ABIOTIC CORRELATES OF ANURAN CALLING PHENOLOGY: THE IMPORTANCE OF RAIN, TEMPERATURE, AND SEASON

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ABSTRACT: We surveyed anuran calls nightly at eight ponds in eastern Texas from 1 January 2001 through 31 December 2002. Air temperatures and daily rainfall also were recorded for each of the sites. Eastern Texas contains a diverse temperate anuran fauna and a climate that provides a range of conditions for anuran reproduction. During our study, we measured air temperatures that fluctuated seasonally with extremes from 0 to 29 C at 2100 h. We found rainfall to be generally abundant with occasional flooding events, however, prolonged periods of no precipitation were also observed. Given the level of anuran diversity and the amount of seasonal variation in temperature and rainfall in our temperate climate we expected to find a variety of breeding strategies. Results from our analyses did indeed suggest five basic breeding strategies based on anuran calling: (1) breeding within a predictable season (summer) independent of local weather patterns; (2) breeding opportunistically within a predictable season (summer) dependent on local rainfall; (3) breeding opportunistically within a predictable season (winter) dependent on local temperature; (4) breeding opportunistically dependent on local flood level rainfall events; (5) breeding opportunistically year round dependent on local temperature in the winter and local rainfall in the summer.

Key words: Anurans; Breeding phenology; Calling; Climate; Frogs; Toads.

ALTHOUGH understanding what determines the composition of many ecological communities remains elusive, abiotic mechanisms have been shown to play a key role in the organization of anuran communities. Clearly, both biotic and abiotic factors play important roles in structuring anuran community composition (Dayton and Fitzgerald, 2001; Duellman, 1990), however a consensus view has emerged that breeding activity is more strongly influenced by abiotic factors (Blair, 1960, 1961; Blankenhorn, 1972; Dixon and Heyer, 1968; Obert, 1975). Indeed, many researchers have reported the influence of rainfall and temperature on anuran breeding, but results from these studies indicate that each species may respond in its own way (Bertoluci, 1998; Moriera and Lima, 1991; Salvador and Carrascal, 1990; Wiest, 1982).

We suggest the phenology of breeding is directly linked to anuran community structure because the sequence of breeding events among species, combined with their use of breeding sites that vary in hydroperiod, largely determines the makeup of anuran communities at local scales. Breeding activity in some species may be highly correlated to specific abiotic conditions such as temperature, for example, whereas other species may have more generalized breeding cues, and still others may be linked to a unique set of abiotic cues or constraints. Reproductive strategies and timing of reproduction also vary greatly among anuran species (Aichinger, 1987; Bertoluci and Rodrigues, 2002; Bevier, 1997). Where temperature and rainfall vary, seasonal changes should allow for diversification of breeding strategies among anurans by providing a greater diversity of environmental conditions (Bertoluci and Rodrigues, 2002). Moreover, many anurans that occur in areas with little seasonal differences in weather patterns breed year-round (Crump, 1974; Duellman, 1978). Anuran assemblages in the southeastern USA, for example, consist of species that co-occur at breeding sites during winter (winter-breeding guild) or summer (summer-breeding guild). Within the summer-breeding guild, species may exhibit an explosive breeding strategy, or have prolonged

breeding periods (Oseen and Wassersug, 2002).

There are contradictory views on how anuran species with different breeding strategies might respond to abiotic cues of breeding activity. Explosive breeding is characterized by a response en masse to some localized cue. Depending on the species, explosive breeders may experience breeding events over several months. Prolonged breeders presumably begin and end breeding in response to more generalized, regional cues and they exhibit breeding activity more continuously during their breeding season, albeit with variation in breeding intensity.

It has been suggested that prolonged breeders might not be sensitive to weather-related cues to stimulate breeding activities such as calling (Bevier, 1997; Cousineau, 1990). A contrasting viewpoint suggests once the breeding season begins for explosive breeders, explosive breeding events should not be very sensitive to abiotic factors. According to this view, prolonged breeders should be more sensitive to abiotic conditions in order to maintain energy reserves during their longer breeding seasons (Oseen and Wassersug, 2002). However, as discussed by Oseen and Wassersug (2002), most previous research attempting to assess the effects of multiple abiotic factors on calling activity has been short-term with intermittent data collection. We suggest both viewpoints have merit, but at different levels of ecological resolution. For example, rain events clearly stimulate chorusing in typical explosive breeders such as spadefoot toads (Pelobatidae), and it is obvious that some prolonged breeding species do not exhibit breeding activity every night of their breeding season. Clearly, a more thorough analysis of anuran communities from seasonal environments that consist of both prolonged and explosive breeders is needed to further resolve the extent to which abiotic factors influence breeding phenology, and ultimately the composition of anuran communities at local scales. We suggest such an analysis would reveal that abiotic cuing of breeding events may be important for both explosive and prolonged breeders, but in different ways.

Herein, we examine relationships between breeding activity and the abiotic factors that cue calling in a diverse community of 13 anuran species in eastern Texas. The anuran fauna in eastern Texas presents an excellent opportunity to evaluate the abiotic factors influencing community composition because both winter-breeding and summer-breeding guilds are present, and the region is characterized by strong temperature fluctuations and rain events. All anuran species in eastern Texas advertise for mates by calling at potential breeding sites. All species lay their eggs aquatically (Conant and Collins, 1998; Garrett and Barker, 1987), with tadpoles developing through metamorphosis into sub-adults (Gosner, 1960). No anuran species in eastern Texas have direct development, foam nests, aerial nests, or parental care. Hence, any effects of life history strategy on analyses of the importance of abiotic factors as drivers of community structure should be minimal. We used daily monitoring of advertisement calls as a surrogate to breeding activity at multiple sites, combined with associated data on weather-related parameters, to test for associations among abiotic variables and calling in the winter and summer-breeding guilds, and to draw comparisons among species with prolonged or explosive-breeding strategies. Additionally, we describe and classify the breeding phenology of the anuran community in eastern Texas. Together, these analyses allow us to understand how abiotic factors, breeding strategy, and breeding phenology work in concert to determine the composition of anuran communities at breeding sites in a seasonal environment.

METHODS

Study System

Our study sites were located in eastern Texas, USA at approximately 31° N latitude. This region experiences occasional freezing temperatures that fall below the known thermal limits for anuran reproduction (Zimmitti, 1999) due to southward movement of arctic air masses or cold fronts, yet is far enough south to have occasional warm winter days and extremely hot summers (Chang et al., 1996). In winter, cold air masses often

meet warm moist air pushed up from the Gulf of Mexico resulting in frequent rain events, placing the study sites in one of the wettest regions of Texas (Bomar, 1995). The region is far enough from the Gulf of Mexico so as not to be severely affected by high winds associated with tropical storms and hurricanes, but massive rainfall events from these major storms often occur during the summer. Rainfall is generally abundant (see Chang et al., 1996) with occasional flooding events; however, prolonged periods of no precipitation are common, providing a range of conditions for anuran reproduction.

Anuran Vocalization Recordings

We collected audio recordings of nocturnally vocalizing anurans at eight study sites. Four of the study sites were in the Davy Crockett National Forest (DCNF) in Houston County and four in the Stephen F. Austin Experimental Forest (SFAEF) in Nacogdoches County in eastern Texas. Each study site was located in secondary growth upland loblolly (*Pinus taeda*) and shortleaf (*P. echinata*) pine forest. Each recording site was adjacent to a pond constructed for wildlife habitat improvement. Ponds in the DCNF were built in 1992 and ranged in size from 900 m^2 to 2000 m^2 surface area with a maximum depth of 2.5 m. Ponds in the SFAEF were built in 2000 and were 500–600 m^2 surface area and had a maximum depth of 1 m.

Based on personal experience, we expected all common anuran species in the Piney Woods region of eastern Texas to be detected by our automated recording devices (described below) except for *Scaphiopus holbrookii* because of their known affinity for extremely ephemeral breeding sites (Garrett and Barker, 1987). Therefore, in addition to the eight ponds that we surveyed with recording equipment, we also monitored a known breeding site for *S. holbrookii* within the city limits of Nacogdoches, in Nacogdoches County, Texas. The Nacogdoches site is on well-drained soil and typically does not hold water for any appreciable length of time, except for instances of flood-level rain events. The dimensions of this ephemeral pond are approximately 600 m^2 surface area with a max-

imum depth of 0.5 m. No recording device was used at this site because of its extremely ephemeral nature. Instead, the site was visited each evening following any rain that exceeded 3 cm in a 24-h period to survey for any anuran vocalizations.

