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ARTICLE

Amphibian breeding phenology and reproductive outcome: an examination using terrestrial and aquatic sampling

C.H. Greenberg, S.A. Johnson, R. Owen, and A. Storfer

Abstract: Worldwide amphibian declines highlight the need for programs that monitor species presence and track population trends. We sampled larval amphibians with a box trap at 3-week intervals for 23 months in eight wetlands, and concurrently trapped adults and juveniles with drift fences, to examine spatiotemporal patterns of tadpole occurrence; explore relationships between breeding effort, tadpole abundance, and recruitment; and compare the efficacy of both methods in detecting species presence and reproductive outcome. Intermittent detection of species within and among wetlands suggested high mortality, followed by deposition of new eggs and tadpole cohorts. Breeding effort, tadpole abundance, and juvenile recruitment were generally not correlated. The reasons for this may include differential bias in detecting species or life stages between methods and high incidence of egg or tadpole mortality. Drift fences detected more species than box traps, but each provided insights regarding amphibian presence and recruitment. Our results illustrate shortfalls in the ability of infrequent aquatic sampling to detect local species richness of larval amphibians, as occurrence of many species is spatially and temporally variable. We also show the importance of using different sampling methods to detect species' presence, as well as difficulties associated with both methods in tracking breeding effort, tadpole occurrence, or reproductive outcome.

Key words: anuran reproduction, aquatic sampling, larval amphibian richness, reproductive outcome, terrestrial sampling, tadpole sampling, tadpole phenology.

Résumé : Le déclin des amphibiens à l'échelle planétaire souligne la nécessité de programmes de surveillance de la présence d'espèces et de suivi des tendances démographiques. Nous avons échantillonné des larves d'amphibien à l'aide d'une boîte-piège à des intervalles de 3 semaines pendant 23 mois dans huit milieux humides et, en même temps, avons piégé des adultes et des juvéniles à l'aide de clôtures de dérivation afin d'examiner la distribution spatiotemporelle de la présence de têtards, d'explorer les liens entre l'effort de reproduction, l'abondance de têtards et le recrutement et de comparer l'efficacité des deux méthodes pour détecter la présence d'espèces et déterminer les résultats de la reproduction. La détection intermittente d'espèces dans les milieux humides et entre ces derniers indiquerait une forte mortalité, suivie par le dépôt de nouveaux œufs et cohortes de têtards. L'effort de reproduction, l'abondance de têtards et le recrutement de juvéniles n'étaient généralement pas corrélés, ce qui pourrait s'expliquer, entre autres, par un biais différentiel de la détection des espèces ou des étapes du cycle de vie entre les méthodes et une forte incidence de mortalité d'œufs ou de têtards. Les clôtures de dérivation ont permis de détecter plus d'espèces que les boîtes-pièges, mais chaque méthode a fourni de l'information sur la présence et le recrutement des amphibiens. Les résultats illustrent les difficultés associées à la capacité d'un échantillonnage aquatique peu fréquent de détecter la richesse spécifique locale de larves d'amphibien, étant donné que la présence de nombreuses espèces varie dans l'espace et dans le temps. Nous démontrons également l'importance d'employer différentes méthodes d'échantillonnage pour détecter la présence d'espèces et les difficultés associées aux deux méthodes pour ce qui est de suivre l'effort de reproduction, la présence de têtards et le résultat de la reproduction. [Traduit par la Rédaction]

Mots-clés : reproduction des anoures, échantillonnage aquatique, richesse des larves d'amphibien, résultat de la reproduction, échantillonnage terrestre, échantillonnage de têtards, phénologie des têtards.

Introduction

Many amphibian species breed solely or opportunistically in ephemeral wetlands because they are generally fish-free and have low relative densities of predatory aquatic macroinvertebrates compared with more permanent water bodies (Pearman 1995; Skelly 1997). Nonetheless, reproductive success is uncertain in ephemeral habitats, partially owing to variable duration, frequency, timing, and depth of water; wetland drying before metamorphosis results in larval mortality (Greenberg et al. 2015). However, the timing of wetland drying affects species differently due to differences in breeding seasons and rates of larval developmental. Variable hydroregime characteristics within and among wetlands make it unlikely that suitable conditions for successful breeding and recruitment for all species will be consistently available (Snodgrass et al. 2000). Wetland hydrology is strongly affected by the amount and timing of precipitation, making them — and the amphibian populations they support — especially sensitive to altered weather patterns resulting from climate change (Greenberg et al. 2014, 2015).

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Concern over amphibian population decline, as well as vulnerability to climate change, disease, and other environmental threats, highlights the need for effective biological monitoring programs (Collins and Storfer 2003). Both long-term terrestrial sampling of amphibians near wetlands and aquatic sampling of larvae indicate high interannual variability in detection, breeding effort, and recruitment (Semlitsch et al. 1996; Trenham et al. 2003; Werner et al. 2007*a*, 2007*b*). Terrestrial and aquatic sampling methods are complementary; terrestrial sampling does not explain dynamics of larval abundance or mortality and aquatic sampling may not reflect breeding effort if egg or tadpole mortality rates are high. Neither method detects all species and each elucidates only a component of reproduction dynamics. Yet, we are unaware of any study using both terrestrial and aquatic sampling methods to examine temporal and spatial dynamics of amphibian breeding through recruitment and, ultimately, long-term population health.

Effective amphibian population monitoring programs must incorporate a combination of methods with sampling frequency, timing, and spatial scale that, together, optimize the likelihood of detecting target species, while minimizing errors in demographic inference (Miller et al. 2011). For example, a species may be temporarily absent or undetected from any given wetland, year, or sampling period due to unsuitable weather or wetland conditions, narrow breeding seasons, rapid larval development rates that affect duration of larval presence, or infrequent or unpredictable breeding behavior (Skelly et al. 2003). Underwater dynamics of competition and predation that vary spatially and temporally can also influence larval presence and reproductive outcome (Wilbur 1982; Morin 1983). Thus, an effective sampling regime requires a basic understanding of the suite of species expected, their life-history traits, wetland conditions required for breeding, and a combination of methods that together can detect each species as adults, larvae, and ideally juvenile recruits.

We compared an aquatic sampling method and a terrestrial sampling method to fill a critical knowledge gap in how sampling different life stages, and using different sampling methods, provide complementary information and insight into amphibian presence and reproductive success. We used a box trap to sample larval amphibians at approximately 3 week intervals for 23 months in eight isolated ephemeral wetlands and concurrently trapped amphibians using drift fences to (*i*) examine spatiotemporal patterns of tadpole occurrence and developmental stage as metrics of breeding and phenology; (*ii*) explore relationships between breeding effort, tadpole abundance, and recruitment; and (*iii*) compare the relative efficacy of drift fences to box trap sampling in detecting amphibian species presence (richness) and tracking reproductive outcome.

Materials and methods

Study area

Our study area consisted of eight small (0.1–0.37 ha), isolated wetlands in longleaf pine – wiregrass sandhills located in the Ocala National Forest in north-central peninsular Florida, USA. The study wetlands were selected in 1994 as part of an ongoing long-term drift fence study of amphibians using ephemeral wetlands and can be considered a representative selection of small, ephemeral, groundwater-driven sinkhole wetlands that are common within xeric uplands of the Floridan Aquifer System region. Excessively drained Entisols are underlain by Ocala limestone (Aydelott et al. 1975), resulting in abundant closed depression sinkholes with limited surface drainage networks (Kalisz and Stone 1984). Wetland elevations at their approximate lowest point ranged from 4.0 to 26.2 m above mean sea level. Mean daily temperatures measured were 20.7 °C (8.9–32.5 °C) in 2000 and 21.3 °C (10.6–32.1 °C) in 2001. Total precipitation was 130.4 cm in 2000 and 164.2 cm in 2001, with >80% occurring April–September both years. Heavy precipitation recharging groundwater was associated with thunderstorms in late May – early October, tropical systems in summer and fall, and wet autumn, winter, or spring frontal systems (Winsberg 1990).

Wetland area and depth zone measurements

We partitioned each wetland into five equal wedge-shaped sections by placing a PVC pipe at center, and benchmark rebars at five, equally distanced azimuths (0°, 72°, 144°, 216°, 288°) around the perimeter. Basin areas were calculated as a circle ($A = \pi r^2$), with radius as the mean distance between the center and the five rebars. Water surface area (WSA) was measured each sample date (visit) and calculated as a circle using the mean of five radii (r) from edge to wetland center. We also calculated WSA of three concentric depth zones (DZs) (Shaffer et al. 1994), if present. DZ3 (≥40 cm) included WSA from 40 cm depth to center; DZ2 (20–39.9 cm) from 20 cm depth to center, minus the area of DZ3; DZ1 (<20 cm) from water edge to center, minus the areas of DZ2 and DZ3. Maximum water depth was measured at wetland centers the same week as box trap sampling dates.

