analyses. All other statistical comparisons used untransformed data. I subjectively defined juveniles based on trends in measurement data as ≤ 50 mm SVL or > 50 mm with a tailbud. Juvenile recruits for each pond were considered to be only emigrating individuals, although some immigrating individuals may also have metamorphosed from the pond where they were captured. I assumed all adults entering or exiting ponds were breeding adults. Only first captures were included in data analyses. I considered a breeding year as May through April based on the following assumptions about R. *capito* in, Florida: adults can breed during fall-spring (R. Franz, pers. comm.; this study) or even year-round (Palis, 1998); larval development requires 90 days to seven months (Palis, 1998); and virtually all juvenile metamorphosis and emigration occurs May to October. These months would presumably encompass the entire period during which breeding might contribute to juvenile recruitment the following year. Because only four complete adult breeding

TABLE 1. Mean (± SE) percent cover of select habitat characteristics and basal area (BA) of trees in hardwood-invaded versus savanna-like longleaf pine-wiregrass sandhills surrounding eight isolated, ephemeral ponds in the Ocala National Forest, Florida. Percentage data were square-root arcsine transformed for t-tests but are presented as untransformed values.

	Upland matrix			
	Hardwood-invaded	Savannah-like	df	*P*
Wiregrass (% cover)	11.6 ± 6.0	66.5 ± 8.6	25.0	<0.0001
Herbaceous (% cover)	4.5 ± 1.4	21.5 ± 4.7	25.0	0.0002
Leaf litter (% cover)	99.3 ± 0.5	68.5 ± 9.6	12.7	0.0023
Bare ground (% cover)	0.4 ± 0.2	9.4 ± 3.7	13.3	0.0072
Coarse woody debris ≥12.5 cm (% cover)	0.7 ± 0.4	1.2 ± 0.6	25.0	0.6208
Shrub <2.5 cm (% cover)	47.5 ± 8.2	27.8 ± 6.4	25.0	0.0548
Light (%)	22.8 ± 3.7	54.0 ± 4.9	25.0	<0.0001
Longleaf pine BA (m^2)	4.5 ± 1.2	4.8 ± 1.1	25.0	0.8475
Hardwoods and sand pine BA (m^2)	2.8 ± 0.7	0.9 ± 0.5	25.0	0.0357
Snag BA (m^2)	0.7 ± 0.3	0.5 ± 0.3	25.0	0.5677

years (May to April) were included in the 5-yr study period, only 4 yr were used in statistical comparisons of pond use by adults (May 1994 to April 1998). Because nearly all juvenile metamorphosis and emigration occurs May to October, all 5 yr of recruitment data (May through April) were included in statistical tests (adding trapnights through April 1999).

Two-way ANOVA was used to test for differences in pond use by adults and juvenile recruitment between upland matrices and among years. However, a small sample size for adults may have precluded statistical detection of existing differences in use of ponds within different upland matrices, or among years. Because the interaction term for upland matrix quality X year was not significant either for adults (F = 0.82, df = 3, P = 0.4944) or juveniles (F = 0.70, df = 4, P = 0.5949), I used Student's t-tests to compare adult breeding and juvenile recruitment between upland matrices. I tested for differences among years (using ponds as replicates) and among ponds (using years as replicates) using one-way ANOVA with least-squares means comparisons. I used simple linear regression to examine the relationship between annual (May through April) adult pond use and juvenile recruitment the following year, using each pond-year as a data point.

Snout-vent length of adult males and females (all first captures) was compared using a Student's t-test. I used two-way ANOVA with least-squares means comparisons to test for the effect of years, ponds, and their interaction on body mass and SVL of emigrating juveniles. Only pond-year combinations with sufficient sample size (N ≥ 10) were included in statistical comparisons. Monthly (if N ≥ 10) differences in SVL, body mass, and tailbud length of juvenile recruits within ponds and years were tested using ANOVA. I used chi-square tests to test whether the monthly proportion of recruits with tailbuds differed significantly from expected values (the average of monthly proportions) for each tested pond-year combination. The relationship between annual recruitment from ponds and mean body mass or SVL of recruits (one data point per pond per year) was examined using simple linear regression. The relationship between SVL and length of tailbud also was examined using simple linear regression.

I obtained an azimuth from the center of each pond to every pitfall trap using a compass. Assuming that captures by intermittent, equally spaced drift fences permitted detection of directional movement in some (if not 50%) proportion to its occurrence, I used the nonparametric Rayleigh test (Zar, 1984) to determine whether the annual movement of adults or juveniles into or from ponds ($N \geq 6$) was nonrandom. Significance is reported at the $P < 0.05$ level unless otherwise stated.

RESULTS

Upland Matrix Characteristics-Basal area of longleaf pine, snags, and coarse woody debris did not significantly differ between upland matrices, but BA of hardwoods and sand pine was significantly greater in hardwood-invaded treatment than savanna-like treatment (Table 1). There was significantly more light at breast height in the savanna-like treatment. Percent cover of wiregrass, and herbaceous plants was significantly higher in savanna-like than hardwood-invaded upland matrices. Percent cover of shrubs and leaf litter was significantly higher, and bare ground lower in hardwood-invaded uplands (Table 1).