The automated recorders used in this study, termed frogloggers, were based on a modified version designed by Peterson and Dorcas (1994). The components were three D-cell batteries, a six-cycle timer (six on/off cycles per 24 h), a voice clock (talking watch), a standard cassette recorder, and a condenser microphone. The components were linked via a circuit board that allowed the timer to activate and deactivate the recorder, microphone, and voice clock simultaneously at predetermined time intervals. All components, except the microphone, were housed in a weatherproof military ammunition box. The microphone wire protruded from a hole drilled in the side of the box that was sealed with silicon.

Frogloggers were placed within 2 m of the pond edge (one per pond) with the microphone oriented towards the center of the pond. Frogloggers were used to record calling frogs simultaneously at each site continuously for two years, from 1 January 2001 through 31 December 2002. The frogloggers were set to record for one minute at the start of each hour from 2100 h to 0200 h Central DST, for a total of six minutes per night. Sampling six times throughout each night should minimize daily variation in calling activity and increase the probability of detecting all species vocalizing at a pond (Bridges and Dorcas, 2000; Mohr and Dorcas, 1999; Murphy, 1999). All species expected to occur in the study areas were detected between 2100 h and 0200 h (D. Saenz, personal observations), confirming the appropriateness of the sampling period. Tapes were retrieved weekly, vocalizations were identified to species, and the number of calling individuals was estimated. When the number of frogs calling was ≤4, we felt confident that we could record the exact number of calling individuals of a given species. The number of species calling at one time did not affect our ability to count individuals of each species. However, when >4 individuals of a given species were calling,

it was not possible to determine the exact number; therefore, we assigned a value of 5. A maximum value of 30 (summed across the six sampling minutes) could be scored as an index of call intensity for a single species in a given night.

Temperature, Rainfall, and Day Length

Variation in calling behavior is known to occur over very small spatial scales that also vary in climatic conditions (Obert, 1975; Runkle et al., 1994). Therefore, we measured temperature and daily rainfall at each site to obtain site-specific data for assessing climatic effects on anuran vocalization behavior (Corn, 2003).

Temperature was measured to the nearest 0.01 C hourly using HOBO® Pro series data loggers (Onset Computer Corporation, Pocasset, Massachusetts) attached to trees 2 m above ground. A plastic cover was used to prevent direct sunlight and precipitation from contacting the logger. To compute the number of hours of daylight according to Julian date and latitude, we used 31° N latitude for all our study sites (http://www.qpais.co.uk/modb-iec/dayleng.htm).

Daily rainfall was measured in both the DCNF and the SFAEF to the nearest 0.1 mm. The rain gauge in the DCNF was monitored daily by Davy Crockett National Forest personnel and was located 5 km from the farthest sampling site. The rain gauge at the SFAEF was monitored daily and was <2 km from any anuran sampling sites.

Statistical Analyses

We used multiple logistic regression to test the statistical hypotheses of no relationships between daily anuran calling activity (0 = no calling or 1 = calling) and air temperature at 2100 DST to the nearest 0.01 C and daily rainfall to the nearest 0.1 mm. Because daily calling samples at a given pond were autocorrelated, we used a first order autoregressive GEE model, (Proc GENMOD [SAS 1996]), for all regression analyses with α set to 0.05. Because some anuran species called for several days after a rain event, it was not clear if species were responding to precipitation immediately or if there was a lag or build-up in calling activity. Therefore, we tested for

the association between rain events and calling activity for each species, using a one-day lag period and two-day lag period. For example, the one-day lag modeled daily rainfall from the prior day and the two-day lag used rainfall data from two days prior to the calling data.

By using multivariate logistic regression models we tested the hypotheses of no significant association between each variable (i.e., abiotic factors, lag periods) and whether the species was calling or not. Additionally, the slope estimate indicates if the relationship is positive or negative. The odds ratio reflects the predicted effect of the variable on the odds of the species calling. An odds ratio of 1.00 would indicate zero change in the odds of calling, for example, while a ratio of 1.50 would indicate that 1 unit increase in the variable results in a 50% increase in the odds of calling.

The odds of calling was nearly constant at temperatures ≥25 C for most summer-breeding species, even considering the majority of sampling days had temperatures ≥25 C. Thus, in addition to the overall regressions, separate analyses were performed for the summer-breeding species for temperatures ≤24 C and ≥25 C. The separate analyses allowed better ability to detect the influence of temperature on odds of calling (Allison, 1999).

To determine the probability of a species calling on nights at a given temperature we first determined the range of available air temperatures at 2100 hours to the nearest 1.0 C for each individual species during their respective breeding seasons. Then for each 1.0 C increment in temperature, we determined the number of nights that a species called or did not call, and we calculated the probability of calling as the percentage of nights where each species was calling at a given temperature. For example, if the air temperature was 15 C on 10 nights during a species' breeding season and the species was detected calling on 5 of those nights, then the species would have a 50% probability of calling at 15 C.

Analyses of calling activity were conducted independently for each species because each species has its own breeding season. We

TABLE 1.—Calling activity of 13 species of anurans in eastern Texas by month from 2001 to 2002. The symbol X indicates that the species was observed calling in the month indicated. Blank cells represent no calling detected in that month for a given species.

Species	Month											
	Jan	Feb	Mar	Apr	May	Jun	Jul	Aug	Sep	Oct	Nov	Dec
Bufonidae												
B. valliceps				X	X	X	X					
B. woodhousii			X	X	X	X	X	X	X			
Hylidae												
A crepitans				X	X	X	X	X				
H. cinerea				X	X	X	X	X				
H. vers./chryso.	X		X	X	X	X	X	X	X			
P. crucifer	X	X	X	X								
P. triseriata	X	X	X									
Microhylidae												
G. carolinensis				X	X	X	X		X			
Pelobatidae												
S. holbrookii		X		X								
Ranidae												
R. catesbeiana				X	X	X	X	X		X		
R. clamitans			X	X	X	X	X	X	X	X	X	
R. palustris	X	X	X	X								
R. sphenocephala	X	X	X	X	X	X	X	X	X	X	X	X

defined a species' breeding season by the number of days from the earliest date to the latest date the species was detected calling over the two-year period. For example, the earliest date we detected *Pseudacris triseriata* was Julian day 24 and the latest date was Julian day 89; therefore analyses for this species included data only for 66 d, a very short breeding season in our system. The species with the longest breeding season was *R. sphenocephala*, which called all months of the year; therefore data from every day of the two-year period were analyzed. For this species only, we categorized the data according to three seasons, Julian days 1–122 (spring), 123–244 (summer), and 245–365 (fall), respectively.

RESULTS

We detected 13 anuran species representing 5 families of frogs and toads at our nine survey sites (Table 1). There were two members of the Family Bufonidae: *Bufo valliceps* and *B. woodhousii*, five Hylidae: *Acris crepitans*, *Hyla cinerea*, *H. versicolor/chrysoscelis*, (we combined data for these two cryptic species and refer to them collectively as *H. vers./chryso.* throughout this study because of the difficulty in distinguishing the species from one another reliably from our recordings), *Pseudacris crucifer*, and *P. triseriata*, one Pelobatidae: *Scaphiopus holbrookii*, one Microhylidae: *Gastrophryne carolinensis*, and four Ranidae: *R. catesbeiana*, *R. clamitans*, *R. palustris*, and *R. sphenocephala*. As expected, *S. holbrookii* was only detected at the extremely ephemeral site in Nacogdoches. *Acris crepitans* and *R. palustris* were both only detected at two ponds in the DCNF, and the remaining 10 species were detected at both the SFAEF and the DCNF sites. We only failed to detect one species known from our research area, *R. areolata*. However, this was not unexpected because the species has become extremely rare in Texas (Dixon, 2000).

