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# ARTICLE

# Relative influence of weather and season on anuran calling activity

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**Abstract:** Drivers of anuran reproductive activity may include multiple and independent environmental variables. To determine the relative influence of season, temperature, and precipitation in initiating frog reproduction, we monitored a species-rich frog assemblage in south-central Alabama for 3 years and modeled calling activity of vocalizing males, who call to attract mates. We evaluated multiple hypotheses potentially explaining calling activity and we were able to identify significant influences of calling activity for all 11 anuran species considered in the analysis. Eight species were significantly influenced by month of survey and four of these were influenced by at least one additional environmental variable. In our study, precipitation was relatively unimportant in influencing calling activity, likely because breeding pools at the site are semipermanent and the species we sampled are not generally reliant on ephemeral wetlands. In general, our data suggest that different species within the same wetlands respond to different cues when initiating reproduction and calling activity is largely based on a combination of both environmental conditions and either seasonal changes or endogenous drivers.

*Key words:* Anaxyrus, amphibian, frog, *Lithobates*, *Pseudacris*, toad, vocalization.

**Résumé :** Les moteurs de l'activité de reproduction des anoures peuvent comprendre de multiples variables environnementales indépendantes. Afin de déterminer l'influence relative des saisons, de la température et des précipitations dans le déclenchement de la reproduction des grenouilles, nous avons examiné un assemblage de grenouilles de grande richesse spécifique dans le centre-sud de l'Alabama pendant 3 ans et modélisé l'activité de chant de mâles pour attirer des compagnes. Nous avons évalué plusieurs hypothèses qui pourraient expliquer l'activité de chant et avons pu cerner des influences significatives sur l'activité de chant pour les 11 espèces d'anoures examinées dans le cadre de l'analyse. Huit espèces étaient significativement influencées par le mois d'observation et quatre d'entre eux étaient influencées par au moins une autre variable environnementale. Dans notre étude, l'importance des précipitations était relativement faible pour ce qui est d'influencer l'activité de chant, probablement en raison du fait que les bassins servant à la reproduction en ce site sont semi-permanents et que les espèces échantillonnées n'ont généralement pas besoin de milieux humides éphémères. Nos données donnent généralement à penser que, dans un même milieu humide, le début de la reproduction est déclenché par différents signaux selon l'espèce, et que l'activité de chant dépend en bonne partie d'une combinaison de conditions environnementales d'une part, et de changements saisonniers ou de déclencheurs endogènes, d'autre part. [Traduit par la Rédaction]

*Mots-clés :* Anaxyrus, amphibien, grenouille, *Lithobates*, *Pseudacris*, crapaud, vocalisation.

## Introduction

For vertebrates residing within heterogeneous environments, reproductive activity patterns may be the result of adaptive strategies (Giesel 1976). Reproduction is often energetically expensive (Ryser 1989); therefore, breeding may be timed to coincide with conditions that will maximize fitness (Emerson et al. 2008). As amphibians, most anurans in temperate zones rely on wet conditions for breeding and recruitment of young. For species that breed in permanent or semipermanent wetlands, the reproductive season may occur over relatively long periods of time (Saenz et al. 2006). On the other hand, for species that breed within ephemeral wetlands, reproductive activity may be timed to coincide with rainfall; this ensures the presence of water within breeding habitats and facilitates overland movements with low risk of desiccation (e.g., Jensen et al. 2003).

Some frog species are thought to reproduce in a particular season regardless of weather patterns or climate (prolonged breeders). Other species are thought to breed opportunistically in response to local environmental conditions regardless of timing (explosive breeders; Wells 1977). In temperate regions, anuran reproductive activity may be considered to be influenced primarily by temperature and rainfall (Blair 1961; Oseen and Wassersug 2002). However, either cyclical endogenous drivers or variables that change seasonally, such as photoperiod (e.g., Both et al. 2008; Canavero et al. 2008; Canavero and Arim 2009), are also likely important influences. As a result, species may be designated as midsummer or early-spring breeders, (e.g., Gibbs and Breisch 2001). Few studies have concurrently examined the relative influence of seasonal changes and environmental variables on amphibian reproduction over long temporal scales. Perhaps consequently, contradictory views persist regarding how frogs respond to abiotic cues (Saenz et al. 2006). In addition, frogs may require multiple environmental variables to pass certain thresholds before conditions are considered suitable for reproduction (e.g., Meshaka and Woolfenden 1999).