Rainfall and Hydroperiod.—Pond depths ranged 0-2 m during February 1994 through January 1999 (Fig. 1). Depth and hydroperiod were similar among most ponds, with the ex-

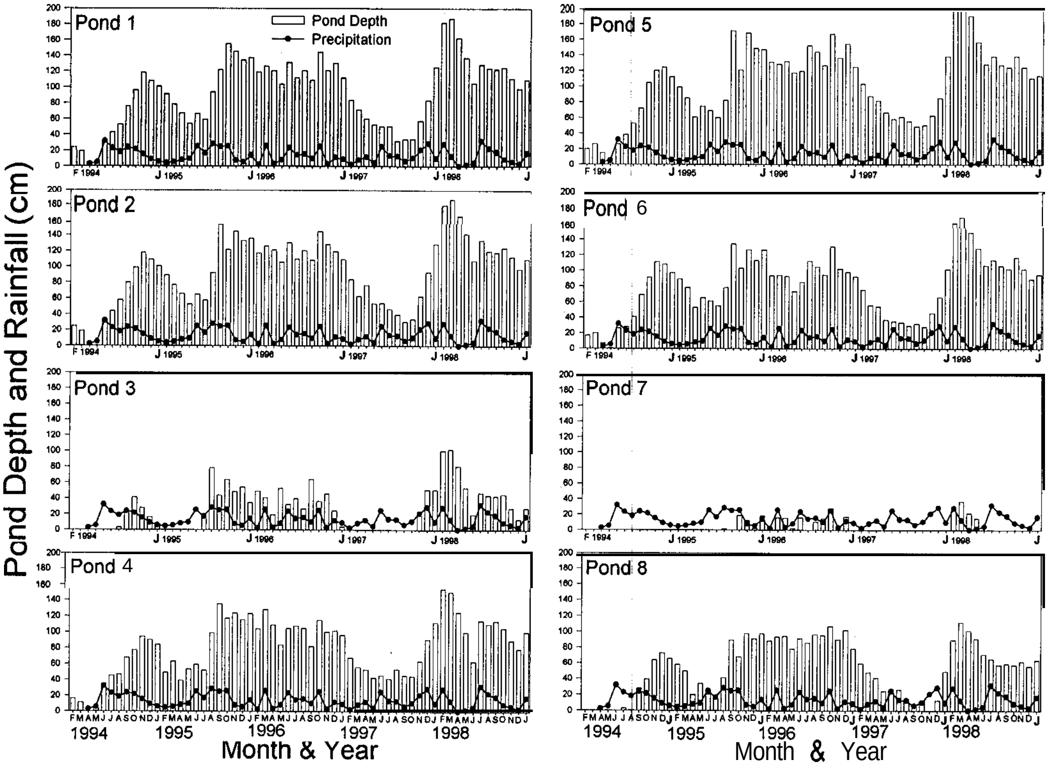

FIG. 1. Monthly rainfall and water depth in eight isolated, ephemeral ponds in the Ocala National Forest, Florida.

ception of one intermittently dry or very shallow pond in each upland matrix quality type (ponds 3 and 7). All ponds dried in April and May 1994. In many years, water levels tended to peak during late fall through January and decline during late winter through summer, reaching lowest levels in May. Rainfall tended to be the highest during June to October and the lowest during winter and spring. Rainfall associated with el Nino in 1998 resulted in record high water levels in ponds, flooding many traps from mid-February through May (Fig. 1).

Population Structure.-A total of 1444 individuals was captured 1504 times from eight ponds February 1994 to January 1999 (Fig. 2). Only 8.4% (N = 121) of all captures were adults. Of these, 33 were female, 65 male, and 23 unknown gender. Adult females had significantly longer SVLs (mean ± 1 SE = 82.4 ± 1.9) than males (mean = 76.1 ± 1.1; t = 3.03, df = 94, P = 0.0032). Most juveniles (72.8%) were captured exiting ponds (vs. 27.2% captured entering ponds).

Upland Matrix Effects.—Adult captures did not differ significantly between ponds within the savanna-like uplands (mean = 0.016 ± 0.004/100 trapnights) versus hardwood-invaded uplands (mean = 0.014 ± 0.004/100 trapnights; t = 0.50, P = 0.6184, df = 15,15). Recruitment of juvenile *R. capito* was significantly higher from ponds within the savanna-like uplands (mean = 0.168 ± 0.048/100 trapnights) than from ponds within the hardwood-invaded uplands (mean = 0.050 ± 0.013/100 trapnights; t = 2.24, P = 0.0327, df = 19,19).

Spatio-Temporal Dynamics Pond Use.-The number of adults captured per 100 trapnights did not differ significantly among years (F = 1.02, df = 3, P = 0.3997). February to April 1994 data were not included in statistical analyses of annual pond use, but the number of adults during that Period appeared similar to the number captured in other years (Fig. 2). However, the number of adults captured per 100 trapnights differed significantly among ponds (F = 4.81; df = 7, P = 0.0017). Use of ponds by adults did not consistently correlate with juvenile recruitment from those ponds the following year. The number of adults using ponds during May 1997 to April 1998 positively correlated with the number of juvenile recruits from those ponds the following year (May 1998 to April 1999; F = 18.21, P = 0.0053, r^2 = 0.7522) but not in other tested years (P = 0.3421–0.9228).