Seasonal and Daily Call Patterns

There was large seasonal variation in calling activity among species. At the extremes, *S. holbrookii* was heard calling on only two nights of the two-year study while *R. sphenocephala* was detected calling every month of the year. *Rana palustris* and the two *Pseudacris* species called only during cooler months while the remaining eight species called primarily during warmer months (Table 1).

Although *R. sphenocephala* called every month, daily call patterns were variable

(Fig. 1). *Rana sphenocephala* was occasionally detected in large numbers and sometimes was not detected for periods of several days to weeks at a time.

Rana palustris and *P. triseriata* called only during a narrow window during the winter (Fig. 1). *Pseudacris crucifer* had a more extensive breeding season and nights with higher calling intensity than the other two winter breeding species (Fig. 1). There also was considerable variation in daily call patterns among the eight species that breed in the warmer months. Duration of calling was much longer and more consistent for *R. clamitans*, *A. crepitans*, and *H. vers./chryso.* (Fig. 1), whereas the calling patterns of the remaining five warm-season species (*H. cinerea*, *R. catesbeiana*, *B. valliceps*, *B. woodhousii*, and *G. carolinensis*) exhibited spikes in calling activity and extended periods of little to no detectable vocalization (Fig. 1). Finally, while *S. holbrookii* was detected on only two nights during the study, >5 individuals were heard calling simultaneously at the breeding site on both occasions.

Temperature, Rainfall, and Day Length

The mean air temperature at 2100 h during this study was 18.1 C with a low of −0.3 C and a high of 29.3 C (Fig. 2). The SFAEF (310 cm rain during the study) experienced over 50% more rain than the DCNF (200 cm rain during the study) over the two-year period (Fig. 3) despite their close proximity to one another, approximately 30 km. Temperature and rainfall varied inversely and were strongly influenced by season. Rainfall was more frequent from December through March, with detectable precipitation occurring on 22% of the days. Winter rain events and temperature are associated with periodic frontal systems (Bomar, 1995; Fig. 3). Warm-season rainfall events were less frequent, with detectable precipitation occurring approximately 17% of the days, April through August. Summer rains were associated with isolated thunderstorms or tropical weather systems (Fig. 3).

There was a clear association between day length and temperature, with temperature increases lagging 4–6 weeks behind the day with the most daylight (Chang et al., 1996).

Although air temperatures warmed gradually during both winter and summer, winter-breeding species experienced greater daily temperature fluctuations due to irregular cold fronts that dramatically dropped the temperature. Summertime air temperatures were less variable from one day to the next because summertime frontal systems had less effect on air temperature.

Associations Between Temperature and Calling

There was a wide range of associations between calling activity and temperature in this anuran assemblage. *Rana sphenocephala* called over the widest range of temperatures (Fig. 4), including the maximum and minimum temperatures recorded for any species detected calling. *Rana sphenocephala* called when the 2100 h air temperature was 4 C, the lowest temperature at which any species was observed calling in this study, and was also detected calling on nights when the 2100 h temperature was 29 C, the highest recorded temperature. Both and *P. crucifer* and *P. triseriata* called at temperatures ranging from 5 C up to 22 C (Fig. 4). *Rana palustris* had a tendency to call at intermediate temperatures (10 to 22 C) in relation to the other winter and summer breeding species (Fig. 4).

When temperatures exceeded 15 C, the probability of detecting calling *R. clamitans*, a summer-breeding species, increased by over 50% (Fig. 4). *Acris crepitans* exhibited a similar calling pattern. It had ≥50% probability of calling when temperatures exceeded 20 C (Fig. 4).

Rana catesbeiana, *B. valliceps*, and *G. carolinensis* all called sporadically at relatively warm temperatures. The probability of any of these species calling was <20% at any temperature (Fig. 4). The pattern was similar for *B. woodhousii*, *H. vers./chryso.*, and *H. cinerea* except they tended to have a slightly higher probability of calling (Fig. 4). On the two nights *S. holbrookii* was observed calling, temperatures were 17 C (27 February 2001) and 20 C (7 April 2002).

Abiotic Correlates of Calling Activity

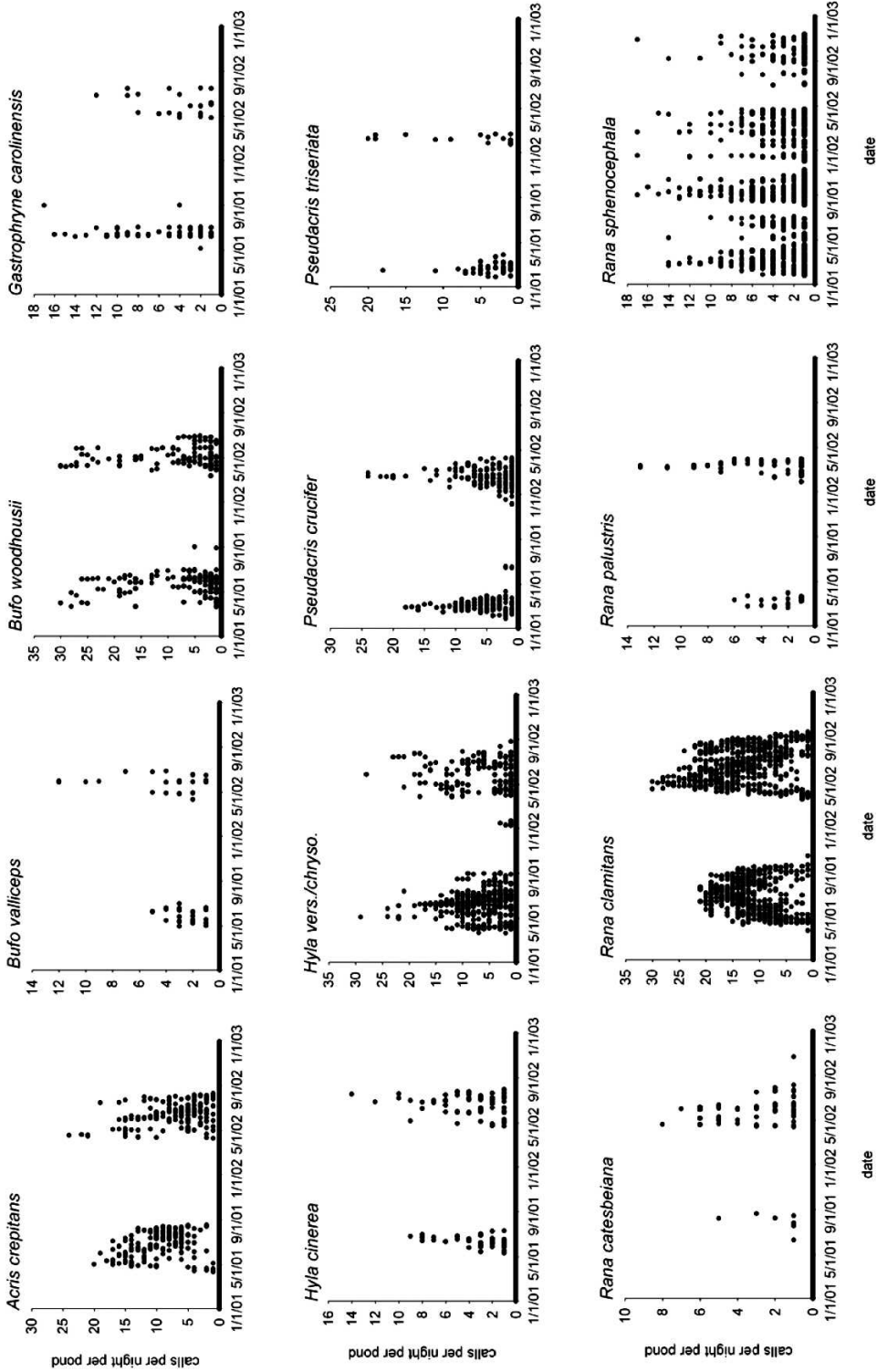The logistic regressions revealed significant associations among abiotic variables and

