# ECOLOGICAL CORRELATES OF ANURAN BREEDING ACTIVITY AND COMMUNITY STRUCTURE

A Dissertation

by

DANIEL SAENZ

Submitted to the Office of Graduate Studies of
Texas A&M University
in partial fulfillment of the requirements for the degree of

DOCTOR OF PHILOSOPHY

December 2004

Major Subject: Wildlife and Fisheries Sciences

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Approved as to style and content by:

| | |
|---|---|
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# ABSTRACT

Ecological Correlates of Anuran Breeding Activity and Community Structure.

(December 2004)

Daniel Saenz, B.S., Stephen F. Austin State University;

M.S., Stephen F. Austin State University

Chair of Advisory Committee: Dr. Lee A. Fitzgerald

Multiple ecological factors can simultaneously affect species activity and community structure. The goal of my dissertation was to examine the effects of abiotic factors, biotic factors, and succession on anuran communities. I took a three pronged approach dividing the study into three major chapters.

First I focused on abiotic factors that affect anuran breeding activity. I found that weather, rainfall and temperature affect the breeding activity of each species differently, and species in my study area can be placed into 5 different groups based on their association with weather and season: 1) breed within a predictable season (summer) independent of local weather patterns 2) breed opportunistically within a predictable season (summer) dependent on local rainfall 3) breed opportunistically within a predictable season (winter) dependent on local temperature 4) breed opportunistically dependent on local flood level rainfall events and 5) breed opportunistically year round dependent on local temperature in the winter and local rainfall in the summer.

In the second part of the study, I created a simulation model of an anuran community using published life history parameters of the anuran species in my study system. Results of the model suggest colonizing ability is important for species with low fecundity and high susceptibility to predation. These early succession species tend to be constrained from later stages of succession by predators. Species that are resistant to predators are generally poor colonizers and tend to arrive late in succession, but once they colonize a pond they tend to persist and recruit successfully.

Finally, I explored biotic mechanisms that might be important in structuring anuran communities. I found that with the exception of *Rana sphenocephala*, anuran species occupying sites with shorter hydroperiods had higher activity rates and were more susceptible to predation. *Rana sphenocephala* appeared to be better at escaping predation than the other species despite a relatively high activity rate. Examination of published phylogenies indicates *R. sphenocephala* is derived from a species group that uses permanent water suggesting that *R. sphenocephala* has retained many anti-predator defenses inherited from its ancestors, even though the species now exploits sites with low predator densities.

# ACKNOWLEDGEMENTS

I thank my advisory committee: Drs. Lee A. Fitzgerald, William E. Grant, Kirk O. Winemiller, and Thomas W. Boutton for their advice and patience during my graduate studies and development of this research project. Special thanks to Dr. Lee Fitzgerald for accepting me as his graduate student and for his guidance and friendship.

My graduate studies would not have been possible without the unselfish support that was given to me by mentor and friend, Dr. Richard (Dick) Conner. Dick, at a sacrifice to his own research program, allowed me to temporarily leave my post as his professional support at the Southern Research Wildlife Laboratory to complete my coursework in College Station.

Gage Dayton and Kristen Baum were instrumental in helping me develop many of the ideas and assisted me in the field and in the lab. Nancy Koerth was a great help with some difficult statistical analyses, and she also checked my work on simpler tasks. Cory Adams, Brad Johnson, Jim McCormick, Chris Collins, and Robert Allen all provided valuable assistance in the field and in the lab. Philip Blackburn provided his expertise in electronics by building me the best and most reliable automated audio recorders available. Finally I would like to thank all of my friends at the Wildlife and Silviculture Laboratory in Nacogdoches, Texas for all of their support.

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# CHAPTER I

# INTRODUCTION

Species composition can sometimes be explained by a few assembly rules (Diamond 1975), but natural communities appear to be structured by multiple factors. For example, 1) species interactions have often been reported as important mechanisms influencing community composition (Cody and Diamond 1975, Connell and Slayter 1977, Schoener 1983), 2) abiotic factors also can limit species from inhabiting a particular area at a given time (Roberts and Lewin 1979, Stewart 1995, Pounds et al. 1999, Porter et al. 2000), and 3) time is also a critical correlate of community structure in natural communities (Connell and Slayter 1977, Pickett et al. 1987, Lichter 1998).

In lentic environments, water permanency is a resource continuum that affects community structure across the gradient. Virtually every species, from virtually every class of animal that lives in freshwater habitats, is restricted to some portion of the hydroperiod continuum, and is constrained either by the amount of time water is available or the distribution of predators (Wellborn et al. 1996). An interesting link between predation and water permanency exists in the complex behavioral and life-

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This dissertation follows the style and format of Ecology.

history trade-offs among the prey communities in freshwater systems. Faster development rates in temporary pond species may require high energy intake levels that lead to more time spent feeding or looking for food, which would lower primary anti-predator defenses (the ability to avoid being detected by predators) in these species (Low 1976, Woodward 1983, Lawler 1989, Richards and Bull 1990, Skelly 1994). onversely, species that inhabit relatively more permanent aquatic environments spend less time engaged in feeding and consequently less time in motion (Skelly 1994).

The goals of my dissertation were to identify biotic, abiotic, and time correlates of anuran breeding activity and community assembly and to test current paradigms in anuran community ecology that suggest a link between water permanency and life-history trade-offs among the prey communities in freshwater systems (Woodward 1983, Lawler 1989, Skelly 1994). Specifically, I will address the following objectives.

1) Determine the relationships between weather, season, and breeding activity of an anuran community and explore the role of different anuran life-history traits and how they are correlated to responses to environmental factors.
2) Examine the relationships between anuran life-history traits such as length of larval stage, fecundity, and breeding phenology with changes in community structure over time by simulating succession over a ten-year period.
3) Test the paradigms about behavioral and life-history trade-offs among anuran tadpoles occupying different portions on the hydroperiod continuum and identify mechanisms that regulate community assembly.

## BACKGROUND

The Order Anura (frogs and toads) is comprised of approximately 30 Families and 5,000 species that occur throughout most of the world with the exception of the Polar Regions. The order is a monophyly supported by numerous unique features including a urostyle, nine or fewer presacral vertebrae, compound radioulna and tibiofibula, elongate tarsal elements and unusual larvae (Pough et al. 1998).

Most anurans, like other amphibians, go through an aquatic stage as tadpoles and a terrestrial adult stage at some point in their lives. Typically, adults will return to the water to breed and deposit eggs. Male frogs and toads produce, species specific, breeding advertisement calls intended to attract gravid females. Females are known to respond positively to conspecific calls while responding indifferently to calls from other species (Littlejohn 1965, Snyder and Jameson 1965). Acoustic resource partitioning in anuran communities has been the subject of much study (Duellman and Pyles 1983, Schwartz et al. 1983, Narins 1995). While species specific calls act as important premating isolating mechanisms, they are also distinguishable by humans and can be used to determine breeding activity in species of anurans.

## STUDY SYSTEM

The eastern Texas region, with its variable climate, is a hotspot for temperate zone anuran diversity and has proven to be an ideal location for studying the effects of climate on anuran calling behavior. My study sites are at high enough latitudes (approximately 31º N) to experience occasional freezing temperatures due to southward movement of arctic air masses or cold fronts and 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 my study sites in one of the wettest regions of Texas (Bomar 1995). Nacogdoches and Houston Counties are far enough from the Gulf of Mexico that they are not severely affected by high winds associated with tropical storms and hurricanes, but they seem to be the perfect distance from the Gulf to receive massive amounts of rainfall from these major summertime storms. My study sites are in a very humid region of the country, experience temperatures that likely fall below the known thermal limits for anuran reproduction (Zimmitti 1999), and they also experience some of the highest temperatures in the United States. Rainfall is generally abundant with occasional flooding events and prolonged periods of no precipitation providing a range of stresses on and opportunities for anuran reproduction.

In eastern Texas, no anuran species have direct development, foam nests, aerial nests, or parental care. All species lay their eggs aquatically (Garrett and Barker 1987, Conant and Collins 1998) and the tadpoles develop through multiple stages (Gosner 1960), metamorphosing into a sub-adult frog. All of the frog species in eastern Texas must advertise by calling for mates at potential breeding sites. Hence, the opportunity exists to monitor breeding activity among all species and measure their call intensity at breeding sites.

This dissertation is written in chapter format, with a separate chapter for each major objective and minor objectives within the chapters. After the general introduction

(Chapter I), the second chapter explores the relationships between anuran calling activity, weather, and season in eastern Texas. These relationships were used to classify the species into 5 breeding strategy groups. In the third chapter, I develop a simulation model to predict the change in anuran community composition over a ten year period in a new pond. I also evaluated how anuran life history parameters such as fecundity and length of larval stage affect colonization of a species to a breeding site and a species' persistence over time. The fourth chapter explores habitat associations of winter breeding anurans in eastern Texas and the role of predation on anuran communities. Finally, the fifth chapter provides and overall summary of the conclusions resulting from the objectives in the previous chapters.

# CHAPTER II

# ABIOTIC CORRELATES OF BREEDING ACTIVITY IN AN ANURAN COMMUNITY

## INTRODUCTION

Both biotic and abiotic mechanisms have been proposed for the organization of anuran communities. Crump (1971) suggested interspecific competition for breeding resources, such as perch sites and oviposition sites, may be important in determining community composition. Many researchers have reported on the influence of rainfall and temperature on anuran breeding (Blair 1960, 1961, Dixon and Heyer 1968, Blankenhorn 1972, Obert 1975, Wiest 1982, Salvador and Carrascal 1990, Moriera and Lima 1991, Donnelly and Guyer 1994, Bertoluci 1998). However, Duellman (1990) suggested that both biotic and abiotic factors, such as predation, greatly influence anuran community composition, yet the determinants of community composition remain speculative in many ecological communities.

The consensus view among ecologists is that in anuran communities, breeding activity is strongly influenced by abiotic factors such as rain and temperature, and each species may respond in its own way. However, the makeup of assemblages breeding at the same place and time is also influenced by similarities in breeding biology among subsets of the species present in the entire anuran community. Breeding activity in some species may be highly correlated to specific abiotic conditions, for example, while other species may have more generalized breeding cues, or others may be linked to a different set of abiotic cues or constraints.

Reproductive strategies and timing of reproduction vary greatly among anuran species (Aichinger 1987, Beiver 1997, Bertoluci and Rodrigues 2002). Many anurans that occur in areas with little seasonal differences in weather patterns breed year-round (Crump 1974, Duellman 1978). However, where temperature and rainfall vary, seasonal changes should allow for diversification of breeding strategies among anurans by providing a greater diversity of environments (Bertoluci and Rodrigues 2002).

Currently there are contradictory views on how species using different breeding strategies might respond to abiotic factors. For example, Oseen and Wassersug (2002) suggest that explosive breeders are less sensitive to abiotic factors than prolonged breeders, but Wells (1977), Cousineau (1990), and Bevier (1997), come to the opposite conclusion. However, as pointed out by Oseen and Wassersug (2002), most previous research attempting to assess the effects of multiple abiotic factors on calling activity have been short-term with intermittent data collection.

Identifying the mechanisms that regulate breeding activity among individual species may help explain co-occurrence of species in an anuran community. In this chapter, I examine abiotic mechanisms that regulate breeding activity in a community of 13 anuran species in eastern Texas. The anuran assemblage in eastern Texas presents an excellent opportunity to determine the biotic and abiotic factors influencing community composition by monitoring breeding activity. All frog species in eastern Texas advertise by calling for mates at potential breeding sites. All species lay their eggs aquatically

(Garrett and Barker 1987, Conant and Collins 1998) and the tadpoles develop through multiple stages (Gosner 1960), metamorphosing into a sub-adult frog. No anuran species have direct development, foam nests, aerial nests, or parental care. Initially, I explored seasonal patterns of anuran calling behavior. In addition, I examined relationships between calling behavior of each anuran species to nightly temperature and daily rainfall. I also compared responses of species that called during different seasons in response to the abiotic factors. Additionally, I compare responses of explosively breeding species and species that breed for prolonged periods to abiotic factors.

## METHODS

### Study system

The eastern Texas region, with its variable climate, is a hotspot for Temperate Zone anuran diversity and has proven to be an ideal location for studying the effects of climate on anuran calling behavior. My study sites are at a high enough latitude (approximately 31° N) to experience occasional freezing temperatures due to southward movement of arctic air masses or cold fronts and 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 my study sites in one of the wettest regions of Texas (Bomar 1995). Nacogdoches and Houston Counties are far enough from the Gulf of Mexico that they are not severely affected by high winds associated with tropical storms and hurricanes, but they also receive massive amounts of rainfall from these major summertime storms.

My study sites are in a very humid region of the country, experience temperatures that fall below the known thermal limits for anuran reproduction (Zimmitti 1999), and also experience some of the highest temperatures in the United States. Rainfall is generally abundant with occasional flooding events and prolonged periods of no precipitation providing a range of stresses on and opportunities for anuran reproduction.

### Anuran vocalization recordings

I collected audio recordings of nocturnally vocalizing anurans at eight sites in the Davy Crockett National Forest (DCNF, n = 4) in Houston County and the Stephen F. Austin Experimental Forest (SFAEF, n = 4) 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 immediately adjacent to a pond constructed for wildlife habitat improvement. Ponds in the DCNF were built in 1992 and ranged in size from 900 $m^2$ - 2,000 $m^2$ 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 a maximum depth of 1 m.