We sampled anurans for over 3 years in a wetland matrix in south-central Alabama to identify variables influencing reproductive activity. High-quality studies have been conducted to determine the relative influence of seasonal changes and environmental variables on anuran vocalizations (i.e., reproduction; Oseen and Wassersug 2002; Saenz et al. 2006; Steelman and Dorcas 2010). We

**Table 1.** Models (and associated hypotheses) used to describe anuran calling activity within four wetlands of Tuskegee National Forest, Alabama, 2007–2009.

| Model | Hypothesis |
|---|---|
| Null | Calling activity does not change along with recorded variables |
| Year | Calling activity is different between years |
| Month | Calling activity increases or decreases during the year |
| Month² | Calling activity peaks during the year |
| Mean monthly temperature | Calling activity varies due to mean daily temperature within a month |
| Monthly precipitation | Calling activity varies due to total monthly precipitation |
| Daily temperature | Calling activity varies due to temperature on day of survey |
| Daily precipitation | Calling activity varies due to precipitation on day of survey |
| Month + daily temperature | Calling activity increases or decreases during the year and also varies due to temperature on day of survey |
| Month + daily precipitation | Calling activity increases or decreases during the year and also varies due to precipitation on day of survey |
| Month² + daily precipitation | Calling activity peaks during the year and also varies due to precipitation on day of survey |
| Month² + daily temperature | Calling activity peaks during the year and also varies due to temperature on day of survey |
| Time | Calling activity varies between day and night surveys |

attempted to generate novel insights into drivers of anuran calling activity by using multimodel inference and Akaike's information criterion (AIC) (Burnham and Anderson 2002) to evaluate the relative strength of multiple competing hypotheses.

## Materials and methods

### Study site

This research was conducted in Tuskegee National Forest (32.4532°N, 85.644°W), in Macon County, Alabama (Graham et al. 2012). The site is generally mixed-bottomland forest and is located within the Fall Line transitional zone. Three of the studied wetlands were ~2 ha beaver impoundments. The fourth wetland was an oxbow pond approximately the same size as the beaver impoundments, contained evidence of beaver activity, and was characterized by similar vegetation. During the study period, these wetlands were semipermanent to permanent, and some dried substantially or completely during the autumn. However, these ponds are part of a complex of impounded streams, and therefore they were quickly recolonized by predatory fish (for example, flier (*Centrarchus macropterus* Lacepède, 1801), bluegill (*Lepomis macrochirus* Rafinesque, 1819), warmouth (*Lepomis gulosus* (Cuvier, 1829)), and bowfin (*Amia calva* L., 1766); S.P. Graham, unpublished data).

Wetlands contained large areas of open water with emergent vegetation, such as spadderdock (genus *Nuphar* Sm.), sugarcane plumegrass (*Erianthus giganteus* (Walter) Pers.), waterpod (genus *Hydrolea* L.), watershield (*Brasenia schreberi* J.F. Gmel.), bladderwort (genus *Utricularia* L.), and American bur-reed (*Sparganium americanum* Nutt.). Each pond contained zones with patches of common buttonbush (*Cephalanthus occidentalis* L.) or isolated shrub hummocks, usually made up of Virginia sweetspire (*Itea virginica* L.). The only living trees found within the ponds were occasional swamp blackgums (*Nyssa sylvatica* Marsh.).

The margins of these ponds were made up of a shrub–vine thicket, which included coastal doghobble (*Leucothoe axillaris* (Lam.) D. Don), alders (genus *Alnus* Mill.), American snowbell (*Styrax americanus* Lam.), grapes (genus *Vitis* L.), greenbriers (genus *Smilax* L.), and American wisteria (*Wisteria frutescens* (L.) Poir.). Each pond occurred within a matrix of lowland pine – hardwood forest, which contained loblolly pine (*Pinus taeda* L.), pond pine (*Pinus serotina* Michx.), southern red oak (*Quercus falcata* Michx.), water oak (*Quercus nigra* L.), and laurel oak (*Quercus laurifolia* Michx.) as dominants.