Box trap sampling for larval amphibians

We used a rigid, open-ended 0.5 m^2 (92 cm × 54 cm; 8 cm height) box trap (Shaffer et al. 1994) to sample tadpoles in all DZs at each wetland at approximately 3-week intervals, from 3 February 2000 to 23 December 2001. The box trap was the same width as our dip net, fitted with green-dipped, 0.95 cm mesh (Memphis Net and Twine; net Model HDD2). Tadpole sampling entailed pressing the box trap through the water column into the mucky substrate, then removing all tadpoles using repeated dip net sweeps (≥3 sweeps until 2 successive sweeps yielded no additional larvae). We avoided dense mats of vegetation that impeded sampling; thus, sampling was biased toward open water. Because wetlands gradually filled or dried, all DZs were not present each visit. Dry wetlands were not sampled and we assumed larvae were absent, although rarely a "dry" wetland contained small puddles and, potentially, some amphibian larvae or egg masses.

We used a randomized sampling design stratified by DZ, designed to account for spatial variability in tadpole distribution. Each DZ in each of the five wetland sections ("wedges") was sampled with 1 "throw", for a total of 15 throws when all three DZs were present, or fewer if wetlands were shallow. We varied sample locations where possible and observed little if any damage to aquatic vegetation over time. We attempted to maintain at least 4 m between each throw, but distances were less when WSA was low.

Captured tadpoles were identified to species in the field and scored into three developmental classes (Gosner 1960) — class 1: no distinct rear limbs formed (up to Gosner stage 35); class 2: rear limbs formed and discernable toes (Gosner stages 36–41); class 3: ≥1 front limb erupted (Gosner stage 41–46). Larvae were released after processing.

Drift fence sampling for adults and juveniles

Drift fences, spaced 7.6 m apart and 7.6 m in length, encircled 50% of each wetland perimeter as part of the longer term study. Pitfall traps (19 L buckets) were positioned inside and outside of each fence at both ends, with a funnel trap at the fence midpoint on both sides allowing us to ascertain whether amphibians were immigrating to or emigrating from wetlands. A PVC pipe was placed between fences to attract treefrogs. Drift fence traps were open continuously and checked approximately three times weekly throughout the study period. Amphibians toe-clipped by wetland number and year, categorized as adult or juvenile based on a specified snout–vent length (SVL) cutoff for each species (Table 1), and released. Because all wetlands were sampled in proportion to size, we did not further adjust for trap nights.

Table 1. Time intervals used to define breeding effort (total first-captured adults) and recruitment (juveniles exiting from wetlands) based on drift fence sampling, and snout–vent length (SVL) cutoffs used to designate adults and recruits.

Species	Adult breeding effort	Juvenile emigration	Juvenile SVL (mm)
Southern Cricket Frog, *Acris gryllus*	Intermittent[a]	Intermittent[b]	<15
Oak Toad, *Anaxyrus quercicus*	May, week 1 – October, week 4	June, week 1 – December, week 4	<20
Southern Toad, *Anaxyrus terrestris*	Feb, week 1 – October, week 4	March, week 4 – December, week 4	<25
Narrowmouth Toad, *Gastrophryne carolinensis*	May, week 1 – October, week 4	June, week 1 – December, week 4	<23
Pinewoods Treefrog, *Hyla femoralis*	May, week 1 – October, week 4	September, week 1 – August, week 4[c]	<24
Barking Treefrog, *Hyla gratiosa*	Intermittent[a]	Intermittent[b]	<40
Little Grass Frog, *Pseudacris ocularis*	Intermittent[a]	Intermittent[b]	<12
Florida Gopher Frog, *Lithobates capito*	May, week 1 – April, week 4	April, week 1 – October, week 4	<50
American Bullfrog, *Lithobates catesbeianus*	May, week 1 – April, week 4	April, week 4 – December, week 4	<59
Pig Frog, *Lithobates grylio*	Intermittent[a]	Intermittent[b]	<56
Southern Leopard Frog, *Lithobates sphenocephalus*	May, week 1 – April, week 4	April, week 4 – December, week 4	<52
Spadefoot Toad, *Scaphiopus holbrookii*[d]	If ≥30 within 1 week[d]	12 weeks after breeding event[e]	<18

[a] Sum of adult captures during the interval starting when prior tadpole cohort is no longer detected in wetland, until the new cohort (resulting from that breeding effort) is first detected, and until that cohort is no longer detected.

[b] Sum of exiting juvenile captures starting when a new cohort of tadpoles is first detected in a wetland, through the period when that cohort is no longer detected, and until the next, new cohort of tadpoles is first detected.

[c] Sum of exiting juvenile captures starting in September when tadpoles are first detected, until the following August, or until wetland dries and then refills for opportunity for new breeding and cohort.

[d] Explosive breeding events.

[e] Tadpoles metamorphose within 3 weeks of explosive breeding events, so we used a longer time period to include emigrating juvenile "stragglers".

Data analyses

For each visit, we averaged the number of amphibian larvae per 0.5 m^2 WSA and expanded to number per m^2 WSA within each DZ present ($n = 5$ per DZ), then multiplied by the total DZ WSA to estimate total density per DZ; we summed across DZs to estimate total number per wetland. Density estimates were based on number per m^2 WSA rather than volume, but should accurately represent total numbers within DZs and wetlands, because box traps sampled the entire water column. We examined whether densities of each species differed among DZs when three or (separate analysis) two DZs were available using repeated-measures ANOVAs (Proc Mixed in SAS version 9.3; SAS Institute, Inc. 2009) with wetlands as a random factor.

We examined relationships between adult breeding effort (defined as all first-captured adults), tadpole abundance, and juvenile recruitment (defined as all first-captured juveniles emigrating from ponds) within defined breeding cycles for each species (Table 1). We used longer term drift fence data for adults captured before and recruits captured after our larval sampling study period to increase sample size of complete breeding cycles for some species and wetlands. We performed Spearman's correlations to test the relationships between (*i*) breeding effort and maximum tadpole abundance and between (*ii*) maximum tadpole abundance and total recruits. Each wetland and breeding cycle was considered an independent observation. Wetlands were included if any adults, tadpoles, or recruits were captured; incomplete breeding cycles were omitted. Correlations were not performed on American Bullfrog (*Lithobates* (*Rana*) *catesbeianus* (Shaw, 1802)) and Pig Frog (*Lithobates* (*Rana*) *grylio* (Stejneger, 1901)) because of inadequate sample size.

We used a paired *t* test to compare amphibian richness sampled by box traps and drift fences over the same period. We included Striped Newts (*Notophthalmus perstriatus* (Bishop, 1941)) in estimates of species richness, but focused only on anurans for other analyses.

Results

Wetlands 3, 7, and 8 were dry for most of the study period (Fig. 1). In the year 2000, wetlands dried by mid-May through early September, refilling with higher rainfall in September, including Tropical Storm Gordon on 17–18 September that dropped 8.1 cm of rain. In 2001, all wetlands were completely or nearly dry from late spring through late September (Fig. 1), refilling after Tropical Storm Gabrielle dropped 28.8 cm of rain on 14–16 September. WSA was positively correlated with depth ($p < 0.01$, r^2 ranged 0.64–0.99); depths and number of DZs corresponded with WSA.

We sampled a total of 3306 larval amphibians including 12 anuran species, and both larval and paedomorphic *N. perstriatus* (Table 2; Fig. 2). Because larvae were unmarked, we were unable to determine if individuals were sampled more than once during the study period. Species richness of larval amphibians on any given date, across all wetlands, ranged from 2 to 10 (Fig. 2). Within wetlands, total richness over the entire study period ranged from 2 to 11 and generally corresponded with the number of visits a wetland held water (Table 2; Fig. 3). Pinewoods Treefrog (*Hyla femoralis* Bosc in Daudin, 1800) tadpoles were the most abundant (27.3%), followed by Florida Gopher Frog (*Lithobates* (*Rana*) *capito* (LeConte, 1855)) (18.6%), Spadefoot Toad (*Scaphiopus holbrookii* (Harlan, 1836)) (16.1%), and Southern Leopard Frog (*Lithobates* (*Rana*) *sphenocephalus* (Cope, 1886)) (15.6%) (Table 2). Each wetland was sampled (hence, held water) 2–21 times during the 23-month study period (Table 2).