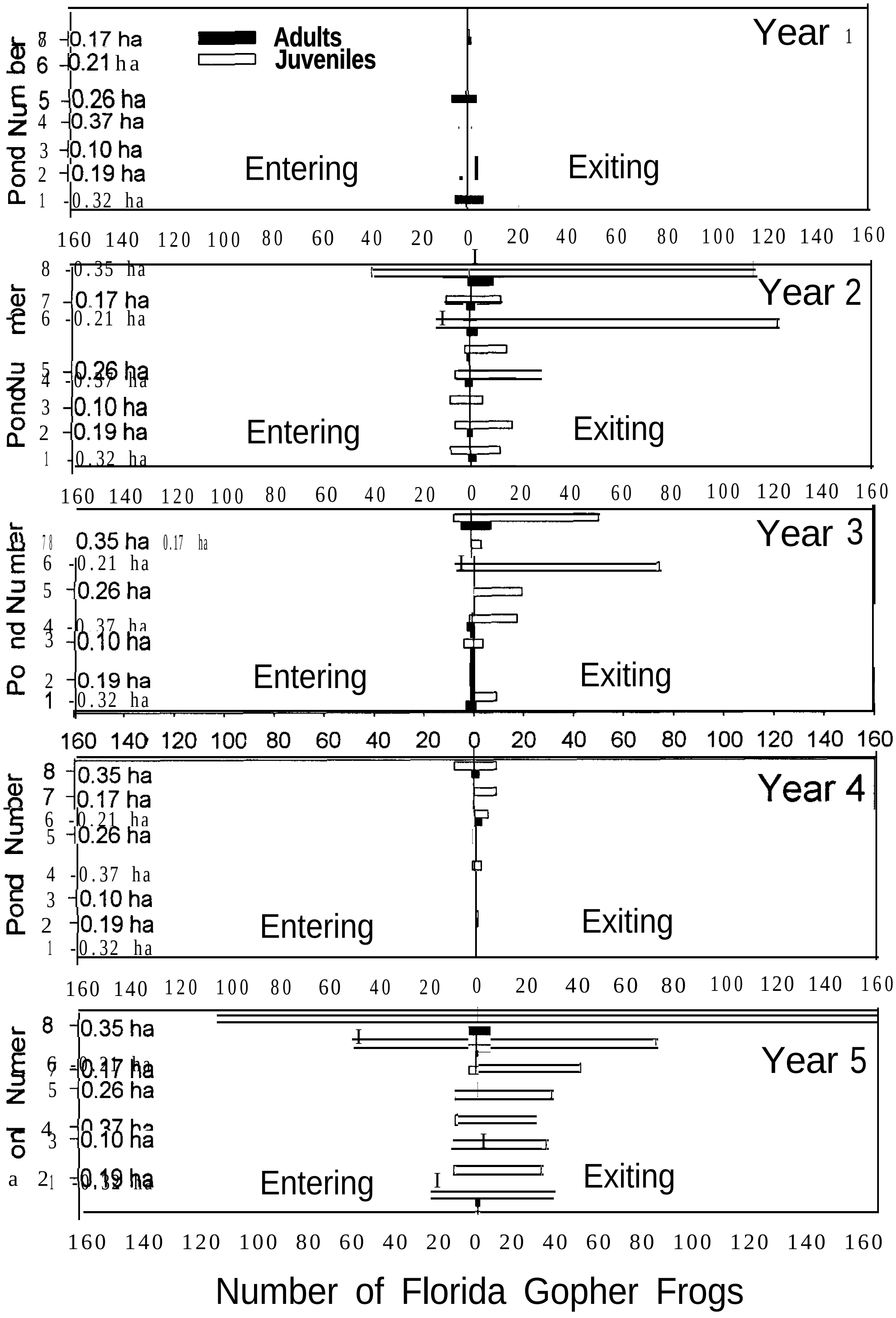

FIG. 2. Total annual (February through January) number (excluding recaptures) of adult and juvenile *Rana capito* captured entering and exiting eight isolated, ephemeral ponds February 1994 to January 1999, Ocala National Forest, Florida. Pond size (ha) also is indicated.

TABLE 2. Mean (± SE) body mass (g) and SVL (mm) of metamorphic juvenile *Rana capito aesopus* exiting 8 ponds February 1994 to January 1999 in the Ocala National Forest, Florida. Only pond-year combinations having N ≥ 1.0 exiting juveniles were included in ANOVA. Results of two-way ANOVA indicate significant differences in body mass and SVL among ponds, years, and pond X year interaction ($P = 0.0001$ for all). Nonsignificant differences are shown for body mass or SVL within years (Y) among ponds (P), and among ponds within years. All body mass and SVL means for pond-year combinations not shown are significantly different.