### Call surveys

The majority of anuran vocalizations are efforts by males to attract mates (Gerhardt 1994). Vocalizing probability (i.e., the probability an individual will make an auditory noise and is thus available for detection) varies within a year and within a breeding season due to environmental conditions (e.g., Bridges and Dorcas

2000; Kirlin et al. 2006; Smith et al. 2006). Thus, seasonal variation in vocalizations may be best conceptualized as relative availability to be sampled, which is a function of animal behavior (e.g., McClure et al. 2011). Auditory surveys undertaken to detect anuran calls are a common and standardized method of determining the presence of frogs in a particular wetland (Heyer et al. 1994; Dorcas et al. 2009).

Weekly anuran calling surveys were conducted for approximately 2 h, 1–4 h after dark during April through October 2007–2009 on a rotational basis. On the day following night surveys at a given pond, this pond was sampled for approximately 2 h between the hours of 1000 and 1500 such that each wetland was sampled twice per month (one day survey and one night survey), concomitant with visual encounter surveys conducted for other research (Burkett-Cadena et al. 2008, 2011).

We also sampled all wetlands during January–March of 2008, although with some differences in methodology. Specifically, these winter surveys were conducted within 1 h of dark once every 2 weeks at all wetlands. Surveys were conducted for 5 min at each site. To reduce observer bias, the same observer (S.P.G.) conducted all surveys to listen for calling male anurans (Heyer et al. 1994) at the four wetlands.

We focused on detection–nondetection data. Although the sampling methodology differed between the winter and the other surveys, all surveys consisted of the minimum amount of time required to detect most species (e.g., listening for 5 min), which has become the standard used in frog monitoring efforts (Heyer et al. 1994). Thus, each calling survey was treated identically in the data analysis, resulting in a total of 199 surveys per species. Our focus on detection–nondetection data, rather than indices of abundance, allowed us to limit bias between the two protocols.
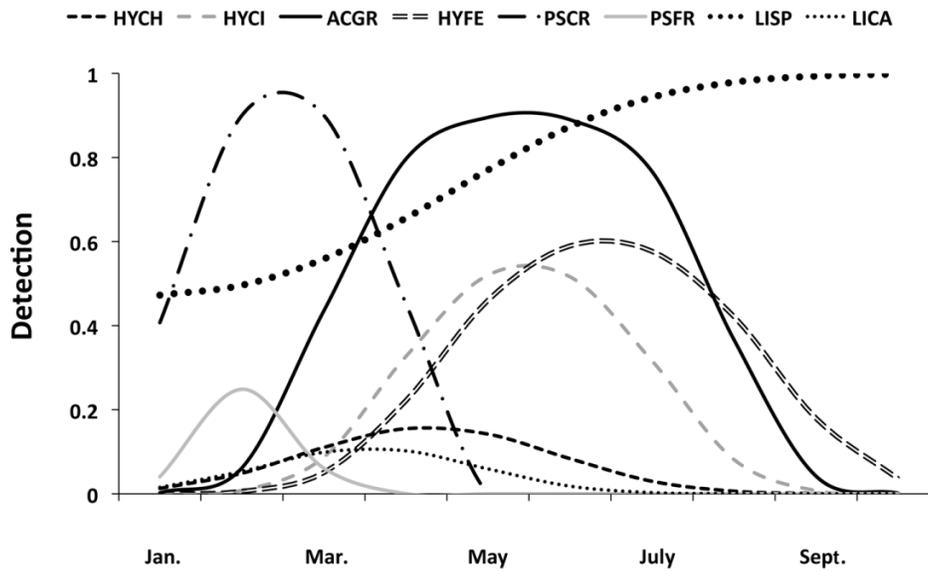
### Environmental data

We collected temperature and precipitation data from the Global Summary of the Day, National Climatic Data Center (http://www.ncdc.noaa.gov). We used data from the weather station located in Opelika, Alabama (32.616°N, 85.433°W), roughly 26 km from our study site. We determined the temperature and total precipitation for each survey date. We also calculated the mean daily temperature and total precipitation for each month in which our calling surveys were conducted, hereafter mean monthly temperature and monthly precipitation, respectively.