Most larval amphibian species were detected in only a subset of wetlands over the study period. Only *H. femoralis* and Little Grass Frog (*Pseudacris ocularis* (Bosc and Daudin in Sonnini de Manoncourt and Latrielle, 1801)) tadpoles were detected at all eight wetlands; *L. capito* and *L. sphenocephalus* were detected at seven wetlands, followed by Narrowmouth Toad (*Gastrophryne carolinensis* (Holbrook, 1835)) and *L. grylio* (six wetlands); Southern Cricket Frog (*Acris gryllus* (LeConte, 1825)), Barking Treefrog (*Hyla gratiosa* LeConte, 1856), and *N. perstriatus* (five wetlands); *L. catesbeianus* (four wetlands); and *S. holbrookii* (three wetlands) (Table 2; Fig. 3). Oak Toad (*Anaxyrus* (*Bufo*) *quercicus* (Holbrook, 1840)) (Dodd 1994; Greenberg and Tanner 2005*a*) and Southern Toad (*Anaxyrus* (*Bufo*) *terrestris* (Bonnaterre, 1789)) (Dodd 1994) tadpoles were detected at only one wetland in September and April 2001, respectively (Table 2; Fig. 3). On any given date, a species detected in ≥1 wetland (e.g., potentially present) was rarely detected in all available (holding water) wetlands (Table 3; Fig. 3). Frequently, species were not detected within available wetlands where they were detected the visit prior, or vice versa (Fig. 3). Most tadpole species were detected intermittently, with apparent disappearances and subsequent reappearance commonly occurring within wetlands and breeding cycles (Fig. 3).

The seasonal timing of tadpole occurrence also differed among some species. *Acris gryllus* tadpoles were detected in all seasons

Fig. 1. Total water surface area and surface area of three depth zones (<20, 20–39.9, ≥40 cm) in eight isolated ephemeral wetlands sampled at approximately 3-week intervals (from 2/3/2000 to 12/23/2001; format is month/day/year), Ocala National Forest, Florida, USA.

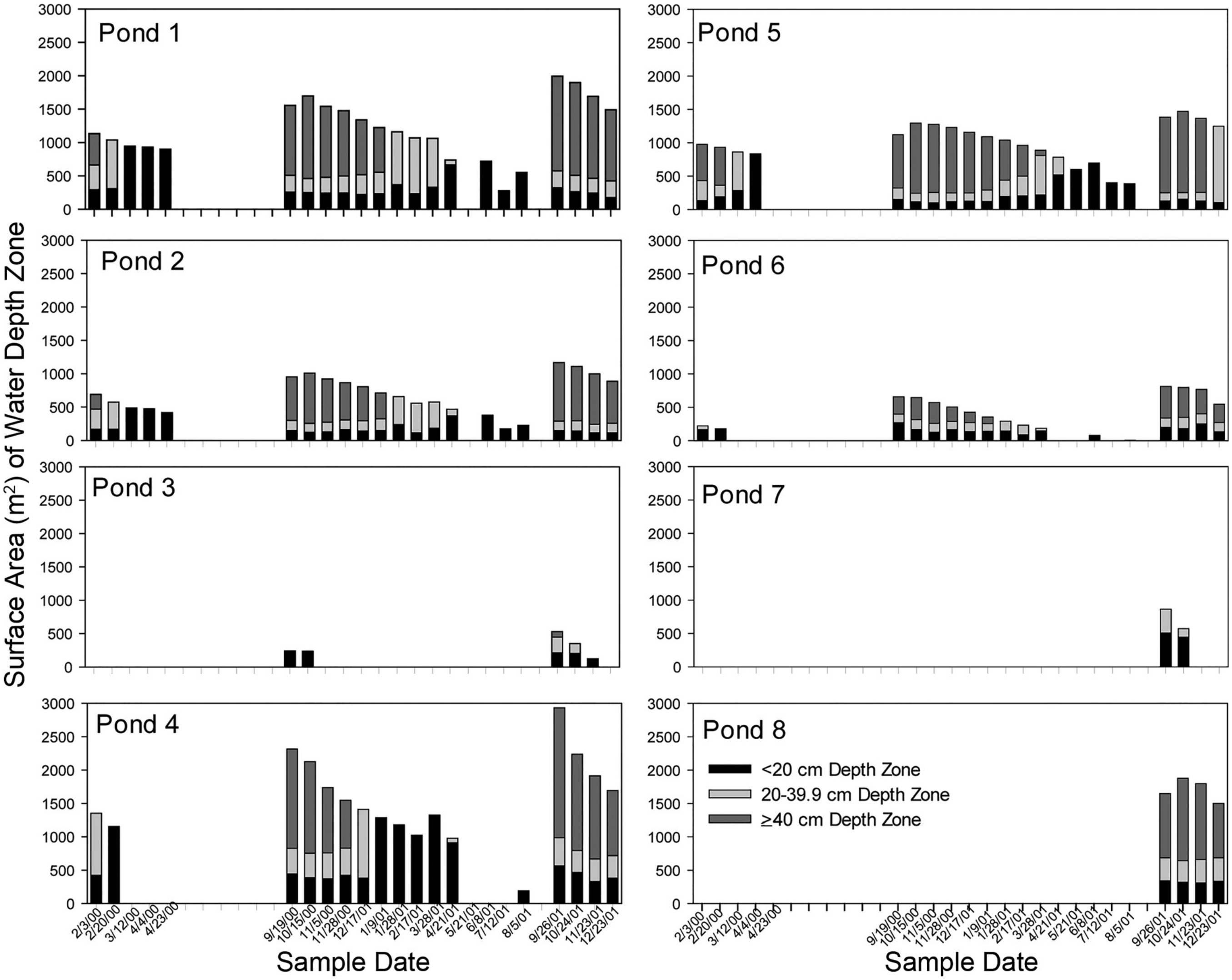
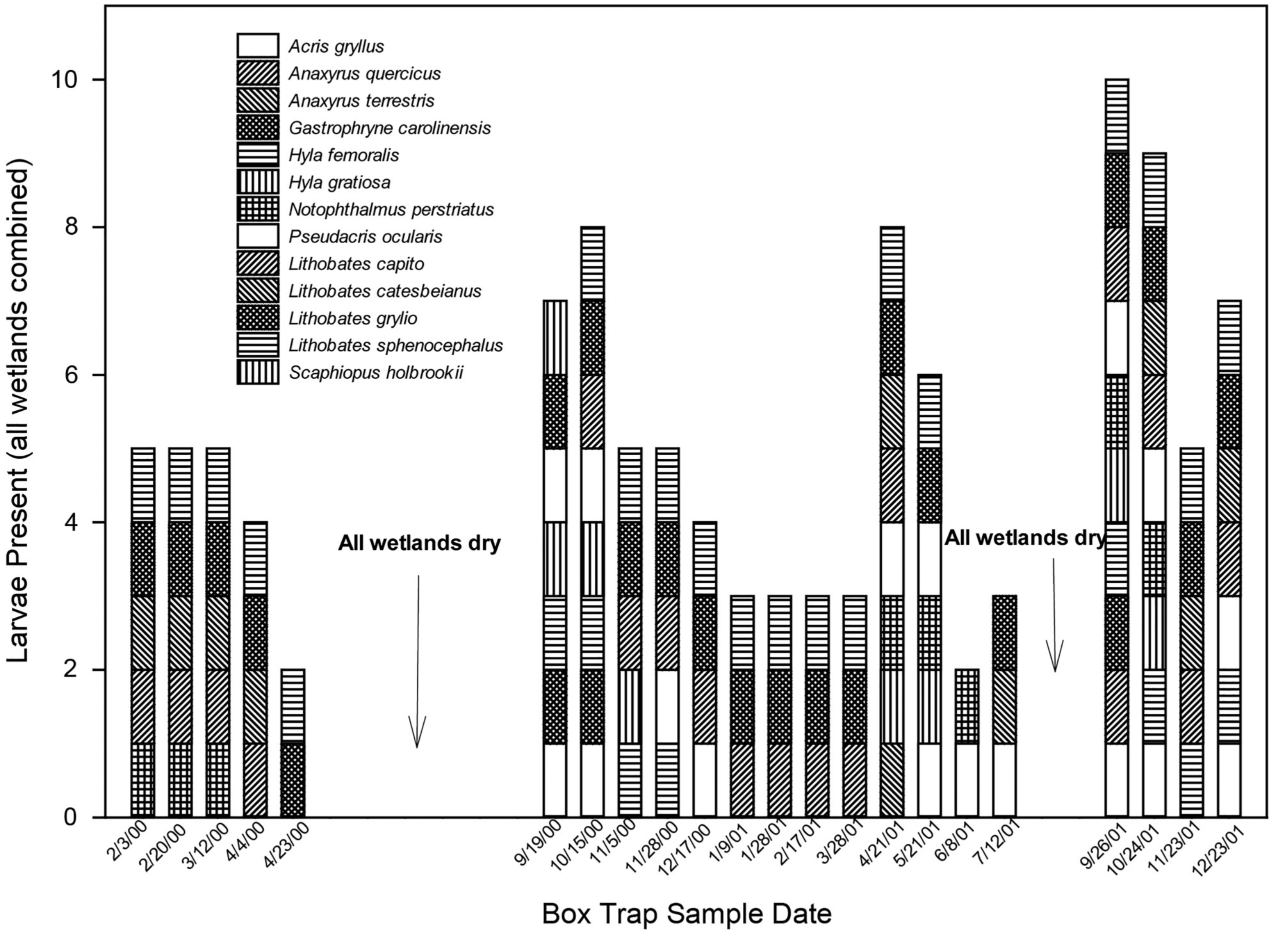


Table 2. Total number of amphibian larvae, times sampled (wetlands not sampled if dry), and number of box trap throws (5 per depth zone when present, per visit).