Based on personal experience, I expected all common anuran species in the Piney Woods region of eastern Texas to use my study ponds in the DCNF and the SFAEF for breeding and to be detected by my automated recording devices (description provided below) except for *Scaphipous holbrookii* because of their known affinity for extremely ephemeral breeding sites (Garrett and Barker 1987). Therefore, in addition to the eight ponds that I surveyed with recording equipment, I 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 pond dimensions are approximately 600 $m^2$ surface area with a maximum depth of 0.5 m. No recording device was used at this site because its use by anurans is so infrequent due to the extremely ephemeral nature of the site that rarely holds water. Instead the site was visited each evening following any rain that exceeded 3 cm in a 24-hour period to listen for any anuran vocalizations.

The automated recorders I used in this study, termed frogloggers, were modeled after Peterson and Dorcas' (1994) design and built by Philip Blackburn of Blackburn Transmitters™. The components were three D-cell batteries, a six-cycle timer (six on/off cycles per 24 hours), 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 the voice clock simultaneously at predetermined intervals. All components, except the microphone are housed in a weatherproof military ammunition box. The microphone wire extruded through a hole drilled in the side of the box that was sealed with silicon (Figures 1, 2).

Frogloggers were placed within 2 m of the pond's edge (one per pond) with the microphone oriented towards the center of the pond. Frogloggers were in place for 720 days, from 1 January 2001 through 31 December 2002, and were programmed to record simultaneously at each site every night for one minute at the start of each hour from 2100 hours to 0200 hours Central DST, for a total of six minutes per night. Sampling 6 times throughout each night should help overcome daily variation in calling activity and increase the chances that all species vocalizing at a pond were detected (Mohr and Dorcas 1999, Murphy 1999, Bridges and Dorcas 2000). Tapes were retrieved weekly, the vocalizations were identified to species, and the number of calling individuals was estimated. Also, recording every night of the year for two years enabled me to observe and compare seasonal variation in calling behavior among anuran species. When the number of frogs calling was < 4, I could determine the exact number of calling individuals of a given species. However, when > 4 individuals of a given species were calling, it was not possible to determine the exact number, therefore I assigned a value of 5 for that species during that sampling minute. A maximum value of 30 could be scored as an index of call intensity for a single species in a given night. The number of species calling at one time did not affect my ability to count individuals of each species.

### Temperature, rainfall, and day length

Daily rainfall was measured in both the DCNF and the SFAEF using English unit plastic rain gauges; measurements were converted to the nearest 0.01 cm. The rain gauge in the DCNF was monitored daily by Davy Crockett National Forest, U S Forest Service personnel (Bobbi Styles) and was located 2 km from the nearest anuran sampling point and 5 km from the farthest sampling site. The rain gauge at the SFAEF was monitored daily by East Texas Plant Materials Center, Natural Resource Conservation

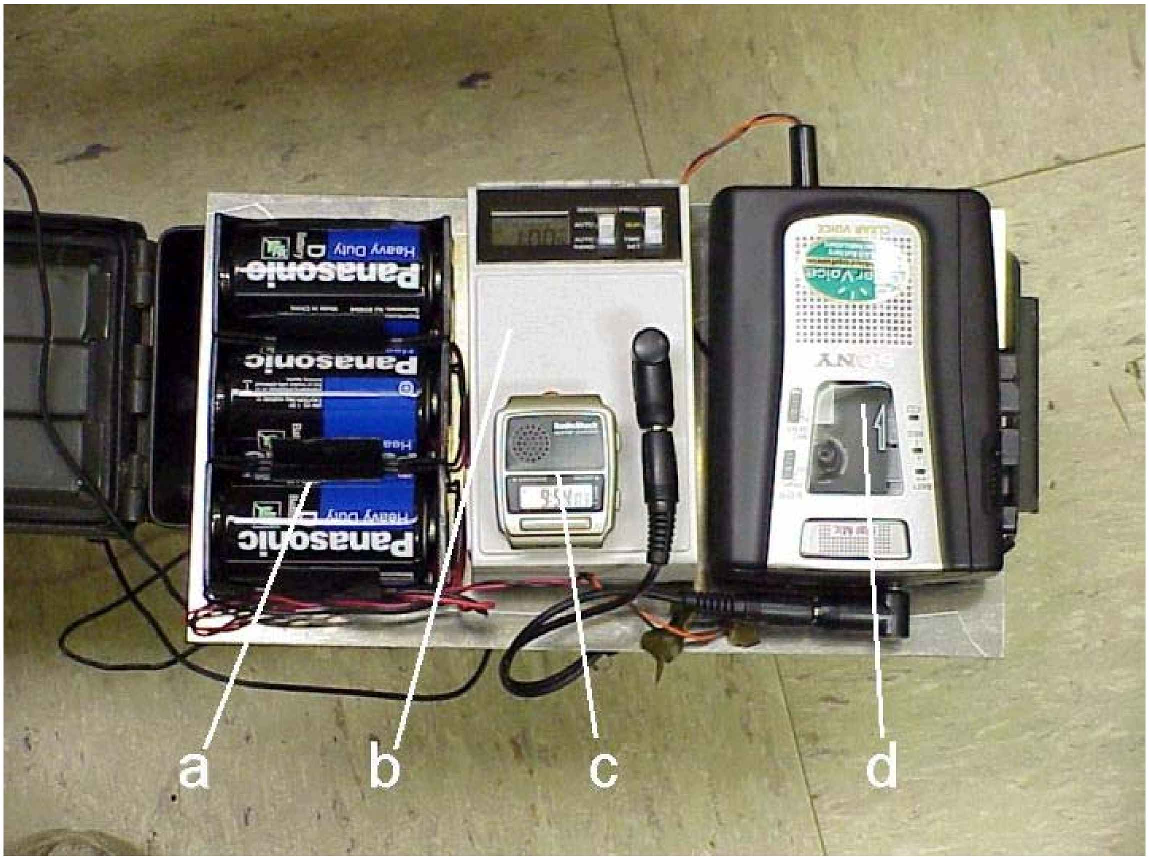


Figure 1. Internal components of automated recording device (froglogger). Components have been removed from protective ammunition box for display: a) three D-cell batteries, b) six-cycle timer, c) voice clock, and d) cassette recorder.

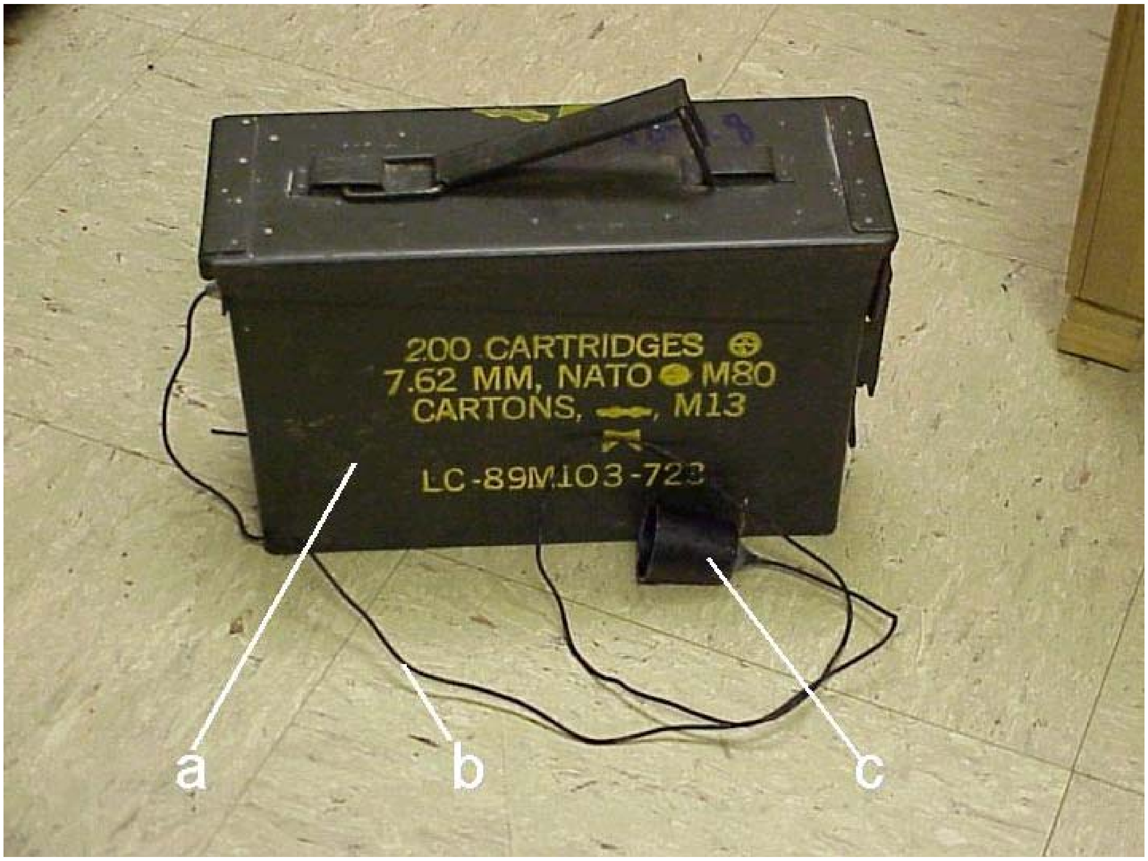


Figure 2. External components of automated recording device (froglogger): a) ammunition box, b) microphone wire, and c) microphone. Internal components were placed in the protective ammunition box as they would be when the froglogger is in use.

Service personnel (Jim Stevens and others) and was < 2 km from any anuran sampling sites.

Variation in calling is known to occur over very small spatial scales that are also affected by weather (Obert 1975, Runkle et al. 1994). Therefore, I measured weather at the anuran sampling sites in order to provide accurate, site-specific data for assessing climatic effects on anuran vocalization behavior (Corn 2003). Temperature was measured to the nearest 0.01° C and relative humidity was measured to the nearest 0.1% hourly at each individual anuran sampling location using HOBO® Pro series data loggers (Onset Computer Corporation, Pocasset, Massachusetts). The loggers were attached to trees 2 m above the ground with wood screws. Care was taken to select sites that were shaded, and a plastic cover was used to prevent direct sunlight and precipitation from contacting the logger.

I used a day-length calculator (http://www.qpais.co.uk/modb-iec/dayleng.htm) to computes the number of hours of daylight according to Julian date and latitude. I used 31° N latitude for the day length calculation for all my study sites.

## Statistical analyses

I used multiple logistic regression to test the statistical hypotheses of no relationships between daily anuran calling activity (0 = no calling or 1= calling) and abiotic parameters, air temperature at 2100 DST to the nearest 0.01 C° and daily rainfall to the nearest 0.1 mm. Some frog species called for a few days after a rain, and it is not clear if species were responding to precipitation immediately or if there was a lag, or build-up, in calling activity. Therefore, I tested 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. Because daily calling samples at a given pond were not independent from day to day (samples were autocorrelated), I used a first order autoregressive model GEEMOD in SAS (SAS 1996) for all regression analyses with $\alpha \leq 0.05$.

The multivariate logistic regression models 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, an estimate of the slope indicates if the relationship is positive or negative. The odds ratio reflects the predicted effect of the variable on the probability of the species calling. An odds ratio of 1.00 would indicate zero change in probability of calling, for example, while a ratio of 1.50 would indicate a 50% change in the probability of calling.

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

To determine the probability of a species calling on nights at a given temperature I 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 given temperature I determined the number of nights that a species called and did not call. I then calculated the percentage of nights where each species was calling at a given temperature to determine the probability of calling. For example, if the air temperature was 15º C on 10 nights during a species' breeding season and the species was detected calling on 5 of those nights, then the species would be determined to have a 50% probability of calling at 15º C. This was repeated for each species at all available temperatures then graphed.

Analyses of calling activity were conducted independently for each species because each species has its own breeding season. I 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 I detected *Psuedacris 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 contrast, *Rana clamitans* had a much longer breeding season, Julian day 88 through 261 (174 d). Because *R. sphenocephala* called all months of the year, data from every day of the two-year period were analyzed. Due to the different weather conditions that occurred throughout the year, I categorized the data according to three seasons, Julian days 1-122 (spring), 223-244 (summer), and 245-365 (fall), respectively, for this species only.

## RESULTS

I detected 13 different anuran species representing 5 different families of frogs and toads at my nine survey sites. There were two members of the Family Bufonidae: *Bufo valliceps* and *B. woodhouseii*, five Hylidae: *Acris crepitans*, *Hyla cinerea*, *H. versicolor/chrysocelis,* (I lumped these two cryptic species and refer to them collectively as *H. versicolor* throughout this study because call differences are known for some populations they can only be distinguished reliably based on chromosomes from one another, Conant and Collins 1998), *Pseudacis crucifer*, and *P. triseriata*, one Pelobatidae: *Scaphiopus holbrookii*, one member of the Family Microhylidae: *Gastrophryne carolinensis*, and four Ranidae: *R. catesbeiana*, *R. clamitans*, *R. palustris*, and *R. sphenocephala*. As expected, *S. holbrookii* were only detected at the extremely ephemeral site in Nacogdoches. *Acris crepitans* and *R. palustris* were each only detected at two ponds in the DCNF, and the remaining 10 species were detected at both the SFAEF and the DCNF.

### Seasonal and daily call patterns

There was large seasonal variation among species in calling activity. At the extremes, *S. holbrookii* was observed 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 *Psuedacris* species called only during cooler months while the remaining 8 species called primarily during warmer months (Table 1).

Despite the fact *R. sphenocephala* called every month, daily call patterns were variable (Figure 3). *Rana sphenocephala* were occasionally detected in large numbers and sometimes 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 (Figures 4, 5, respectively). *Pseudacris crucifer* had a more extensive breeding season and nights with higher calling intensity than the other two winter breeding species (Figure 6). There was also 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. versicolor* (Figures 7, 8, 9, respectively), whereas the calling patterns of the remaining five warm-season species (*H. cinerea*, *R. catesbeiana*, *B. valliceps*, *B. woodhouseii*, and *G. carolinensis*) exhibited spikes in calling activity and extended periods of little to no detectable vocalization (Figures 10-14, respectively). Finally, while *S. holbrookii* was only detected on 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 hrs during this study was 18.1º C with a low of – 0.3º C and a high of 29.3º C (Figure 15). The SFAEF (310 cm rain during the study) experienced over 50 percent more rain than the DCNF (200 cm rain during the study) over the two-year period despite their close proximity, approximately 30 km.