### Analysis

We developed multiple hypotheses explaining variation in calling activity; models included those with only seasonal components (i.e., linear or quadratic effects of month of survey), large-scale climatic variables (i.e., mean daily temperature within a month and total precipitation for a given month), or survey level

**Fig. 1.** Association between anuran calling activity and month of survey within Tuskegee National Forest, Macon County, Alabama, from January to October, 2007–2009. Graphs are based on predictions for night surveys. Species codes are presented in Table 2.



environmental conditions (i.e., temperature and precipitation on the day of the survey), as well as models containing a combination of the above, and a model including the year in which surveys were conducted (Table 1). By including mean monthly temperature and monthly precipitation in a given month in models, we attempted to determine whether a species was likely to be detected during a particular month due to typical weather conditions associated with that month. We considered quadratic effects of month of study as a proxy for photoperiod because of their close relationship. Because anurans call primarily after sunset (Dorcas et al. 2009), we included a binary factor indicating whether each survey was conducted during the day or at night (night = 1, day = 0), and also tested a model which only included the factor for time of survey. If month of survey appeared in top models, we interpreted this as evidence for either cyclical endogenous drivers or a seasonal environmental change that we did not explicitly quantify.

We evaluated calling activity using generalized linear mixed models with a binomial distribution and a logit-link or mixed logistic regression (Bolker et al. 2009). To correct for repeated measures and different sampling methods, we included random intercepts for a site factor and a season factor that coded for surveys conducted under either summer or winter protocols. We also included a linear effect in all models that included a quadratic effect. We ranked models with AIC adjusted for small-sample size (AIC$_c$) (Hurvich and Tsai 1989). We then averaged to produce the unconditional coefficient estimates and standard errors used for inference (Burnham and Anderson 2002). We used covariates that were within models with $\Delta AIC_c < 2$ and had 95% unconditional confidence intervals that did not include zero for inference and considered covariates that fit these criteria as significant. We present graphs for these significant covariates only. Because of potential problems associated with low samples sizes or detection, we only analyzed data for species detected on >30 occasions. All analyses were performed using R version 2.13.1 (R Development Core Team 2011). We used lme4 (Bates et al. 2011) to fit our models using Laplace estimation and MuMIn (Barton 2009) for model selection. We based figures on modeled calling activity in March because this was the month when all species were reasonably detectable (Fig. 1).

## Results

Temperature on the day of survey averaged 20.4 °C (SD = 7.25 °C, range = 1.9–31 °C) and precipitation on the day of survey averaged 0.19 cm (SD = 0.54 cm, range = 0.0–2.87 cm). Monthly mean temperature averaged 20.3 °C (SD = 6.6 °C, range = 6.7–28.7 °C) and monthly precipitation averaged 9.0 cm (SD = 5.9 cm, range = 0.33–22.12 cm). The only highly correlated variables were mean daily temperature and month ($R^2$ = 0.5). We detected 16 species of anurans over the course of our study. However, we detected five species on fewer than 30 surveys so they were excluded from the analyses; these species included the Eastern Narrow-mouthed Toad (*Gastrophryne carolinensis* (Holbrook, 1836)) (15 surveys), Fowler's Toad (*Anaxyrus fowleri* (Hinckley, 1882)) (14 surveys), Squirrel Treefrog (*Hyla squirrela* Bosc, 1800) (8 surveys), Southern Toad (*Anaxyrus terrestris* (Bonnaterre, 1789)) (6 surveys), and Barking Treefrog (*Hyla gratiosa* LeConte, 1857) (3 surveys).