	Wetland number								
Species	1	2	3	4	5	6	7	8	Total
Southern Cricket Frog, *Acris gryllus*	11	14	0	0	59	8	0	2	94
Oak Toad, *Anaxyrus quercicus*	0	4	0	0	0	0	0	0	4
Southern Toad, *Anaxyrus terrestris*	0	0	0	56	0	0	0	0	56
Narrowmouth Toad, *Gastrophryne carolinensis*	1	1	1	0	5	15	0	0	23
Pinewoods Treefrog, *Hyla femoralis*	185	159	8	77	167	179	10	118	903
Barking Treefrog, *Hyla gratiosa*	25	1	0	14	32	1	0	0	73
Striped Newt, *Notophthalmus perstriatus*	18	1	0	0	22	7	0	1	49
Little Grass Frog, *Pseudacris ocularis*	7	2	28	2	19	19	18	54	149
Florida Gopher Frog, *Lithobates capito*	115	14	1	6	160	223	0	95	614
American Bullfrog, *Lithobates catesbeianus*	31	0	0	0	7	35	0	7	80
Pig Frog, *Lithobates grylio*	93	23	0	3	83	7	0	2	211
Southern Leopard Frog, *Lithobates sphenocephalus*	47	7	8	12	314	117	0	12	517
Spadefoot Toad, *Scaphiopus holbrookii*	396	0	0	0	26	111	0	0	533
Total larvae sampled	929	226	46	170	894	722	28	291	3306
Total species sampled	11	10	5	7	11	11	2	8	13
Total times wetland sampled	21	21	4	16	21	15	2	4	23
Total 0.5 m² box trap throws	235	230	35	155	250	200	15	60	1180

Note: Wetlands containing water were sampled at approximately 3-week intervals, from 3 February 2000 to 23 December 2001, at eight small, ephemeral wetlands in the Ocala National Forest, Florida, USA.

Fig. 2. Species occurrence of amphibian larvae in one or more of the eight study wetlands, based on box trap samples taken at approximately 3-week intervals (from 2/3/2000 to 12/23/2001; format is month/day/year), Ocala National Forest, Florida, USA. Samples were not taken if wetland(s) were dry or nearly dry.



except winter (mid-November – April). *Hyla gratiosa* and *P. ocularis* tadpoles were detected in fall and spring, whereas *H. femoralis* tadpoles were detected only in fall – early winter (Table 3; Figs. 3, 4). *Gastrophryne carolinensis* tadpoles were detected once in each of four wetlands during September or October 2000 and in one wetland on September 2001 (Table 3; Figs. 3, 4). *Lithobates capito* and *L. sphenocephalus* were detected in ≥1 wetland during most fall–spring months in both years; *L. grylio* and *L. catesbeianus* were detected in most calendar months (Table 3; Figs. 3, 4).

Generally, species with rapid larval development were detected for fewer consecutive visits than those with slow larval development. *Acris gryllus*, *H. gratiosa*, *P. ocularis*, *H. femoralis*, *G. carolinensis*, and *S. holbrookii* tadpoles, all known to complete development in ≤8 weeks (Ashton and Ashton 1988), were detected for 1–3 consecutive visits within individual wetlands (Fig. 3), and tadpoles in class 2 or 3 were found within days to weeks of ponds refilling (Fig. 4). In contrast, tadpoles of *Lithobates* spp., which require ≥3 months to >1 year to complete development (Ashton and Ashton 1988), were detected on one to several (*L. capito*: 8 visits; *L. sphenocephalus*: 7 visits; *L. grylio*: 11 visits; *L. catesbeianus*: 3 visits) consecutive visits within individual wetlands (Fig. 3), and class 2 *Lithobates* tadpoles were first found months after first detections; no class 3 tadpoles were found during the study period (Fig. 4). Class 2 *L. capito* and *L. sphenocephalus* tadpoles were detected in March–April of one or both years, about 6 months after wetlands refilled; additionally, *L. capito* tadpoles were detected in one wetland on November 2000 (Fig. 4). Class 2 *L. grylio* tadpoles were detected in the months of February, March, April, May, and October, and *L. catesbeianus* in February 2000 (Fig. 4). *Scaphiopus holbrookii* tadpoles, all class 1, were detected in three wetlands on 19 September 2000, 6–8 days after an explosive breeding event.

When all 3 DZs were available, abundance of *L. sphenocephalus* was greater in DZ1 than DZ2 or DZ3 ($F_{[2,15]} = 6.3$, $p = 0.01$); abundance of *A. gryllus* ($F_{[2,12]} = 4.8$, $p = 0.03$) and *L. capito* ($F_{[2,15]} = 6.2$, $p = 0.01$) was greater in DZ1 than DZ3 (Fig. 5). Abundance of *G. carolinensis*, *H. femoralis*, *P. ocularis*, *L. catesbeianus*, *L. grylio*, and *S. holbrookii* did not differ ($p \geq 0.12$) among DZs when all three were available (Fig. 5). In contrast, abundance of *H. gratiosa* was higher in DZ3 than DZ1 ($F_{[2,9]} = 5.0$, $p = 0.03$). When only DZ1 and DZ2 were present, abundance of *P. ocularis*, *L. capito*, *L. catesbeianus*, *L. grylio*, and *L. sphenocephalus* did not differ ($p \geq 0.21$). *Acris gryllus*, *G. carolinensis*, *H. femoralis*, and *H. gratiosa* generally occurred only when all three DZs were present. *Anaxyrus quercicus* and *A. terrestris* occurred once, and thus data on depth selection were not analyzed.

We found a positive correlation between breeding effort and maximum tadpole abundance for *H. femoralis* ($p = 0.01$, $r_S = 0.61$) and *S. holbrookii* ($p = 0.01$, $r_S = 0.83$), but not for the other eight species tested ($p \geq 0.17$) (Figs. 6A–6J). Maximum *H. femoralis* tadpole abundance was positively correlated with total recruits ($p = 0.02$, $r_S = 0.56$), but we found no relationship for the other eight species tested ($p \geq 0.19$) (Figs. 7A–7J).

Total amphibian species richness detected by drift fences averaged 4.9 ± 0.8 higher (mean ± SE) ($t = 6.18$, $p < 0.01$) than richness detected by box trap sampling.

Fig. 3. Estimated number of amphibian larvae per wetland based on box trap samples taken at approximately 3-week intervals from eight isolated ephemeral wetlands (from 2/3/2000 to 12/23/2001; format is month/day/year), Ocala National Forest, Florida, USA. Samples were not taken if wetland(s) were dry or nearly dry.