FIG. 1.—Call intensity scores for 12 species of anurans each night at eight ponds during 2001 and 2002. Four ponds were located in the Davy Crockett National Forest in Houston County, Texas, and four were in the Stephen F. Austin Experimental Forest in Nacogdoches County, Texas. *Scaphiopus holbrookii* was excluded because they were only heard calling on two occasions during the study.
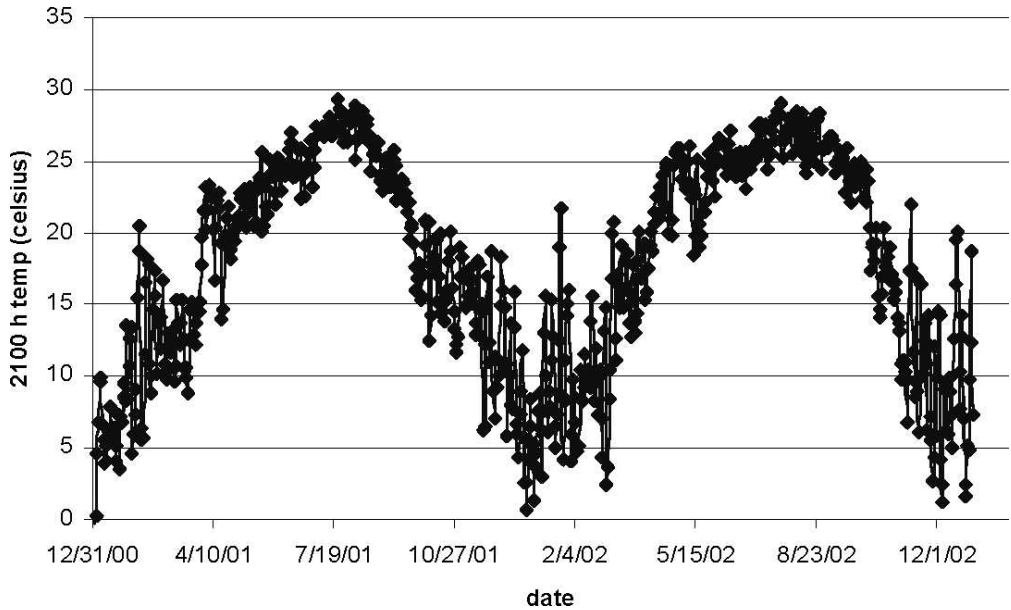
Fɪɢ. 2.—Mean nightly temperatures at 2100 hrs for eight sites in Nacogdoches County, Texas and Houston County, Texas during 2001and 2002.

calling activity, and the relationships were complex and distinct for different species. In spring (Julian day 1–122), calling by *R. sphenocephala* was significantly and positively associated with temperature and rain and the 1-day and 2-day lags after a rainfall event (Table 2). In summer (Julian days 123–244), calling by *R. sphenocephala* was positively associated only with the 2-day lag after rains; temperature and rainfall were no longer significant predictors of calling. In the fall (Julian day 245–365), calling by *R. sphenocephala* was associated with temperature and both 1-day and 2-day lags, but not rainfall.

Calling activity in the winter-breeding species, *P. triseriata* and *R. palustris*, was statistically and positively associated with temperature; rainfall and lags after rainfall were not significant predictors of calling for these species (Tables 3, 4). However, temperature, rainfall, and 1-day lag were all significant, positive predictors of calling by *P. crucifer* (Table 5).

There were interesting differences in abiotic predictors of calling activity among the eight summer-breeding species. Separate analyses for all temperatures, for days ≤24 C, and days >24 C reveal temperature

thresholds for calling (see Fig. 4). In general, calling by species that use permanent water was negatively associated with rainfall. Calling in *R. catesbeiana* with all temperatures included in the analysis was negatively associated with rainfall; one unit increase in rainfall predicted a 43% decrease in odds of detecting calling activity (Table 6). In the analysis using only data from nights ≤24 C, calling was positively associated with temperature, and negatively associated with rainfall and a 1-day lag after rain. Above 25 C, calling was negatively associated with rain.

For *R. clamitans*, another species that uses permanent water sites, temperature and a one-day lag in rainfall were significantly and positively associated with calling in the overall model (Table 7). Below 24 C, however, temperature was the only significant predictor of calling. Above 24 C, there was a negative association with rain, but temperature was not a good predictor of calling. Calling in the hylids that used permanent water, *A. crepitans* and *H. cinerea*, was positively associated with temperature in the overall models (Tables 8, 9). Calling in *Acris crepitans* was negatively associated with lags in rain and positively associated with temperature during days
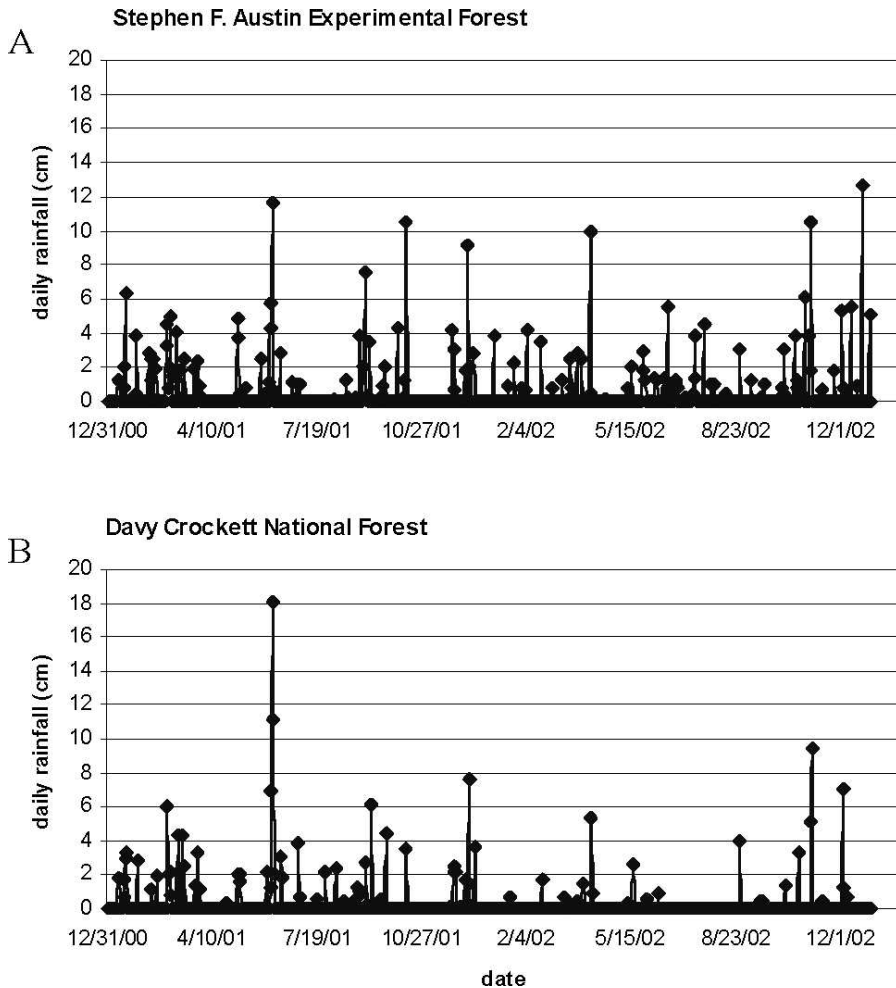
FIG. 3.—Daily rainfall in (A) the Stephen F. Austin Experimental Forest in Nacogdoches County, Texas, and (B) the Davy Crockett National Forest in Houston County, Texas during 2001 and 2002.

≤24 C. Above 24 C, however, calling by *A. crepitans* was negatively associated with rain only (Table 8). Only increasing temperature significantly predicted calling by *H. cinerea* in the overall model and at temperatures ≤24 C; calling by this species was not predictable when temperature was >24 C (Table 9).

Calling by *H. vers./chryso.*, *B. valliceps*, *B. woodhousii*, and *G. carolinensis*, the summer-breeding species that use ephemeral breeding sites, exhibited a very different calling response to rain than species that used permanent water. Calling by all four species was positively and significantly associated with lags following rain, regardless of temperature

(Tables 10, 11, 12, 13). Calling was positively and significantly associated with air temperature ≤ 24 C and negatively associated when temperature exceeded 24 C.

