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Weather, hydroregime, and breeding effort influence juvenile recruitment of anurans: implications for climate change

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Abstract. Amphibians that primarily breed in ephemeral wetlands are especially vulnerable to climate change because they rely on rainfall or temperature to initiate breeding and create suitable hydroregimes (water duration, timing, frequency, depth) for reproductive success. Hydroregime effects on reproductive success are likely to differ among species because of differences in reproductive strategies: the length and timing of breeding period, rate of larval development, and timing of metamorphosis. We applied an information-theoretic approach to 22 consecutive years of continuous amphibian trapping data at eight ephemeral wetlands to test hypotheses regarding environmental (hydroregime, weather) and biological (adult breeding effort) factors affecting juvenile recruitment (JR) by six focal species representing four reproductive strategies. We hypothesized that (1) JR by species with similar reproductive strategies would be influenced by similar variables; (2) JR would be higher for all species when models encompassed the maximum time span of potential tadpole occurrence and development; and (3) JR rates within individual wetlands and breeding cycles would correlate most closely between species with similar breeding strategies. The best model for all focal species (except *Scaphiopus holbrookii*) encompassed the maximum time span and indicated that ≥1 hydroregime variable, total precipitation, or both were important drivers of reproductive success; average air temperature was not. Continuous hydroperiod through peak juvenile emigration was an important predictor of JR for species with prolonged breeding periods, slow larval development, and a "fixed" late spring start date for juvenile emigration (regardless of when oviposition occurred, or cohort age; *Lithobates capito*, *Lithobates sphenocephalus*), but not for species with rapid larval development and continual emigration as cohorts complete metamorphosis (*Anaxyrus terrestris, Anaxyrus quercicus, Gastrophryne carolinensis, S. holbrookii*). Total rainfall was positively associated with recruitment for most species; depth characteristics affected species differently. Annual JR was positively correlated among species with similar reproductive strategies. Our results indicate that weather and hydroregime characteristics interact with reproductive strategies that differ among amphibian species and influence reproductive plasticity, opportunity, and success. Effects of altered weather patterns associated with climate change on amphibian reproductive success may correspond more closely among species having similar reproductive strategies, with critical implications for population trends and assemblages.

Key words: amphibian recruitment; *Anaxyrus quercicus; Anaxyrus terrestris;* anuran reproduction; breeding strategy; climate and amphibians; ephemeral wetland; *Gastrophryne carolinensis;* hydroregime; *Lithobates capito; Lithobates sphenocephalus; Scaphiopus holbrookii.*

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INTRODUCTION

Climate change is already evident. Since the 1970s, global mean average temperature has risen by nearly 1°C, with the greatest seasonal increase during winter (Vose and Klepzig 2014). Temporal precipitation pattern changes, including severe drought, have affected much of the southeastern United States over the past three decades. For example, mean summer precipitation has decreased, whereas mean fall precipitation has increased by 30% since 1901; severity and patterns of storms are changing, with more heavy downpours in many parts of the southeast and more powerful Atlantic hurricanes (Karl et al. 2009). Climate models project a 2–10°C increase in temperature by 2100 (IPCC 2007) in the southeastern United States. Historically, climate change has been an important driver in range shifts, extinction, colonization, and evolution through adaptation of species (Greenberg et al. 2014). Amphibians have evolved diverse life history strategies allowing them to persist under stochastic and changing environmental conditions. Yet, it remains unknown whether climate change will outpace their adaptive potential (Walls et al. 2013*a*).

Amphibians that primarily breed in ephemeral wetlands are especially vulnerable to altered weather patterns resulting from climate change because of their reliance on precipitation-driven hydroregime characteristics such as the timing, depth, frequency, and duration of water in wetlands (Brooks 2009, Greenberg et al. 2014). Changes in weather patterns including temperature, and the amount, frequency, timing, and severity of precipitation will almost certainly alter wetland hydroregimes (Greenberg et al. 2015), with critical implications for population viability of wetland-breeding amphibians. Hydroregime effects on reproductive success (i.e., juvenile recruitment [JR]) are likely to differ among species because of differences in reproductive strategies: the length and timing of breeding period, rate of larval development, and timing of metamorphosis (Snodgrass et al. 2000, Babbitt et al. 2003). Dry wetlands are unavailable for breeding; likewise, wetlands that dry before larval development is complete will result in egg or tadpole mortality and reproductive failure (Walls et al. 2013*b*).

Many amphibian species depend on ephemeral wetlands completely or facultatively for reproduction because they are generally fish-free, and host lower densities of predatory aquatic macroinvertebrates (Moler and Franz 1987). Several studies report high stochastic variation in amphibian reproductive success related to hydroregime or unknown biotic factors such as larval competition and predation on eggs and larvae (Pechmann et al. 1989, Dodd 1994, Semlitsch et al. 1996, Richter et al. 2003, Greenberg and Tanner 2005*a*). Widespread reproductive failure for even one year can severely reduce populations of short-lived species and alter amphibian assemblages (Stewart 1995, McMenamin et al. 2008, Cole et al. 2016). Given their limited dispersal ability and reliance on weather patterns for reproductive success, ephemeral wetland-breeding amphibians represent an ideal system to examine vulnerabilities of species with different reproductive strategies to climate change.

In this paper, we used 22 yr (March 1994–December 2015) of continuous, concurrent amphibian trapping data at eight ephemeral wetlands to examine the influence of weather, hydroregime, and breeding effort (adult captures during defined breeding periods) on reproductive success of six anuran species representing four reproductive strategies (Table 1). Reproductive strategies and representative species were (1) prolonged, continuous, or intermittent breeding period, slow larval development (minimum 2.5 months), and a "fixed" late spring start date for juvenile emigration, regardless of when oviposition occurred (cohort age), represented by fall-through-spring breeding *Lithobates capito* and *Lithobates sphenocephalus*; (2) prolonged breeding period, rapid larval development (4–8 weeks), and juvenile emigration continual as cohorts complete metamorphosis, represented by late winter-through-fall breeding *Anaxyrus terrestris*; (3) season-limited breeding period, rapid larval development (4–8 weeks), and juvenile emigration continual as cohorts complete metamorphosis, represented by summer-breeding *Anaxyrus quercicus* and *Gastrophryne carolinensis*; and (4) aseasonal, explosive breeding, very rapid larval development (2–3 weeks), and most juvenile emigration immediately after completing metamorphosis, represented by *Scaphiopus holbrookii*.

Table 1. Life history attributes† of *Lithobates capito* (LCAP), *L. sphenocephalus* (LSPH), *Anaxyrus terrestris* (ATER), *A. quercicus* (AQUE), *Gastrophryne carolinensis* (GCAR), and *Scaphiopus holbrookii* (SHOL) related to reproductive strategy (breeding, rate of larval development, and timing of metamorphosis and juvenile emigration) and explanations of select variables and time spans used in statistical analyses.

Species	Reproductive Strategy‡	Breeding period	Eggs/ Female	Larval development (days)	Breeding adult variable§	Juvenile recruits (JR variable)#	Time spans analyzed (breeding through peak J emigration)‖
LCAP	PB-SLD-SE	Fall–Winter–Spring	1200–2200	85–225	May Wk1 Yr1-Apr Wk4 Yr2	Apr Wk1-Oct Wk4 (J if <50 mm SVL)	Sept Wk1 Yr1-**May Wk4** Yr2 (35 weeks) Jan Wk1-**May Wk4** (19 weeks) Mar Wk1-**May Wk4** (11 weeks)
LSPH	PB-SLD-SE	Fall–Winter–Spring	>1000	67–230	May Wk1 Yr1-Apr Wk4 Yr2	Apr Wk1-Dec Wk4 (Juv <52 mm SVL)	Sept Wk1-**Jun Wk1** (36 weeks) Jan Wk1-**Jun Wk1** (20 weeks) Mar Wk1-**Jun Wk1** (12 weeks)
ATER	PB-RLD-CE	Late winter–Fall	Several thousand	28–55	Feb Wk1 Yr1-Oct Wk4 Yr1	Mar Wk4-Dec Wk4 (J < 25 mm SVL)	Feb Wk1-**May Wk2** (13 weeks) Mar Wk4-**May Wk2** (6 weeks)
AQUE	SB-RLD-CE	Summer	420 max	33–44	May Wk1 Yr1-Oct Wk4 Yr1	Jun Wk1-Dec Wk4 (J < 20 mm SVL)	May Wk1-**Jul Wk4** (11 weeks) Jun Wk2-**Jul Wk4** (6 weeks)
GCAR	SB-RLD-CE	Summer	800	23–67	May Wk1 Yr1-Oct Wk4 Yr1	Jun Wk1-Dec Wk4 (J < 23 mm SVL)	May Wk1-**Aug Wk4** (15 weeks) Jun Wk2-**Aug Wk4** (10 weeks)
SHOL	EB-VRLD-IE	Explosive aseasonal	Av 2872	14–30	Wk of explosive breeding ±1 week (3 weeks in total)¶	4 weeks following breeding event (J < 18 mm SVL)	Breeding event **+2 weeks** Breeding event **+3 weeks**

† Ashton and Ashton (1988), Dodd (1995), Phillips (1995), Semlitsch et al. (1995), Palis (1998), Bridges and Dorcas (2000), Greenberg (2001), Wright (2002), Greenberg and Tanner (2004), McCallum et al. (2004), Greenberg and Tanner (2005*a*, *b*), Richter et al. (2009).

‡ PB-SLD-SE = prolonged breeding period, slow larval development, juvenile emigration not initiated until late spring, regardless of when oviposition occurred (cohort age); PB-RLD-CE = prolonged breeding period, rapid larval development, juvenile emigration continual as cohorts complete metamorphosis; SB-RLD-CE = season-limited breeding period; rapid larval development; juvenile emigration continual as cohorts complete metamorphosis; EB-VRLD-IE = explosive aseasonal breeding, very rapid larval development, most juvenile emigration immediately after completing metamorphosis.

§ All first-captures, summed across specified time periods; most breeding initiated later, ended earlier than dates here, but defined conservatively to include "stragglers."

¶ Explosive breeding defined as ≥30 adults captured at an individual wetland within a one-week period.

All exiting (emigrating) first-captured juveniles, summed across specified time intervals; most emigration initiated later, ended earlier than dates here, but defined conservatively to include "stragglers."

‖ Week of peak emigration (see Fig. 4) bolded.

We used the information-theoretic (IT) approach (Burnham and Anderson 2002) to model the reproductive success of each species in relation to (1) hydroregime variables only; (2) weather variables only; (3) hydroregime and weather variables together; (4) model sets 1–3 (above) repeated with the addition of the number of breeding adults as a factor influencing reproductive success. The environmental and hydrologic variables in these models represented conditions over specified time intervals, defined as the period(s) between potential onset, mid-, or late breeding season and peak juvenile emigration (PJE), to assess their relative importance during shorter or longer time spans prior to tadpole metamorphosis. We also examined whether JR rates were most closely correlated among species with similar breeding strategies. We hypothesized that (1) JR by species with similar reproductive strategies would be influenced by the same environmental (hydroregime and weather variables) and biological (adult breeding effort) variables; (2) JR would be higher for all species when models encompassed the maximum period (time span) of potential tadpole occurrence and development within wetlands; and (3) JR rates within individual wetlands and breeding cycles would correlate most closely between species with similar breeding strategies.

METHODS

Study area

Our eight study wetlands were a representative selection of small (0.1–0.37 ha), ephemeral, groundwater-driven sinkhole wetlands, embedded within xeric longleaf pine-wiregrass uplands of the Floridan Aquifer System region, Ocala National Forest, Marion and Putnam Counties, Florida (Fig. 1; Greenberg et al. 2015). Average weekly temperatures (February 1997–December 2015) ranged from 13.9°C in December to 28.6°C in August (Fig. 2a). Average annual precipitation (March 1994–2015) at our study areas was 132 cm, with more than half occurring during late spring and summer (Fig. 2a). Heavy precipitation providing groundwater recharge was associated with thunderstorms and tropical systems in summer and fall, and wet autumn, winter, or spring frontal systems (Fig. 2a; Winsberg 1990). Wetland depths were generally highest in winter and lowest in summer due to rainfall patterns and groundwater recharge, as well as low evapotranspiration in winter (Figs. 2b and 3; Knowles et al. 2002).