Table 1. Presence of calling activity by month from 2001 to 2002. The symbol X indicates that the species in the row was observed calling in the month indicated at the top of the column. Blank cells represent no calling detected in that month for a given species.

| | Month | | | | | | | | | | | |
|---|---|---|---|---|---|---|---|---|---|---|---|---|
| Species | Jan | Feb | Mar | Apr | May | Jun | Jul | Aug | Sep | Oct | Nov | Dec |
| | Ranidae | | | | | | | | | | | |
| *R. sphenoceph.* | X | X | X | X | X | X | X | X | X | X | X | X |
| *R. clamitans* | | | X | X | X | X | X | X | X | X | X | |
| *R. palustris* | X | X | X | X | | | | | | | | |
| *R. catesbeiana* | | | | X | X | X | X | X | | X | | |
| | Hylidae | | | | | | | | | | | |
| *H. versicolor* | X | | X | X | X | X | X | X | X | | | |
| *H. cinerea* | | | | X | X | X | X | X | | | | |
| *P. triseriata* | X | X | X | | | | | | | | | |
| *P. crucifer* | X | X | X | X | | | | | | | | |
| *A crepitans* | | | | X | X | X | X | X | | | | |
| | Bufonidae | | | | | | | | | | | |
| *B. valliceps* | | | | X | X | X | X | | | | | |
| *B. woodhouseii* | | | X | X | X | X | X | X | X | | | |
| | Microhylidae | | | | | | | | | | | |
| *G. carolinensis* | | | | X | X | X | X | | X | | | |
| | Pelobatidae | | | | | | | | | | | |
| *S. holbrookii* | | X | | X | | | | | | | | |

Temperature and rainfall varied inversely and were strongly influenced by season. Rainfall was more frequent December through March, with detectable precipitation occurring on 22% of the days. Winter rain and temperature are associated with periodic frontal systems (Bomar 1995, Figure 16). Summer rainfall events were less frequent, with detectable precipitation occurring approximately 17% of the days, April through August. Summer rains were associated with isolated thunder storms or tropical weather systems (Figure 16).

There is 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). While air temperatures warmed gradually during both winter and summer breeding seasons, winter breeding species experienced greater daily fluctuations influenced by irregular cold fronts that dramatically dropped the temperature. Summertime air temperatures were less variable from one day to the next because summertime frontal systems have less effect on air temperature.

## Associations between temperature and calling

The anuran species displayed a wide range of associations between calling activity and temperature. *Rana sphenocephala* called over the widest range of temperatures (Figure 17), including the maximum and minimum recorded temperatures where any calls of any species were detected. *Rana sphenocephala* called on a night where the 2100 air temperature was 4° C, the lowest temperature at which any species

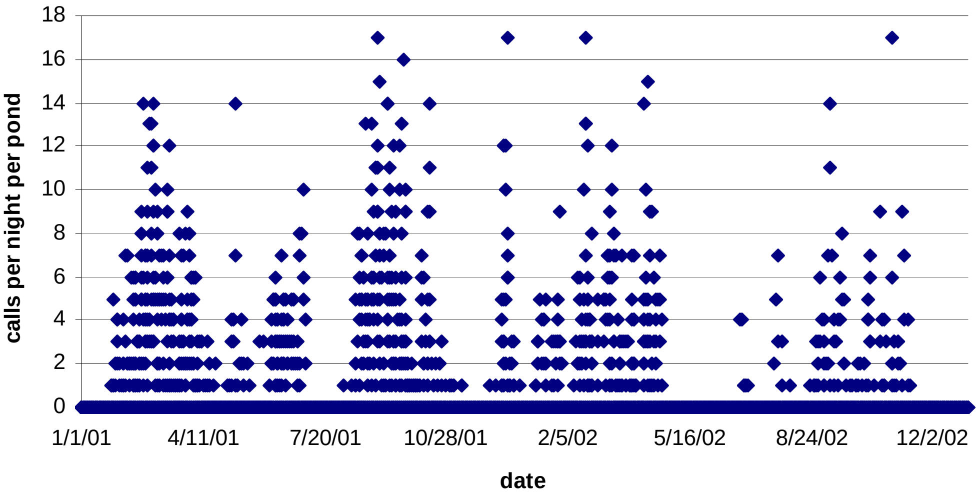


Figure 3. Call intensity scores for *R. sphenocephala* each night at eight ponds during 2001 and 2002. Four ponds were located in the Davy Crockett National Forest in Houston County, Texas, and four were in the Stephen F. Austin Experimental Forest in Nacogdoches County, Texas.

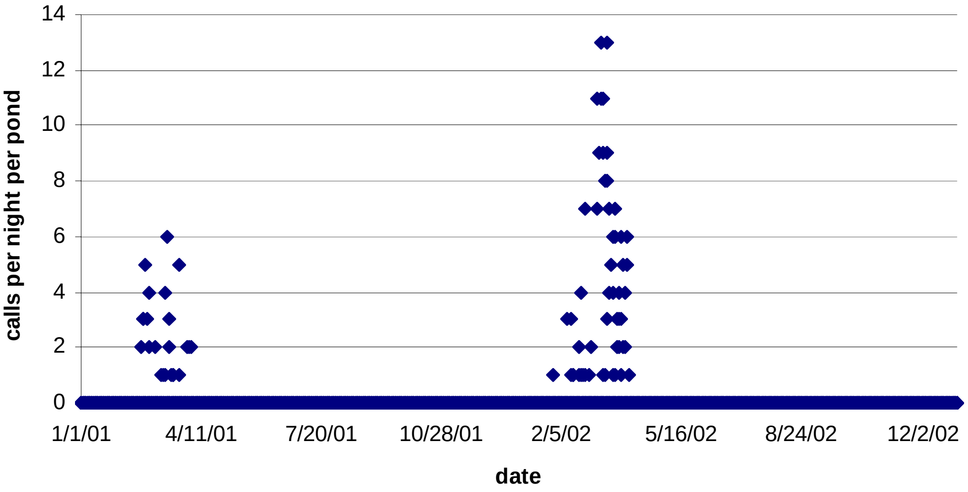


Figure 4. Call intensity scores for *R. palustris* each night at eight ponds during 2001 and 2002. Four ponds were located in the Davy Crockett National Forest in Houston County, Texas, and four were in the Stephen F. Austin Experimental Forest in Nacogdoches County, Texas.

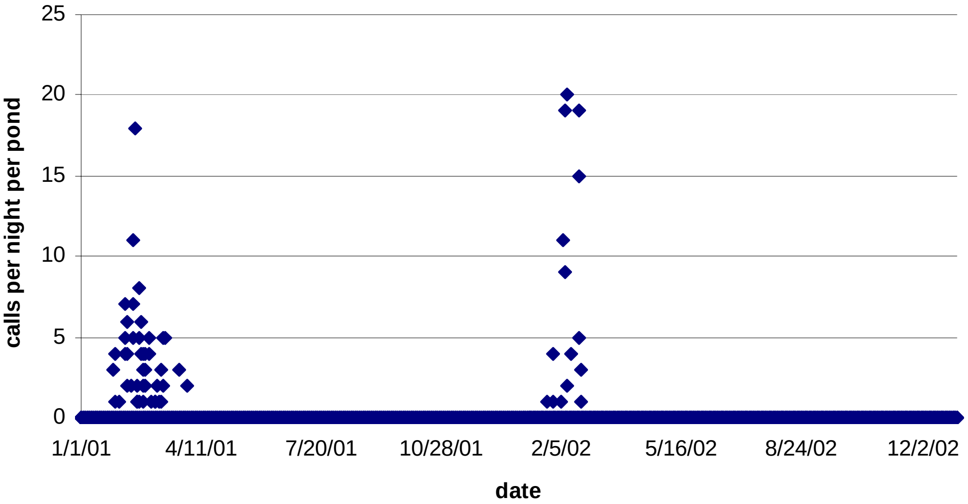


Figure 5. Call intensity scores for *P. triseriata* each night at eight ponds during 2001 and 2002. Four ponds were located in the Davy Crockett National Forest in Houston County, Texas, and four were in the Stephen F. Austin Experimental Forest in Nacogdoches County, Texas.

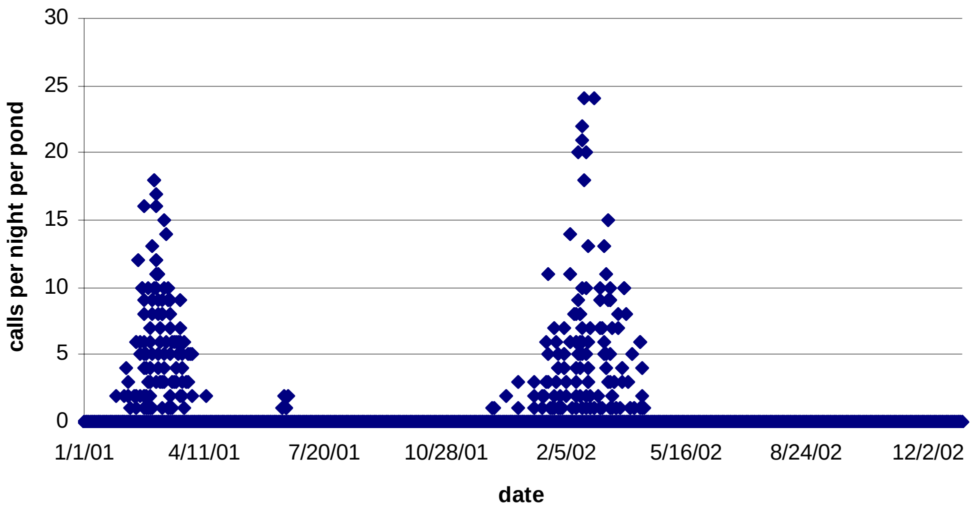


Figure 6. Call intensity scores for *P. crucifer* each night at eight ponds during 2001 and 2002. Four ponds were located in the Davy Crockett National Forest in Houston County, Texas, and four were in the Stephen F. Austin Experimental Forest in Nacogdoches County, Texas.

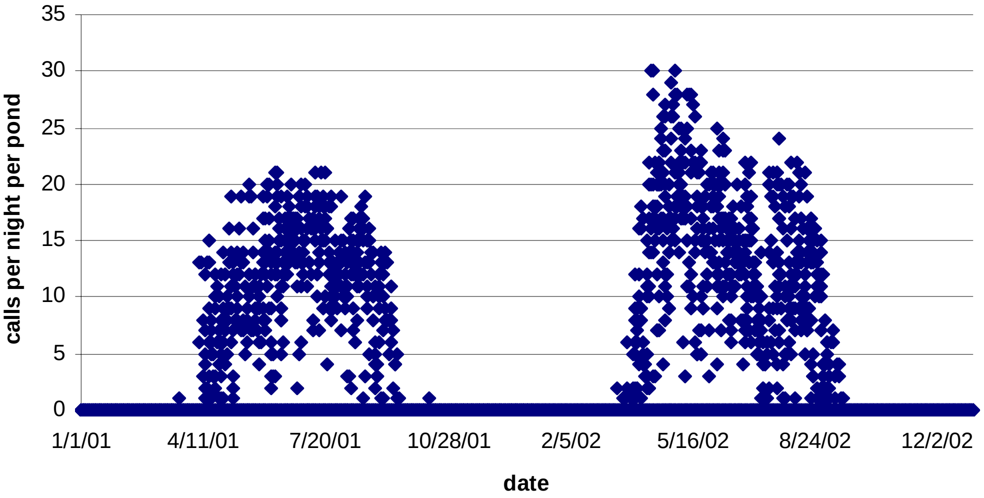


Figure 7. Call intensity scores for *R. clamitans* each night at eight ponds during 2001 and 2002. Four ponds were located in the Davy Crockett National Forest in Houston County, Texas, and four were in the Stephen F. Austin Experimental Forest in Nacogdoches County, Texas.

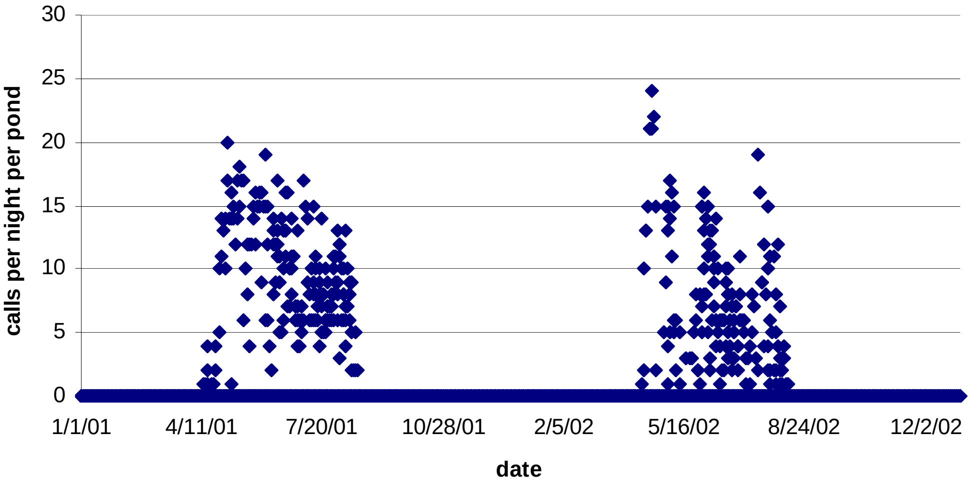


Figure 8. Call intensity scores for *A. crepitans* each night at eight ponds during 2001 and 2002. Four ponds were located in the Davy Crockett National Forest in Houston County, Texas, and four were in the Stephen F. Austin Experimental Forest in Nacogdoches County, Texas.