DISCUSSION

Although air temperature and rainfall were clearly important factors driving calling activity of anurans in eastern Texas, similarities and differences among species' responses to these abiotic factors resulted in seasonal patterns of calling among the 13 species present. Oseen and Wassersug (2002) reported water temperature and time of day were the most
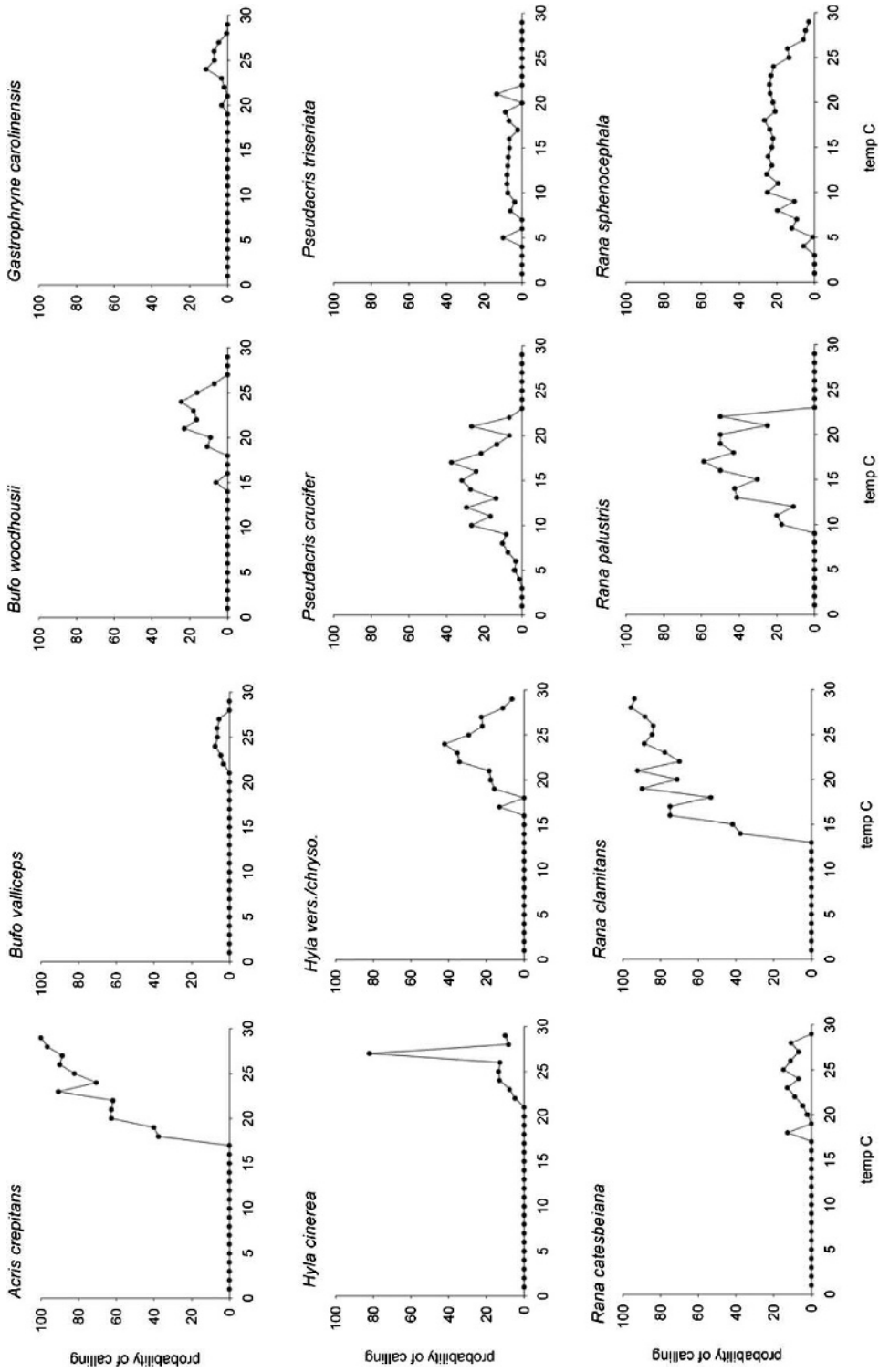
Fig. 4.—Probability of 12 species of anurans calling over the range of observed temperatures at 2100 h during 2001and 2002 in Nacogdoches County, Texas, and Houston County, Texas. *Scaphiopus holbrookii* was excluded because they were only heard calling on two occasions during the study.

TABLE 2.—Results of multiple logistic regression model for *Rana sphenocephala*. The probability of *R. sphenocephala* calling was modeled with the following variables: 2100 h air temperature, daily rainfall, one-day and two-day lag in rainfall. Since *Rana sphenocephala* called year-round, analyses were conducted separately for the spring, summer, and fall seasons.

Model	Variable	Estimate[1]	SE[2]	χ^{2}[3]	$P > \chi^{2}$[4]	Odds ratio
J-day 1–122						
Spring	Intercept	−1.85	0.43			
	Temp	0.07	0.02	13.24	<0.001	1.08
	Rain[5]	0.17	0.04	14.48	<0.001	1.18
	Lag 1[6]	0.19	0.03	38.05	<0.001	1.21
	Lag 2[7]	0.29	0.06	21.75	<0.001	1.33
J-day 123–244						
Summer	Intercept	1.28	2.42			
	Temp	−0.12	0.09	1.81	0.178	0.89
	Rain[5]	0.04	0.04	1.27	0.259	1.04
	Lag 1[6]	0.06	0.03	2.65	0.104	1.06
	Lag 2[7]	0.15	0.03	23.43	<0.001	1.16
J-day 245–365						
Fall	Intercept	−4.55	1.29			
	Temp	0.13	0.04	8.77	0.003	1.14
	Rain[5]	0.08	0.07	1.27	0.261	1.08
	Lag 1[6]	0.21	0.04	29.32	<0.001	1.24
	Lag 2[7]	0.23	0.03	46.39	<0.001	1.26

[1] Estimate of explanatory slope (β_x).
[2] Standard error of slope estimate.
[3] χ^2 statistic testing H_o: slope estimate = 0.
[4] Probability to reject H_o.
[5] Rainfall the day of anuran calls.
[6] Rainfall one day prior to anuran calls.
[7] Rainfall two days prior to anuran calls.

important factors influencing calling activity of anurans at a single pond, and suggested species differed in their responses to these exogenous factors depending on whether they were spring versus summer breeders or whether they were explosive versus prolonged breeders. Our results on call intensity, probability of calling, and predictability of calling based on logistic regressions were in general agreement with the view by Oseen and Wassersug (2002) that calling activity in response to abiotic factors corresponds to the breeding strategies of anurans. However, the pattern in our study was more complex. Calling activity in the eastern Texas anurans was assorted by species that breed only in

TABLE 3.—Results of multiple logistic regression model for *Pseudacris triseriata*. The probability of *Pseudacris triseriata* calling was modeled with the following variables: 2100 h air temperature, daily rainfall, one-day, and two-day lag in rainfall. *Pseudacris triseriata* breeding season was defined as Julian day 24 through 89 based on earliest and latest calling observations during this study.

Model	Variable	Estimate[1]	SE[2]	χ^{2}[3]	$P > \chi^{2}$[4]	Odds ratio
All temps						
	Intercept	−5.01	0.67			
	Temp	0.06	0.01	18.13	<0.001	1.06
	Rain[5]	0.17	0.12	1.94	0.164	1.18
	Lag 1[6]	0.09	0.06	2.09	0.148	1.09
	Lag 2[7]	0.03	0.04	0.33	0.565	1.03

[1] Estimate of explanatory slope (β_x).
[2] Standard error of slope estimate.
[3] χ^2 statistic testing H_o: slope estimate = 0.
[4] Probability to reject H_o.
[5] Rainfall the day of anuran calls.
[6] Rainfall one day prior to anuran calls.
[7] Rainfall two days prior to anuran calls.

TABLE 4.—Results of multiple logistic regression model for *Rana palustris*. The probability of *R. palustris* calling was modeled with the following variables: 2100 h air temperature, daily rainfall, one-day, and two-day lag in rainfall. *Rana palustris* breeding season was defined as Julian day 29 through 92 based on earliest and latest calling observations during this study.