Year	Pond	N (mass)	Mean ± SE mass (g)	No difference ($P \geq 0.05$)	N (SVL)	Mean ± SE SVL (mm)	No difference ($P \geq 0.05$)
1995	2	12	11.2 ± 0.5	none	12	41.7 ± 0.9	Y2-P4, 5; Y3-P5, 6 8; Y5-P1, 2, 4, 5, 6
	4	21	9.2 ± 0.4	Y2-P5; Y3-P4	25	39.9 ± 0.5	Y2-P2, 5; Y5-P3, 4, 5, 8
	5	11	9.5 ± 0.9	Y2-P4; Y3-P4	12	40.3 ± 1.2	Y2-P2, 4; Y3-P5, 6; Y5-P1, 2, 3, 4, 5, 8
	6	110	6.3 ± 0.1	Y2-P8; Y5-P2, 6	113	37.4 ± 0.3	Y2-P8; Y5-P3, 7
	8	45	6.1 ± 0.3	Y2-P6; Y5-P1, 2. 6	45	36.8 ± 0.5	Y2-P6: Y5-P7
1996	4	14	9.2 ± 0.7	Y2-P4, 5	16	45.1 ± 1.0	none
	5	16	7.8 ± 0.4	Y3-P6, 8	16	42.3 ± 0.7	Y2-P2, 5; Y3-P6, 8; Y5-P1, 2, 5, 6
	6	61	6.9 ± 0.2	Y3-P5	64	41.8 ± 0.3	Y2-P2, 5; Y3-P5, 8; Y5-P1, 2, 5, 6
	8	38	7.7 ± 0.3	Y3-P5	42	42.9 ± 0.5	Y2-P2; Y3-P5, 6; Y5-P1, 2, 6
1998	1	27	5.6 ± 0.2	Y5-P2, 3, 4, 5, 6, 8	29	41.7 ± 0.6	Y2-P2, 5; Y3-P5, 6 8; Y5-P2, 5, 6
	2	19	6.0 ± 0.3	Y5-P1, 5, 6; Y2-P6, 8	23	42.5 ± 0.6	Y2-P2, 5; Y3-P5, 6, 8; Y5-P1, 6
	3	25	4.9 ± 0.3	Y5-P1, 4, 5, 8	26	38.5 ± 0.8	Y2-P5, 6; Y5-P4, 7, 8
	4	22	4.8 ± 0.2	Y5-P1, 3, 5, 8	23	39.5 ± 0.8	Y2-P2, 5; Y5-P3, 4, 5, 8
	5	29	5.3 ± 0.3	Y5-P1, 2, 3, 4, 8	29	40.7 ± 0.7	Y2-P2, 4, 5; Y3-P5, 6; Y5-P1, 4
	6	38	6.1 ± 0.2	Y2-P8; Y3-P5; Y5-P1, 2	41	42.4 ± 0.4	Y2-P2; Y3-P5, 6, 8; Y5-P1, 3
	7	52	3.9 ± 0.1	none	57	37.8 ± 0.4	Y2-P6, 8; Y5-P3
	8	143	4.8 ± 0.1	Y5-Pond 3, 4, 5	160	39.4 ± 0.3	Y2-P4, 5; Y5-P3, 4

The total annual number of emigrating juveniles captured ranged from 2426 (Fig. 2). Differences in juvenile recruitment (number exiting per 100 trapnights) were significant among years ($F = 11.2$, df = 4, $P = 0.0001$). Recruitment was significantly lower in 1994 and 1997 than in other years and higher in 1995 and 1998 (recruitment in 1996 did not differ from 1995). Within years, juvenile recruitment varied dramatically among even similar-sized study ponds (Fig. 2). Recruitment was consistently greater in ponds 6 and 8.

All ponds successfully recruited juveniles in 1998, and most recruited juveniles in at least three of five years studied (Fig. 2). The hydroperiod and water depth in pond 3 appeared similar in 1995-1996 and in 1997-1998, but successful recruitment apparently occurred only in 1998 (low numbers of emigrating juveniles in 1995 probably originated in other ponds, because pond 3 did not hold water February to July 1995). Pond 7 held water continually from breeding through metamorphosis only in 1998, and recruitment was high.

Size at Metamorphosis-Body mass and SVL of metamorphic juveniles (both entering and exiting ponds) differed significantly among ponds (body mass $F = 22.12$, df = 7, MS = 50.04, $P = 0.0001$; SVL $F = 12.25$, df = 7, MS = 122.52, $P = 0.0001$) and years (body mass $F = 158.53$, df = 2, MS = 364.96, $P = 0.0001$; SVL $F = 48.41$, df = 2, MS = 484.14, $P = 0.0001$), and there was a significant pond X year interaction (body mass $F = 19.84$, df = 7, MS = 45.71, $P = 0.0001$; SVL $F = 7.43$, df = 7, MS = 74.30, $P = 0.0001$; Table 2). Especially notable were the much smaller body mass and SVL of juveniles in 1997 (also a very poor year for juvenile recruitment) than in other years and lighter juveniles in 1998 than in 1995 and 1996. For 1995, 1996, and 1998 combined (the only years with sufficient numbers of recruits to analyze), the number of juveniles exiting ponds was significantly negatively correlated with SVL ($F = 6.04$, $P = 0.0267$, $r^2 = 0.2870$) and marginally correlated with body mass ($F = 3.18$, $P = 0.0948$, $r^2 = 0.1749$; Fig. 3). However, examination of individual years revealed that significance was concentrated in only one of those years. The number of recruits was significantly correlated with body mass ($F = 27.11$, $P = 0.0138$, $r^2 = 0.9003$) and SVL ($F = 25.51$, $P = 0.0150$, $r^2 = 0.8948$) in 1995 but not in 1996 (body mass $F = 3.65$, $P = 0.1961$; SVL $F = 1.27$, $P = 0.3774$) or 1998 (body mass $F = 1.01$, $P = 0.3540$; SVL $F = 0.75$, $P = 0.4200$; Fig. 4).