Top models explaining calling activity varied among the species (Table 2). Calling activity for Cope's Gray Treefrog (*Hyla chrysoscelis* Cope, 1880), Green Treefrog (*Hyla cinerea* (Schneider, 1799)), Southern Cricket Frog (*Acris gryllus* (LeConte, 1825)), Pine Woods Treefrog (*Hyla femoralis* Bosc, 1800), Spring Peeper (*Pseudacris crucifer* (Wied-Neuwied, 1838)), Upland Chorus Frog (*Pseudacris ferarium* (Baird, 1854)), American Bullfrog (*Lithobates catesbeianus* (Shaw, 1802)), and Southern Leopard Frog (*Lithobates sphenocephalus* (Cope, 1886)) was influenced by month of survey (Fig. 1). Of these species, *H. femoralis* and *P. crucifer* were also influenced by mean monthly temperature (Fig. 2), *A. gryllus* was also influenced by monthly precipitation (Fig. 3), and *L. sphenocephalus* was also influenced by mean monthly temperature and daily precipitation (Figs. 3, 4). Calling activity for the Bird-voiced Treefrog (*Hyla avivoca* Viosca, 1928) was only significantly influenced by mean monthly temperature (Fig. 2), calling activity for Eastern Cricket Frog (*Acris crepitans* (Baird, 1854)) was only influenced by monthly precipitation (detection rates for this species were too low to include within a figure), and calling activity for Green Frog (*Lithobates clamitans* (Latreille, 1801)) was only influenced by temperature on the day of survey (Fig. 5).

## Discussion

Because many amphibians rely on ephemeral environmental conditions for successful reproduction, we expected some degree

**Table 2.** Total number of detections, unconditional coefficient values ($\beta$), unconditional standard error (SE), and Akaike weights ($w_i$) obtained by model averaging, describing calling activity of anurans within Tuskegee National Forest, Alabama, from January to October, 2007–2009.

| Species | No. of detections | Intercept $\beta$ (SE) | $w_i$ | Month $\beta$ (SE) | $w_i$ | Month$^2$ $\beta$ (SE) | $w_i$ | Daily temperature $\beta$ (SE) | $w_i$ | Monthly temperature $\beta$ (SE) | $w_i$ | Monthly precipitation $\beta$ (SE) | $w_i$ | Daily precipitation $\beta$ (SE) | $w_i$ | Nocturnal surveys $\beta$ (SE) | $w_i$ |
|---|---|---|---|---|---|---|---|---|---|---|---|---|---|---|---|---|---|
| *Acris gryllus* (ACGR) | 103 | –11.47 (1.93)* | — | 4.57 (0.75)* | 1 | –0.42 (0.06)* | 1 | 0.03 (0.09) | 0.16 | 0.02 (0.04) | 0 | 0.06 (0.03)* | 0 | 0.74 (0.62) | 0.4 | 1.29 (0.46)* | 1 |
| *Lithobates clamitans* (LICL) | 81 | –8.43 (4.47) | — | –0.45 (1.17) | 1 | –0.07 (0.13) | 0.32 | 0.24 (0.09)* | 0.91 | 0.03 (0.05) | 0 | 0.04 (0.03) | 0 | 0.09 (0.37) | 0.32 | 3.54 (0.52)* | 1 |
| *Hyla cinerea* (HYCI) | 78 | –13.73 (2.62)* | — | 4.49 (1.21)* | 1 | –0.41 (0.09)* | 1 | 0.15 (0.09) | 0.5 | 0.03 (0.04) | 0 | 0.04 (0.03) | 0 | 0.22 (0.36) | 0.15 | 1.6 (0.41)* | 1 |
| *Hyla avivoca* (HYAV) | 77 | 0.21 (3.12) | — | –0.48 (0.84) | 1 | –0.09 (0.07) | 0.41 | 0.05 (0.08) | 0.26 | –0.16 (0.04)* | 0 | 0.03 (0.02) | 0 | 0.14 (0.37) | 0.2 | 1.27 (0.43)* | 1 |
| *Acris crepitans* | 56 | –8.83 (6.37) | — | 1.41 (1.74) | 1 | –0.22 (0.11) | 0.78 | –0.11 (0.11) | 0.27 | –0.08 (0.05) | 0 | 0.07 (0.03)* | 0.35 | 0.49 (0.35) | 0 | 1.68 (0.45)* | 1 |
| *Pseudacris crucifer* (PSCR) | 46 | –17.94 (9.49)* | — | 15.15 (7.69)* | 1 | –3.02 (1.54)* | 1 | –0.16 (0.16) | 0.08 | –0.38 (0.06)* | 0 | 0 (0.06) | 0 | 2.24 (1.28) | 0.79 | 5.43 (3.38) | 1 |
| *Lithobates sphenocephalus* (LISP) | 45 | –1.4 (1.64) | — | –0.14 (0.44) | 0.18 | 0.08 (0.04)* | 0.02 | –0.04 (0.05) | 0.08 | –0.17 (0.03)* | 0.18 | 0.06 (0.04) | 0.16 | 0.71 (0.35)* | 0.36 | 1.35 (0.56)* | 0.98 |
| *Lithobates catesbeianus* (LICA) | 43 | –8.81 (4.49)* | — | 2.24 (1.98) | 1 | –0.31 (0.07)* | 0.72 | 0.05 (0.1) | 0.26 | –0.1 (0.05) | 0 | –0.02 (0.03) | 0 | –0.22 (0.42) | 0.21 | 2.72 (0.57)* | 1 |
| *Hyla chrysoscelis* (HYCH) | 38 | –7.76 (3.34)* | — | 2.11 (1.45) | 1 | –0.25 (0.07)* | 0.81 | 0.03 (0.09) | 0.23 | –0.04 (0.05) | 0 | 0.02 (0.03) | 0 | –0.28 (0.44) | 0.23 | 1.55 (0.47)* | 1 |
| *Hyla femoralis* (HYFE) | 33 | –13.03 (3.63)* | — | 3.68 (1.27)* | 0.96 | –0.29 (0.1)* | 0.96 | –0.07 (0.1) | 0.23 | 0.18 (0.05)* | 0.03 | –0.05 (0.03) | 0 | 0.34 (0.37) | 0.25 | 1.63 (0.51)* | 1 |
| *Pseudacris feriarum* (PSFR) | 31 | –11.32 (8.47) | — | 7.59 (2.78)* | 0.92 | –1.84 (0.55)* | 0.88 | 0.22 (0.13) | 0.46 | 0.18 (0.14) | 0 | 0.22 (0.14) | 0.01 | 2.65 (4.72) | 0.21 | 2.41 (1.6) | 0.99 |