Model	Variable	Estimate[1]	SE[2]	χ^2[3]	$P > \chi^2$[4]	Odds ratio
All temps	Intercept	−4.30	0.68			
	Temp	0.25	0.03	111.71	<0.001	1.28
	Rain[5]	0.08	0.21	0.15	0.697	1.08
	Lag 1[6]	−0.02	0.13	0.03	0.861	0.98
	Lag 2[7]	−0.13	0.13	0.97	0.325	0.88

[1] Estimate of explanatory slope (β_x).
[2] Standard error of slope estimate.
[3] χ^2 statistic testing H_o: slope estimate = 0.
[4] Probability to reject H_o.
[5] Rainfall the day of anuran calls.
[6] Rainfall one day prior to anuran calls.
[7] Rainfall two days prior to anuran calls.

winter, during summer, year-round, or explosive breeding following infrequent large rain events.

Rana sphenocephala was the only year-round caller in the assemblage, and this breeding generalist apparently had a wide range of tolerances for climatic conditions with respect to calling behavior. Calling was cued by rain, temperature, or lags after rain, depending on season. In winter, calling in *R. sphenocephala* was associated with rainy days, but with a 2-day lag during summer. Because rain events were less frequent in summer, this species may have been less active which could have prolonged migration to the ponds from their retreats. Calling in winter by *R. sphenocephala* was also associated with temperature. Cold temperatures did appear to limit calling to some extent, as *R. sphenocephala* only called when temperatures exceeded 3 C. Apparently the summer heat during this study

was never too high for calling by *R. sphenocephala*, as individuals called at the highest recorded temperatures.

Pseudacris crucifer, *P. triseriata*, and *R. palustris* made up the winter-breeding assemblage. Calling in these species was generally intense, of relatively short duration, and positively associated with temperature. Winter air temperatures frequently drop below the apparent lower limit for breeding activity for these species. Therefore, it was not surprising that calling activity of these winter breeders was mostly dependent on nightly air temperature; rainfall was only important to *P. crucifer*. Winter rainfall is common in eastern Texas, and winter precipitation was normal in both 2001 and 2002 (Chang et al., 1996). Breeding sites do not appear to be limited by a lack of water during wet years (D. Saenz, personal observation). It is not known if the winter-breeding species might respond more

TABLE 5.—Results of multiple logistic regression model for *Pseudacris crucifer*. The probability of *Pseudacris crucifer* calling was modeled with the following variables: 2100 h air temperature, daily rainfall, one-day, and two-day lag in rainfall. *Pseudacris crucifer* breeding season was defined as Julian day 339 through 92 based on earliest and latest calling observations during this study.

Model	Variable	Estimate[1]	SE[2]	χ^2[3]	$P > \chi^2$[4]	Odds ratio
All temps	Intercept	−2.05	0.38			
	Temp	0.11	0.02	35.43	<0.001	1.11
	Rain[5]	0.14	0.05	7.54	0.006	1.15
	Lag 1[6]	0.06	0.02	5.91	0.015	1.06
	Lag 2[7]	0.03	0.04	0.90	0.342	1.03

[1] Estimate of explanatory slope (β_x).
[2] Standard error of slope estimate.
[3] χ^2 statistic testing H_o: slope estimate = 0.
[4] Probability to reject H_o.
[5] Rainfall the day of anuran calls.
[6] Rainfall one day prior to anuran calls.
[7] Rainfall two days prior to anuran calls.

TABLE 6.—Results of multiple logistic regression model for *Rana catesbeiana*. The probability of *Rana catesbeiana* calling was modeled with the following variables: 2100 h air temperature, daily rainfall, one-day, and two-day lags in rainfall. *Rana catesbeiana* breeding season was defined as Julian day 104 through 233 based on earliest and latest calling observations during this study. Days 24 C or below at 2100 h were analyzed separately from warmer days because a threshold temperature for calling behavior may occur in summer breeding species. Analyses including all days also were conducted.

Model	Variable	Estimate[1]	SE[2]	χ^{2}[3]	$P > \chi^{2}$[4]	Odds ratio
All temps						
	Intercept	−3.07	1.14			1.04
	Temp	0.04	0.02	2.96	0.086	1.04
	Rain[5]	−0.57	0.09	40.20	<0.001	0.57
	Lag 1[6]	−0.03	0.15	0.06	0.812	0.97
	Lag 2[7]	0.02	0.89	0.04	0.845	1.02
≤24 C						
	Intercept	−6.23	2.28			
	Temp	0.17	0.05	14.48	<0.001	1.19
	Rain[5]	−0.57	0.06	98.90	<0.001	0.57
	Lag 1[6]	−0.35	0.07	25.90	<0.001	0.70
	Lag 2[7]	0.07	0.12	0.38	0.539	1.07
>24 C						
	Intercept	1.75	2.74			
	Temp	−0.15	0.06	6.24	0.125	0.86
	Rain[5]	−0.62	0.17	12.98	<0.001	0.54
	Lag 1[6]	0.09	0.12	0.57	0.452	1.09
	Lag 2[7]	0.03	0.06	0.28	0.599	1.03

[1] Estimate of explanatory slope (β_x).
[2] Standard error of slope estimate.
[3] χ^2 statistic testing H_o: slope estimate = 0.
[4] Probability to reject H_o.
[5] Rainfall the day of anuran calls.
[6] Rainfall one day prior to anuran calls.
[7] Rainfall two days prior to anuran calls.

TABLE 7.—Results of multiple logistic regression model for *Rana clamitans*. The probability of *Rana clamitans* calling was modeled with the following variables: 2100 h air temperature, daily rainfall, one-day, and two-day lags in rainfall. *Rana clamitans* breeding season was defined as Julian day 88 through 261 based on earliest and latest calling observations during this study. Days 24 C or below at 2100 h were analyzed separately from warmer days because a threshold temperature for calling behavior may occur in summer breeding species. Analyses including all days also were conducted.

Model	Variable	Estimate[1]	SE[2]	χ^{2}[3]	$P > \chi^{2}$[4]	Odds ratio
All temps						
	Intercept	−1.22	0.58			
	Temp	0.12	0.06	4.39	0.036	1.12
	Rain[5]	−0.07	0.08	0.67	0.413	0.93
	Lag 1[6]	0.06	0.03	4.62	0.032	1.06
	Lag 2[7]	−0.03	0.06	0.22	0.641	0.97
≤24 C						
	Intercept	−2.30	0.81			
	Temp	0.17	0.07	6.54	0.011	1.19
	Rain[5]	−0.06	0.09	0.55	0.459	0.94
	Lag 1[6]	0.02	0.02	0.71	0.401	1.02
	Lag 2[7]	0.01	0.05	0.00	0.984	1.00
>24 C						
	Intercept	0.34	2.23			
	Temp	0.05	0.14	0.11	0.744	1.05
	Rain[5]	−0.19	0.09	4.64	0.031	0.83
	Lag 1[6]	0.26	0.16	2.64	0.104	1.30
	Lag 2[7]	−0.02	0.06	0.08	0.781	0.98

[1] Estimate of explanatory slope (β_x).
[2] Standard error of slope estimate.
[3] χ^2 statistic testing H_o: slope estimate = 0.
[4] Probability to reject H_o.
[5] Rainfall the day of anuran calls.
[6] Rainfall one day prior to anuran calls.
[7] Rainfall two days prior to anuran calls.

TABLE 8.—Results of multiple logistic regression model for *Acris crepitans*. The probability of *Acris crepitans* calling was modeled with the following variables: 2100 h air temperature, daily rainfall, one-day, and two-day lags in rainfall. *Acris crepitans* breeding season was defined as Julian day 102 through 226 based on earliest and latest calling observations during this study. Days 24 C or below at 2100 h were analyzed separately from warmer days because a threshold temperature for calling behavior may occur in summer breeding species. Analyses including all days also were conducted.