Amphibian sampling

We installed drift fences 7.6 m long and spaced 7.6 m apart around the perimeter of each wetland near the high water line, such that 50% of each wetland was fenced, with fences and spaces equally distributed and encircling wetlands. Pitfall traps (19-L buckets) were positioned inside and outside of each end of each fence (four per fence), and a double- or single-ended funnel trap (one of each per fence) was positioned at the midpoint of each fence on both sides, to detect directional movement by amphibians to and from wetlands. We placed a sponge in each pitfall trap, and moistened as needed during trap checks to reduce the likelihood of desiccation. All traps were checked approximately three times weekly from late March 1994 through December 2015. We identified, sexed, and measured snout-vent length (SVL) and weight of captured frogs, and assigned age (adult or recent metamorph/first-year juvenile) based on a specified SVL cutoff for each species (Table 1). All individuals were marked by wetland number and year of capture by toe clipping. Exceptions were newly metamorphosed *A. quercicus* and *S. holbrookii* that were not marked, as they were too small to toe-clip. Because all wetlands were sampled continuously and in proportion to basin size, we did not further adjust for trapnights. However, we discarded data from one or more wetlands during some years when most traps were flooded for prolonged periods during defined adult breeding or juvenile emigration periods, which differed among species (Table 1).

Weather and water depth measurements

We measured local precipitation using a rain gauge placed in the open near Wetland 1, daily from 28 March 1994 through mid-2006, and approximately three times weekly thereafter. Maximum and minimum air temperatures were measured using a max-min thermometer (in the shade, also near Wetland 1) daily beginning 22 February 1997 through mid-2006 and approximately three times weekly through 2015. We also measured water depth approximately weekly at polyvinyl chloride pipe (PVC) staff gauges that were permanently established at the approximate lowest point within each of the eight wetland basins. Our statistical models required complete environmental data for the explanatory variables, which for some time periods or wetlands were missing. To avoid discarding entire breeding cycles for analyses and hypothesis testing, we estimated missing depth data (22 total weeks for seven wetlands; 42 total weeks for one wetland) using an existing model (developed using data from our study wetlands) that predicts wetland depth based on known depth and rainfall the prior week (Greenberg et al. 2015). Missing rainfall data (54 total weeks) were estimated by reversing the model to predict rainfall the prior week based on change in wetland depth from the prior week (Greenberg et al. 2015). We discarded entire breeding cycles (which differed among species)

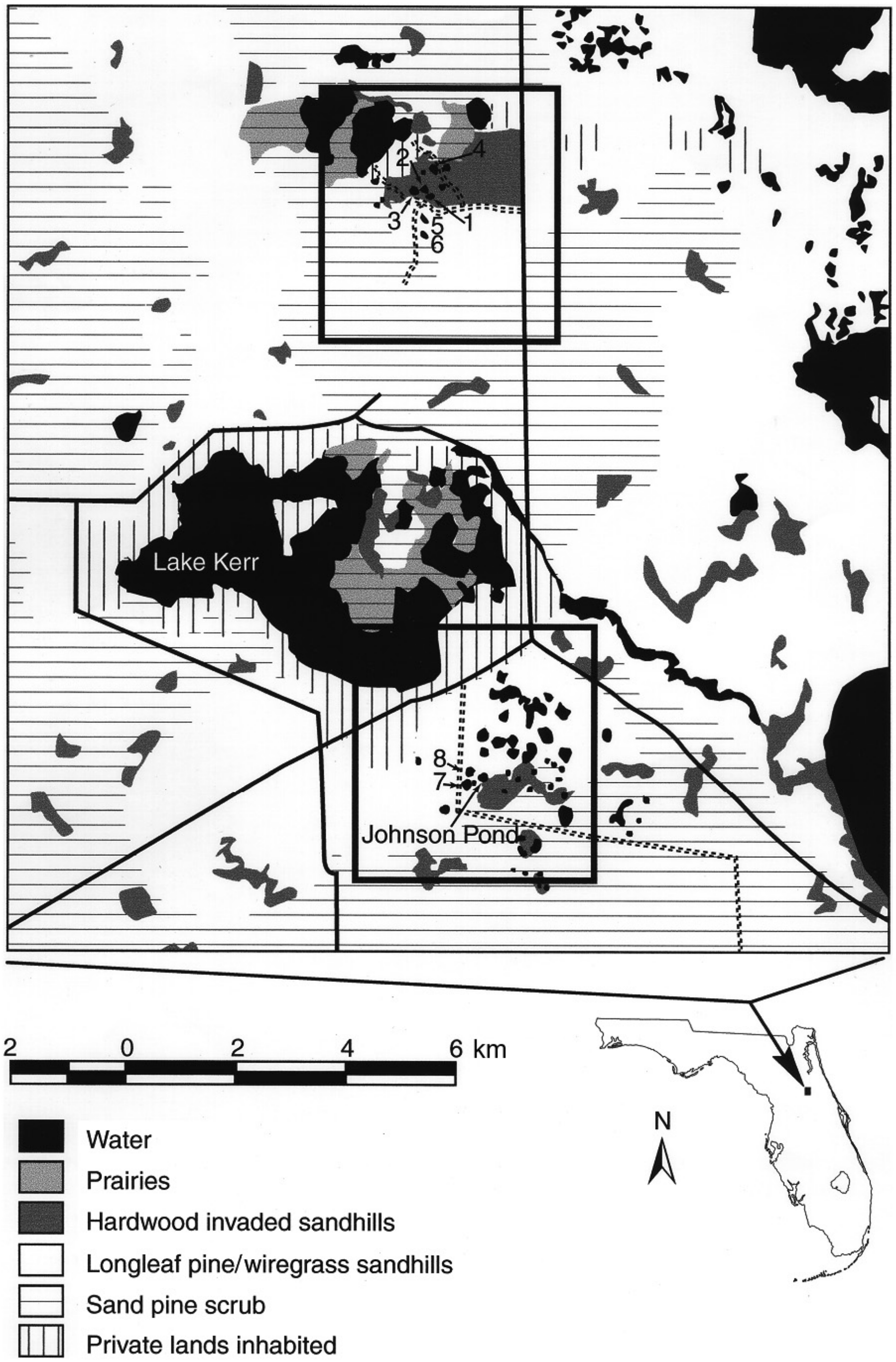

Fig. 1. Locations of study wetlands in the Ocala National Forest, Putnam and Marion Counties, Florida (courtesy of Dale Johnson). Double-dashed and heavy lines represent sand and paved roads, respectively.

from statistical analyses requiring temperature data, if temperature data were missing. We coupled weekly weather data and wetland depth measurements with corresponding anuran capture totals at four, approximately weekly intervals (7.6 ± 0.06 d per "week") per month, using dates when all environmental variables were sampled simultaneously.

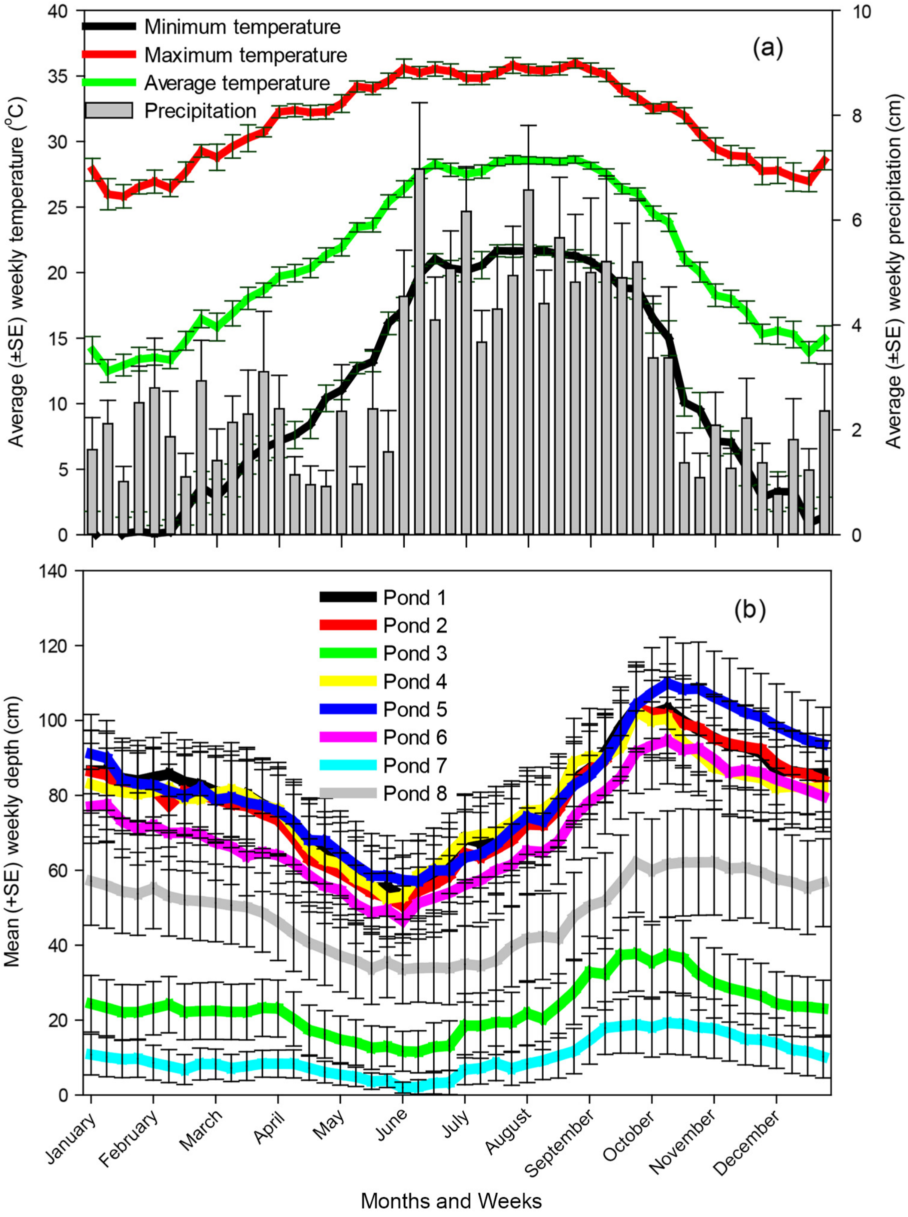

Fig. 2. Mean (±SE) (a) weekly temperature (minimum, maximum, average; February 1997–December 2015) and precipitation (March 1994–December 2015) and (b) approximate maximum depth (March 1994–December 2015) of eight study wetlands, Ocala National Forest, Florida.