Juvenile SVL was positively correlated with body mass ($F = 846.80$, $P = 0.0001$, $r^2 = 0.4585$). The relationship between juvenile SVL and tailbud length was positive and significant but poorly explained variation ($F = 8.63$, $P = 0.0035$,’ $r^2 = 0.0240$). This suggests that smaller recruits are not necessarily exiting ponds prematurely relative to their larger counterparts. The proportion of recruits with tailbuds differed significantly among months in 1995 (pond 6, χ^2

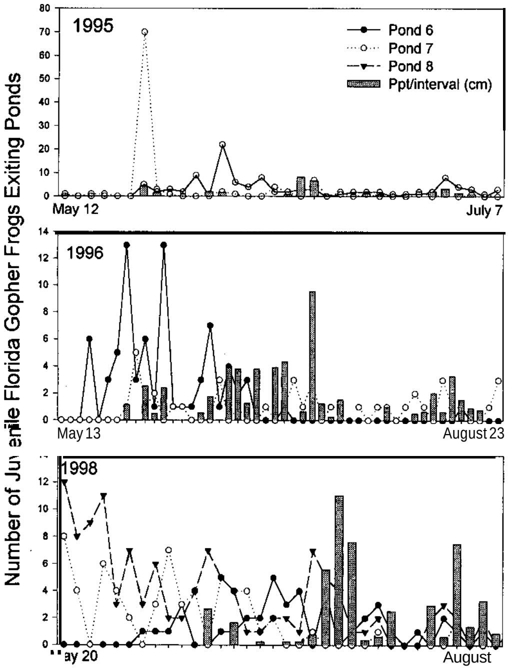

FIG. 3. Capture rate per trap check (2-3 day intervals) of juvenile *Rana capito* recruits (exiting only) in relation to rainfall during the preceding interval between trap checks. The emigration period shown includes dates wherein ≥ 80% of recruit captures occurred. Only ponds having > 50 captures are represented here.

= 6.14, $P < 0.05$) and 1998 (pond 6, $\chi^2 = 21.41$, $P < 0.001$; pond 8, $\chi^2 = 25.71$, $P < 0.001$), but not in 1996 (pond 6, $\chi^2 = 1.29$, $P < 0.50$; Table 3). However, where differences were significant, no trend (increase or decrease) was apparent among months, and in most months, the proportion was relatively high. Mean length of tailbud did not significantly differ among months for any pond-year tested ($P \geq 0.0662$; Table 3), suggesting that emigrating recruits were at similar developmental stages in all months. Some immigrating juveniles (13.9% over the 5-yr study period) also had tailbuds. Body mass and SVL of metamorphic juveniles exiting ponds were significantly higher in the first month of emigration for all pond-year combinations tested except one (Table 3).

Activity Patterns and Orientation.—The low capture rate of adults renders interpretation of breeding periods difficult. Capture rates were slightly higher in September and October and again from January through March in some years. During both periods, adult frogs entered and exited ponds. Low sample size precluded correlation of adult capture rates to rainfall, but no trend was readily apparent. Directional movement of adults into or from ponds did not significantly differ from random in any year ($P > 0.20$).

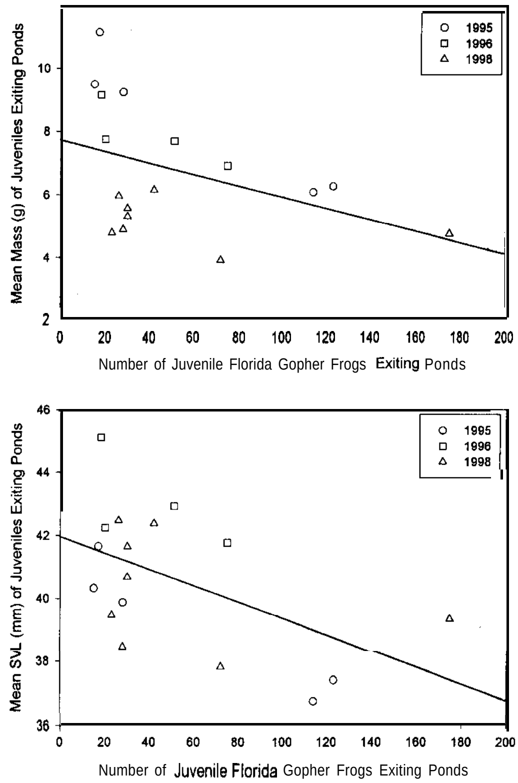

FIG. 4. Relationship between the number of juvenile *Rana capito* recruits (exiting only) and mean body mass (g) and snout-vent length (mm). Each point represents data from one year in one pond (pond-year datasets were included only if $N \geq 10$ for body size data). The regression line is calculated based on all pond-years, but individual years are represented separately by symbols.

Movement of metamorphic juveniles was highly seasonal, with most emigration (and immigration) occurring from May through July (Table 4). Only 4 juveniles, all < 39 mm SVL, were captured in winter. One exited pond 8 on 27 February 1998; another entered pond 8 on 4 March 1998. Two were captured at pond 7 (which had been dry for a year) on 3 and 26 December 1997.

Dates of first emergence varied by several weeks, and emigration periods extended for variable lengths of time among ponds and years (Table 4). The earliest recorded date of metamorphic emigration (with the exceptions mentioned above) was 28 April in 1995. The latest record of an emigrating juvenile was 12 October 1998. Length of emigration period ranged from 33 to 159 days (Table 4). Among individual ponds, most emigration (≥ 80%) by metamor-

TABLE 3. Mean (± SE) monthly body mass (g), snout-vent length (SVL; mm), proportion with tails, and tailbud length (TBL) of metamorphic *Rana capito aesopus* exiting ponds in the Ocala National Forest, Florida. ANOVA was conducted on pond-year combinations having ≥2 months and tested for significant differences in body mass and SVL (if N ≥ 9) and tailbud length (if N ≥ 6; $P \geq 0.0662$) among months within ponds and years. Different letters within columns indicate significant differences among months for that pond and year.