**Note:** An asterisk indicated that the 95% confidence intervals did not overlap with zero. Codes for each species are in parentheses next to scientific name. Common names are as follows in order of appearance in the table: Southern Cricket Frog, *Acris gryllus*; Green Frog, *Lithobates clamitans*; Green Treefrog, *Hyla cinerea*; Bird-voiced Treefrog, *Hyla avivoca*; Eastern Cricket Frog, *Acris crepitans*; Spring Peeper, *Pseudacris crucifer*; Southern Leopard Frog, *Lithobates sphenocephalus*; American Bullfrog, *Lithobates catesbeianus*; Cope's Gray Treefrog, *Hyla chrysoscelis*; Pine Woods Treefrog, *Hyla femoralis*; Upland Chorus Frog, *Pseudacris feriarum*.
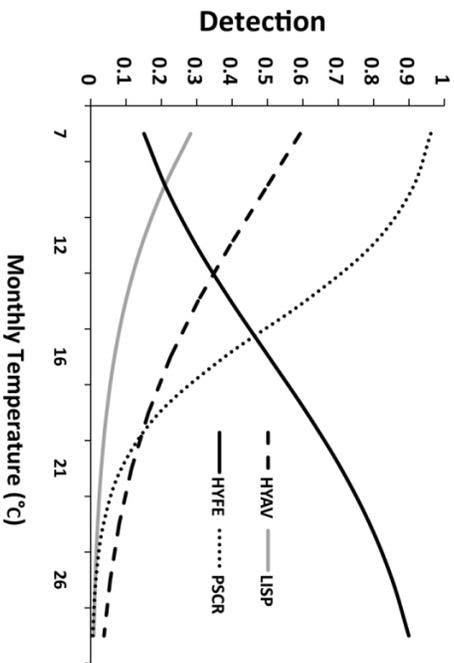