Determining reproductive cycles

We used long-term drift fence capture data of adults and emigrating juveniles (Figs. 4 and 5), tadpole sampling data from study wetlands (2000–2001; Greenberg et al., *in press*), and published literature to determine approximate breeding periods, rates of larval development to metamorphosis, and juvenile emigration periods for each species (Table 1, Fig. 4), recognizing that each can vary somewhat among years and wetlands (Fig. 5). We defined a single breeding cycle as the period between the potential onset of breeding through the completion of juvenile emigration from wetlands resulting from that

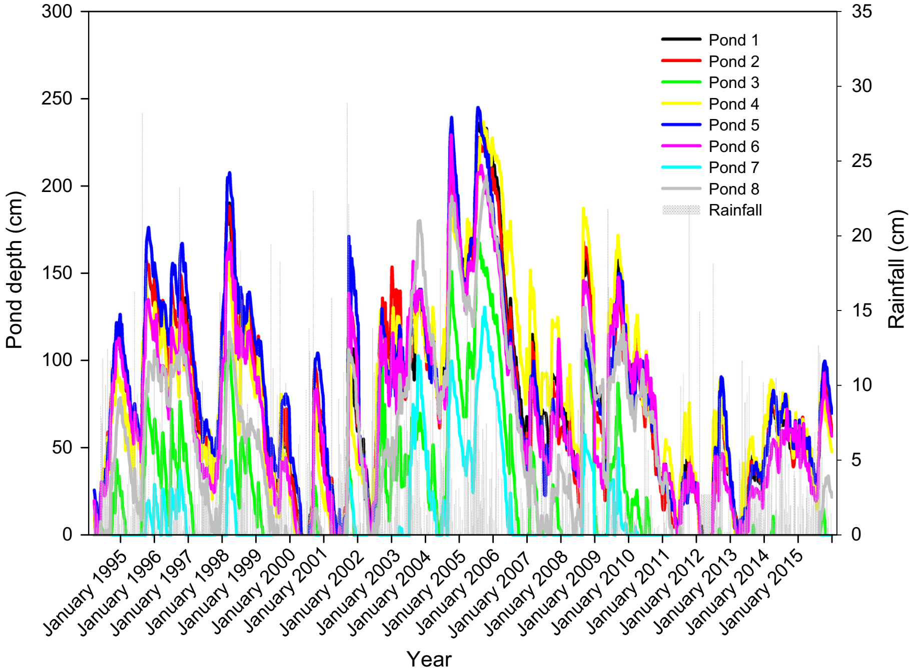

Fig. 3. Weekly (March 1994–2015) total precipitation and depths of eight study wetlands, Ocala National Forest, Florida.

breeding effort (Table 1, Fig. 4), and used that definition for all years. We defined breeding adults as all first-captures entering or exiting wetlands within their defined breeding period (Table 1, Fig. 4), recognizing that adult migration to wetlands (Greenberg et al., *in press*), or even calling activity (D. Saenz, *personal communication*), is not always indicative of breeding. We conservatively defined juvenile recruits as total first-captures exiting (only) wetlands within their defined emigration period (Table 1, Fig. 4). Breeding and juvenile emigration periods partially overlapped within a breeding cycle, for all species except *S. holbrookii* (Table 1, Fig. 4).

For some species, the breeding cycle was complete within a given calendar year. In our study area, *A. terrestris* bred February through the end of October, and juveniles emerged beginning the last week of March through the end of December; both *A. quercucis* and *G. carolinensis* bred May through October, and juveniles emerged June through December (Table 1, Fig. 4). For *L. capito* and *L. sphenocephalus*, breeding extended from one calendar year into the next (Table 1, Fig. 4). Breeding season for both species was difficult to determine with confidence because adult capture rates were low, and breeding can occur continuously or intermittently during fall through spring (Palis 1998) or even summer (Godley 1992); however, juveniles of both species emigrate in late spring through early fall within our study area (Greenberg 2001; Table 1, Fig. 4). Thus, we defined breeding adults as all first-captures May (calendar year 1) through the following April (calendar year 2) as potentially contributing to JR for that breeding cycle, and we defined juvenile recruits within that breeding cycle as all first-captured emigrating juveniles April through October for *L. capito*, or April through December for *L. sphenocephalus*, calendar year 2 (Table 1, Fig. 4). *Scaphiopus holbrookii* are explosive breeders that can breed nearly any time of year after heavy rainfall, and sometimes go several years without breeding; larval development is rapid, and up to thousands of juveniles metamorphose and emigrate from wetlands two to three weeks later (Greenberg and Tanner 2004). Because they do not have a distinctive breeding season, we included only wetlands and years when breeding events occurred in our analyses. We defined a

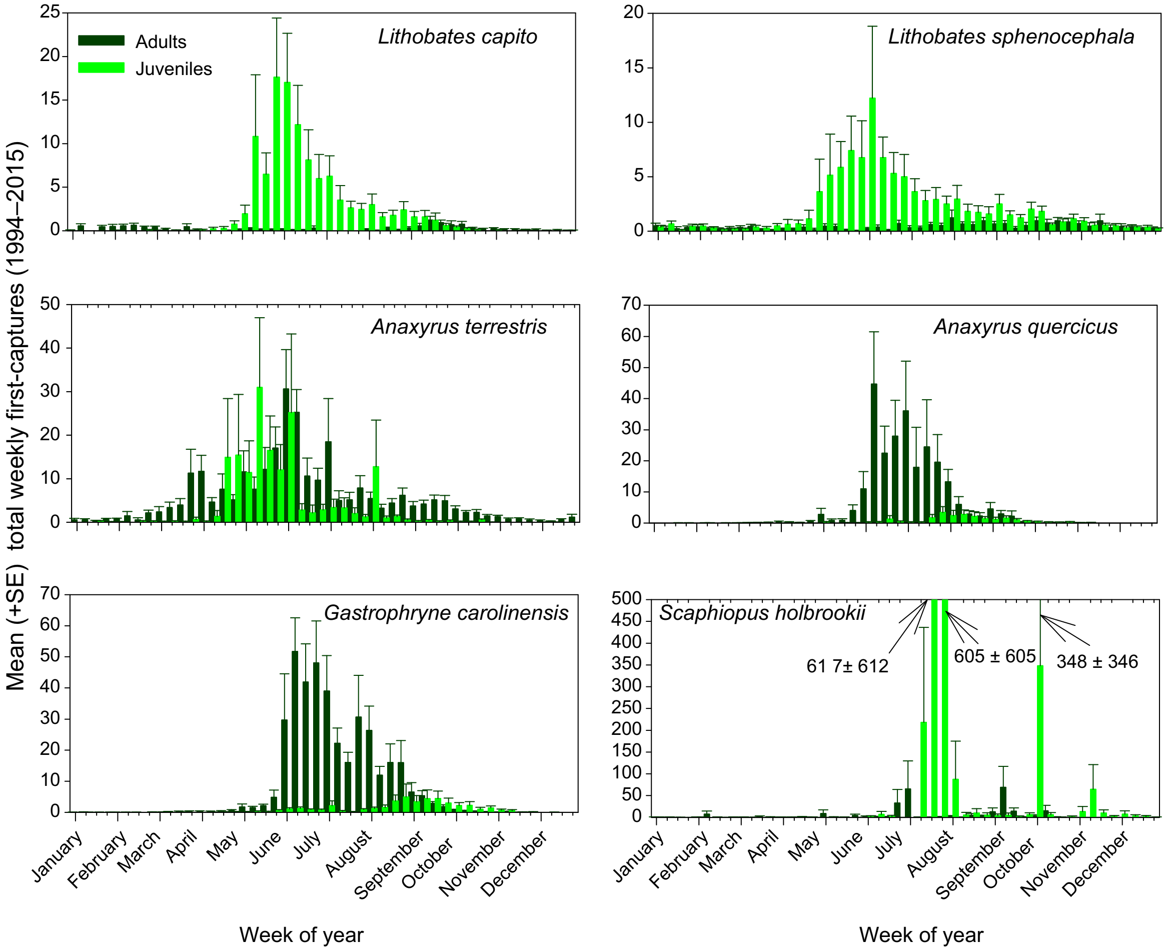

Fig. 4. Mean (+SE) (1994–2015) number of adult and juvenile first-captures (all wetlands combined) per week of year (approximately four weeks per month; 48 weeks per year) of six anuran species at isolated ephemeral wetlands in the Ocala National Forest, Florida.

breeding event as ≥30 adults captured at a particular wetland within a single week, but included adult first-captures during the week prior and after that event as "breeding adults." We defined *S. holbrookii* juvenile recruits to include all emigrating juveniles within four weeks after a breeding event to include peak emigration and potential "stragglers" exiting wetlands (Table 1, Fig. 4).

Defining time spans of larval vulnerability to weather and hydroregime

We focused our analyses on periods when eggs and tadpoles were potentially present and developing to metamorphosis, assuming that larval vulnerability to weather or hydroregime variables would occur within the aquatic stage (eggs through metamorphosis and juvenile emigration). We defined two time periods ("time spans") for focal species with rapid larval development (*A. terrestris*, *A. quercicus*, *G. carolinensis*, *S. holbrookii*), or three for those with protracted larval development (*L. capito* and *L. sphenocephalus*). We determined the average PJE week for each species (Fig. 4) and then defined the potential periods for larval development as beginning at the onset, mid-, or late breeding period (or presumed oviposition), extending through PJE (Table 1, Fig. 4). Because *S. holbrookii* can breed explosively during any month

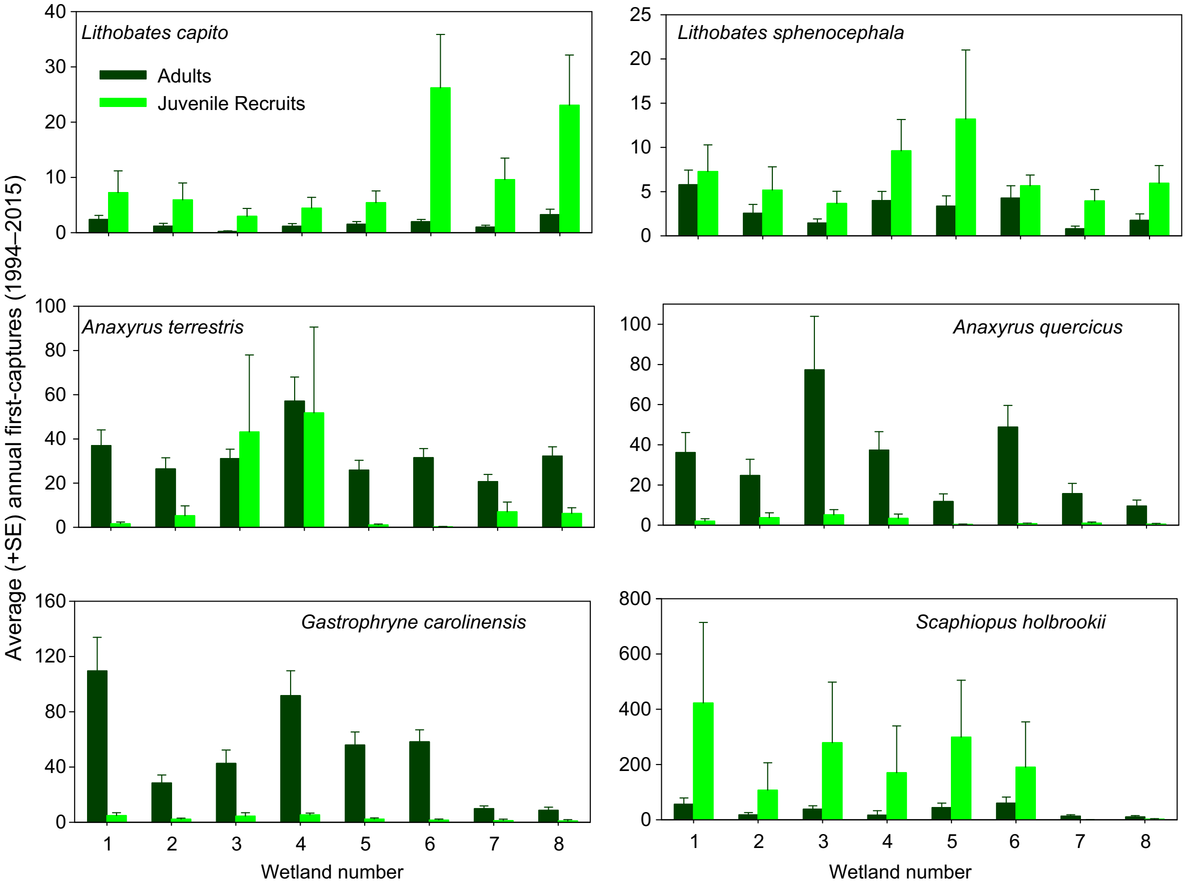

Fig. 5. Mean (+SE) annual (1994–2015) number of first-captured adults and juvenile recruits per wetland of six anuran species, Ocala National Forest, Florida.

of the year, with metamorphs emerging a few weeks later, we defined the time spans for this species as (1) two weeks or (2) three weeks after a breeding event, to encompass the period when tadpoles would be developing to metamorphosis. The dates and time spans encompassed differed among our focal species because of differences in the timing and lengths of breeding periods, larval developmental rates, and juvenile emigration periods (Table 1, Fig. 4).