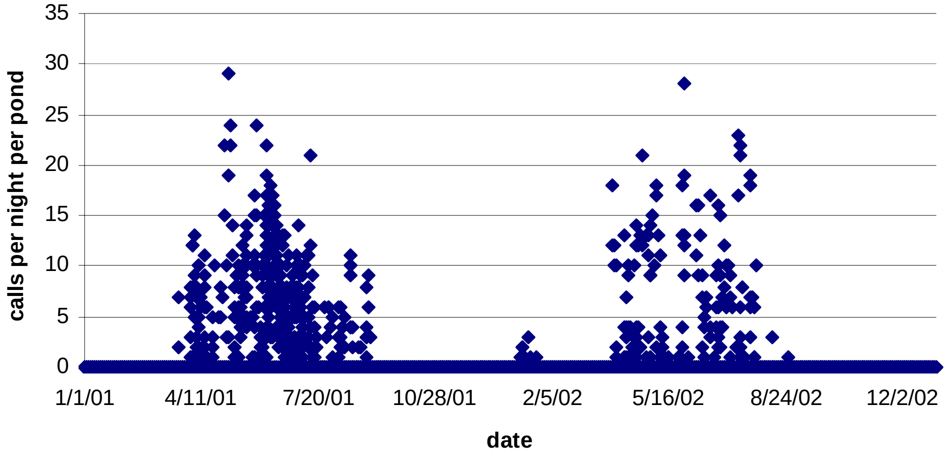


Figure 9. Call intensity scores for *H. versicolor* each night at eight ponds during 2001 and 2002. Four ponds were located in the Davy Crockett National Forest in Houston County, Texas, and four were in the Stephen F. Austin Experimental Forest in Nacogdoches County, Texas.

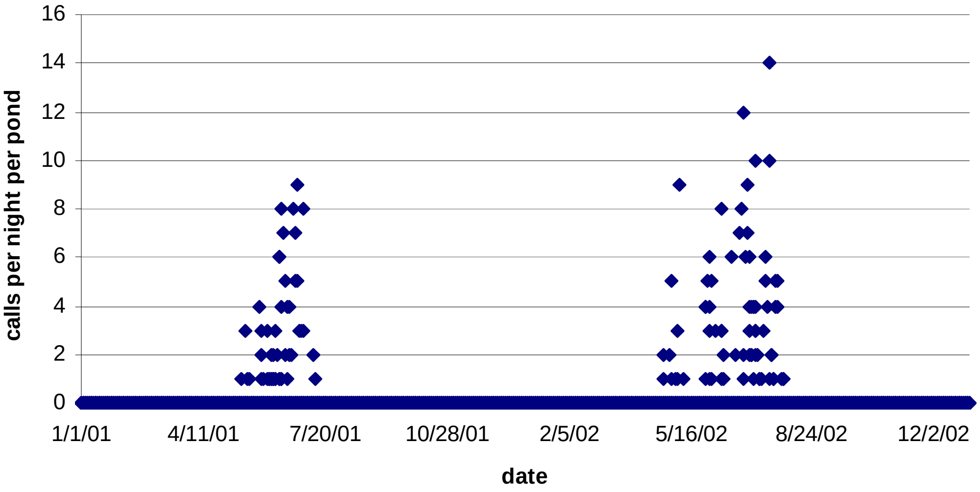


Figure 10. Call intensity scores for *H. cinerea* each night at eight ponds during 2001 and 2002. Four ponds were located in the Davy Crockett National Forest in Houston County, Texas, and four were in the Stephen F. Austin Experimental Forest in Nacogdoches County, Texas.

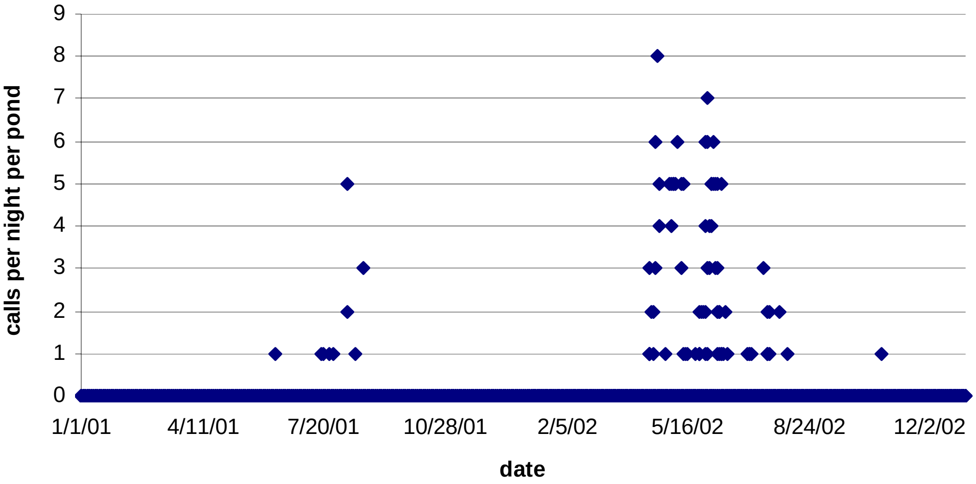


Figure 11. Call intensity scores for *R. catesbeiana* each night at eight ponds during 2001 and 2002. Four ponds were located in the Davy Crockett National Forest in Houston County, Texas, and four were in the Stephen F. Austin Experimental Forest in Nacogdoches County, Texas.

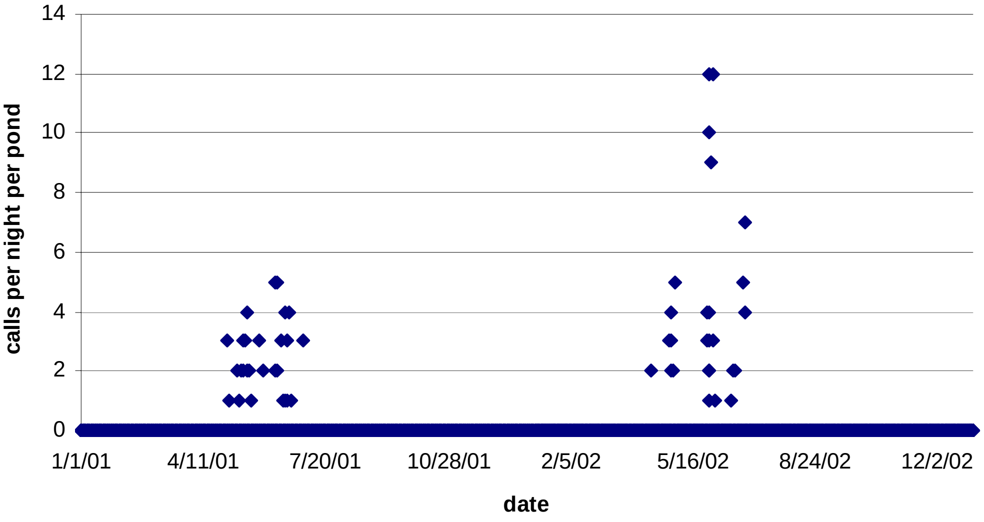


Figure 12. Call intensity scores for *B. valliceps* each night at eight ponds during 2001 and 2002. Four ponds were located in the Davy Crockett National Forest in Houston County, Texas, and four were in the Stephen F. Austin Experimental Forest in Nacogdoches County, Texas.

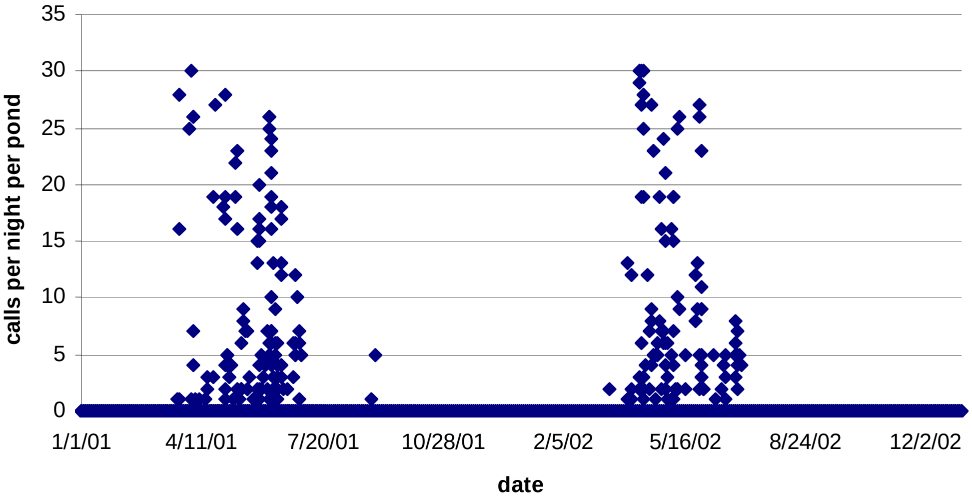


Figure 13. Call intensity scores for *B. woodhouseii* each night at eight ponds during 2001 and 2002. Four ponds were located in the Davy Crockett National Forest in Houston County, Texas, and four were in the Stephen F. Austin Experimental Forest in Nacogdoches County, Texas.

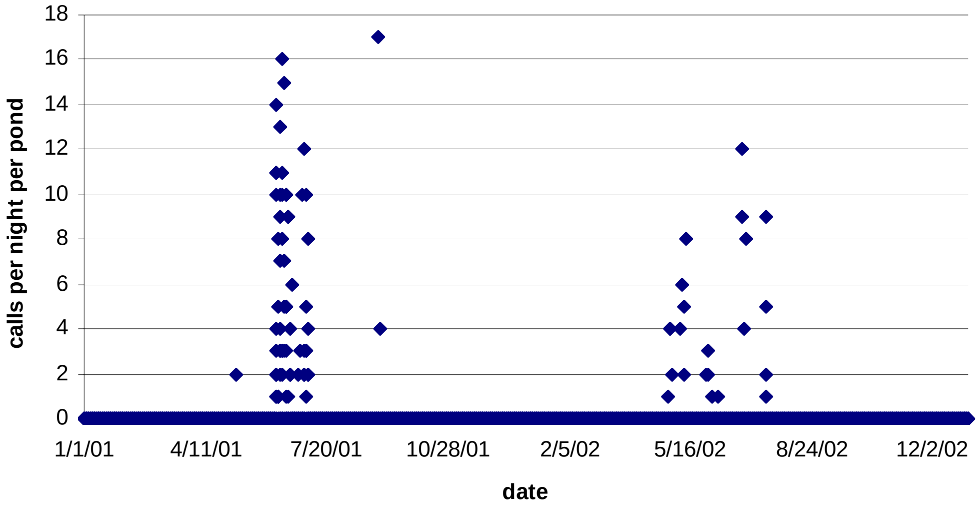


Figure 14. Call intensity scores for *G. carolinensis* each night at eight ponds during 2001 and 2002. Four ponds were located in the Davy Crockett National Forest in Houston County, Texas, and four were in the Stephen F. Austin Experimental Forest in Nacogdoches County, Texas.

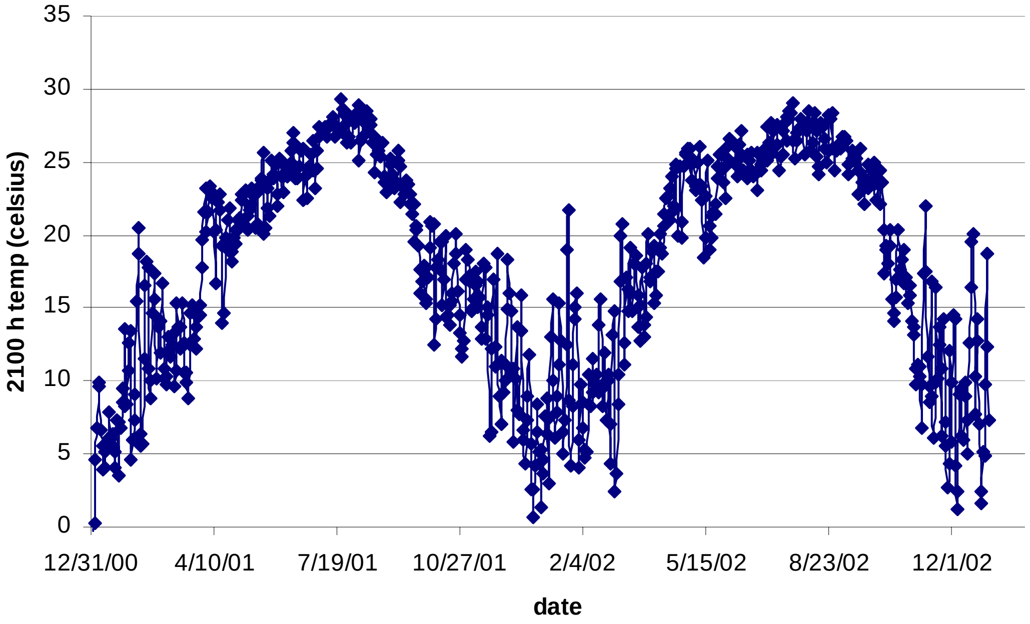


Figure 15. Nightly temperature at 2100 hrs in Nacogdoches and Houston counties, Texas, during 2001and 2002.

was observed calling in this study and was also detected calling on nights when the 2100 temperature was 29º C, the highest recorded temperature. Both *P. crucifer* and *P. triseriata* called at temperatures ranging from 5º C up to the lower 20sº C (Figures 18, 19, respectively). *Rana palustris* had a tendency to call at intermediate temperatures (10 - 22º C) in relation to the other winter and summer breeding species (Figure 20).