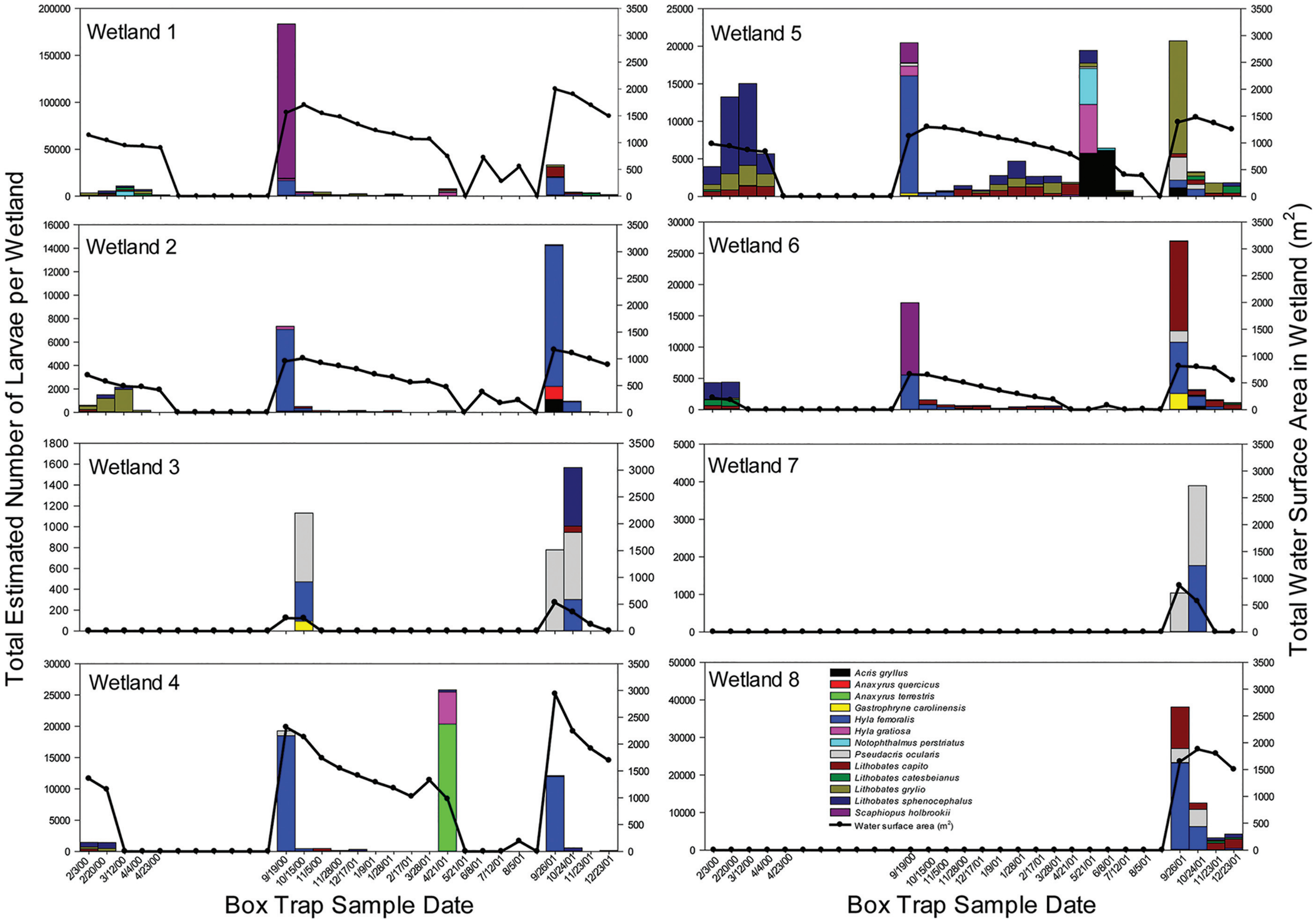


Table 3. Number of eight total study wetlands with water on each visit, and number of wetlands where each larval amphibian species was detected with box trap sampling at approximately 3-week intervals, from February 2000 to December 2001, in the Ocala National Forest, Florida, USA.

	Species[a]													
Date (mm/dd/yy)	H_2O	AGRY	AQUE	ATER	GCAR	HFEM	HGRA	NPER	POCU	LCAP	LCAT	LGRY	LSPH	SHOL
2/3/00	5	0	0	0	0	0	0	4	0	5	2	5	4	0
2/20/00	5	0	0	0	0	0	0	1	0	4	2	5	5	0
3/12/00	3	0	0	0	0	0	0	1	0	2	2	3	3	0
4/4/003	3	0	0	0	0	0	0	0	0	2	1	3	2	0
4/23/00	2	0	0	0	0	0	0	0	0	0	0	1	1	0
After 4/23/00, all wetlands dry; next visit with water on 9/19/00														
9/19/00	6	3	0	0	2	5	3	0	2	0	0	2	0	3
10/15/00	6	2	0	0	2	6	1	0	2	4	0	2	1	0
11/15/00	5	0	0	0	0	2	1	0	0	4	0	2	1	0
11/28/00	5	0	0	0	0	1	0	0	1	4	0	2	3	0
12/17/00	5	0	0	0	0	0	0	0	1	2	0	3	5	0
1/9/01	5	0	0	0	0	0	0	0	0	4	0	2	3	0
1/28/01	5	0	0	0	0	0	0	0	0	4	0	1	3	0
2/17/01	5	0	0	0	0	0	0	0	0	3	0	2	3	0
3/28/01	5	0	0	0	0	0	0	0	0	2	0	1	3	0
4/21/01	4	0	0	1	0	0	3	1	2	2	1	1	2	0
5/21/01	1	1	0	0	0	0	1	1	1	0	0	1	1	0
6/8/01	4	1	0	0	0	0	0	1	0	0	0	0	0	0
7/12/01	3	1	0	0	0	0	0	0	0	0	1	1	0	0
8/5/01	4	0	0	0	0	0	0	0	0	0	0	0	0	0
All wetlands dry; next visit with water on 9/26/01														
9/26/01	8	4	1	0	1	6	1	1	7	5	0	2	1	0
10/26/01	8	3	0	0	0	7	1	1	5	6	1	2	4	0
11/23/01	7	0	0	0	0	1	0	0	0	4	4	3	4	0
12/23/01	6	1	0	0	0	1	0	0	1	5	4	2	3	0

[a] Agry, *Acris gryllus* (Southern Cricket Frog); Aque, *Anaxyrus quercicus* (Oak Toad); Ater, *Anaxyrus terrestris* (Southern Toad); Gcar, *Gastrophryne carolinensis* (Narrowmouth Toad); Hfem, *Hyla femoralis* (Pinewoods Treefrog); Hgra, *Hyla gratiosa* (Barking Treefrog); Nper, *Notophthalmus perstriatus* (Striped Newt); Pocu, *Pseudacris ocularis* (Little Grass Frog); Lcap, *Lithobates capito* (Florida Gopher Frog); Lcat, *Lithobates catesbeianus* (American Bullfrog); Lgry, *Lithobates grylio* (Pig Frog); Lsph, *Lithobates sphenocephalus* (Southern Leopard Frog); Shol, *Scaphiopus holbrookii* (Spadefoot Toad).

Discussion

Our study demonstrates the importance of using both aquatic and terrestrial sampling methods concurrently to more accurately detect amphibian presence and gauge reproductive success. We found that the occurrence, or detectability, of amphibian larvae is highly variable among and within wetlands. Furthermore, the detection of adults or larvae with just aquatic or terrestrial sampling is not a reliable indicator of reproductive success. Use of integrated sampling protocols to accurately detect amphibian presence and population trends is especially important in light of potentially altered weather patterns, wetland hydrology, and amphibian reproductive phenology or outcome associated with climate change (Greenberg et al. 2014, 2015).

Hydroregime was an obvious and important influence on anuran reproductive outcome, but not the sole determining factor. Dry wetlands during both summers prohibited successful breeding and recruitment by exclusively summer-breeding *A. quercicus* (Dodd 1994; Greenberg and Tanner 2005*a*) and *G. carolinensis* (Dodd 1995), and reduced opportunity for other species. Additionally, wetlands dried just prior to potential completion of *L. capito* and *L. sphenocephalus* metamorphosis and juvenile emigration in late spring – summer (Greenberg 2001) of both years, likely resulting in total tadpole mortality and recruitment failure. Similarly, we detected *A. terrestris* tadpoles in one wetland that dried shortly thereafter, likely resulting in complete mortality.

Stochastic factors other than hydroperiod apparently also caused mortality of entire egg or tadpole cohorts. Even within prolonged hydroperiods detection of individual tadpole species within breeding cycles was spatially and temporally variable. Tadpoles of a given species rarely occurred simultaneously in all available wetlands; most occurred in a subset of available wetlands throughout the study period. Intermittent detection of tadpole species within continuously filled wetlands suggests high mortality, followed by deposition of eggs resulting in new tadpole cohorts. Other studies have shown high stochastic variation in amphibian reproductive success. Semlitsch et al. (1996) reported that high amphibian recruitment occurred in only 1–7 of 16 years, depending on the species, in South Carolina. Dodd (1994) reported no *A. quercicus* or *A. terrestris* recruitment from a pond in north-central Florida over a 5-year period. Greenberg and Tanner (2005*a*) reported *A. quercicus* recruitment from three of eight wetlands in only 2 of 10 years. Richter et al. (2003) reported high variability in the Dusky Gopher Frog (*Lithobates* (*Rana*) *sevosus* (Goin and Netting 1940)) reproductive success in Mississippi, with no consistent relationship between the number of females, eggs, or metamorphs.