**Fig. 2.** Association between anuran calling activity and mean monthly temperature and within Tuskegee National Forest, Macon County, Alabama, from January to October, 2007–2009. Species codes are presented in Table 2.
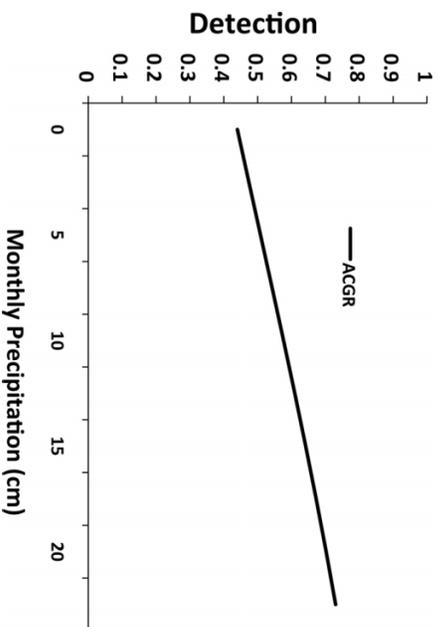


**Fig. 3.** Association between Southern Cricket Frog (*Acris gryllus*) calling activity and mean monthly precipitation within Tuskegee National Forest, Macon County, Alabama, from January to October, 2007–2009. This relationship was also significant for Eastern Cricket Frog (*Acris crepitans*), but detection rates were too low to graph trends. Species codes are presented in Table 2.

of change in male vocalization to correspond to variation in the environmental conditions most important to facilitating reproduction for a given species. By decoupling season (i.e., month), environmental conditions associated with a given month, and environmental conditions on the day of a given survey while evaluating multiple working hypotheses, we were able to identify important influences of calling activity. Thus, we could evaluate whether anuran calling activity was best predicted by environmental conditions on a given day, environmental conditions for a given month, or whether breeding activity is endogenous and (or) cyclical on an annual basis. Our results suggest different species respond to different cues, and sometimes a combination thereof, when initiating reproductive activity. However, weather conditions on the day of calling surveys were important influences of calling activity for only two species.

Within this study, season was an important factor influencing anuran vocalization for most species. For four species (*H. chrysoscelis*, *H. cinerea*, *L. catesbeianus*, and *P. ferarium*), it was the only important variable. This suggests that for at least these four species, anuran reproduction is largely cyclical, recurring in a given month regardless of environmental conditions. This may be the

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**Fig. 4.** Association between Leopard Frog (*Lithobates sphenocephalus*) calling activity and precipitation on the day of survey within Tuskegee National Forest, Macon County, Alabama, from January to October, 2007–2009. Species codes are presented in Table 2.
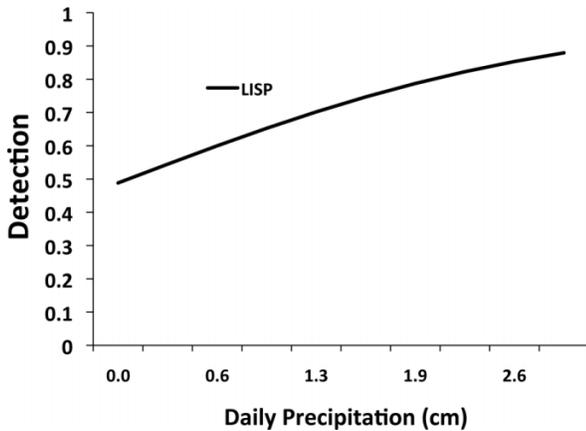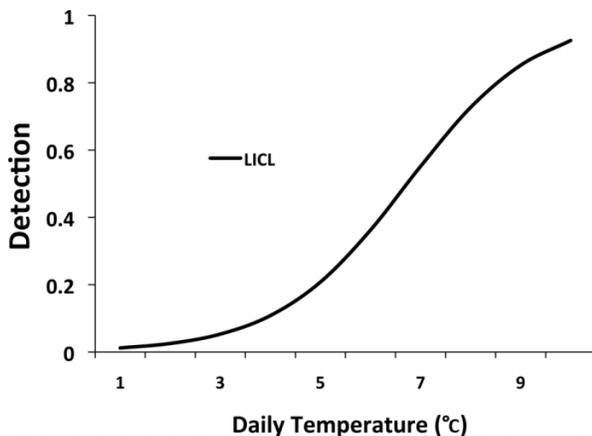