*Rana clamitans* called at the coolest temperatures (14º C) of any of the 8 summer breeding species. However, when temperatures exceeded 15º C, the probability of detecting calling *R. clamitans* increased by over 50% (Figure 21). *Acris crepitans* calling was similar pattern in that they were consistent callers above a temperature threshold of 18º C and had at least a 50 % probability of calling when temperatures exceeded 20º C (Figure 22).

*Rana catesbeiana*, *B. valliceps*, and *G. carolinensis* all called at relatively warm temperatures, but the probability of any of these species calling was below 20% at any given temperature within the calling range (Figures 23, 24, 25, respectively). The pattern was similar for the *B. woodhouseii*, *H. versicolor*, and *H. cinerea* except they tended to have a slightly higher probability of calling (Figures 26, 27, 28, respectively). On the two nights *S. holbrookii* were observed calling, temperatures were 16.74º C (27 February 2001) and 20.12º C (7 April 2002).

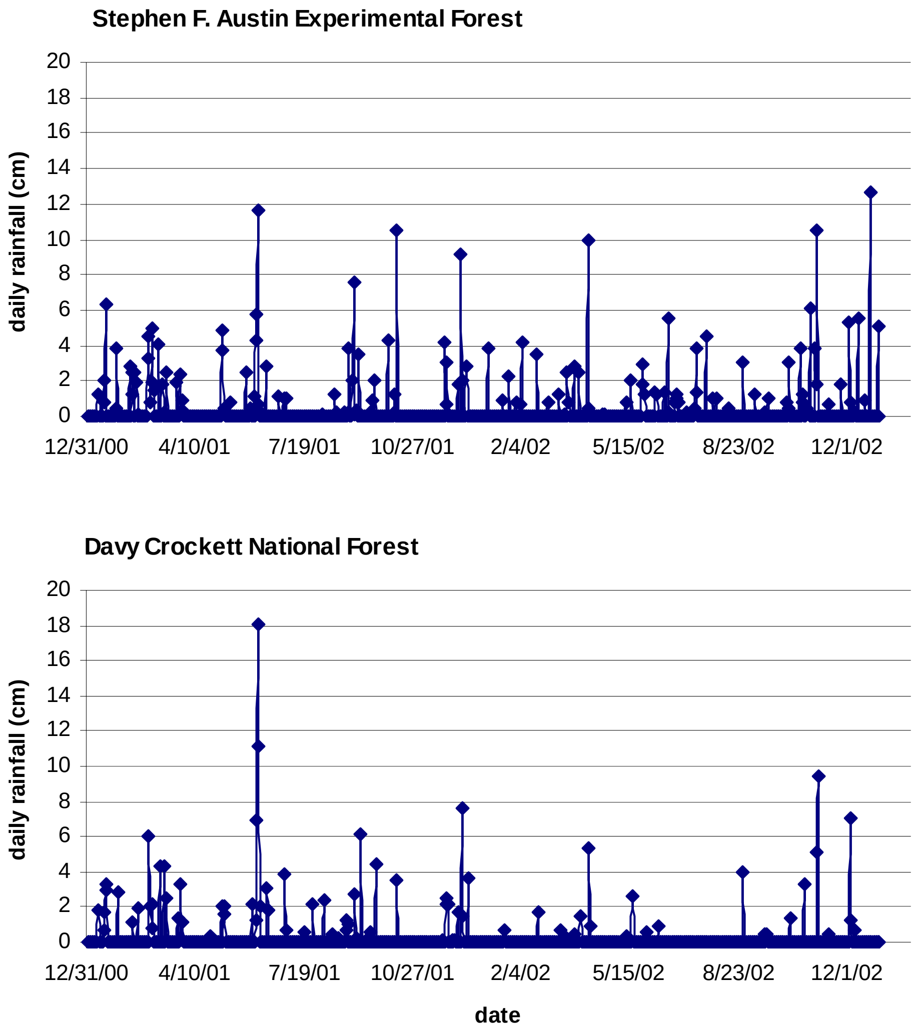


Figure 16. Daily rainfall in Nacogdoches and Houston counties, Texas, during 2001and 2002.

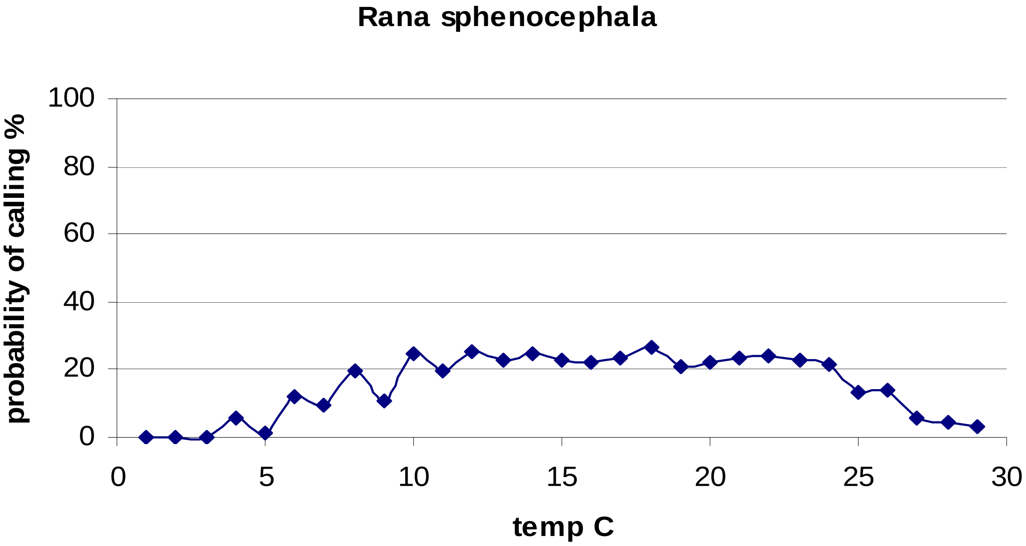


Figure 17. Probability of *Rana sphenocephala* calling over the range of observed temperatures at 2100 h during 2001and 2002 in Nacogdoches and Houston counties, Texas.

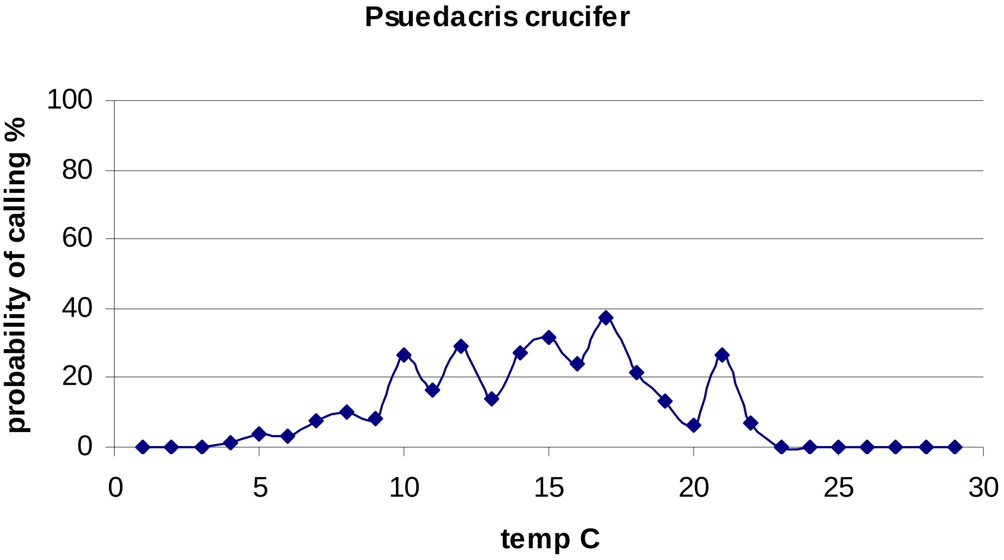


Figure 18. Probability of *Psuedacris crucifer* calling over the range of observed temperatures at 2100 h during 2001and 2002 in Nacogdoches and Houston counties, Texas.

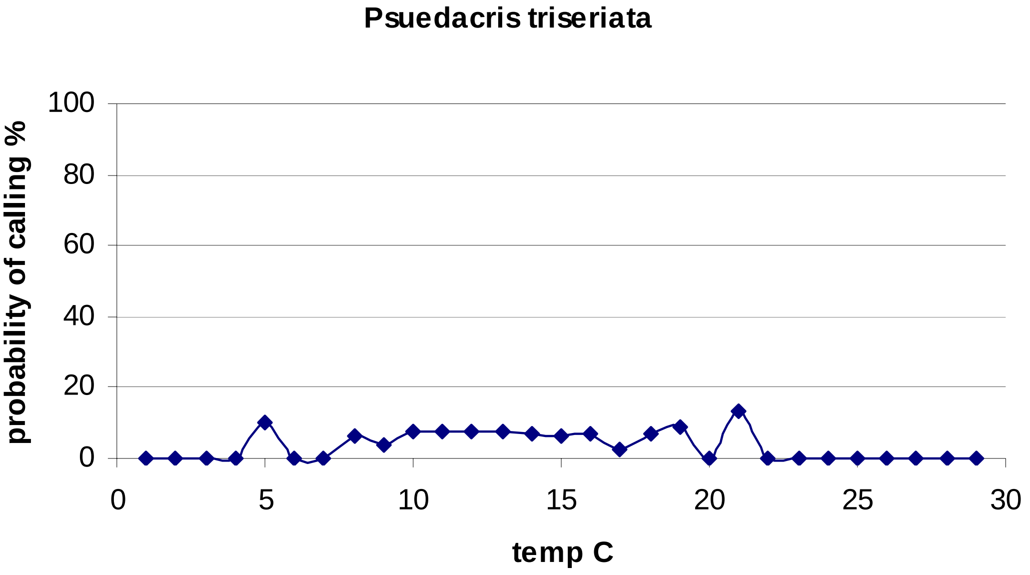


Figure 19. Probability of *Psuedacris triseriata* calling over the range of observed temperatures at 2100 h during 2001and 2002 in Nacogdoches and Houston counties, Texas.

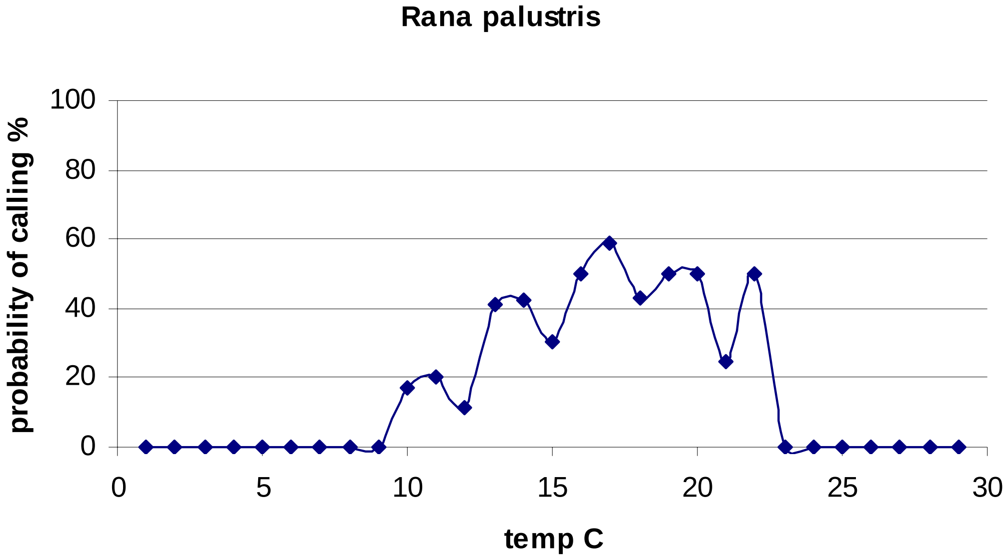


Figure 20. Probability of *Rana palustris* calling over the range of observed temperatures at 2100 h during 2001and 2002 in Nacogdoches and Houston counties, Texas.

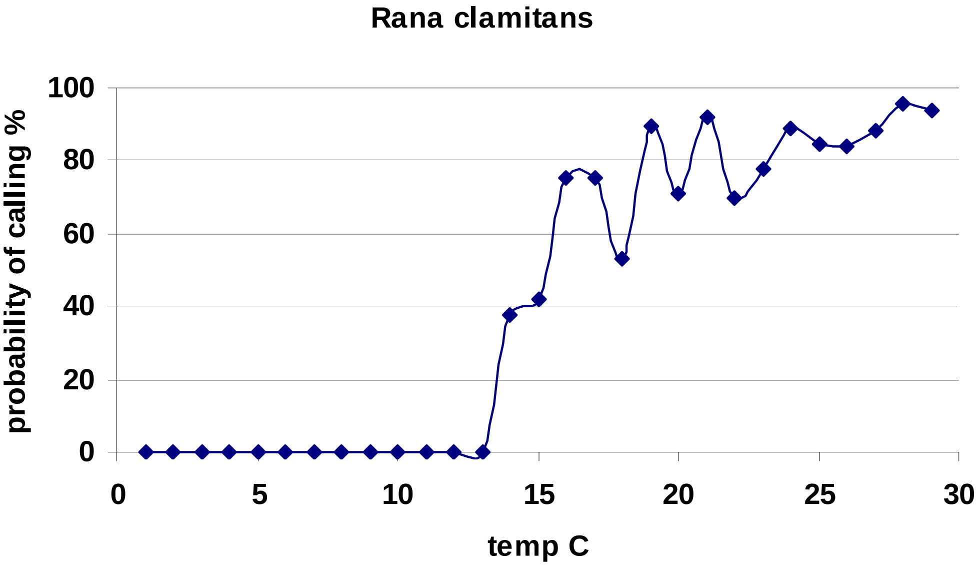


Figure 21. Probability of *Rana clamitans* calling over the range of observed temperatures at 2100 h during 2001and 2002 in Nacogdoches and Houston counties, Texas.