Although our study did not elucidate mechanisms for reproductive failure, likely causes were predation or competition within wetlands. Due to frequent drying and isolation from larger water bodies, our study wetlands lacked fish and most predatory aquatic salamander species, including ambystomids. *Notophthalmus perstriatus*, the only potentially predatory salamander species detected, is relatively small, gape-limited, and apparently occurred at low densities, likely limiting its impact on tadpoles. On the other hand, wetlands hosted several predatory macroinvertebrate species including darner (Aeshnidae) and skimmer (Libellulidae) dragonfly nymphs, adult and larval predaceous diving beetles (Dytiscidae), giant water bugs (Belostomatidae), creeping water bugs (Naucoridae), and water scorpions (Nepidae) (S.A. Johnson, personal observation) that were likely a primary source of mortality.

We found no consistent relationship between apparent anuran breeding effort and tadpole abundance, or between tadpole abundance and recruitment for most species. Aside from stochastic factors, reasons may include the following: (*i*) tadpoles may be present but go undetected; this likelihood may be higher for species that exhibit schooling behavior; (*ii*) adult captures during breeding seasons are not necessarily indicative of breeding; others

Fig. 4. Mean proportion of tadpoles in developmental class 1, 2, or 3 sampled using box traps at approximately 3-week intervals (from 2/3/2000 to 12/23/2001; format is month/day/year) at eight isolated ephemeral wetlands, Ocala National Forest, Florida, USA. Samples were not taken if wetland(s) were dry or nearly dry. Mean proportions for each visit and species include only wetlands where larvae of respective species were sampled.

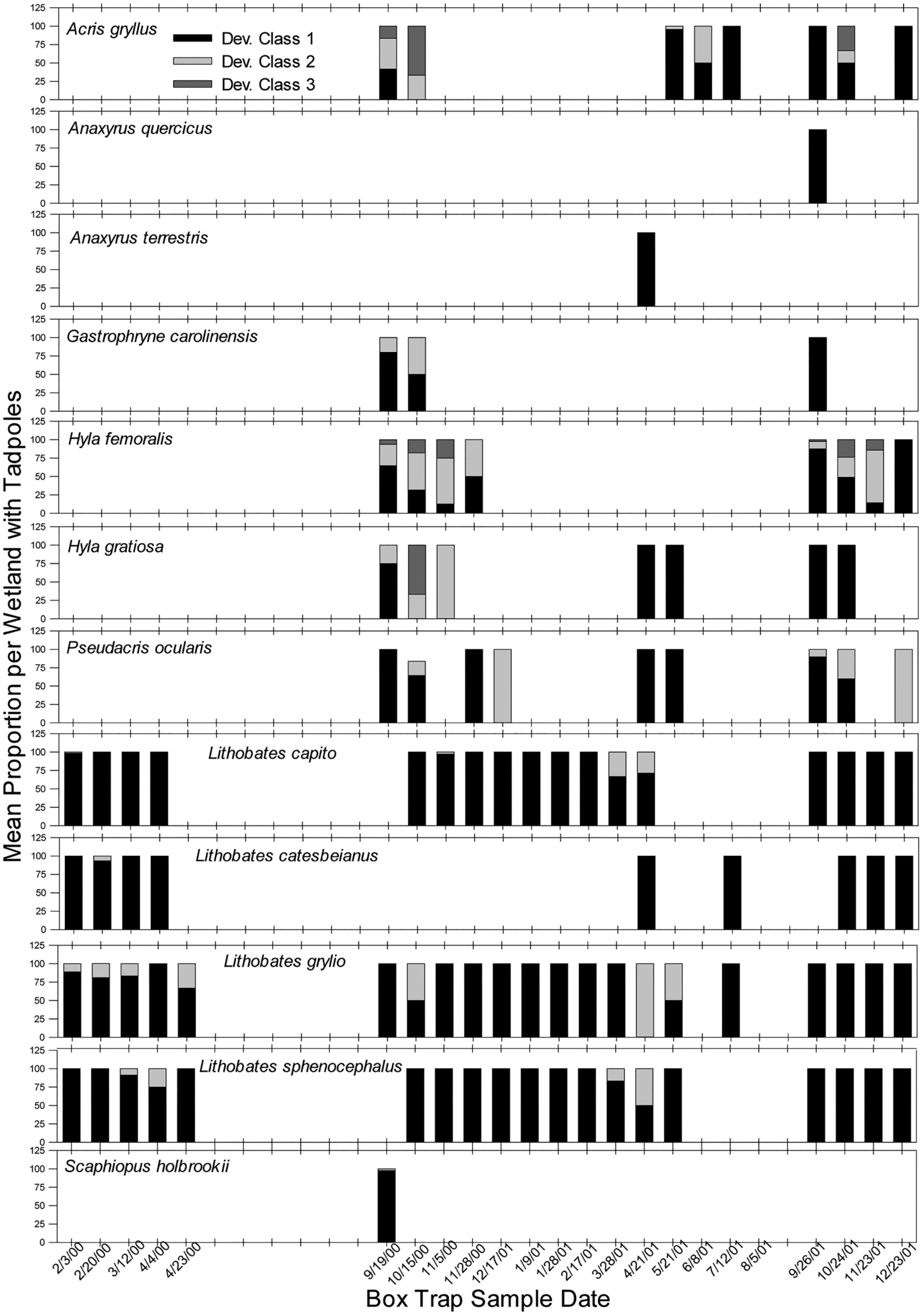
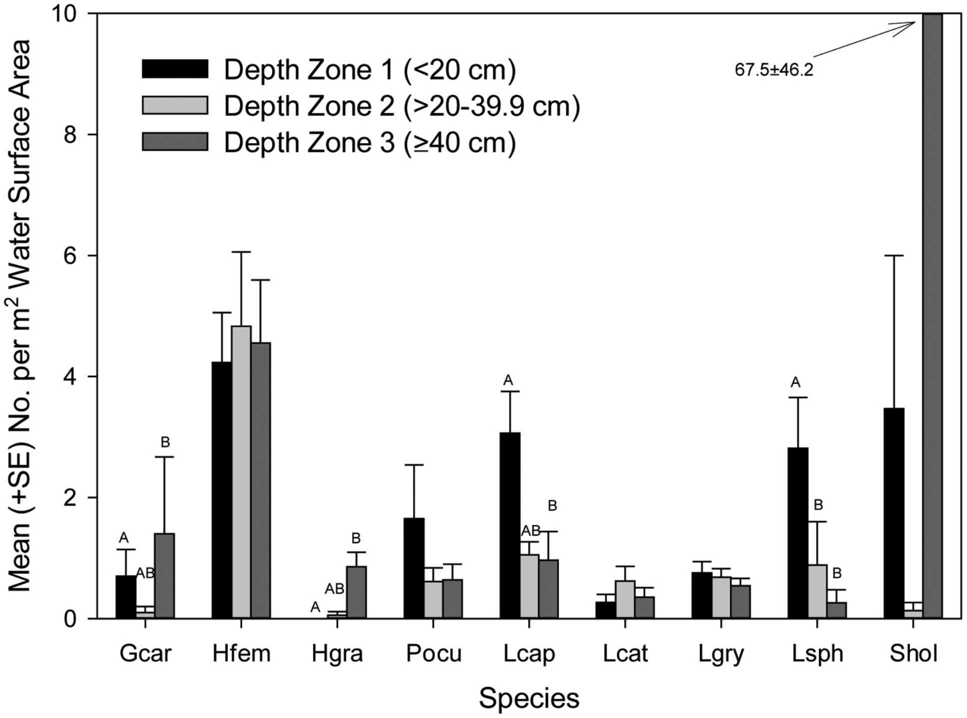


Fig. 5. Mean (+SE) density (number per m² water surface area) of amphibian larval species in each of three water depth zones (DZs) based on box trap samples taken at approximately 3-week intervals (from 2/3/2000 to 12/23/2001; format is month/day/year) in each of eight isolated ephemeral wetlands, Ocala National Forest, Florida, USA. Mean values are based on visits and wetlands when all three DZs were present and larvae of respective species were detected. Different letters among DZs denote significantly different densities within species. Gcar, *Gastrophryne carolinensis* (Narrowmouth Toad); Hfem, *Hyla femoralis* (Pinewoods Treefrog); Hgra, *Hyla gratiosa* (Barking Treefrog); Pocu, *Pseudacris ocularis* (Little Grass Frog); Lcap, *Lithobates capito* (Florida Gopher Frog); Lcat, *Lithobates catesbeianus* (American Bullfrog); Lgry, *Lithobates grylio* (Pig Frog); Lsph, *Lithobates sphenocephalus* (Southern Leopard Frog); Shol, *Scaphiopus holbrookii* (Spadefoot Toad).