Model	Variable	Estimate[1]	SE[2]	χ^2[3]	$P > \chi^2$[4]	Odds ratio
All temps						
	Intercept	−6.36	1.17			
	Temp	0.33	0.06	36.5	<0.001	1.40
	Rain[5]	−0.20	0.06	12.31	<0.001	0.82
	Lag 1[6]	0.01	0.10	0.00	0.984	1.00
	Lag 2[7]	0.14	0.10	2.02	0.155	1.15
≤24 C						
	Intercept	−11.70	4.86			
	Temp	0.47	0.22	4.62	0.032	1.59
	Rain[5]	−0.09	0.05	3.23	0.072	0.92
	Lag 1[6]	−0.29	0.01	54.36	<0.001	0.75
	Lag 2[7]	−0.28	0.07	18.01	<0.001	0.75
>24 C						
	Intercept	−5.58	1.77			
	Temp	0.30	0.18	2.68	0.102	1.35
	Rain[5]	−0.20	0.05	18.16	<0.001	0.82
	Lag 1[6]	0.02	0.11	0.03	0.867	1.02
	Lag 2[7]	0.12	0.14	0.71	0.398	1.12

[1] Estimate of explanatory slope (β_x).
[2] Standard error of slope estimate.
[3] χ^2 statistic testing H_o: slope estimate = 0.
[4] Probability to reject H_o.
[5] Rainfall the day of anuran calls.
[6] Rainfall one day prior to anuran calls.
[7] Rainfall two days prior to anuran calls.

TABLE 9.—Results of multiple logistic regression model for *Hyla cinerea*. The probability of *Hyla cinerea* calling was modeled with the following variables: 2100 h air temperature, daily rainfall, one-day, and two-day lags in rainfall. *Hyla cinerea* breeding season was defined as Julian day 113 through 211 based on earliest and latest calling observations during this study. Days 24 C or below at 2100 h were analyzed separately from warmer days because a threshold temperature for calling behavior may occur in summer breeding species. Analyses including all days also were conducted.

Model	Variable	Estimate[1]	SE[2]	χ^2[3]	$P > \chi^2$[4]	Odds ratio
All temps						
	Intercept	−5.90	0.96			
	Temp	0.15	0.05	8.76	0.003	1.16
	Rain[5]	0.02	0.03	0.50	0.478	1.02
	Lag 1[6]	0.09	0.06	2.35	0.125	1.09
	Lag 2[7]	−0.02	0.03	0.58	0.446	0.98
≤24 C						
	Intercept	−14.75	1.41			
	Temp	0.51	0.06	19.77	<0.001	1.67
	Rain[5]	0.01	0.04	0.04	0.850	1.01
	Lag 1[6]	0.08	0.07	1.52	0.220	1.09
	Lag 2[7]	−0.03	0.03	1.00	0.316	0.97
>24 C						
	Intercept	−0.88	2.66			
	Temp	−0.06	0.11	0.24	0.623	0.95
	Rain[5]	−0.03	0.06	0.36	0.551	0.97
	Lag 1[6]	0.07	0.07	0.92	0.337	1.07
	Lag 2[7]	0.02	0.06	0.09	0.758	1.02

[1] Estimate of explanatory slope (β_x).
[2] Standard error of slope estimate.
[3] χ^2 statistic testing H_o: slope estimate = 0.
[4] Probability to reject H_o.
[5] Rainfall the day of anuran calls.
[6] Rainfall one day prior to anuran calls.
[7] Rainfall two days prior to anuran calls.

TABLE 10.—Results of multiple logistic regression model for *Hyla vers./chryso*. The probability of *Hyla vers./chryso.* calling was modeled with the following variables: 2100 h air temperature, daily rainfall, and one-day, and two-day lags in rainfall. *Hyla vers./chrys.* breeding season was defined as Julian day 88 through 246 based on earliest and latest calling observations during this study. Days 24 C or below at 2100 h were analyzed separately from warmer days because a threshold temperature for calling behavior may occur in summer breeding species. Analyses including all days also were conducted.

Model	Variable	Estimate[1]	SE[2]	χ^2[3]	$P > \chi^2$[4]	Odds ratio
All temps						
	Intercept	−0.99	0.82			
	Temp	0.02	0.03	0.30	0.585	1.02
	Rain[5]	0.02	0.03	6.90	0.009	1.20
	Lag 1[6]	0.10	0.07	2.02	0.155	1.11
	Lag 2[7]	0.14	0.03	21.62	<0.001	1.15
≤24 C						
	Intercept	−4.75	1.02			
	Temp	0.26	0.03	6.87	<0.001	1.25
	Rain[5]	0.13	0.09	1.42	0.156	1.12
	Lag 1[6]	0.09	0.10	0.92	0.355	1.10
	Lag 2[7]	0.12	0.05	2.57	0.010	1.11
>24 C						
	Intercept	8.10	1.98			
	Temp	−0.34	0.08	20.88	<0.001	0.71
	Rain[5]	0.11	0.06	3.08	0.079	1.11
	Lag 1[6]	0.05	0.08	0.45	0.500	1.05
	Lag 2[7]	0.21	0.05	20.07	<0.001	1.24

[1] Estimate of explanatory slope (β_x).
[2] Standard error of slope estimate.
[3] χ^2 statistic testing H_o: slope estimate = 0.
[4] Probability to reject H_o.
[5] Rainfall the day of anuran calls.
[6] Rainfall one day prior to anuran calls.
[7] Rainfall two days prior to anuran calls.

TABLE 11.—Results of multiple logistic regression model for *Bufo valliceps*. The probability of *Bufo valliceps* calling was modeled with the following variables: 2100 h air temperature, daily rainfall, one-day, and two-day lags in rainfall. *Bufo valliceps* breeding season was defined as Julian day 92 through 183 based on earliest and latest calling observations during this study. Days 24 C or below at 2100 h were analyzed separately from warmer days because a threshold temperature for calling behavior may occur in summer breeding species. Analyses including all days also were conducted.

Model	Variable	Estimate[1]	SE[2]	χ^2[3]	$P > \chi^2$[4]	Odds ratio
All temps						
	Intercept	−8.93	0.83			
	Temp	0.22	0.04	32.31	<0.001	1.25
	Rain[5]	−0.05	0.01	14.75	<0.001	0.95
	Lag 1[6]	0.06	0.01	23.92	<0.001	1.06
	Lag 2[7]	0.08	0.03	5.44	0.020	1.08
≤24 C						
	Intercept	−10.21	0.63			
	Temp	0.27	0.04	54.10	<0.001	1.31
	Rain[5]	−0.08	0.02	25.99	<0.001	0.92
	Lag 1[6]	0.09	0.02	26.75	<0.001	1.09
	Lag 2[7]	0.07	0.04	3.40	0.065	1.07
>24 C						
	Intercept	−11.08	4.99			
	Temp	0.27	0.19	2.18	0.140	1.31
	Rain[5]	−0.06	0.01	18.49	<0.001	0.94
	Lag 1[6]	0.08	0.01	61.32	<0.001	1.08
	Lag 2[7]	1.12	0.08	2.24	0.135	1.12

[1] Estimate of explanatory slope (β_x).
[2] Standard error of slope estimate.
[3] χ^2 statistic testing H_o: slope estimate = 0.
[4] Probability to reject H_o.
[5] Rainfall the day of anuran calls.
[6] Rainfall one day prior to anuran calls.
[7] Rainfall two days prior to anuran calls.

TABLE 12.—Results of multiple logistic regression model for *Bufo woodhousii*. The probability of *Bufo woodhousii* calling was modeled with the following variables: 2100 h air temperature, daily rainfall, one-day, and two-day lags in rainfall. *Bufo woodhousii* breeding season was defined as Julian day 73 through 245 based on earliest and latest calling observations during this study. Days 24 C or below at 2100 h were analyzed separately from warmer days because a threshold temperature for calling behavior may occur in summer breeding species. Analyses including all days also were conducted.