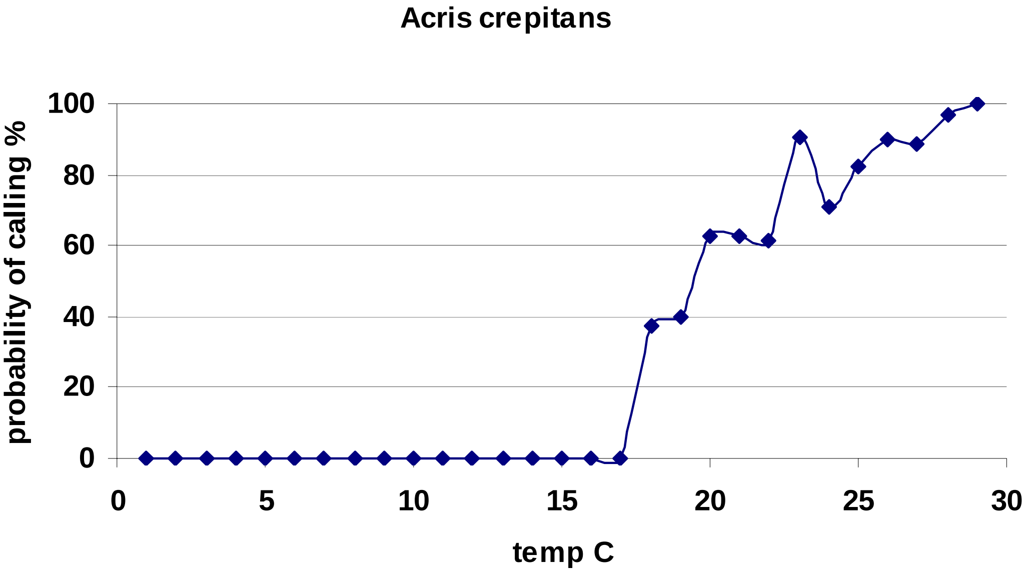


Figure 22. Probability of *Acris crepitans* calling at over the range of temperatures at 2100 h during 2001and 2002 in Nacogdoches and Houston counties, Texas.

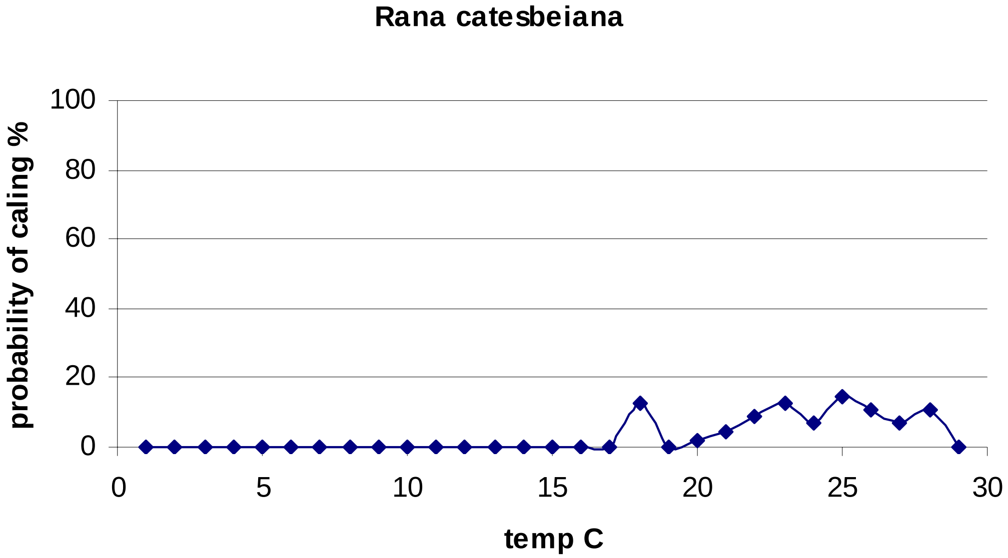


Figure 23. Probability of *Rana catesbeiana* calling over the range of observed temperatures at 2100 h during 2001and 2002 in Nacogdoches and Houston counties, Texas.

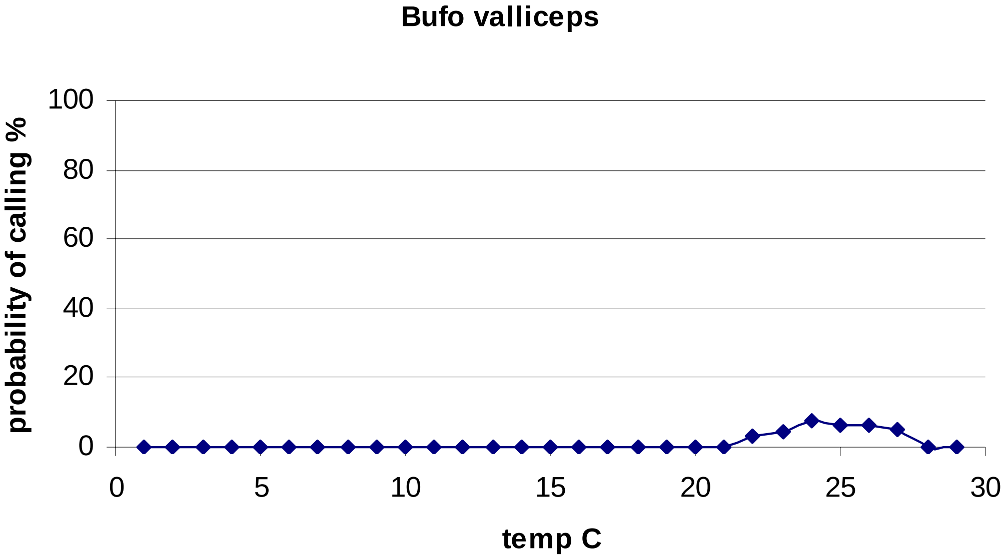


Figure 24. Probability of *Bufo valliceps* calling over the range of observed temperatures at 2100 h during 2001and 2002 in Nacogdoches and Houston counties, Texas.

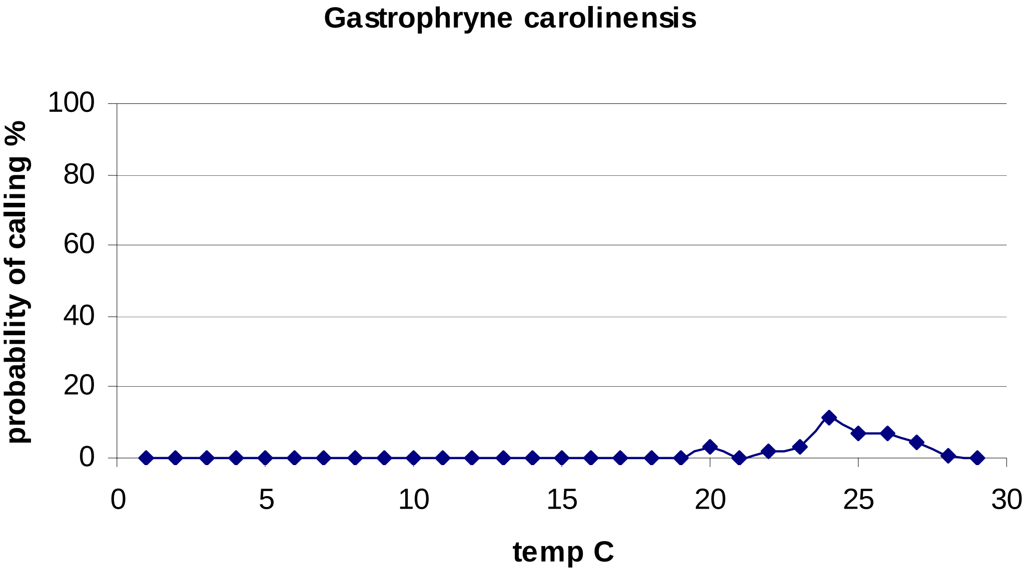


Figure 25. Probability of *Gastrophryne carolinensis* calling over the range of observed temperatures at 2100 h during 2001and 2002 in Nacogdoches and Houston counties, Texas.

## Abiotic correlates of calling activity

The repeated-measures logistic regressions revealed significant associations among abiotic variables and calling activity, but the relationships were complex and distinct for different species. In spring (Julian day 1-122), calling by *R. sphenocephala* was significantly associated with the abiotic variables and the 1-day and 2-day lags after rainfall. In summer (Julian day 123-244), calling by *R. sphenocephala* was only statistically associated with the 2-day lag after rains. In the fall (Julian day 245-365), was associated with temperature and both 1 and 2-day lags (Table 2).

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 (Table 3; Table 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 8 summer-breeding species. 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. A unit increase in rainfall predicted a 43% decrease in calling activity. In the analysis using only data from nights $\leq 24^{o}$C, calling was positively associated with temperature, and negatively associated with rainfall and a 1-day lag after rain. Above 25 $^{o}$C, calling was negatively associated with rain (Table 6).

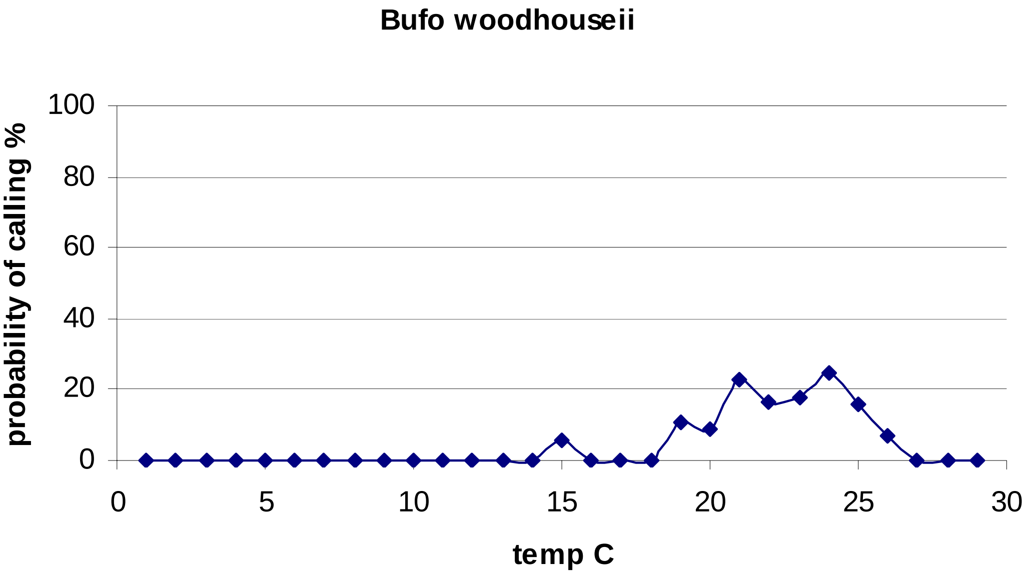


Figure 26. Probability of *Bufo woodhouseii* calling over the range of observed temperatures at 2100 h during 2001and 2002 in Nacogdoches and Houston counties, Texas.

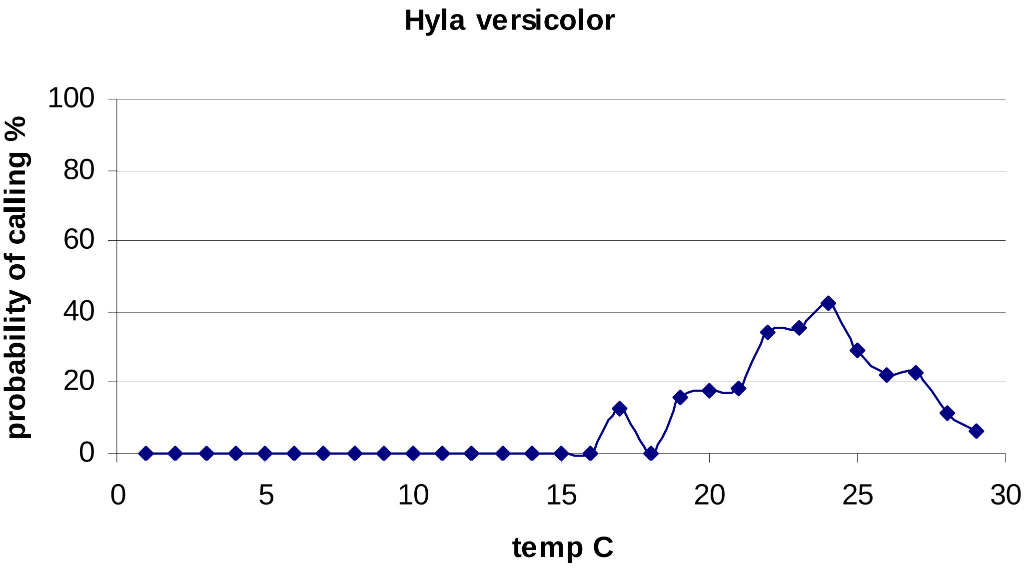


Figure 27. Probability of *Hyla versicolor* calling over the range of observed temperatures at 2100 h during 2001and 2002 in Nacogdoches and Houston counties, Texas.