Pond	Year	Month	*N* (mass)	Mass ± SE (g)	*F* (*P*) (mass)	*N* (SVL)	SVL ± SE (mm)	F (P) (SVL)	% w/ TB (% w/ TB)	χ^2 (*P*)	TBL ± SE (mm)
6	1995	5	58	7.0 ± 0.2^{a}		60	38.4 ± 0.4^{a}		41.7		4.4 ± 0.7
6	1995	6	26	5.7 ± 0.2^{b}	13.7	27	36.4 ± 0.3^{b}	7.27	66.7	6.14	5.4 ± 0.9
6	1995	7	12	5.3 ± 0.3”	(0.0001)	12	36.0 ± 0.6^{b}	(0.0012)	50.0	($0.025 < P < 0.05$)	2.5 ± 0.4
6	1996’	5	40	7.4 ± 0.2^{a}	14.56	41	42.7 ± 0.4’	18.56	80.5	1.29	6.0 ± 0.5
6	1996	6	19	6.0 ± 0.2”	(0.0003)	21	40.1 ± 0.4^{b}	(0.0001)	0.0	($0.25 < P < 0.50$)	5.4 ± 0.7
8	1996	7	9	7.0 ± 0.5	0.6	10	41.7 ± 0.9	0.76	18.8		—
8	1996	8	15	7.7 ± 0.6	(0.4457)	16	43.2 ± 1.2	(0.3923)		NA	4.7 ± 0.3
6	1998	6	10	6.6 ± 0.3’	3.0	10	44.0 ± 0.6^{a}	4.77	10.0	21.41	1.0
6	1998	7	23	6.1 ± 0.1^{b}	(0.0932)	25	42.4 ± 0.4^{b}	(0.0361)	44.0	($P < 0.001$)	3.7 ± 0.6
8	1998	5	28	5.7 ± 0.2’		37	41.7 ± 0.5’		37.8		5.1 ± 0.5
8	1998	6	50	4.6 ± 0.2^{b}		56	39.1 ± 0.4^{b}		12.5		3.7 ± 0.6
8	1998	7	28	4.4 ± 0.2^{b}		28	38.5 ± 0.5^{b}		50.0		4.9 ± 0.6
8	1998	8	20	4.3 ± 0.3^{b}	5.8	21	37.7 ± 0.5^{b}	7.09	47.6	25.71	2.7 ± 0.9
8	1998	9	15	4.8 ± 0.4^{b}	0.0002	16	38.9 ± 1.0^{b}	(0.0001)	50.0	($P < 0.001$)	3.7 ± 0.8

phic juveniles occurred within a 14–86 day period (Table 4). Rainfall did not appear to trigger emigration, and had a negligible influence on daily emigration rates of recruits (Fig. 3).

Directional movement was significant (Rayleigh test, $P < 0.05$) for juveniles entering ponds, exiting ponds, or both only in eight of 32 possible pond-year combinations (omitting 1994). Where directional movement was nonrandom, the distribution of directions was usually wide (≤ about 180”). Each year from 1995 to 1998, juveniles entered pond 7 predominantly from a west-southwest direction. In 1995, they exited predominantly to the northeast, and in 1998, they exited in an arc ranging southeast to west. Juveniles captured at pond 8 also exhibited significantly nonrandom movement into ponds in 1997 and 1998. In each year, most entered from the east (northeast and southeast). In 1997, most juveniles exited from pond 8 in a southerly direction; this trend was not apparent in other years. There was an abundance of unmarked juveniles entering most ponds in high-recruitment years (Fig. 2). The low incidence of immigrating marked recruits from other study ponds suggests that many originated at untrapped ponds within the vicinity.

Interpond Movement and Multiple-Year Recaptures.—Minimal movement of *R. capito* among ponds was detected. On 24 June 1998, a juvenile first captured at pond 6 was recaptured entering pond 5 (about 480 m away) in the same year. On 25 May 1998, a juvenile first captured at pond 2 was recaptured entering pond 5 (about 280 m away) the same year. A male **that was** first captured (unknown whether it was then an adult or juvenile) in year 2 at pond 7 was recaptured as an adult about 360 m away exiting pond 8 on 4 October 1996 (year 3). The minimum time between recaptures for this individual was more than 14 months, because the last *R. capito* (a juvenile) captured in 1995 was on 26 July. Only one other animal was recaptured in multiple years. This male was first captured at pond 4 in year 1 and recaptured exiting that pond on 20 February 1995. Because it was one of only three first-captures from 21 September through 24 October 1994 at pond 4 in year 1, the time between captures was 4-5 months.

DISCUSSION

Upland Matrix Effects.-Adult use of ponds did not appear to be influenced by hardwood invasion and associated characteristics of surrounding uplands, but juvenile recruitment was significantly lower in hardwood-invaded than in savanna-like habitats (Table 4). Reasons for this are not readily apparent, because the level of hardwood invasion in the hardwood-invaded upland matrix was patchy and distance (on one side) between three ponds in the hardwood-invaded upland matrix and the savanna-like upland matrix was < 30 m.