Statistical analyses

Selection of weather and hydroregime variables.— For each species, we performed initial exploratory analyses using simple and stepwise regressions to determine the most important weather and hydroregime variables influencing JR, and to narrow down pertinent variables for developing hypotheses and models. For the purpose of this paper, we considered each breeding cycle within a wetland to be an independent sample point. Initial hydroregime variables explored for all species, within each defined time span, were maximum hydroperiod (duration of continuous water, even if interrupted before PJE); the number of weeks with continuous water (>0 cm), including and preceding PJE week; total number of hydroperiods (>1 if water was intermittent); total weeks dry (even if intermittent); maximum number of weeks continuously dry (we re-tested these variables using alternative definitions of "dry" [e.g., <5 cm and <10 cm depth] to examine whether very shallow water might be functionally dry, regarding influence on tadpoles); water depth (average, minimum, maximum); and depth fluctuations (maximum increase, decrease, or maximum change). The observed precipitation variable was weekly total; these were used to create four predictor variables, defined as minimum, maximum, average, and total precipitation over the course of a given time span. The observed temperature variables were weekly minimum, maximum, and average (more representative of the entire week than maximum or minimum extremes); these were used to create three predictor variables defined as minimum, maximum, and average temperature over the course of a given time span.

Initial, preliminary analyses consisted of univariate graphical plots, correlations, simple linear regressions, and stepwise multiple regressions (PROC GLMSELECT SAS 2011) of square-root-transformed juvenile recruits on the environmental and weather variables within species-specific time spans. Our goal was to narrow down the most important weather and hydroregime variables to use in model development, minimize the use of strongly correlated variables, and assess whether some variables were shared or differed among species.

Preliminary analyses were followed by using a generalized linear mixed model to explain JR as a function of environmental and climatic variables. The response variable (JR) for all six species exhibited a negative binomial distribution; variance greatly exceeded the mean, plots of the distribution showed more observations at low and high values than expected based on randomness, and analyses revealed that the dispersion parameter was not zero. To further ensure that the distribution was negative binomial, we also fitted zero-inflated Poisson and zero-inflated negative binomial distributions; comparison of their corrected Akaike information criterion (AICc) values to the negative binomial did not justify using them in further modeling. The final model assumed the response variable (JR) was negative binomial distributed and data were analyzed with wetlands as a fixed factor with no repeated-measures factor for years using PROC GLIMMIX (SAS 2011).

We used preliminary stepwise regression to liberally select independent variables for inclusion and deletion in the models based on the 0.25 significance level. In addition, we considered known biological relationships to help develop meaningful models for further consideration. Second-order interactions between the main independent variables were entertained in model fits, and used if they were significant and meaningful. Resulting models were examined by plotting observed over predicted values, and inspecting plots of the residuals over the independent variables.

Hypothesis testing and model development.—We used the IT approach (Burnham and Anderson 2002) to test hypotheses designed to examine relative importance of individual wetlands, hydroregime, weather, time span prior to PJE, and the number of breeding adults on JR by our six focal species with different breeding strategies. Including individual wetland in our models likely reduced effects of some hydroregime variables, but also reduced variability associated with wetland-specific characteristics or potential philopatry. We elected to use the number of breeding adults, rather than females only because the number of females was often zero, or very low, when split out by wetland and breeding cycle, which was the basis for our models. Preliminary analyses indicated that the female sex ratio was <0.5 for most species (range 0.34 for *A. terrestris*, to 0.46 for *L. sphenocephalus*) when pooled over all wetlands and breeding cycles, but deviated above and below 0.5 across the breeding cycles. The somewhat lower level of captures of female adults may be due to an unknown differential capture bias between females and males. Moreover, 24% of the 6676 adults captured over the course of the study could not be sexed accurately and were classified as "unknown"; these could represent a disproportionate number of females. Thus, we determined that total first-captured adults, both male and female, was a more stable metric of the adult female breeding population than females only.

For each species, numerous models were developed based on a priori hypotheses and then evaluated to determine which ones were most plausible. For a given species, we included the base model which consisted of the effect of the individual wetland alone on JR. We then evaluated initial sets of three models for each species for their power to predict JR. Each model set included individual wetland and (1) two to three selected hydroregime variables only, (2) one to three selected weather variables only, or (3) the selected hydroregime and weather variables and none or one interaction between hydroregime and weather variables. Each model set was repeated to encompass two (onset and mid-breeding period through PJE for *A. terrestris, A. quercicus, G. carolinensis*) or three time spans (onset, mid-, and late breeding period through PJE for *L. capito* and *L. sphenocephalus*); *Scaphiopus holbrookii* was the exception, with time spans encompassing the period between explosive breeding events and the subsequent two or three weeks, as described above. Finally, all model sets and time spans were repeated, to include the number of breeding adults as a potential influence on JR. Thus, we tested a total of 13 models for *A. terrestris, A. quercicus, G. carolinensis*, and *S. holbrookii*, and 19 models for *L. capito, L. sphenocephalus*.

Model sets for all species (except *S. holbrookii*) and defined time spans contained the same two basic hydroregime variables—(1) the number of weeks with continuous water (>0 cm), including and preceding PJE week, and (2) average water depth—and the same two basic weather variables: (1) total precipitation and (2) average temperature (maximum + minimum temperature/2), selected a priori based on preliminary exploratory analysis and biological considerations. For some species, model sets included one additional hydroregime, weather, or hydroregime–weather interaction variable, if preliminary analyses suggested its particular importance for that species. We did not include weeks with continuous water in *S. holbrookii* model sets due to virtual absence of variability (all wetlands continuously held water for two or three weeks after $n = 34$ explosive breeding events used in analyses, with two exceptions). Similarly, we did not use average temperature in *S. holbrookii* models because missing temperature data would have (1) reduced the sample size too much and (2) produced various models with different sample sizes which cannot be validly compared with the AICc criterion. We assumed that *S. holbrookii* tadpoles are less likely to be temperature sensitive at our Florida study sites than some other species, given their potential for explosive breeding events at any time of year. For each set of models, the AICcs and Akaike weights were computed and parameter estimates, standard errors, and 95% confidence intervals obtained using PROC GLIMMIX (SAS 2011).

Is recruitment success correlated between species with similar breeding strategies?.—We used Kendall's tau rank correlations to test the hypothesis that JR would be most similar among species with similar breeding strategies, using each wetland-breeding cycle as one data point. Kendall's was selected over Pearson's tests because the response variable, JR, exhibited a negative binomial distribution. *Scaphiopus holbrookii* was not included because it breeds infrequently (e.g., missing values for many years) and has no defined breeding or JR period for comparison with other species. We also used Kendall's tau rank correlations to examine the relationship between breeding effort and JR within species, using each wetland-breeding cycle as one data point.

RESULTS

Our results indicated that one or more precipitation-driven hydroregime variable was a strong influence on JR for all tested species except *A. terrestris*, but variables differed among species. In contrast, temperature played a relatively minor role, within the range of variation tested. Continuous hydroperiod through PJE was an important predictor of recruitment for species with prolonged breeding periods, slow larval development, and a "fixed" late spring start date for juvenile emigration—regardless of when oviposition occurred, or cohort age (*L. capito and L. sphenocephalus*)—but not for species with rapid larval development and continual emigration as cohorts complete metamorphosis (*A. terrestris, A. quercicus, G. carolinensis, S. holbrookii*). The best-fitting models for all species included the maximum time span tested, from onset of breeding season through PJE. Total rainfall was positively associated with recruitment for most species, and depth characteristics (maximum, average, or maximum change) affected species differently. Total breeding adults was a significant, important predictor of JR for *A. terrestris, G. carolinensis*, and *S. holbrookii* and improved model strength for *A. quercicus*, but was not significant or important for *Lithobates* spp. Annual JR was correlated among species with similar reproductive strategies.

Our best-fitting model for predicting JR by *L. capito* (model 10; $w = 0.467$) was a function of individual wetland, hydroregime, and weather variables, and interactions between them during the maximum time span tested (onset of breeding period through PJE; September week 1 through May week 4; Table 2). Among hydroregime variables, continuous water (>0 cm) and maximum depth change were significantly positively correlated with JR, while average depth was not. Among weather variables, only total precipitation was significant and positively correlated with JR. Average temperature alone was not a significant predictor, but its interaction with continuous water was significantly negatively associated with JR. Weather variables alone during the same time span (model 9; *w* = 0.030) had a greater influence than hydroregime variables alone (model 8; *w* = 0.000). Addition of total breeding adults was not significant, but slightly weakened model strength (see model 19; *w* = 0.429 vs. model 10; Table 2).

Our best-supported model for predicting JR by *L. sphenocephalus* (model 10; *w* = 0.362) was also a function of individual wetland, hydroregime, and weather variables, and an interaction between them during the maximum time span tested (onset of breeding period through PJE; September week 1 through June week 1; Table 3). Among significant hydroregime variables, average wetland depth was negatively associated, and continuous water (>0 cm) was positively associated with JR. No weather variables alone were significant, but an interaction between total rainfall and maximum depth change was positively associated with JR. Weather variables alone, including total rainfall (positively associated) and average temperature (nonsignificant) during the same time span (model 9; *w* = 0.011), had a greater influence on JR than hydroregime variables alone, including maximum depth change and continuous water (both positively associated) (model 8; *w* = 0.000). Addition of total breeding adults reduced model strength considerably (see model 19; *w* = 0.104 vs. model

Table 2. Information-theoretic model (M) results† for *Lithobates capito* juvenile recruitment (1995–2015; *n* = 118) from eight isolated, ephemeral wetlands, Ocala National Forest, Florida.

M	Time span to May Wk4	W	MCD	Cont0	DAv	PptTot	TAv	Cont0xTAv	A	AICc	Akaike Wt
1		x								660.0	0.00000
2	Mar Wk1	x*	–	+	+*					639.8	0.00000
3	Mar Wk1	x				+*	–*			644.1	0.00000
4	Mar Wk1	x*	+	+*	+*	+*	+	–*		624.6	0.00019
5	Jan Wk1	x*	+	+*	+					642.9	0.00000
6	Jan Wk1	x*				+*	–			614.2	0.03422
7	Jan Wk1	x*	+	+	–	+*	+	–		619.2	0.00273
8	Sept Wk1	x*	+*	+*	–					643.8	0.00000
9	Sept Wk1	x*				+*	–*			614.4	0.03004
10	**Sept Wk1**	x*	+*	+*	–	+*	–	–*		**608.9**	**0.46674**
11	Mar Wk1	x*	–	+	+*				+	640.4	0.00000
12	Mar Wk1	x				+*	–*		+	645.3	0.00000
13	Mar Wk1	x	+	+*	+*	+*	+	–*	+	625.9	0.00010
14	Jan Wk1	x*	+	+*	+				+	643.7	0.00000
15	Jan Wk1	x				+*	–		+	615.1	0.02170
16	Jan Wk1	x	+	+*	–	+*	+	–	+	619.3	0.00263
17	Sept Wk1	x*	+*	+*	–				+	644.0	0.00000
18	Sept Wk1	x				+*	–*		+	616.2	0.01260
19	**Sept Wk1**	x*	+	+*	–	+*	–	–*	+	**609.1**	**0.42906**

Notes: Models were run for each of three time spans "pegged" on peak week of juvenile emigration (May week 4), to the preceding onset, mid-, and late breeding period (breeding cycle) and include hydroregime variables (MCD, Cont0, DAv)‡ only; weather variables (PptTot, TAv)§ only; both hydroregime and weather variables with an interaction effect (Cont0xTAv); all models repeated with adult breeding effort (A) included. Wetland (W) was considered a fixed effect and included in all models.