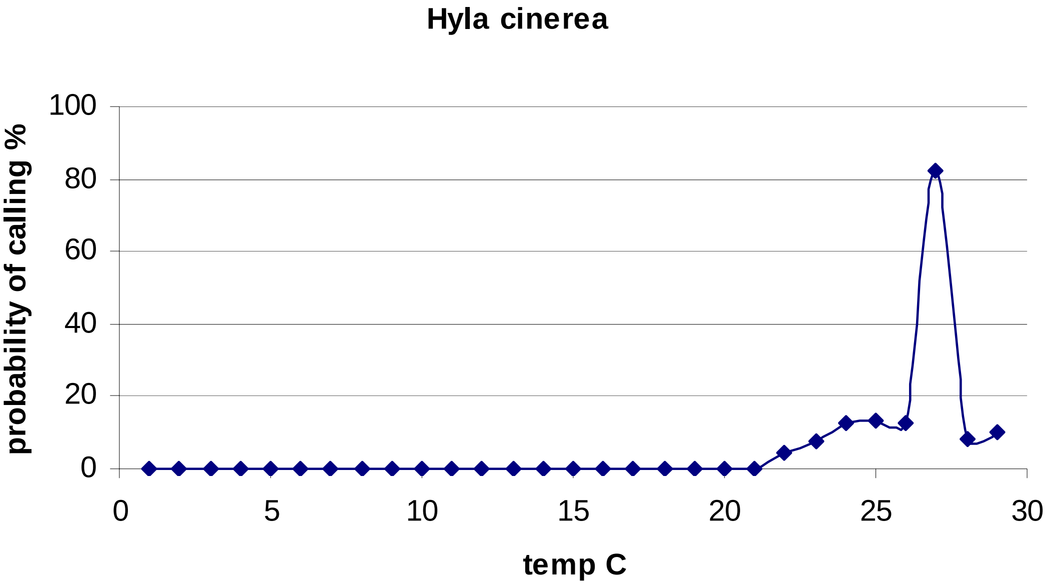


Figure 28. Probability of *Hyla cinerea* calling over the range of observed temperatures at 2100 h during 2001and 2002 in Nacogdoches and Houston counties, Texas.

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

| Model | Variable | Estimate[a] | SE[b] | $\chi^{2c}$ | $P > \chi^{2d}$ | Odds ratio |
|---|---|---|---|---|---|---|
| J-day 1-122 | | | | | | |
| Spring | Intercept | -1.85 | 0.43 | | | |
| | Temp | 0.07 | 0.02 | 13.24 | <0.001 | 1.08 |
| | Rain[e] | 0.17 | 0.04 | 14.48 | <0.001 | 1.18 |
| | Lag 1[f] | 0.19 | 0.03 | 38.05 | <0.001 | 1.21 |
| | Lag 2[g] | 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[e] | 0.04 | 0.04 | 1.27 | 0.259 | 1.04 |
| | Lag 1[f] | 0.06 | 0.03 | 2.65 | 0.104 | 1.06 |
| | Lag 2[g] | 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[e] | 0.08 | 0.07 | 1.27 | 0.261 | 1.08 |
| | Lag 1[f] | 0.21 | 0.04 | 29.32 | <0.001 | 1.24 |
| | Lag 2[g] | 0.23 | 0.03 | 46.39 | <0.001 | 1.26 |

[a] Estimate of explanatory slope ($\beta_x$).

[b] Standard error of slope estimate.

[c] $\chi^2$ statistic testing $H_o$: slope estimate = 0.

[d] Probability to reject $H_o$.

[e] Rainfall the day of frog calls.

[f] Rainfall one day prior to frog calls.

[g] Rainfall two days prior to frog calls.

Table 3. Results of repeated-measures logistic regression model for *R. palustris*. The probability of *R. palustris* calling was modeled with the variables, 2100 h air temperature, daily rainfall, one-day, and two-day lag in calling. *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[a] | SE[b] | $\chi^{2c}$ | $P > \chi^{2d}$ | Odds ratio |
|---|---|---|---|---|---|---|
| All temps | | | | | | |
| | Intercept | -4.30 | 0.68 | | | |
| | Temp | 0.25 | 0.03 | 111.71 | <0.001 | 1.28 |
| | Rain[e] | 0.08 | 0.21 | 0.15 | 0.697 | 1.08 |
| | Lag 1[f] | -0.02 | 0.13 | 0.03 | 0.861 | 0.98 |
| | Lag 2[g] | -0.13 | 0.13 | 0.97 | 0.325 | 0.88 |

[a] Estimate of explanatory slope ($\beta_x$).
[b] Standard error of slope estimate.
[c] $\chi^2$ statistic testing $H_o$: slope estimate = 0.
[d] Probability to reject $H_o$.
[e] Rainfall the day of frog calls.
[f] Rainfall one day prior to frog calls.
[g] Rainfall two days prior to frog calls.

Table 4. Results of repeated-measures logistic regression model for *P. triseriata*. The probability of *P. triseriata* calling was modeled with the variables, 2100 h air temperature, daily rainfall, one-day, and two-day lag in calling. *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[a] | SE[b] | $\chi^{2}$[c] | $P > \chi^{2}$[d] | Odds ratio |
|---|---|---|---|---|---|---|
| All temps | | | | | | |
| | Intercept | -5.01 | 0.67 | | | |
| | Temp | 0.06 | 0.01 | 18.13 | <0.001 | 1.06 |
| | Rain[e] | 0.17 | 0.12 | 1.94 | 0.164 | 1.18 |
| | Lag 1[f] | 0.09 | 0.06 | 2.09 | 0.148 | 1.09 |
| | Lag 2[g] | 0.03 | 0.04 | 0.33 | 0.565 | 1.03 |

[a] Estimate of explanatory slope ($\beta_x$).

[b] Standard error of slope estimate.

[c] $\chi^2$ statistic testing $H_o$: slope estimate = 0.

[d] Probability to reject $H_o$.

[e] Rainfall the day of frog calls.

[f] Rainfall one day prior to frog calls.

[g] Rainfall two days prior to frog calls.

Table 5. Results of repeated-measures logistic regression model for *P. crucifer*. The probability of *P. crucifer* calling was modeled with the variables, 2100 h air temperature, daily rainfall, one-day, and two-day lag in calling. *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[a] | SE[b] | $\chi^{2}$[c] | $P > \chi^{2}$[d] | Odds ratio |
|---|---|---|---|---|---|---|
| All temps | | | | | | |
| | Intercept | -2.05 | 0.38 | | | |
| | Temp | 0.11 | 0.02 | 35.43 | <0.001 | 1.11 |
| | Rain[e] | 0.14 | 0.05 | 7.54 | 0.006 | 1.15 |
| | Lag 1[f] | 0.06 | 0.02 | 5.91 | 0.015 | 1.06 |
| | Lag 2[g] | 0.03 | 0.04 | 0.90 | 0.342 | 1.03 |

[a] Estimate of explanatory slope ($\beta_x$).
[b] Standard error of slope estimate.
[c] $\chi^2$ statistic testing $H_o$: slope estimate = 0.
[d] Probability to reject $H_o$.
[e] Rainfall the day of frog calls.
[f] Rainfall one day prior to frog calls.
[g] Rainfall two days prior to frog calls.

For *R. clamitans*, another species that uses permanent water, temperature was significantly and positively associated with calling in the overall model. Below 25°C, temperature was the only abiotic predictor of calling. Above 24°C, there was a negative association with rain, but temperature was not a good predictor of calling (Table 7). Calling in the hylids that use permanent water, *A. crepitans* and *H. cinerea*, was positively associated with with temperature in the overall models. At lower temperatures, all the abiotic variables were significant predictors of calling in *A. crepitans*. Above 24°C, 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; no abiotic factors predicted calling by this species when temperature was ≥25°C (Table 9).

Calling by *H. versicolor*, *B. valliceps*, *B. woodhouseii*, and *G. carolinensis*, the summer-breeding species use ephemeral breeding sites, exhibited a very different calling response to rain than the species that use permanent water. Calling by *H. versicolor* and *G. carolinensis* was positively and strongly associated with 2-day lag following rain, regardless of temperature. Probability of calling was negatively associated with rain, and positively associated with lags following rain events for *B. valliceps* regardless of temperature, and especially so for *B. woodhouseii* when temperatures were ≤24°C. (Tables 10-13).

Table 6. Results of repeated-measures logistic regression model for *R. catesbeiana*. The probability of *R. catesbeiana* calling was modeled with the variables, 2100 h air temperature, daily rainfall, one-day, and two-day lagged calling. *Rana catesbeiana* breeding season was defined as Julian day 104 through 233 based on earliest and latest calling observations during this study. Days below 25º C 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[a] | SE[b] | $\chi^{2c}$ | $P > \chi^{2d}$ | Odds ratio |
|---|---|---|---|---|---|---|
| All temps | | | | | | |
| | Intercept | -3.07 | 1.14 | | | |
| | Temp | 0.04 | 0.02 | 2.96 | 0.086 | 1.04 |
| | Rain[e] | -0.57 | 0.09 | 40.20 | <0.001 | 0.57 |
| | Lag 1[f] | -0.03 | 0.15 | 0.06 | 0.812 | 0.97 |
| | Lag 2[g] | 0.02 | 0.89 | 0.04 | 0.845 | 1.02 |
| $\leq$ 24º C | | | | | | |
| | Intercept | -6.23 | 2.28 | | | |
| | Temp | 0.17 | 0.05 | 14.48 | <0.001 | 1.19 |
| | Rain[e] | -0.57 | 0.06 | 98.90 | <0.001 | 0.57 |
| | Lag 1[f] | -0.35 | 0.07 | 25.90 | <0.001 | 0.70 |
| | Lag 2[g] | 0.07 | 0.12 | 0.38 | 0.539 | 1.07 |
| $\geq$ 25º C | | | | | | |
| | Intercept | 1.75 | 2.74 | | | |
| | Temp | -0.15 | 0.06 | 6.24 | 0.125 | 0.86 |
| | Rain[e] | -0.62 | 0.17 | 12.98 | <0.001 | 0.54 |
| | Lag 1[f] | 0.09 | 0.12 | 0.57 | 0.452 | 1.09 |
| | Lag 2[g] | 0.03 | 0.06 | 0.28 | 0.599 | 1.03 |

[a] Estimate of explanatory slope ($\beta_x$).
[b] Standard error of slope estimate.
[c] $\chi^2$ statistic testing $H_o$: slope estimate = 0.
[d] Probability to reject $H_o$.
[e] Rainfall the day of frog calls.
[f] Rainfall one day prior to frog calls.
[g] Rainfall two days prior to frog calls.

Table 7. Results of repeated-measures logistic regression model for *R. clamitans*. The probability of *R. clamitans* calling was modeled with the variables, 2100 h air temperature, daily rainfall, one-day, and two-day lag in calling. *Rana clamitans* breeding season was defined as Julian day 88 through 261 based on earliest and latest calling observations during this study. Days below 25º C 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[a] | SE[b] | $\chi^{2c}$ | $P > \chi^{2d}$ | Odds ratio |
|---|---|---|---|---|---|---|
| All temps | | | | | | |
| | Intercept | -1.22 | 0.58 | | | |
| | Temp | 0.12 | 0.06 | 4.39 | 0.036 | 1.12 |
| | Rain[e] | -0.07 | 0.08 | 0.67 | 0.413 | 0.93 |
| | Lag 1[f] | 0.06 | 0.03 | 4.62 | 0.032 | 1.06 |
| | Lag 2[g] | -0.03 | 0.06 | 0.22 | 0.641 | 0.97 |
| ≤ 24º C | | | | | | |
| | Intercept | -2.30 | 0.81 | | | |
| | Temp | 0.17 | 0.07 | 6.54 | 0.011 | 1.19 |
| | Rain[e] | -0.06 | 0.09 | 0.55 | 0.459 | 0.94 |
| | Lag 1[f] | 0.02 | 0.02 | 0.71 | 0.401 | 1.02 |
| | Lag 2[g] | 0.01 | 0.05 | 0.00 | 0.984 | 1.00 |
| ≥ 25º C | | | | | | |
| | Intercept | 0.34 | 2.23 | | | |
| | Temp | 0.05 | 0.14 | 0.11 | 0.744 | 1.05 |
| | Rain[e] | -0.19 | 0.09 | 4.64 | 0.031 | 0.83 |
| | Lag 1[f] | 0.26 | 0.16 | 2.64 | 0.104 | 1.30 |
| | Lag 2[g] | -0.02 | 0.06 | 0.08 | 0.781 | 0.98 |

[a] Estimate of explanatory slope ($\beta_x$).

[b] Standard error of slope estimate.

[c] $\chi^2$ statistic testing $H_o$: slope estimate = 0.

[d] Probability to reject $H_o$.

[e] Rainfall the day of frog calls.

[f] Rainfall one day prior to frog calls.

[g] Rainfall two days prior to frog calls.