High variation in juvenile recruitment levels among ponds and years suggests that four replicates per upland matrix quality type may be inadequate to place great confidence even in highly significant differences. Palis (1998) reported high usage (301 adults) and egg mass deposition at a pond within a fire-suppressed

TABLE 4. Emigration dates of juvenile *Rana capito aesopus* recruits exiting eight isolated, ephemeral ponds during 1995, 1996, and 1998 (1994 and 1997 omitted due to insufficient sample size) in the Ocala National Forest, Florida. Dates of first and last capture (total days in parentheses) are given in the first line; dates (total days in parentheses) wherein ≥80% of captures occurred are in the second line, and total number captured are in the third line. [a] One juvenile was captured exiting on 27 February 1998.

	Pond number							
Year	1	2	3	4	5	6	7	8
1995	5/8–8/14 (98) 5/8–6/6 (29) N = 12	5/1–7/5 (66) 5/1–6/6 (37) N = 17	5/12–7/7 (56) 5/12–5/26 (14) N = 5	5/3–7/30 (88) 5/8–5/31 (23) N = 28	5/15–6/22 (38) 5/15–6/2 (18) N = 15	5/12–9/18 (129) 5/12–7/7 (56) N = 123	5/12–7/26 (75) 5/12–6/9 (28) N = 12	4/28–10/4 (159) 5/12–6/7 (26) N = 114
1996	5/24–8/26 (94) 5/24–8/16 (84) N = 9	NA	5/24–6/26 (33) 5/24–6/26 (33) N = 4	5/7–8/8 (93) 5/7–6/21 (45) N = 18	5/31–9/11 (104) 5/31–7/8 (39) N = 20	5/13–8/14 (93) 5/13–6/12 (30) N = 75	6/3–8/16 (74) 6/3–8/16 (50) N = 4	5/22–9/23 (124) 5/22–8/23 (63) N = 51
1998	5/25–7/13 (49) 5/25–6/24 (30) N = 30	5/20–10/12 (145) 5/20–7/11 (52) N = 26	6/1–9/7 (99) 6/1–7/27 (57) N = 28	5/25–8/28 (95) 5/25–7/11 (47) N = 23	5/20–8/5 (77) 5/20–7/3 (44) N = 30	6/10–9/21 (103) 6/10–7/22 (42) N = 42	5/27–10/4 (130) 5/27–7/11 (45) N = 72	5/11–10/2[a] (144) 5/20–8/14 (86) N = 175

longleaf pine-turkey oak **sandhill** upland. He also reported a tendency for adult *R. capito* to immigrate from the direction of an early successional bombing range versus a hardwood-invaded sandhill, suggesting heavier use of the more open habitat.

Spatio-Temporal Dynamics of Pond Use.-The low capture rate of adults may be the result of escape from pitfalls, trespass, or evasion of drift fences. Alternative or additional explanations include (1) *R. cupito* populations are relatively low, and (2) relatively few adults enter ponds each year. The low rate of multiple-year recaptures could indicate that (1) adults reproduce infrequently, (2) adult survival among years is low, or (3) toe regeneration precludes detection of multiple-year recaptures. Richter (1998) reported a 17-18% rate of adult recaptures between two sets of consecutive breeding seasons, suggesting that some *R. capito* attempt to breed every year.

Recruitment of juveniles from individual ponds in any year appeared to be substantially lower in this study (maximum 175 exiting and 104 entering pond 8 in 1998) than in some others (2488 from a single 440-m circumference pond reported by Richter, 1998). However, study comparisons may be invalid given differences in drift fence placement design (50% encircling drift fences in this study versus 100% in others). Nonetheless, juveniles were recruited from many study ponds in three of five years and from all ponds in 1998. Unmarked juveniles entering ponds in those years suggest that recruitment also occurred in other nearby ponds.

Semlitsch et al. (1995) reported that < 10 adults were collected at any continuously monitored pond in any year at the Savannah River Site and that breeding frequency among years was low (0.06-0.67) at four well-studied ponds. Juvenile recruitment also appeared to be low ($N \leq 50$ per studied pond) at the SRS. They noted that breeding populations and juvenile recruitment remained low but stable for the past 25 years. However, they suggested that a small effective population size, high inbreeding potential, and infrequent recruitment of juveniles renders *R. cupito* vulnerable to rapid local extinction Population characteristics at the Ocala National Forest appear similar to that at Savannah River Site; relatively few juveniles are produced from a high number of isolated, ephemeral ponds in some years.

Although adult use of ponds appeared similar among years, recruitment was highly variable, and correlation between adult breeding effort and juvenile recruitment the next was significant in only 1 yr. Causes of recruitment success or failure could not be attributed solely to pond hydrology except in 1994. Variation in recruitment rate was high among years (1995 vs. 1997) and among ponds having similar hydrologies. Richter (1998) also reported variable recruitment success (O-2488 from 1996 through 1998 at Glens Pond, Mississippi) that could not be attributed strictly to hydroperiod and suggested that observed mortality of egg masses in 1 yr was the result of infestation by larval caddisflies. Hence, underwater dynamics, such as predation, competition, or both, may influence recruitment success. Clearly, influences acting at both landscape-level (such as pond-drying or flooding) and within-pond level (such as predation or competition) affect the short-term population dynamics of *R. capito.*

Variation in body mass and SVL among years, ponds, and within ponds in different years suggests that resources, competition, or both can affect body size. The negative correlation between number of juveniles exiting ponds and body size was significant in only 1 yr, suggesting that intraspecific competition plays some role in metamorphic body size. However, other factors also may affect body size.