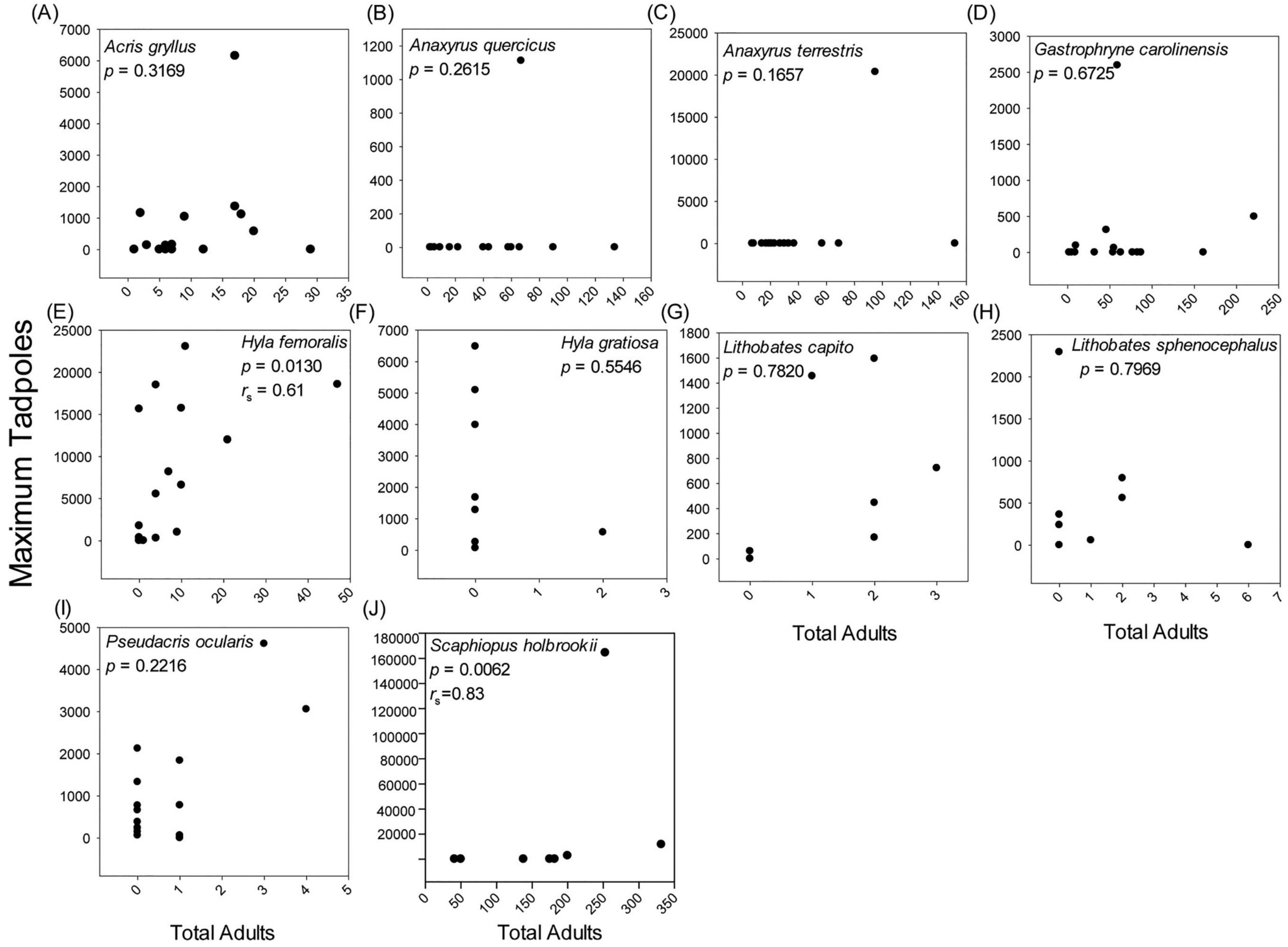
have noted that anuran calling does not always correspond with breeding and egg deposition (D. Saenz, personal communication); (*iii*) primarily aquatic species, such as *A. gryllus* and *L. grylio*, inhabit wetlands year-round; thus, drift fence captures may not be indicative of breeding; (*iv*) adult or juvenile capture rates may be unreliable indicators of breeding effort or recruitment, respectively, due to trap evasion or escape. For example, adult *A. gryllus*, *P. ocularis*, and *Hyla* spp. can potentially climb out of pitfall traps (Dodd 1991), and large *Lithobates* spp. adults can potentially jump out of pitfall traps or evade fences entirely (Pechmann et al. 1989; Semlitsch et al. 1996). Similarly, juvenile *A. gryllus*, *P. ocularis*, and *H. gratiosa* can potentially climb from pitfall traps (Pechmann et al. 1989); juvenile *Lithobates* spp. are generally unable to jump from pitfall traps (Pechmann et al. 1989; C.H. Greenberg, personal observation); (*v*) relatively few adults could potentially contribute to large numbers of tadpoles; consistently low adult capture rates of all four *Lithobates* spp. suggested this as an alternative explanation to trap escape or evasion; (*vi*) adults, such as *A. quercicus*, *G. carolinensis*, and *A. terrestris*, migrate to dry wetlands during breeding season, without potential for reproductive success.

Habit or reproductive strategy could partially account for the few positive relationships that we observed among breeding effort, tadpole abundance, and juvenile recruitment. Adult *H. femoralis* captures were generally greater at wetlands with water, thereby increasing the likelihood of tadpole occurrence in those wetlands. Similarly, the positive correlation between *H. femoralis* tadpole abundance and juvenile recruitment was likely influenced by increased capture probability of new recruits using PVC pipes as refugium for protracted periods. The explosive breeding habit of *S. holbrookii*, with dozens to hundreds of adults breeding simultaneously (Greenberg and Tanner 2004, 2005*b*), could decrease the likelihood of complete cohort mortality in all wetlands where breeding occurred. Even then, apparent mortality of entire egg or tadpole cohorts was common; *S. holbrookii* tadpoles were detected in only three of five wetlands where explosive breeding occurred in 2000 and in none of the four wetlands where explosive breeding occurred in 2001 (see Greenberg and Tanner 2004, 2005*b*).

Our results indicate that nondetection of a given tadpole species does not necessarily indicate that adults were absent, or did not breed, within a given year or wetland, and highlights the complementary information yielded by using both aquatic and terrestrial sampling methods. Werner et al. (2007*b*) found high interannual variability in tadpole species occurrence among multiple wetlands in Michigan, with only half of the expected species detected in any given year. Our findings suggest that their results could be partially attributed to 8- to 9-week intervals between their May and July visits, potentially resulting in missed detections of spatially and temporally intermittent tadpole occurrences. Our results highlight the importance of box trap sampling frequently and concurrently at multiple wetlands for monitoring species presence, since detectability and presence of larval amphibians frequently "blinks" on and off among sampling dates and wetlands.

Our study illustrates difficulties in comparing results of drift fence and aquatic sampling due to inherent biases of both methods. Drift fences detected more amphibian species than box trap sampling at regular intervals, likely in part because they were continuously open. Additionally, nonaquatic-breeding species such as the Greenhouse Frog (*Eleutherodactylus planirostris* (Cope, 1862)), Dwarf Salamander (*Eurycea quadridigitata* (Holbrook, 1842)), and Southeastern Slimy Salamander (*Plethodon grobmani* Allen and Neill, 1949) are likely to be detected only by drift fences. Furthermore, some species such as the Green Treefrog (*Hyla cinerea* (Schneider, 1799)) and Southern Chorus Frog (*Pseudacris nigrita*

Fig. 6. Results of Spearman's correlations between adult anuran first-captures, sampled with drift fences (assumed breeding effort), and maximum estimated number of tadpoles, sampled with box traps, per wetland and breeding cycle, at eight isolated ephemeral wetlands, Ocala National Forest, Florida, USA. Rho (r_S) is presented only if $p < 0.05$. Correlations could not be performed on American Bullfrog (*Lithobates catesbeianus*) and Pig Frog (*Lithobates grylio*) due to inadequate sample size.