† Models with the smallest AICc and highest Akaike weights have more support. The + or – indicates positive or negative relationship with juvenile recruitment. Significant (where confidence intervals did not include zero) variables are denoted by the * symbol, and models with the smallest AICc and highest Akaike weights are bolded.

‡ Maximum change in depth (MCD); weeks with continuous water (>0 cm) (Cont0); average depth (DAv); within specified time span.

§ Total precipitation (PptTot); mean average temperature (TAv); interaction Cont0xTAv; within specified time span.

Table 3. Information-theoretic model (M) results† for *Lithobates sphenocephalus* juvenile recruitment (1995–2015; n = 118) from eight isolated, ephemeral wetlands, Ocala National Forest, Florida.

M	Time span to Jun Wk1	W	MCD	DAv	Cont0	PptTot	TAv	MCDxPptTot	A	AICc	Akaike Wt
1		x								618.1	0.00000
2	Mar Wk1	x*	+	$+^{*}$	–					598.6	0.00005
3	Mar Wk1	x				+	–			617.6	0.00000
4	Mar Wk1	x	$+^{*}$	$+^{*}$	$-^{*}$	$+^{*}$	$+^{*}$	$-^{*}$		585.0	0.04908
5	Jan Wk1	x	+	$+^{*}$	–					601.9	0.00001
6	Jan Wk1	x				$+^{*}$	+			586.0	0.03021
7	**Jan Wk1**	x*	–	+	$-^{*}$	+	$+^{*}$	+		**582.5**	**0.17817**
8	Sept Wk1	x*	$+^{*}$	–	$+^{*}$					602.9	0.00001
9	Sept Wk1	x*				$+^{*}$	–			588.0	0.01122
10	**Sept Wk1**	x*	–	$-^{*}$	$+^{*}$	+	–	$+^{*}$		**581.9**	**0.36223**
11	Mar Wk1	x*	+	$+^{*}$	–				–	601.1	0.00002
12	Mar Wk1	x				+	–		+	717.4	0.00000
13	**Mar Wk1**	x*	$+^{*}$	$+^{*}$	$-^{*}$	$+^{*}$	$+^{*}$	$-^{*}$	$-^{*}$	**582.4**	**0.18461**
14	Jan Wk1	x*	+	$+^{*}$	–				–	604.1	0.00000
15	Jan Wk1	x				$+^{*}$	+		+	587.6	0.01402
16	Jan Wk1	x*	–	+	$-^{*}$	+	$+^{*}$	+	–	584.5	0.06348
17	Sept Wk1	x	$+^{*}$	–	$+^{*}$				+	605.3	0.00000
18	Sept Wk1	x*				$+^{*}$	–		+	590.5	0.00327
19	Sept Wk1	x*	–	$-^{*}$	$+^{*}$	+	–	$+^{*}$	+	583.6	0.10361

Notes: Models were run for each of three time spans "pegged" on peak week of juvenile emigration, to the preceding onset, mid-, and late breeding period (breeding cycle) and include hydroregime variables (MCD, DAv, Cont0)‡ only; weather variables (PptTot, TAv)§ only; both hydroregime and weather variables with an interaction effect (MCDxPptTot); all models repeated with adult breeding effort (A) included. Wetland (W) was considered a fixed effect and included in all models.

† Models with the smallest AICc and highest Akaike weights have more support. The + or − indicates positive or negative relationship with juvenile recruitment. Significant (where confidence intervals did not include zero) variables are denoted by the * symbol, and models with the smallest AICc and highest Akaike weights are bolded.

‡ Maximum change in depth (MCD); average depth (DAv); weeks with continuous water (>0 cm) through peak juvenile emigration week (Cont0); within specified time span.

§ Total precipitation (PptTot); mean average temperature (TAv); interaction MCD × PptTot; within specified time span.

10). The next best two models (model 7; w = 0.178 and model 13; w = 0.185) included both hydroregime and weather variables within shorter time spans (mid- or late breeding season through PJE, respectively).

Our best-fitting model for predicting JR by *A. terrestris* (model 12; w = 0.389) was a function of individual wetland, total precipitation (positively associated), and total breeding adults during the maximum time span tested (onset of breeding period through PJE; February week 1 through May week 2; Table 4). Total breeding adults was significantly positively associated with JR and substantially improved model strength (see model 6; w = 0.000 vs. model 12), whereas addition of hydroperiod variables did not (see model 13; w = 0.316 vs. model 12).

Our best-fitting model for predicting JR by *A. quercicus* (model 11; w = 0.392) was a function of hydroregime variables and total breeding adults during the maximum time span tested (onset of breeding period through PJE; May week 1 through July week 4; Table 5); individual wetland was not a significant predictor of JR. Among hydroregime variables tested, only maximum (positively associated) and average depth (negatively associated) were significant predictors of JR. Total breeding adults was not a significant predictor, but nonetheless slightly improved model strength (see model 5; w = 0.275 vs. model 11). Similarly, addition of weather variables did not improve model strength (see model 13; w = 0.162 vs. model 11).

Our best-fitting model for predicting JR by *G. carolinensis* (model 13; w = 0.994) was a function of individual wetland, hydroregime, and weather variables, and total breeding adults, during the maximum time span tested (onset of breeding period through PJE; May week 1 through

Table 4. Information-theoretic model (M) results† for *Anaxyrus terrestris* juvenile recruitment (1994–2015; n = 118) from eight isolated, ephemeral wetlands, Ocala National Forest, Florida.

M	Time span to Jun Wk1	W	D5	DAv	Cont0	PptTot	TAv	A	AICc	Akaike Wt
1		x*							477.7	0.00003
2	Mar Wk4	x*	–*	–	–				471.5	0.00059
3	Mar Wk4	x*				+	+		479.4	0.00001
4	Mar Wk4	x*	–*	–	–	+	+		472.5	0.00036
5	Feb Wk1	x*	–	–	–				473.9	0.00018
6	Feb Wk1	x*				+*	+		472.3	0.00040
7	Feb Wk1	x*	–	–*	–	+*	+		469.5	0.00163
8	Mar Wk4	x*	–	–	–			+*	460.5	0.14689
9	Mar Wk4	x*				+	+	+*	463.5	0.03244
10	Mar Wk4	x*	–*	–	–	+	+	+*	462.6	0.05019
11	Feb Wk1	x*	–	–*	+			+*	462.2	0.06221
12	**Feb Wk1**	x*				+*	+	+*	**458.5**	**0.38944**
13	**Feb Wk1**	x*	–	–*	–	+*	+	+*	**459.0**	**0.31563**

Notes: Models were run for each of two time spans "pegged" on peak week of juvenile emigration, to the preceding onset and mid-breeding period (breeding cycle) and include hydroregime variables (D5, DAv, Cont0)‡ only; weather variables (PptTot, TAv)§ only; both hydroregime and weather variables; all models repeated with adult breeding effort (A) included. Wetland (W) was considered a fixed effect and included in all models.

† Models with the smallest AICc and highest Akaike weights have more support. The + or − indicates positive or negative relationship with juvenile recruitment. Significant (where confidence intervals did not include zero) variables are denoted by the * symbol, and models with the smallest AICc and highest Akaike weights are bolded.

‡ Total number of weeks (not necessarily continuous) when depth ≤5 cm (D5); weeks with continuous water (>0 cm) through peak juvenile emigration week (Cont0); average depth (DAv); within specified time span.

§ Total precipitation (PptTot); mean average temperature (TAv); within specified time span.

Table 5. Information-theoretic model (M) results† for *Anaxyrus quercicus* juvenile recruitment (1994–2015; n = 118) from eight isolated, ephemeral wetlands, Ocala National Forest, Florida.

M	Time span to Jun Wk1	W	DMax	DAv	Cont0	PptTot	TAv	A	AICc	Akaike Wt
1		x							218.4	0.00213
2	Jun Wk2	x	+	–*	+				219.5	0.00121
3	Jun Wk2	x				+	+		220.5	0.00074
4	Jun Wk2	x	+	–	+	+	+		224.4	0.00011
5	**May Wk1**	x	+*	–*	–				**208.7**	**0.27526**
6	May Wk1	x				+*	+		217.2	0.00376
7	May Wk1	x	+*		–*	–	+	+	210.8	0.09604
8	Jun Wk2	x	+	–	+			+	217.2	0.00394
9	Jun Wk2	x				+	–	+	215.5	0.00923
10	Jun Wk2	x	+	–	+	+	–	+	222.0	0.00036
11	**May Wk1**	x	+*	–*	–			+	**208.0**	**0.39197**
12	May Wk1	x				+*	+	+	212.0	0.05289
13	May Wk1	x	+*	–*	–	+	–	+	209.7	0.16236

Notes: Models were run for each of two time spans "pegged" on peak week of juvenile emigration, to the preceding onset and mid-breeding period (breeding cycle) and include hydroregime variables (DMax, DAv, Cont0)‡ only; weather variables (PptTot, TAv)§ only; both hydroregime and weather variables; all models repeated with adult breeding effort (A) included. Wetland (W) was considered a fixed effect and included in all models.

† Models with the smallest AICc and highest Akaike weights have more support. The + or − indicates positive or negative relationship with juvenile recruitment. Significant (where confidence intervals did not include zero) variables are denoted by the * symbol, and models with the smallest AICc and highest Akaike weights are bolded.

‡ Maximum depth (DMax); weeks with continuous water (>0 cm) (Cont0); average depth (DAv); within specified time span.

§ Total precipitation (PptTot); mean average temperature (TAv).

Table 6. Information-theoretic model (M) results† for *Gastrophryne carolinensis* juvenile recruitment (1994–2015; *n* = 126) from eight isolated, ephemeral wetlands, Ocala National Forest, Florida.

M	Time span to Jun Wk1	W	DMin	DAv	Cont0	PptTot	TMaxAv	TAv	A	AICc	Akaike Wt
1		x*								387.5	0.00000
2	Jun Wk2	x*	−*	−	+					352.5	0.00000
3	Jun Wk2	x				+*	+*	+*		367.4	0.00000
4	Jun Wk2	x*	+	−*	+	+*	+*	+		336.4	0.00005
5	May Wk1	x*	−*	−	−					342.7	0.00000
6	May Wk1	x*				+*	+*	−		372.7	0.00000
7	May Wk1	x*	−	−*	+	+*	+	−		331.1	0.00066
8	Jun Wk2	x*	−*	+	−				+*	343.8	0.00000
9	Jun Wk2	x*				+*	+*	+	+*	352.6	0.00000
10	Jun Wk2	x*	+	−	−	+*	+*	+	+*	327.3	0.00448
11	May Wk1	x*	−*	+	−				+*	332.3	0.00036
12	May Wk1	x*				+*	+*	−	+*	353.8	0.00000
13	**May Wk1**	x*	+	−*	−	+*	+	+	+*	**316.5**	**0.99445**

Notes: Models were run for each of two time spans "pegged" on peak week of juvenile emigration, to the preceding onset and mid-breeding period (breeding cycle) and include hydroregime variables (DMin, DAv, Cont0)‡ only; weather variables (PptTot, TMaxAvTav)§ only; both hydroregime and weather variables; all models repeated with adult breeding effort (A) included. Wetland (W) was considered a fixed effect and included in all models.

† Models with the smallest AICc and highest Akaike weights have more support. The + or − indicates positive or negative relationship with juvenile recruitment. Significant (where confidence intervals did not include zero) variables are denoted by the * symbol, and models with the smallest AICc and highest Akaike weights are bolded.

‡ Minimum depth (DMin); weeks with continuous water (>0 cm) (Cont0); average depth (DAv); within specified time span.

§ Total precipitation (PptTot); mean maximum temperature (TMaxAv); mean average temperature (TAv); within specified time span.

August week 4; Table 6). Among hydroregime variables, only average depth was significantly negatively correlated with JR. Among weather variables, only total precipitation was significantly positively associated with JR. Total breeding adults was significantly positively associated with JR and substantially improved model strength (see model 7; *w* = 0.001 vs. model 13).