Model	Variable	Estimate[1]	SE[2]	χ^2[3]	$P > \chi^2$[4]	Odds ratio
All temps						
	Intercept	−1.88	0.50			
	Temp	−0.01	0.01	0.01	0.925	0.99
	Rain[5]	0.21	0.08	7.94	0.005	1.24
	Lag 1[6]	−0.02	0.02	0.99	0.321	0.98
	Lag 2[7]	0.11	0.07	2.74	0.098	1.12
≤24 C						
	Intercept	−8.36	0.91			
	Temp	0.33	0.03	91.68	<0.001	1.38
	Rain[5]	0.25	0.06	17.75	<0.001	1.28
	Lag 1[6]	−0.38	0.12	9.59	0.002	0.69
	Lag 2[7]	0.25	0.10	5.94	0.015	1.29
>24 C						
	Intercept	49.98	6.62			
	Temp	−2.02	0.26	58.43	<0.001	0.13
	Rain[5]	0.03	0.22	0.03	0.873	1.04
	Lag 1[6]	−0.32	0.44	0.52	0.472	0.73
	Lag 2[7]	−1.57	0.83	3.60	0.058	0.21

[1] Estimate of explanatory slope (β_x).
[2] Standard error of slope estimate.
[3] χ^2 statistic testing H_o: slope estimate = 0.
[4] Probability to reject H_o.
[5] Rainfall the day of anuran calls.
[6] Rainfall one day prior to anuran calls.
[7] Rainfall two days prior to anuran calls.

to rain during drought years. Marsh (2000) found breeding activity in a tropical frog was correlated with rain in a dry year, but rain was not important in a wet year. Although we expect a similar response could occur in the eastern Texas community, it is also clear that temperature was the critical abiotic correlate of calling in winter-breeding anurans in eastern Texas.

The summer-breeding assemblage of eight species could be separated into species that used permanent water for breeding sites and those that used ephemeral sites. Although calling in summer-breeding species was apparently not constrained by temperature as in the winter species, there did appear to be a threshold temperature above which calling activity was most likely to occur. Calling by all the summer breeders was positively influenced by temperature when nightly temperatures were ≤24 C.

Rana catesbeiana, *R. clamitans*, *A. crepitans*, and *H. cinerea* used permanent water and were also prolonged breeders. Calling in

these species was negatively associated with, or not influenced by rain. Conversely, the summer-breeding species that used ephemeral sites, *B. valliceps*, *B. woodhousii*, *H. vers./chryso.*, and *G. carolinensis*, were positively associated with rain and lags after rainfall. Desiccation is a known risk to larval anurans that use ephemeral breeding sites (Dayton and Fitzgerald, 2001). Hence, it was not unexpected that rainfall had a very strong positive effect on species that typically breed in ephemeral pools.

Ephemeral breeding species are often characterized by explosive breeding events (Oseen and Wassersug, 2002), whereas permanent pond breeders tend to exhibit prolonged breeding (Oseen and Wassersug, 2002; Wells, 1977). Oseen and Wassersug (2002) found prolonged breeders were more sensitive to weather than explosive breeders. They reasoned that once explosive breeders begin calling, they were less responsive to their abiotic environment because their breeding period is short and intense. Conversely,

TABLE 13.—Results of multiple logistic regression model for *Gastrophryne carolinensis*. The probability of *Gastrophryne carolinensis* calling was modeled with the following variables: 2100 h air temperature, daily rainfall, one-day, and two-day lags in rainfall. *Gastrophryne carolinensis* breeding season was defined as Julian day 119 through 245 based on earliest and latest calling observations during this study. Days 24 C or below at 2100 h were analyzed separately from warmer days because a threshold temperature for calling behavior may occur in summer breeding species. Analyses including all days also were conducted.

Model	Variable	Estimate[1]	SE[2]	χ^2[3]	$P > \chi^2$[4]	Odds ratio
All temps						
	Intercept	−2.17	0.71			
	Temp	−0.03	0.03	0.92	0.339	0.97
	Rain[5]	−0.05	0.05	0.82	0.365	0.95
	Lag 1[6]	0.13	0.04	9.29	0.002	1.14
	Lag 2[7]	0.22	0.08	8.02	0.005	1.25
≤ 24 C						
	Intercept	−14.76	2.97			
	Temp	0.52	0.12	18.87	<0.001	1.68
	Rain[5]	−0.12	0.05	7.37	0.007	0.88
	Lag 1[6]	0.16	0.04	13.11	<0.001	1.18
	Lag 2[7]	1.18	0.09	4.25	0.039	1.19
> 24 C						
	Intercept	8.60	2.58			
	Temp	−0.45	0.10	20.06	<0.001	0.63
	Rain[5]	−0.09	0.06	2.62	0.105	0.91
	Lag 1[6]	0.12	0.06	4.15	0.042	1.13
	Lag 2[7]	0.24	0.08	10.40	0.001	1.13

[1] Estimate of explanatory slope (β_x).
[2] Standard error of slope estimate.
[3] χ^2 statistic testing H_o: slope estimate = 0.
[4] Probability to reject H_o.
[5] Rainfall the day of anuran calls.
[6] Rainfall one day prior to anuran calls.
[7] Rainfall two days prior to anuran calls.

prolonged breeders must sustain calling for extended periods. *Rana clamitans* in this study, for example, was detected calling for over 150 consecutive days. The opposing view that explosive breeders should be more sensitive to weather patterns is more prevalent in the literature. Cousineau (1990) and Beveir (1997) each predicted no positive relationship between rainfall and breeding activity in species with prolonged breeding seasons that inhabit relatively wet environments, while others (Blankenhorn, 1972; Wells, 1977) concluded species with explosive breeding showed greater responses to weather than prolonged breeders.

Scaphiopus holbrookii is an explosive breeder that depends on highly ephemeral sites and large rain events. Our findings are consistent with past research that concludes that *S. holbrookii* do not have a well-defined breeding season and only breed during or soon after very heavy rain (Bragg, 1945; Gosner and Black, 1955; Pearson, 1955). Gosner and Black (1955) suggested that in New Jersey a day-long air temperature of 10 C is a lower limit that may control breeding activity early in the year. However, with only two breeding observations in a two-year period in this study, it is impossible to make any more inferences into the effects of temperature on this species.

Clearly, community-level interpretations of how abiotic factors drive breeding behavior by anurans are complex, and our results on calling intensity over a 2-year period serve to illustrate linkages between use of ephemeral versus permanent breeding sites, and prolonged versus explosive breeding. Species in eastern Texas that exhibited explosive breeding (based on call intensity and personal observations) were *S. holbrookii*, *B. valliceps*, *B. woodhousii*, *H. vers./chryso.*, and *G. carolinensis* all of which use ephemeral breeding sites in eastern Texas (Conant and Collins, 1998; Garrett and Barker, 1987; D. Saenz, personal observations). However, they also can use permanent ponds, such as the ones monitored during this study, with the

exception of *S. holbrookii* that only used ephemeral sites. Our results support the view that calling by the explosive-breeding species that use ephemeral sites was clearly associated with rainfall, and more importantly, 1- or 2-day lags after rain. The lags in response time from the onset of rain to the time that ephemeral-breeding anurans were detected calling are presumed to be due to the time it takes individuals to migrate to breeding ponds. Therefore, increase in calling activity was usually detected one or two days after a rain event.

Conversely, prolonged breeders were summer-breeding species that used permanent water. The species that breed in permanent ponds in eastern Texas have relatively long larval periods and spend much of their lives in and around sites that hold water year-round (Conant and Collins, 1998; Garrett and Barker, 1987). These sites do not require daily rainfall to remain wet, and we found rain did not increase the probability of calling. Actually, rainfall reduced the probability of calling the day of the rain event. Hypotheses put forth by other studies have suggested that storm noise might reduce the efficacy of advertisement calls through acoustic interference and males might reduce their calling during heavy rain storms (Dorcas and Foltz, 1991; Henzi et al., 1995). Interestingly, the multiple logistic regressions revealed that for these species in eastern Texas, a negative response to rain occurred only during the day of rain; there was no negative association between rainfall lags and calling.

Temperature and rain clearly play an extremely important role in cuing breeding behavior of eastern Texas anurans, and our results illuminate complex responses of species to abiotic cues for breeding activity among the relatively speciose eastern Texas anuran community. The entire assemblage can be categorized into five classes of calling behavior (*sensu* Bertoluci and Rodrigues, 2002): year-round callers, winter/spring callers, summer callers independent of weather, summer callers dependent on local rain, and large rainfall event callers. These categories are clearly linked to the breeding strategies of species, in particular whether species breed in permanent or ephemeral sites, and if they exhibit explosive or prolonged breeding. Hence patterns of species co-occurrence, i.e. community structure, should be predictable based mostly on breeding strategy and calling behavior. Changing local abiotic conditions presumably cause patterns of species co-occurrence to shift, which could have unknown consequences, such as changes in breeding seasons for some amphibians that could lead to significant changes in population and community structure (Blaustein et al., 2001).

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