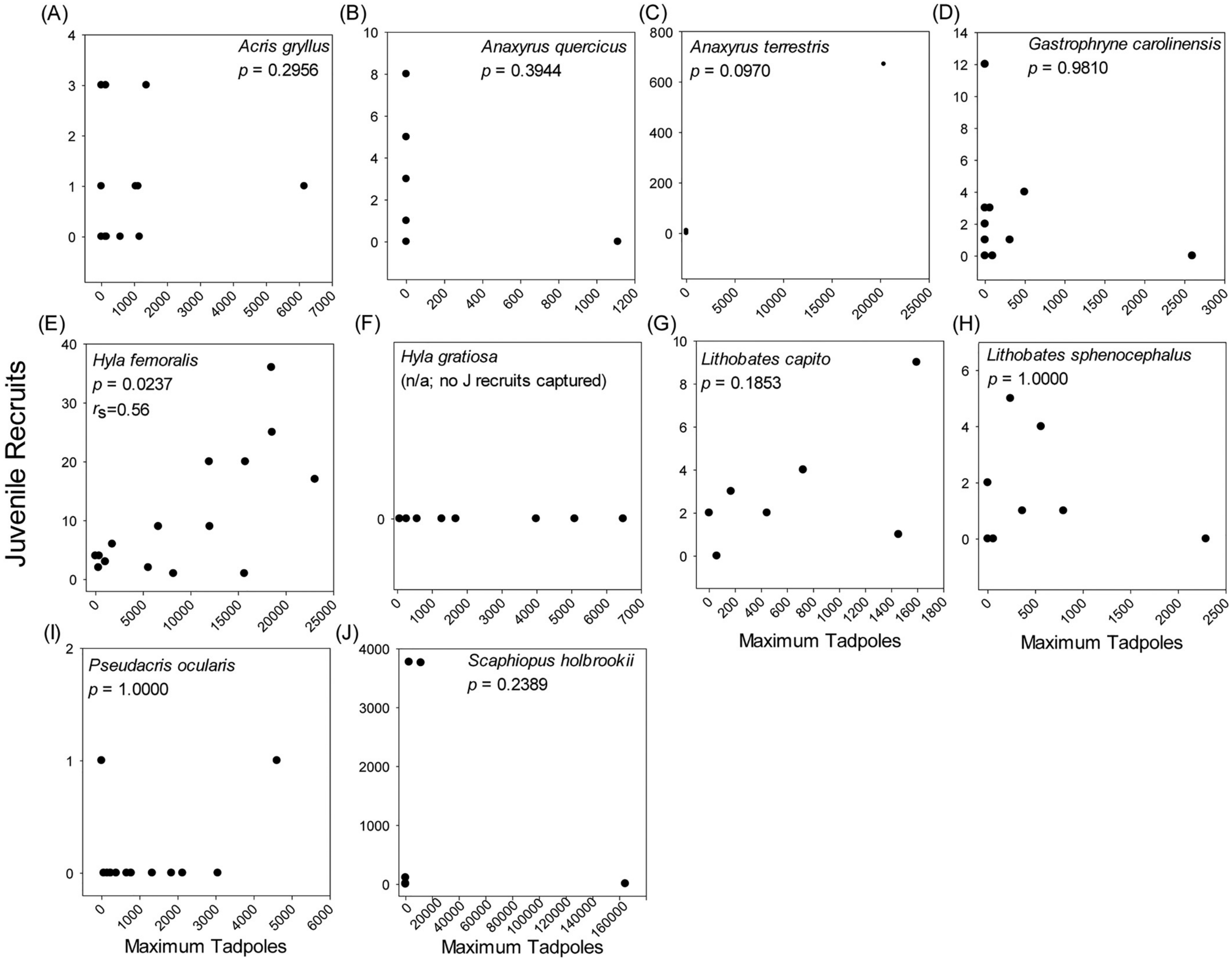


(LeConte, 1825)) may be present in surrounding uplands, but fail to breed every year and thus go undetected by box traps. Moreover, wetlands may be dry during the majority of the breeding season for some species, such as *A. quercicus*, *A. terrestris*, and *G. carolinensis* in our study, and thus undetected by aquatic sampling. Furthermore, species with rapid developmental rate, such as *S. holbrookii*, can be missed by box traps if sampling intervals are too infrequent to detect tadpoles before metamorphosis. Similarly, rapid, complete mortality of eggs or tadpoles could result in species being missed by box trap sampling at 3-week intervals.

Other studies also indicate that amphibian species detections in wetlands are maximized when multiple sampling methods are used at suitable frequencies in relation to interspecific differences in temporal calling patterns, breeding periods, and larval presence (Dodd 2009). Our results additionally illustrate the utility of drift fences in detecting species presence and, perhaps more importantly, apparent breeding effort, and recruitment, for many species. On the other hand, aquatic sampling can detect presence and relative abundance of amphibian larvae. We found that amphibian monitoring methods designed to detect only breeding activity (e.g., acoustic methods) or larvae (e.g., box traps, dip nets) are not reliable indicators of successful recruitment.

Tadpole occurrence in newly filled wetlands in September of both years provided a known approximate "start" date for egg and tadpole phenology. Presence of classes 1 and 2 (*G. carolinensis*, *P. ocularis*) or classes 1, 2, and 3 (*A. gryllus*, *H. femoralis*, *H. gratiosa*) shortly after wetlands refilled indicated rapid developmental rates. Tadpoles of all four *Lithobates* spp. were sampled sporadically, but were present intermittently in ≥1 wetlands during some late fall through early spring months; *L. grylio* and *L. catesbeianus* were also present in some summer months. The presence of classes 1 and 2 *L. grylio* in February–May and October suggested its potential to breed intermittently and metamorphose year-round. Although *L. catesbeianus* tadpoles can take ≥1 year to fully develop, we detected them in individual wetlands for short periods (maximum 9 weeks); most were class 1 regardless of month sampled, suggesting that intermittent breeding with introduction of new cohorts and high mortality occurred throughout much of the year. *Lithobates capito* and *L. sphenocephalus* tadpoles were detected intermittently in some wetlands, but continuously in others for about five (*L. sphenocephalus*) or six (*L. capito*) fall – late spring months; class 2 tadpoles were present only during spring months (except at one wetland, where class 2 *L. capito* tadpoles were detected in November). This suggests that both species can breed intermittently during fall – spring, and younger tadpole cohorts may accelerate development during spring, for a relatively synchronous late spring – summer metamorphosis and emigration by all cohorts (Palis 1998; Greenberg 2001). *Scaphiopus holbrookii* juvenile emigration peaked 16–18 days after an explosive breeding

Fig. 7. Results of Spearman's correlations between maximum estimated number of tadpoles, sampled with box traps, and number of first captured juvenile recruits exiting wetlands, sampled with drift fences, per wetland and breeding cycle, at eight isolated ephemeral wetlands, Ocala National Forest, Florida, USA. Rho (r_S) is presented only if $p < 0.05$. Correlations could not be performed on American Bullfrog (*Lithobates catesbeianus*) and Pig Frog (*Lithobates grylio*) due to inadequate sample size.



event (29 September – 4 October 2000), confirming that larval development was complete within 2.5–4 weeks.

Our results suggest that breeding periods vary somewhat among locations and years. We detected *A. gryllus* tadpoles in all seasons except winter, although they are winter breeders in central Florida (Babbitt and Tanner 2000). We detected *H. femoralis* in September–December and *H. gratiosa* in fall and spring; Babbitt and Tanner (2000) reported that both species breed only in summer in central Florida. *Pseudacris ocularis* bred during fall – early winter, and again in spring, whereas Babbitt and Tanner (2000) reported that they breed year-round in central Florida. In our study, *Lithobates* spp. showed temporal patterns consistent with fall–winter–spring (*L. capito* and *L. sphenocephalus*) or year-round (*L. grylio*, *L. sphenocephalus*) breeding and tadpole development. Palis (1998) reported that *L. capito* breeds intermittently from October to May in the Florida panhandle, whereas *L. sphenocephalus* breeds in winter, spring, and summer (Ashton and Ashton 1988) or year-round (Babbitt and Tanner 2000).

We found that *A. gryllus*, *L. capito*, and *L. sphenocephalus* selected shallow water (<40 cm) and *H. gratiosa* selected deeper water (≥40 cm) when choices were available. Other species exhibited no depth preference. We did not measure water temperature or dissolved oxygen, but suggest that DZ selection could reflect preference for either or both; generally, temperatures are higher and dissolved oxygen are lower in shallow water (e.g., Noland and Ultsch 1981). Additionally, differences in species' distribution among DZs could potentially reduce interspecific competition through resource partitioning (e.g., Whiting 2010). Several studies indicate that reduced competition (Wilbur 1982; Morin 1983) and higher water temperatures increase survival, growth, and developmental rate of tadpoles (e.g., Blaustein et al. 2010). In addition, most species were sampled in wetlands <20 cm depth, illustrating that ephemeral, shallow wetlands can nonetheless provide reproductive opportunity for many amphibian species.

Our results illustrate shortfalls in the ability of infrequent aquatic sampling to detect local species richness of larval amphibians, as the occurrence of many species is spatially and temporally variable. Additionally, we show the importance of using different sampling methods to detect species' presence and the difficulties associated with both methods in tracking breeding effort, tadpole occurrence, or reproductive outcome.

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