Our best-fitting model for predicting JR by *S. holbrookii* (model 8; *w* = 0.670) was a function of individual wetland, total precipitation (the only weather variable tested; negatively associated), and total breeding adults during the time span between explosive breeding events the subsequent two weeks (Table 7). Hydroregime variables alone (see model 9; *w* = 0.004 vs. model 8) or in addition to weather variables (see model 10; *w* = 0.050 vs. model 8) did not improve model strength.

Kendall's tau rank correlations indicated that adult breeding effort was significantly positively correlated with reproductive success for all species, when tested without other model variables; tau values ranged from 0.22842 (*A. terrestris*) to 0.47972 (*S. holbrookii*; Fig. 6).

Annual JR was significantly positively associated between both species having a prolonged breeding period, slow larval development, and a "fixed" late spring start date for juvenile emigration, regardless of when oviposition occurred, or cohort age (*L. capito* and *L. sphenocephalus*; tau = 0.41069). In most cases, associations of JR between both *Lithobates* species, and other species having different reproductive strategies, were negative or nonsignificant; *L. sphenocephalus* and *A. quercicus* JR was weakly positively associated. Annual JR was also positively associated between *A. terrestris* (prolonged breeding period, rapid larval development, and juvenile emigration continual as cohorts complete metamorphosis) and both species having a season-limited breeding period, rapid larval development, and continuous juvenile emigration as cohorts complete metamorphosis: *A. quercicus*, tau = 0.23850; and *G. carolinensis*, tau = 0.16302. Annual JR was also positively associated between *A. quercicus* and *G. carolinensis*, both species having a season-limited breeding period, rapid larval development, and juvenile emigration continual as cohorts complete metamorphosis (tau = 0.45937; Table 8).

Table 7. Information-Theoretic model† (M) results for *Scaphiopus holbrookii* juvenile recruitment (1994–2015; $n = 34$) from eight isolated, ephemeral wetlands, Ocala National Forest, Florida.

M	Time span to Jun Wk1	W	DAv	DMax	PptTot	A	AICc	Akaike Wt
1		x					319.8	0.00068
2	Jun Wk2	x			−		322.8	0.00015
3	Jun Wk2	x	−	+			327.1	0.00002
4	Jun Wk2	x	−*	+*	−*		328.1	0.00001
5	May Wk1	x			−*		320.9	0.00039
6	May Wk1	x	−	−			325.7	0.00004
7	May Wk1	x	+	−	−		329.6	0.00001
8	**Jun Wk2**	x*			−*	+*	**306.0**	**0.67007**
9	Jun Wk2	x	+	−		+*	316.5	0.00350
10	Jun Wk2	x	−	+	−*	+*	311.2	0.05033
11	May Wk1	x			−*	+*	308.6	0.18047
12	May Wk1	x	+	−*		+*	310.5	0.06993
13	May Wk1	x	−	−	−	+*	312.6	0.02441

Notes: Models were run for each of three time spans "pegged" on week of explosive breeding (≥30 individual adults captured at a given wetland within a single week) and the subsequent two or three weeks and include hydroregime variables (DAv, DMax)‡ only; weather variables (PptTot)§ only; both hydroregime and weather variables; all models repeated with adult breeding effort included. Wetland was considered a fixed effect and included in all models.

† Models with the smallest AICc and highest Akaike weights have more support. The + or − indicates positive or negative relationship with juvenile recruitment. Significant (where confidence intervals did not include zero) variables are denoted by the * symbol, and models with the smallest AICc and highest Akaike weights are bolded.

‡ Average depth (DAv); maximum depth (DMax).

§ Total precipitation (PptTot).

Discussion

Our models indicated that environmental variables affecting reproductive success differed among species, but were most similar among those with similar reproductive strategies, characterized by length and timing of breeding period, rates of larval development, and timing of metamorphosis. Strong correlations of annual JR between species with similar reproductive strategies further corroborated those results. This suggests that altered weather patterns associated with climate change will differentially affect reproductive success among amphibian species, but could correspond more closely among those having similar reproductive strategies.

The best-supported models for all focal species (except explosive breeder *S. holbrookii*) encompassed the maximum tested time span (onset of breeding period through PJE) when tadpoles, if present, would be developing to metamorphosis within wetlands. Models encompassing shorter time spans were somewhat supported only for *L. sphenocephalus*. Based on known breeding and tadpole phenology (footnotes, Table 1), all of our focal species could potentially reproduce successfully even if suitable wetland characteristics did not occur until mid- or late breeding season. However, given the extreme variation in reproductive success related to hydroregime, weather, and other, seemingly stochastic factors (Pechmann et al. 1989, Semlitsch et al. 1996, Richter et al. 2003), a protracted time span provides the maximum opportunity for continuous or intermittent breeding and introduction of new egg and tadpole cohorts (Greenberg et al., *in press*), likely increasing chances that some will survive to metamorphosis.

Our strongest models indicated that different hydroregime characteristics, total precipitation, or both were important drivers of reproductive success for most species. Continuous water through PJE was an important predictor of JR for focal species with prolonged breeding seasons and slow larval development (*L. capito and L. sphenocephalus*), but not for those with rapid larval development (*A. terrestris, A. quercicus, G. carolinensis, S. holbrookii*). A continuous hydroperiod during the onset of breeding period through PJE time span (the maximum time span tested) would potentially allow *L. capito* or *L. sphenocephalus* tadpoles originating from

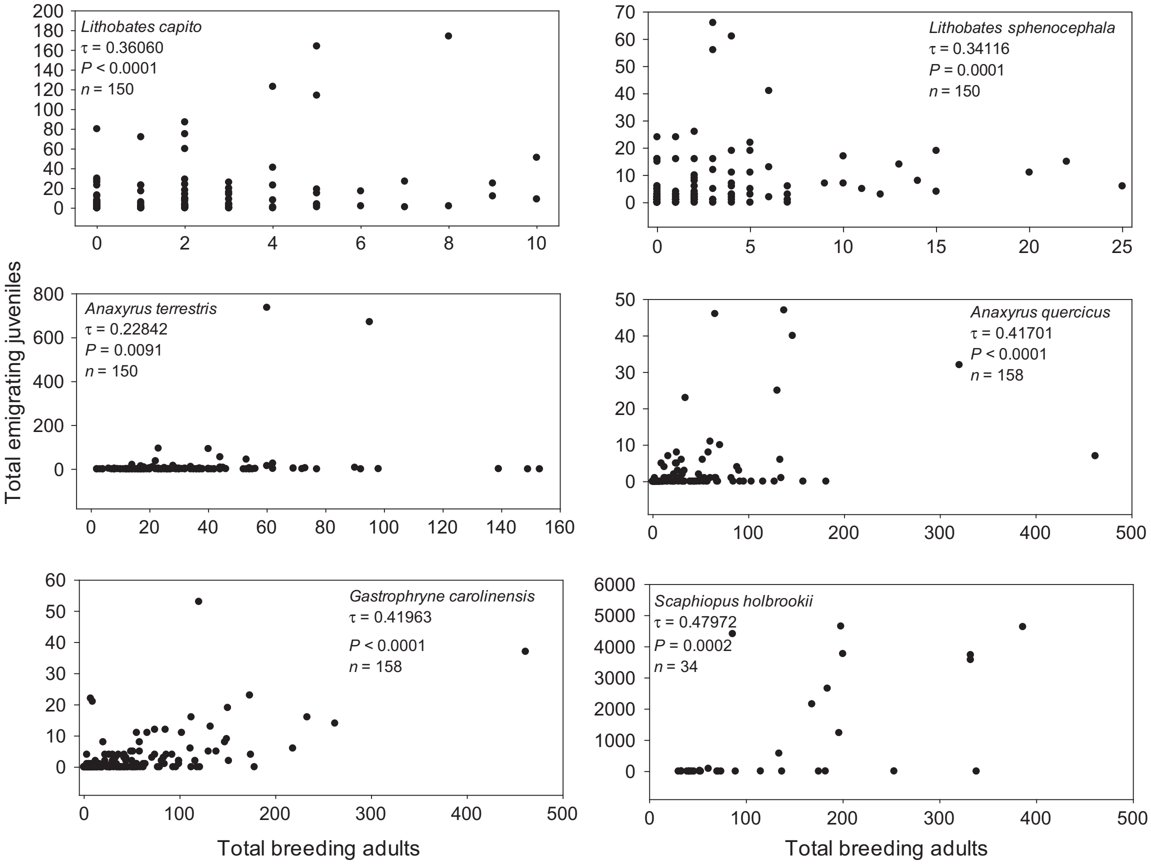

Fig. 6. Kendall's tau rank correlations of adult breeding effort with juvenile recruitment rates of six anuran species from eight isolated, ephemeral wetlands, Ocala National Forest, Florida (1994–2015). Each data point represents adult breeding and juvenile recruitment from one wetland within one breeding cycle (Table 1). For *Scaphiopus holbrookii* only explosive breeding events ($n \geq 30$ adults per wetland within a one-week period) and resulting juvenile recruits were included.

continuous or intermittent fall, winter, or spring breeding to cumulatively survive to metamorphosis, which does not occur until late spring. Alternatively, shorter hydroperiods lasting winter—or spring—through peak metamorphosis would eliminate tadpoles resulting from earlier breeding, providing opportunity only for cohorts from later breeding to survive; wetlands drying prior to spring metamorphosis would eliminate all cohorts within a breeding cycle. In contrast, species with rapid larval development and the ability to metamorphose continually may not require continuous water through PJE because tadpoles could complete metamorphosis in one or multiple shorter hydroperiods within the breeding cycle. A positive association between total rainfall and *A. terrestris* and *G. carolinensis* JR suggests that higher rainfall may provide enough suitable hydroperiods within breeding cycles for successful JR, even if water is not continuously in wetlands through PJE. Thus, both timing and duration of hydroperiods are likely to affect amphibian species differently, in relation to their reproductive strategies.

Influential water depth variables also differed among species and generally corresponded among species with similar breeding strategies. juvenile recruitment rates of *A. quercicus* and *G. carolinensis* were negatively associated with average depth, suggesting that shallow water may increase tadpole survival to metamorphosis for these species. Average depth was negatively

Table 8. Kendall's tau rank correlations of juvenile recruitment rates between all pairs of five anuran species from eight isolated, ephemeral wetlands, Ocala National Forest, Florida (1994–2015).

Species	PB-SLD-SE† *L. capito*	PB-SLD-SE† *L. sphenocephalus*	PB-RLD-C‡ *A. terrestris*	SB-RLD-CE§ *A. quercicus*	SB-RLD-CE§ *G. carolinensis*
Lithobates capito	...	tau = 0.41069 $P < 0.0001$ $n = 161$	tau = 0.04635 $P = 0.4634$ $n = 161$	tau = −0.11155 $P = 0.0982$ $n = 155$	tau = −0.29418 $P < 0.0001$ $n = 155$
L. sphenocephalus	...	...	tau = 0.08248 $P = 0.1869$ $n = 161$	tau = 0.15466 $P = 0.0206$ $n = 155$	tau = −0.04391 $P = 0.4924$ $n = 155$
Anaxyrus terrestris	...	...	...	tau = 0.23850 $P = 0.0006$ $n = 155$	tau = 0.16302 $P = 0.0147$ $n = 155$
A. quercicus	...	...	...	...	tau = 0.45937 $P < 0.0001$ $n = 169$

Notes: Species exhibit three reproductive strategies defined by length and timing of breeding period, rate of larval development, and timing of metamorphosis and juvenile emigration. *Scaphiopus holbrookii* exhibits a fourth reproductive strategy (explosive breeding), but was not included because breeding and juvenile recruitment are unpredictable and aseasonal. Each data point represents juvenile recruitment from one wetland within the same year.

† Prolonged breeding period, slow larval development, spring emigration regardless of when oviposition occurred (cohort age).

‡ Prolonged breeding period, rapid larval development, juvenile emigration continual as cohorts complete metamorphosis.