Most studies report *R. capito* breeding from December (or later) through April, often for only a few days (Mount, 1975; Franz, 1988; Bailey, 1991; Godley, 1992; Semlitsch et al., 1995). In northern Florida, *R. capito* have been recorded as breeding from February to November (Carr, 1940; Wright and Wright, 1949) and possibly year-round under suitable conditions (see Palis, 1998). Palis (1998) reported an eight-month breeding season, with major breeding events in October, February, and April at a pond in the Florida panhandle.

May-July peak emergence of metamorphic juveniles appears to be relatively uniform for studied populations (Semlitsch et al., 1995; Palis, 1998; Richter, 1998). A high proportion of emigrating juveniles with tailbuds and similar tailbud lengths in most months suggests that metamorphosis occurred throughout the emigration period. Individuals emerging during this period may have been derived from different cohorts. Larger juveniles emigrating early (May) may have originated from an earlier breeding. Differences among ponds in dates and length of juvenile emigration periods within years further suggest that the duration of breeding or number of breeding episodes, and rates of larval development, can vary among ponds.

Based on observations from dipnetting ponds throughout the Ocala National Forest in 1993 (S. Telford, unpubl. data), *R. capito* tadpoles may result from both a fall and late winter breeding. Estimations of larval developmental periods include 87-113 days (South Carolina: Semlitsch et al., 1995), 141-155 days (laboratory-reared tadpoles: Volpe, 1958), and 210 days (Florida panhandle: Palis, 1998). Based on the presence of tailbuds, Richter (1998) suggested a wide range in the dates of *R. capito* metamorphosis at Glen's Pond. The prevalence of tailbuds on emigrating and immigrating (from other ponds) juveniles suggests that tailbuds often persist during early dispersal, although they may thereafter be quickly absorbed [R. Franz (pers. comm.) has never observed juveniles with tailbuds in *Gopherus polyphemus* burrows].

Adult capture rates in this study were too low to determine breeding periods. However, the protracted period of juvenile emigration suggests that either (1) breeding was continual or episodic over a period of several months (January-April, assuming a 34 month development period or October-April, assuming a 3-7 month development period), or (2) larval development rates can vary by several months among individuals within the same pond, or both. Richter (1998) reported that adult males remained in ponds for an average of 10 weeks, suggesting that breeding could occur over a relatively long period.

Activity Patterns and Orientation.—Other studies suggest that individual adults enter and exit ponds by the same routes and that adult movement is significantly correlated with rainfall (Franz, 1988; Palis, 1998; Richter, 1998). In this study, cohort markings, rather than individual markings, precluded detection of route use. Orientation data for adults suggest that they inhabited or moved through surrounding uplands without preference.

Richter (1998) suggested that rapid drying of Glens Pond explained a short (20 days) juvenile emigration period in 1998 (compared to 62 days in 1997). However, hydroperiod does not explain differences in emigration periods among ponds and years in this study. As in this study, emigration by metamorphic juveniles at Glen's Pond was not tied to rainfall events.

Directional movement by juveniles to or from ponds was uncommon in this study and varied among ponds and years when it occurred. Unmarked juveniles entering or exiting ponds in a generally uniform direction (e.g., pond 7 1995–1998; pond 8 1997-1998) could have emigrated from other ponds. Several ponds occur within 1 km of ponds 7 and 8, including some known to contain *R. capito* tadpoles (S. Telford, unpubl. data; S. Johnson, pers. comm.). Directional movement by juveniles exiting some ponds could have been a result of aggregation of egg masses, tadpoles, or premetamorphic juveniles (Bailey, 1990). Richter (1998) reported metamorphic *R. capito* emigrating from Glen's Pond using the same specific migratory corridors in 1997 and 1998. In many cases, nonrandom movement observed in this study could be attributed to dispersal from neighboring ponds, and their location relative to study ponds.

Only three cases of interpond movement were detected, and at least two of those involved juveniles. Frequent captures of unmarked juveniles entering ponds suggest that juveniles may frequently move at least a few hundred meters from their natal ponds and at least temporarily into neighboring ponds. This study cannot address *R. capito* movements into uplands except for intervening uplands between ponds. However, adult *R. capito* were regularly observed at inactive G. **polyphemus** burrow entrances within 15 m of ponds 3 and 7 (pers. obs.; J. Beach, pers. comm.). Franz et al. (1988) recorded a R. cupito moving 2 km from a breeding pond. This study documents interpond movements of ≤ 480 m.

Influences on juvenile recruitment success appear to act both at landscape and within-pond scales. The condition of longleaf pine-wiregrass sandhills surrounding ponds may influence levels of juvenile recruitment. The role of multiple ponds in sustaining *R. capito* populations is clearly illustrated in this study. In two of five years, recruitment was negligible; in successful years, recruitment failure in one pond may be offset by success in others. Some ponds appear to consistently produce more recruits than others, although variation among years makes this difficult to detect statistically. Variability in recruitment success among ponds and years illustrates the importance of long-term, multiple-pond studies to gain perspective of spatial and temporal dynamics of amphibian populations.

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