**Fig. 5.** Association between Green Frog (*Lithobates clamitans*) calling activity and temperature on the day of survey within Tuskegee National Forest, Macon County, Alabama, from January to October, 2007–2009. Species codes are presented in Table 2.



case if reproductive activity was influenced solely by endogenous factors (e.g., hormones; Rastogi et al. 2005) or by a seasonal driver such as photoperiod (Bradshaw and Holzapfel 2007); we are unable to distinguish between these two potentials. Because some of the species significantly influenced by month of survey were also influenced by environmental conditions associated with a given month, our results suggest that a combination of both seasonal or endogenous drivers and short-term environmental conditions influence the timing of calling activity. Based on peaks in calling behavior (Fig. 1), we can characterize some frogs within the assemblage that we sampled as either winter (*P. crucifer* and *P. ferarium*), spring (*L. catesbeianus*), late-spring to summer (*A. gryllus*, *H. chrysoscelis*, *H. cinerea*, *H. femoralis*), or fall to winter (*L. sphenocephalus*) breeders.

Most species within our study site were prolonged breeders with relatively consistent breeding activity throughout their reproductive season (Saenz et al. 2006). These prolonged breeders have been suggested to be relatively unaffected by short-term weather patterns (e.g., Bevier 1997; Oseen and Wassersug 2002). Anurans that use wetlands with hydroperiods that fluctuate largely due to patterns of precipitation, a characteristic of many species inhabiting tropical regions that experience discrete wet and dry seasons, are likely to be more influenced by rainfall (e.g., Aichinger 1987; Donnelly and Guyer 1994; Prado et al. 2005). In our

study area, species that depend largely on temporary and fishless wetlands, such as *H. gratiosa*, may be more dependent on precipitation for forming these other wetlands. Rain may also elicit movements of anurans from terrestrial refugia to breeding ponds (Obert 1976), but many of the species included in this study reside within, or in close proximity to, wetlands.

Future research may reveal whether unmeasured environmental factors may influence reproductive activity of anurans at our study site. For example, lunar cycles and water temperature have been shown to influence timing of amphibian reproductive behavior (Oseen and Wassersug 2002; Grant et al. 2009). Environmental influences on survival (of any life stage) may also influence the timing of adult breeding seasons. In addition, calling (Brooke et al. 2000; Oseen and Wassersug 2002) or simply presence of conspecific species (Henzi et al. 1995; Murphy 1999) may influence calling rates. Future studies of these species may indicate whether calling activity is influenced by the presence of conspecifics (Loftus-Hills and Littlejohn 1992). However, variation in calling intensity should not affect our results due to our focus on presence–absence data. Finally, some species may call at different times of the night depending on the season (Bridges and Dorcas 2000). Thus, it is possible that we failed to detect a species that was active during a time outside of our sampling protocol. This would result in a biased impression of breeding season.

There are opportunities to improve upon our study design with the potential for better inference. Although our study was relatively long term, wetlands were sampled only twice per month. Future studies should sample wetlands more intensively, allowing for a greater range of environmental conditions to be encompassed within the samples for a given month. Automated recording devices may facilitate this greater sampling effort (e.g., Steelman and Dorcas 2010). Similarly, we only sampled amphibians during one winter. Repeating our methodology in multiple winters would allow us to ensure that we did not sample in an atypical year. Collecting weather information at the study site, instead of a nearby weather station, may also improve inference.

Previous studies of anuran assemblages have placed species into multiple categories based on their reproductive strategies and suggested complex relationships existed between calling phenology and season and weather conditions (e.g., Bertoluci and Rodrigues 2002; Oseen and Wassersug 2002; Saenz et al. 2006). Our results from a diverse frog assemblage inhabiting a relatively permanent wetland complex corroborate the need for multiple categorizations that incorporate season and environmental conditions at multiple temporal scales.

## Acknowledgements

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