§ Season-limited breeding period, rapid larval development, juvenile emigration continual as cohorts complete metamorphosis.

associated with *L. sphenocephalus* recruitment in the best model encompassing the maximum time span (model 10), but not in other good models encompassing shorter time spans (models 7 and 13), suggesting that effect of average depth may vary with timing. Maximum change in wetland depth and total precipitation, or an interaction between those variables, were important predictors of *L. capito* and *L. sphenocephalus* JR, respectively, suggesting that large, depth fluctuations may have an important influence on *L. capito* and *L. sphenocephalus* recruitment. J. H. K. Pechmann (*personal communication*) observed *L. sevosa* "waiting" until water levels increased to about 55 cm at Glenn's Pond before initiating breeding activity; deeper water could increase the probability of water remaining in wetlands through metamorphosis. Maximum water depth was positively correlated with *A. quercicus* JR, suggesting that deeper water at some point during the breeding cycle is associated with hydroperiod duration adequate for tadpole survival to metamorphosis. Other studies indicate that wetland dry-downs immediately prior to breeding may enhance JR for *G. carolinensis* (Pechmann et al. 1989, Semlitsch et al. 1996), by reducing populations of predatory aquatic macroinvertebrates and salamander larvae.

Our strongest model for *S. holbrookii* indicated a strong, positive association between breeding effort and recruitment, and a negative association between total precipitation and recruitment within two weeks after explosive breeding events. Explosive breeding events are triggered by heavy rainfalls, usually associated with tropical storms or hurricanes that rapidly refill dry wetlands (Greenberg and Tanner 2004). Thus, whereas heavy rainfall is critical in eliciting breeding events, our results suggest that substantial rainfall within the two to three weeks after breeding could negatively affect tadpole survival to metamorphosis. Our results indicate that two weeks post-breeding is the most critical time span affecting JR, as tadpole development is very rapid.

Air temperature variables had little or no influence on JR for most species, suggesting that tadpoles can tolerate a range of temperatures within the seasons they occur in wetlands. *Lithobates capito* was an exception, where a negative interaction effect between continuous water and temperature, in conjunction with a (nonsignificant) association with temperature, suggested that recruitment may be negatively affected by higher temperatures, even when hydroperiod timing and duration are suitable. Clearly, tadpoles of species with prolonged, multi-season breeding periods (e.g., *L. capito*, *L. sphenocephalus*, and *A. terrestris*), or explosive breeding at any time of year (*S. holbrookii*), would require wider temperature tolerance than summer breeders such as *A. quercicus* and *G. carolinensis*. Our models only included temperatures measured within specified time spans relevant to each species' breeding phenology. Thus, we could not address how reproductive success might be affected if breeding phenology (seasonal timing) was substantially altered due to changing temperature or precipitation (Saenz et al. 2006) associated with climate change, thereby exposing eggs and tadpoles to a wider range of temperatures. Additionally, altered changes in hydroregime associated with climate change could increase effects of air temperature on tadpole survival to metamorphosis, as water temperature varies with both air temperature and water depth (Berven 1982, Harkey and Semlitsch 1988). Nonetheless, our results suggest that altered rainfall patterns and hydroregimes associated with climate change are likely to have a much bigger impact on amphibians than temperature alone.

In our models, individual wetland alone (model 1) was not associated with JR for any species except *A. terrestris* and *G. carolinensis*, but was significant in the strongest models for all species except *A. quercicus*. The influence of individual wetland could be a function of (hence correlated with) characteristics such as basin size or shape that, in turn, could affect hydroregime characteristics (Figs. 2b and 3), wetland vegetation, or substrate characteristics important for breeding adults, oviposition sites, or tadpoles. Although all wetlands varied annually in hydroregime characteristics, some contained water more of the time, increasing chances of suitable timing and duration of hydroperiods for multiple species. Philopatry could also influence wetland selection by breeding adults over multiple generations (Pechmann et al. 2001, Semlitsch 2008). Juveniles of many species were produced from wetlands that were dry much of the time, and recruitment failure or low average juvenile production often occurred in wetlands that held water much of the time during our 22-yr study period (Figs. 2b, 3 and 5), highlighting the importance of maintaining multiple ephemeral wetlands within landscapes.

Rank correlations of breeding adults to juvenile recruits indicated that breeding effort was a significant predictor of JR for all species. In contrast, our multivariate models indicated that breeding effort was not an important predictor of JR for *L. capito*, *L. sphenocephalus*, or *A. quercicus*. This seeming inconsistency was likely due to correlation between adult captures and other variables in our models, such as continuous hydroperiod or total rainfall; a strong association between breeding effort and JR for *A. terrestris*, *G. carolinensis*, and *S. holbrookii* suggests that breeding effort was an important predictor of JR, above and beyond the influence of weather and/or hydroregime. The influence of weather and hydroregime on breeding effort was not a focus of our study. However, these factors can strongly influence adult movement (Greenberg and Tanner 2004, 2005*a*), calling activity (Saenz et al. 2006), and (likely) breeding effort and thus have an important, indirect influence on JR.

Sampling bias associated with drift fence trapping (Dodd 1991) potentially affected results associated with influence of breeding effort, as well. For example, low adult capture rates for *L. capito* and *L. sphenocephalus* could be due to pitfall trap escape by jumping, or trap avoidance by going around or over fences; Pechmann et al. (1989) also reported that large *Lithobates* adults (*L. catesbeianus* and *L. sphenocephalus*) were likely able to trespass fences and pitfall traps, although juveniles were not. Alternatively or in addition, adult populations of *L. capito* and *L. sphenocephalus* may be small compared to some other anuran species, and relatively few adults may be able to produce a comparatively large number of juvenile recruits. Similarly, relatively low capture rates of *G. carolinensis* and *A. quercicus* could be due to trespass, or because juveniles may remain in wetlands and grow for prolonged periods post-metamorphosis.

Our results suggest that annual variation in reproductive success was most similar among species having similar reproductive strategies. For example, JR was strongly associated between both species having a prolonged breeding period, slow larval development, and juvenile emigration not initiated until late spring (*L. capito* and *L. sphenocephalus*); both require prolonged hydroperiods through late spring, so that slow-developing tadpoles can complete metamorphosis and emigrate from wetlands. Similarly, JR was significantly positively associated among all species pairs with rapid larval development (*A. quercicus*, *A. terrestris*, and *G. carolinensis*), regardless of breeding period duration. Thus, hydroregime and weather conditions could provide reproductive opportunity for species having a similar reproductive strategy in some years or wetlands, but for species with a different strategy in others. Weather and hydroregime characteristics interact with life history traits, or reproductive strategies, that differ among amphibian species and influence reproductive plasticity, opportunity, and success.

Clearly, reproductive opportunity in ephemeral wetlands is higher for species with rapid larval development than for species with slow larval development because of their ability to exploit shorter hydroperiods. Among species with rapid larval development, a protracted breeding period offers greater reproductive opportunity than a shorter, season-limited breeding season, by increasing chances of one or more suitable hydroperiods. For example, *A. terrestris* could potentially exploit multiple, short-duration hydroperiods during their extended (February through October) breeding season, whereas summer-breeding *A. quercicus* or *G. carolinensis* (33–44 d or 23–67 d, respectively) would likely encounter fewer suitable hydroperiods during their shorter, summer breeding season when ephemeral wetlands are more often dry. For rapidly developing species with a protracted breeding period, either multiple short-duration (4–5 weeks) or prolonged hydroperiods within respective breeding seasons could allow continuous or intermittent breeding and multiple cohorts of juvenile recruits. The explosive breeding strategy and extremely rapid rate of larval development (14 d) confer *S. holbrookii* with high reproductive plasticity. Nonetheless, *S. holbrookii* are constrained by their requirement for specific weather cues (heavy rainfall, usually associated with late summer and fall tropical storms and hurricanes) and wetland conditions (dry wetlands that refill rapidly; Greenberg and Tanner 2004). In contrast, reproductive opportunity in ephemeral wetlands is relatively lower for species with slow larval development, requiring prolonged, continuous hydroperiods for successful reproduction, such as *Lithobates* spp. Reproductive opportunity is further constrained for *L. capito* and *L. sphenocephalus*, as tadpoles do not metamorphose or emigrate until late spring, relative to species that can metamorphose year-round (e.g., *L. catesbeianus* and *L. grylio*; C. H. Greenberg, *unpublished data*). Wetlands drying before metamorphosis in May or June result in reproductive failure for *L. capito* and *L. sphenocephalus*, regardless of prior breeding effort and hydroregime.

Our results illustrate the complexity and uncertainty involved in determining effects of weather and hydroregime on amphibian recruitment. Although our models clearly implicated precipitation and specific hydroregime characteristics as important predictors of anuran JR, much of the variability in JR remained unexplained. Our IT modeling approach used weather and hydroregime variables selected a priori based on initial exploratory analysis and biological considerations. Nonetheless, correlation among multiple variables (both selected and unused) added ambiguity, and rendered it difficult to assess what specific variables or combination of variables was most important in predicting reproductive success. For example, individual wetland basin shape and area, coupled with the amount and timing of precipitation, are likely correlated with hydroregime characteristics such as hydroperiod duration, frequency, timing, and fluctuations in water depth and surface area. In turn, water temperature varies in relation to both air temperature and depth or volume. Precipitation, temperature, and hydroregime characteristics are, in turn, closely correlated with breeding effort by adults (Saenz et al. 2006). Thus, many or all of these correlated variables are likely to influence amphibian reproductive success.

Whereas unsuitable hydroperiod duration during tadpole development can be clearly, causally linked to recruitment failure, many unknown biotic factors, such as competition and predation on eggs and larvae, likely contribute to high stochastic variation in amphibian reproductive success.

Competition within and among species, predation by aquatic macroinvertebrates on eggs and larvae, larval density, and hydroregime can all affect survival, developmental rate, and body size at metamorphosis (Wilbur 1980, 1982, Morin 1983, Semlitsch et al. 1996, Richter et al. 2009, McMenamin and Hadly 2010). These factors are confounded by temporal dynamics, including interspecific differences in the timing of oviposition, rates of larval development, and apparently high mortality rates and reintroduction of new eggs and cohorts (Greenberg et al., *in press*), resulting in continual changes in larval assemblages. Ongoing fluctuation of wetland surface area and depth, driven by precipitation, basin morphology, and groundwater levels (Greenberg et al. 2015), and continually changing competition and predation pressure (Gascon and Travis 1992, Pearman 1993, 1995, Azevedo-Ramos and Magnusson 1999) further confound factors affecting survival to metamorphosis. Water temperature, a dynamic interaction between changing air temperature and fluctuating water depth and surface area (Berven 1982, Harkey and Semlitsch 1988), in turn affects the growth and development rate of tadpoles (e.g., Blaustein et al. 2001, 2010, Corn 2005, Todd et al. 2011). This is further confounded by season and complicates prediction of tadpole survival to metamorphosis because effects could vary with developmental stage. Additionally, amphibian breeding phenology is influenced by both air temperature and precipitation (e.g., Corn 2005, Saenz et al. 2006, Blaustein et al. 2010, Todd et al. 2011, Greenberg et al. 2014).

Our results suggest that moderate climate warming may not directly affect anuran populations, but associated changes with weather patterns including the amount, frequency, timing, and severity of precipitation will almost certainly alter wetland hydroregimes (Greenberg et al. 2014, 2015), breeding activity, and reproductive success among amphibian species. Climate scenarios with substantially reduced summer and fall precipitation would likely result in reduced groundwater recharge and shorter, shallower hydroperiods during the critical fall–winter–spring breeding cycle for *L. capito* and *L. sphenocephalus*. These species may be especially vulnerable because their tadpoles do not metamorphose until late spring; thus, even a prolonged hydroperiod will result in reproductive failure if it dries before then. Alternatively, substantially reduced winter precipitation would likely result in initial groundwater levels too far belowground for summer rains to raise aboveground during spring and summer breeding seasons for species such as *A. terrestris*, *A. quercicus*, and *G. carolinensis*. In contrast, increased frequency of tropical storms or hurricanes (Karl et al. 2009) could provide more frequent reproductive opportunity for *S. holbrookii*, as high-severity storms prompt explosive breeding events and often create suitable wetland conditions for their very rapidly developing larvae. Clearly, altered weather patterns associated with climate warming will differentially affect reproductive success among amphibian species with different breeding strategies, with critical implications for amphibian population trends and assemblages (Greenberg et al. 2014, 2015). Our study highlights the importance of maintaining multiple ephemeral wetlands within landscapes to increase chances for reproductive success by species with different strategies, in at least some years and wetlands.

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LITERATURE CITED

Ashton Jr., R. E., and P. S. Ashton. 1988. Handbook of reptiles and amphibians of Florida, part three: the amphibians. Windward Publishing Inc, Miami, Florida, USA.

Azevedo-Ramos, C., and W. E. Magnusson. 1999. Tropical tadpole vulnerability to predation: association between laboratory results and prey distribution in an Amazonian savanna. Copeia 1999:58–67.

Babbitt, K. J., M. J. Baber, and T. L. Tarr. 2003. Patterns of larval amphibian distribution along a wetland hydroperiod gradient. Canadian Journal of Zoology 81:1539–1552.

Berven, K. A. 1982. The genetic basis of altitudinal variation in the wood frog *Rana sylvatica* II. An experimental analysis of larval development. Oecologia 52:360–369.

Blaustein, A. R., L. K. Belden, D. H. Olson, D. M. Green, T. L. Root, and J. M. Kiesecker. 2001. Amphibian breeding and climate change. Conservation Biology 15:1804–1809.

Blaustein, A. R., S. C. Walls, B. A. Bancroft, J. J. Lawler, C. L. Searle, and S. S. Gervasi. 2010. Direct and indirect effects of climate change on amphibian populations. Diversity 2010:281–313.

Bridges, A. S., and M. E. Dorcas. 2000. Temporal variation in anuran calling behavior: implications of surveys and monitoring programs. Copeia 2000: 587–592.

Brooks, R. T. 2009. Potential impacts of global climate change on the hydrology and ecology of ephemeral freshwater systems of the forests of the northeastern United States. Climatic Change 95:469–483.

Burnham, K. P., and D. R. Anderson. 2002. Model selection and multi-modal inference: a practical information-theoretic approach. Second edition. Springer-Verlag, New York, New York, USA.

Cole, E. M., R. Hartman, and M. P. North. 2016. Hydroperiod and cattle use associated with lower recruitment in an r-selected amphibian with a declining population trend in the Klamath Mountains, California. Journal of Herpetology 50:37–43.

Corn, P. S. 2005. Climate change and amphibians. Animal Biodiversity and Conservation 28:59–67.

Dodd Jr., C. K.. 1991. Drift fence-associated sampling bias of amphibians at a Florida sandhills temporary pond. Journal of Herpetology 25:1991.

Dodd Jr., C. K.. 1994. The effects of drought on population structure, activity, and orientation of toads (*Bufo quercicus* and *B. terrestris*) at a temporary pond. Ethology Ecology and Evolution 6:331–349.

Dodd Jr., C. K.. 1995. The ecology of a sandhills population of the eastern narrow-mouthed toad, *Gastrophryne carolinensis*, during a drought. Bulletin Florida Museum of Natural History and Biological Science 38:11–41.

Gascon, C., and J. Travis. 1992. Does the spatial scale of experimentation matter? A test with tadpoles and dragonflies. Ecology 73:2237–2243.

Godley, J. S. 1992. Threatened: gopher frog *Rana capito* Le Conte. Pages 15–19 *in* P. E. Moler, editor. Rare and endangered biota of Florida, Volume 3. Amphibians and reptiles. University Press of Florida, Gainesville, Florida, USA.

Greenberg, C. H. 2001. Spatio-temporal dynamics of pond use and recruitment in Florida gopher frogs (*Rana capito aesopus*). Journal of Herpetology 35:74–85.

Greenberg, C. H., S. Goodrick, J. D. Austin, and B. R. Parresol. 2015. Hydroregime prediction models for ephemeral groundwater-driven sinkhole wetlands: a planning tool for climate change and amphibian conservation. Wetlands 35:899–911.

Greenberg, C. H., S. E. Johnson, R. Owen, and A. Storfer. *In press*. Amphibian breeding phenology and reproductive success at isolated ephemeral wetlands: an examination using concurrent terrestrial and aquatic sampling. Canadian Journal of Zoology.

Greenberg, C. H., R. W. Perry, K. E. Franzreb, S. C. Loeb, D. Saenz, and D. C. Rudolph. 2014. Climate change and wildlife in the southern United States: potential effects and management options. Pages 379–420 *in* J. M. Vose and K. D. Klepzig, editors. Climate change adaptation and mitigation management options. CRC Press, New York, New York, USA.

Greenberg, C. H., and G. W. Tanner. 2004. Breeding pond selection and movement patterns by eastern spadefoot toads (*Scaphiopus holbrookii*) in relation to weather and edaphic conditions. Journal of Herpetology 38:569–577.

Greenberg, C. H., and G. W. Tanner. 2005*a*. Spatial and temporal ecology of oak toads (*Bufo quercicus*) on a Florida landscape. Herpetologica 61:422–434.

Greenberg, C. H., and G. W. Tanner. 2005*b*. Spatial and temporal ecology of eastern spadefoot toads on a Florida landscape. Herpetologica 61:20–28.

Harkey, G. A., and R. D. Semlitsch. 1988. Effects of temperature on growth, development, and color polymorphism in the ornate chorus frog *Pseudacris ornata*. Copeia 1988:1001–1007.

IPCC. 2007. Climate Change 2007: Synthesis Report. 52 pp. http://www.ipcc.ch/pdf/assessment-report/ar4/syr/ar4/syr.pdf

Karl, T. R., J. M. Melillo, and T. C. Peterson, editors. 2009. Global climate change impacts in the United States. Cambridge University Press, UK. http://www.globalchange.gov/usimpacts

Knowles Jr., L., A. M. O'Reilly, and J. C. Adamski. 2002. Hydrogeology and simulated effects of the ground-water withdrawals from the Floridan aquifer system in Lake County and in the Ocala National Forest and vicinity, north-central Florida. Water-Resources Investigations Report 02-4207. US Geological Society, Tallahassee, Florida, USA.

McCallum, M. L., S. E. Trauth, M. N. Mary, C. McDowell, and B. A. Wheeler. 2004. Fall breeding of the southern leopard frog (*Rana sphenocephala*) in northeastern Arkansas. Southeastern Naturalist 3:401–408.

McMenamin, S. K., and E. A. Hadly. 2010. Developmental dynamics of *Ambystoma tigrinum* in a changing landscape. BMC Ecology 10:10.

McMenamin, S. K., E. A. Hadly, and C. K. Wright. 2008. Climatic change and wetland desiccation cause amphibian decline in Yellowstone National Park. Proceedings of the National Academy of Sciences 105:16988–16993.

Moler, P. E., and R. Franz. 1987. Wildlife values of small, isolated wetlands in the southeastern coastal plain. Pages 234–241 *in* R. R. Odum, K. A. Riddleberger, and J. C. Ozier, editors. Proceedings of the Third Southeastern Nongame and Endangered Wildlife Symposium. Georgia Department of Natural Resources, Atlanta, Georgia, USA.

Morin, P. J. 1983. Predation, competition, and the composition of larval anuran guilds. Ecological Monographs 53:119–138.

Palis, J. G. 1998. Breeding biology of the gopher frog, *Rana capito*, in western Florida. Journal of Herpetology 32:217–223.

Pearman, P. B. 1993. Effects of habitat size on tadpole populations. Ecology 73:1982–1991.

Pearman, P. B. 1995. Effects of pond size and consequent predator density on two species of tadpoles. Oecologia 102:1–8.

Pechmann, J. H. K., R. A. Estes, D. E. Scott, and J. W. Gibbons. 2001. Amphibian colonization and use of ponds created for trial mitigation of wetland loss. Wetlands 21:93–111.

Pechmann, J. H. K., D. E. Scott, J. W. Gibbons, and R. D. Semlitsch. 1989. Influence of wetland and hydroperiod on diversity and abundance of metamorphosing juvenile amphibians. Wetlands Ecology and Management 1:3–11.

Phillips, K. M. 1995. *Rana capito capito*, the Carolina gopher frog, in southeast Georgia: reproduction, early growth, adult movement patterns, and tadpole fright response. M.S. Thesis. Georgia Southern University, Statesboro, Georgia, USA.

Richter, J., L. Martin, and C. K. Beachy. 2009. Increased larval density induces accelerated metamorphosis independently of growth rate in the frog *Rana sphenocephala*. Journal of Herpetology 43:551–554.

Richter, S. C., J. E. Young, G. N. Johnson, and R. A. Seigel. 2003. Stochastic variation in reproductive success of a rare frog, *Rana sevosa*: implications for conservation and for monitoring amphibian populations. Biological Conservation 111:171–177.

Saenz, D., L. A. Fitzgerald, K. A. Baum, and R. N. Conner. 2006. Abiotic correlates of anuran calling phenology: the importance of rain, temperature, and season. Herpetological Monographs 20:64–82.

SAS Institute Inc. 2011. SAS/STAT® 9.3 user's guide. SAS Institute Inc., Cary, North Carolina, USA.

Semlitsch, R. D. 2008. Differentiating migration and dispersal processes for pond-breeding amphibians. Journal of Wildlife Management 72:260–267.

Semlitsch, R. D., J. W. Gibbons, and T. S. Tuberville. 1995. Timing of reproduction and metamorphosis in the Carolina gopher frog (*Rana capito capito*) in South Carolina. Journal of Herpetology 29: 612–614.

Semlitsch, R. D., D. E. Scott, J. H. K. Pechmann, and J. W. Gibbons. 1996. Structure and dynamics of an amphibian community: evidence from a 16-year study of a natural pond. Pages 217–248 *in* M. L. Cody and J. A. Smallwood, editors. Long-term studies of vertebrate communities. Academic Press, San Diego, California, USA.

Snodgrass, J. W., M. J. Komoroski, A. L. Bryan Jr., and J. Burger. 2000. Relationships among isolated wetland size, hydroperiod, and amphibian species richness: implications for wetland regulations. Conservation Biology 14:414–419.

Stewart, M. M. 1995. Climate driven population fluctuations in rain forest frogs. Journal of Herpetology 29:437–446.

Todd, B. D., D. E. Scott, J. H. Pechmann, and J. W. Gibbons. 2011. Climate change correlates with rapid delays and advancements in reproductive timing in an amphibian community. Proceedings of the Royal Society of London B: Biological Sciences 278:2191–2197.

Vose, J. M., and K. D. Klepzig. 2014. Introduction to climate change adaptation and mitigation management options. Pages 1–8 *in* J. M. Vose and K. D. Klepzig, editors. Climate change adaptation and mitigation management options. CRC Press, New York, New York, USA.

Walls, S. C., W. J. Barichivich, M. E. Brown, D. E. Scott, and B. T. Hossack. 2013*a*. Drought, deluge and declines: the impact of precipitation extremes on amphibians in a changing climate. Biology 2013:399–418.

Walls, S. C., W. J. Barichivich, M. E. Brown, D. E. Scott, and B. R. Hossack. 2013*b*. Influence of drought on salamander occupancy of isolated wetlands on the southeastern Coastal Plain of the United States. Wetlands 33:345–354.

Wilbur, H. M. 1980. Complex life cycles. Annual Review of Ecology and Systematics 11:67–93.

Wilbur, H. M. 1982. Competition between tadpoles of *Hyla femoralis* and *Hyla gratiosa* in laboratory experiments. Ecology 63:278–282.

Winsberg, M. D. 1990. Florida weather. University of Central Florida Press, Orlando, Florida, USA.

Wright, A. H. 2002. Life-histories of the frogs of Okefinokee swamp, Georgia. North American Salientia (Anura) No. 2. Cornell University Press, Ithaca, New York, USA.