Table 8. Results of repeated-measures logistic regression model for *A. crepitans*. The probability of *A. crepitans* calling was modeled with the variables, 2100 h air temperature, daily rainfall, one-day, and two-day lag in calling. *Acris crepitans* breeding season was defined as Julian day 102 through 226 based on earliest and latest calling observations during this study. Days below 25º C 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[a] | SE[b] | $\chi^{2c}$ | $P > \chi^{2d}$ | Odds ratio |
|---|---|---|---|---|---|---|
| All temps | | | | | | |
| | Intercept | -6.36 | 1.17 | | | |
| | Temp | 0.33 | 0.06 | 36.5 | <0.001 | 1.40 |
| | Rain[e] | -0.20 | 0.06 | 12.31 | <0.001 | 0.82 |
| | Lag 1[f] | 0.01 | 0.10 | 0.00 | 0.984 | 1.00 |
| | Lag 2[g] | 0.14 | 0.10 | 2.02 | 0.155 | 1.15 |
| $\leq$ 24º C | | | | | | |
| | Intercept | -11.70 | 4.86 | | | |
| | Temp | 0.47 | 0.22 | 4.62 | 0.032 | 1.59 |
| | Rain[e] | -0.09 | 0.05 | 3.23 | 0.072 | 0.92 |
| | Lag 1[f] | -0.29 | 0.01 | 5436.5 | <0.001 | 0.75 |
| | Lag 2[g] | -0.28 | 0.07 | 18.01 | <0.001 | 0.75 |
| $\geq$ 25º C | | | | | | |
| | Intercept | -5.58 | 1.77 | | | |
| | Temp | 0.30 | 0.18 | 2.68 | 0.102 | 1.35 |
| | Rain[e] | -0.20 | 0.05 | 18.16 | <0.001 | 0.82 |
| | Lag 1[f] | 0.02 | 0.11 | 0.03 | 0.867 | 1.02 |
| | Lag 2[g] | 0.12 | 0.14 | 0.71 | 0.398 | 1.12 |

[a] Estimate of explanatory slope ($\beta_x$).

[b] Standard error of slope estimate.

[c] $\chi^2$ statistic testing $H_o$: slope estimate = 0.

[d] Probability to reject $H_o$.

[e] Rainfall the day of frog calls.

[f] Rainfall one day prior to frog calls.

[g] Rainfall two days prior to frog calls.

Table 9. Results of repeated-measures logistic regression model for *H. cinerea*. The probability of *H. cinerea* calling was modeled with the variables, 2100 h air temperature, daily rainfall, one-day, and two-day lag in calling. *Hyla cinerea* breeding season was defined as Julian day 113 through 211 based on earliest and latest calling observations during this study. Days below 25º C 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[a] | SE[b] | $\chi^{2c}$ | $P > \chi^{2d}$ | Odds ratio |
|---|---|---|---|---|---|---|
| All temps | | | | | | |
| | Intercept | -5.90 | 0.96 | | | |
| | Temp | 0.15 | 0.05 | 8.76 | 0.003 | 1.16 |
| | Rain[e] | 0.02 | 0.03 | 0.50 | 0.478 | 1.02 |
| | Lag 1[f] | 0.09 | 0.06 | 2.35 | 0.125 | 1.09 |
| | Lag 2[g] | -0.02 | 0.03 | 0.58 | 0.446 | 0.98 |
| $\leq$ 24º C | | | | | | |
| | Intercept | -14.75 | 1.41 | | | |
| | Temp | 0.51 | 0.06 | 19.77 | <0.001 | 1.67 |
| | Rain[e] | 0.01 | 0.04 | 0.04 | 0.850 | 1.01 |
| | Lag 1[f] | 0.08 | 0.07 | 1.52 | 0.22 | 1.09 |
| | Lag 2[g] | -0.03 | 0.03 | 1.00 | 0.316 | 0.97 |
| $\geq$ 25º C | | | | | | |
| | Intercept | -0.88 | 2.66 | | | |
| | Temp | -0.06 | 0.11 | 0.24 | 0.623 | 0.95 |
| | Rain[e] | -0.03 | 0.06 | 0.36 | 0.551 | 0.97 |
| | Lag 1[f] | 0.07 | 0.07 | 0.92 | 0.337 | 1.07 |
| | Lag 2[g] | 0.02 | 0.06 | 0.09 | 0.758 | 1.02 |

[a] Estimate of explanatory slope ($\beta_x$).
[b] Standard error of slope estimate.
[c] $\chi^2$ statistic testing $H_o$: slope estimate = 0.
[d] Probability to reject $H_o$.
[e] Rainfall the day of frog calls.
[f] Rainfall one day prior to frog calls.
[g] Rainfall two days prior to frog calls.

Table 10. Results of repeated-measures logistic regression model for *H. versicolor*. The probability of *H. versicolor* calling was modeled with the variables, 2100 h air emperature, daily rainfall, and one-day, and two-day lag in calling. *Hyla versicolor* breeding season was defined as Julian day 88 through 246 based on earliest and latest calling observations during this study. Days below 25º C 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[a] | SE[b] | $\chi^{2c}$ | $P > \chi^{2d}$ | Odds ratio |
|---|---|---|---|---|---|---|
| All temps | | | | | | |
| | Intercept | -0.99 | 0.82 | | | |
| | Temp | 0.02 | 0.03 | 0.30 | 0.585 | 1.02 |
| | Rain[e] | 0.02 | 0.03 | 6.90 | 0.009 | 1.20 |
| | Lag 1[f] | 0.10 | 0.07 | 2.02 | 0.155 | 1.11 |
| | Lag 2[g] | 0.14 | 0.03 | 21.62 | <0.001 | 1.15 |
| $\leq$ 24º C | | | | | | |
| | Intercept | -4.75 | 1.02 | | | |
| | Temp | 0.26 | 0.03 | 6.87 | <0.001 | 1.25 |
| | Rain[e] | 0.13 | 0.09 | 1.42 | 0.156 | 1.12 |
| | Lag 1[f] | 0.09 | 0.10 | 0.92 | 0.355 | 1.10 |
| | Lag 2[g] | 0.12 | 0.05 | 2.57 | 0.010 | 1.11 |
| $\geq$ 25º C | | | | | | |
| | Intercept | 8.10 | 1.98 | | | |
| | Temp | -0.34 | 0.08 | 20.88 | <0.001 | 0.71 |
| | Rain[e] | 0.11 | 0.06 | 3.08 | 0.079 | 1.11 |
| | Lag 1[f] | 0.05 | 0.08 | 0.45 | 0.500 | 1.05 |
| | Lag 2[g] | 0.21 | 0.05 | 20.07 | <0.001 | 1.24 |

[a] Estimate of explanatory slope ($\beta_x$).
[b] Standard error of slope estimate.
[c] $\chi^2$ statistic testing $H_o$: slope estimate = 0.
[d] Probability to reject $H_o$.
[e] Rainfall the day of frog calls.
[f] Rainfall one day prior to frog calls.
[g] Rainfall two days prior to frog calls.

Table 11. Results of repeated-measures logistic regression model for *B. valliceps*. The probability of *B. valliceps* calling was modeled with the variables, 2100 h air temperature, daily rainfall, one-day, and two-day lag in calling. *Bufo valliceps* breeding season was defined as Julian day 92 through 183 based on earliest and latest calling observations during this study. Days below 25º C 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[a] | SE[b] | $\chi^{2c}$ | $P > \chi^{2d}$ | Odds ratio |
|---|---|---|---|---|---|---|
| All temps | | | | | | |
| | Intercept | -8.93 | 0.83 | | | |
| | Temp | 0.22 | 0.04 | 32.31 | <0.001 | 1.25 |
| | Rain[e] | -0.05 | 0.01 | 14.75 | <0.001 | 0.95 |
| | Lag 1[f] | 0.06 | 0.01 | 23.92 | <0.001 | 1.06 |
| | Lag 2[g] | 0.08 | 0.03 | 5.44 | 0.020 | 1.08 |
| $\leq$ 24º C | | | | | | |
| | Intercept | -10.21 | 0.63 | | | |
| | Temp | 0.27 | 0.04 | 54.10 | <0.001 | 1.31 |
| | Rain[e] | -0.08 | 0.02 | 25.99 | <0.001 | 0.92 |
| | Lag 1[f] | 0.09 | 0.02 | 26.75 | <0.001 | 1.09 |
| | Lag 2[g] | 0.07 | 0.04 | 3.40 | 0.065 | 1.07 |
| $\geq$ 25º C | | | | | | |
| | Intercept | -11.08 | 4.99 | | | |
| | Temp | 0.27 | 0.19 | 2.18 | 0.140 | 1.31 |
| | Rain[e] | -0.06 | 0.01 | 18.49 | <0.001 | 0.94 |
| | Lag 1[f] | 0.08 | 0.01 | 61.32 | <0.001 | 1.08 |
| | Lag 2[g] | 1.12 | 0.08 | 2.24 | 0.135 | 1.12 |

[a] Estimate of explanatory slope ($\beta_x$).

[b] Standard error of slope estimate.

[c] $\chi^2$ statistic testing $H_o$: slope estimate = 0.

[d] Probability to reject $H_o$.

[e] Rainfall the day of frog calls.

[f] Rainfall one day prior to frog calls.

[g] Rainfall two days prior to frog calls.

Table 12. Results of repeated-measures logistic regression model for *B. woodhouseii*. The probability of *B. woodhouseii* calling was modeled with the variables, 2100 h air temperature, daily rainfall, one-day, and two-day lag in calling. *Bufo woodhouseii* breeding season was defined as Julian day 73 through 245 based on earliest and latest calling observations during this study. Days below 25° C 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[a] | SE[b] | $\chi^{2}$[c] | $P > \chi^{2}$[d] | Odds ratio |
|---|---|---|---|---|---|---|
| All temps | | | | | | |
| | Intercept | -1.88 | 0.50 | | | |
| | Temp | -0.01 | 0.01 | 0.01 | 0.925 | 0.99 |
| | Rain[e] | 0.21 | 0.08 | 7.94 | 0.005 | 1.24 |
| | Lag 1[f] | -0.02 | 0.02 | 0.99 | 0.321 | 0.98 |
| | Lag 2[g] | 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[e] | 0.25 | 0.06 | 17.75 | <0.001 | 1.28 |
| | Lag 1[f] | -0.38 | 0.12 | 9.59 | 0.002 | 0.69 |
| | Lag 2[g] | 0.25 | 0.10 | 5.94 | 0.015 | 1.29 |
| ≥ 25° C | | | | | | |
| | Intercept | 49.98 | 6.62 | | | |
| | Temp | -2.02 | 0.26 | 58.43 | <0.001 | 0.13 |
| | Rain[e] | 0.03 | 0.22 | 0.03 | 0.873 | 1.04 |
| | Lag 1[f] | -0.32 | 0.44 | 0.52 | 0.472 | 0.73 |
| | Lag 2[g] | -1.57 | 0.83 | 3.60 | 0.058 | 0.21 |

[a] Estimate of explanatory slope ($\beta_x$).

[b] Standard error of slope estimate.

[c] $\chi^2$ statistic testing $H_o$: slope estimate = 0.

[d] Probability to reject $H_o$.

[e] Rainfall the day of frog calls.

[f] Rainfall one day prior to frog calls.

[g] Rainfall two days prior to frog calls.

Table 13. Results of repeated-measures logistic regression model for *G. carolinensis*. The probability of *G. carolinensis* calling was modeled with the variables, 2100 h air temperature, daily rainfall, one-day, and two-day lag in calling. *Gastrophryne carolinensis* breeding season was defined as Julian day 119 through 245 based on earliest and latest calling observations during this study. Days below 25º C 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[a] | SE[b] | $\chi^{2c}$ | $P > \chi^{2d}$ | Odds ratio |
|---|---|---|---|---|---|---|
| All temps | | | | | | |
| | Intercept | -2.17 | 0.71 | | | |
| | Temp | -0.03 | 0.03 | 0.92 | 0.339 | 0.97 |
| | Rain[e] | -0.05 | 0.05 | 0.82 | 0.365 | 0.95 |
| | Lag 1[f] | 0.13 | 0.04 | 9.29 | 0.002 | 1.14 |
| | Lag 2[g] | 0.22 | 0.08 | 8.02 | 0.005 | 1.25 |
| $\leq$ 24º C | | | | | | |
| | Intercept | -14.76 | 2.97 | | | |
| | Temp | 0.52 | 0.12 | 18.87 | <0.001 | 1.68 |
| | Rain[e] | -0.12 | 0.05 | 7.37 | 0.007 | 0.88 |
| | Lag 1[f] | 0.16 | 0.04 | 13.11 | <0.001 | 1.18 |
| | Lag 2[g] | 1.18 | 0.09 | 4.25 | 0.039 | 1.19 |
| $\geq$ 25º C | | | | | | |
| | Intercept | 8.60 | 2.58 | | | |
| | Temp | -0.45 | 0.10 | 20.06 | <0.001 | 0.63 |
| | Rain[e] | -0.09 | 0.06 | 2.62 | 0.105 | 0.91 |
| | Lag 1[f] | 0.12 | 0.06 | 4.15 | 0.042 | 1.13 |
| | Lag 2[g] | 0.24 | 0.08 | 10.40 | 0.001 | 1.13 |

[a] Estimate of explanatory slope ($\beta_x$).

[b] Standard error of slope estimate.

[c] $\chi^2$ statistic testing $H_o$: slope estimate = 0.

[d] Probability to reject $H_o$.

[e] Rainfall the day of frog calls.

[f] Rainfall one day prior to frog calls.

[g] Rainfall two days prior to frog calls.

## DISCUSSION

Although air temperature and rainfall were clearly important drivers of calling activity of anurans in eastern Texas, similarities and differences in 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 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. My 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 eastern Texas was more complex. Calling activity in the eastern Texas anurans was assorted by species that breed only in winter, during summer, year-round breeding by *R. sphenocephala*, and explosive breeding by *S. holbrookii* following infrequent large rain events.

*Rana sphenocephala* was the only year-round caller in the assemblage, and this generalist species apparently had a wide range of tolerances for climatic conditions with respect to calling behavior. Calling in this species 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 the 2-day lag during summer. Because rain events were less frequent in summer, this species may have been less active and took longer to migrate to the ponds from their retreats. Calling in winter by *R. sphenocephala* was also associated with temperatures. 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 positively associated with temperature. Calling was intense and of relatively short duration. 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. Breeding sites do not appear to be limited by a lack of water during wet years (personal observation). It is not known if the winter-breeding species might respond more 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 I expect a similar response could occur in the community studied here, it is also clear that temperature was the critical abiotic correlate of calling in winter-breeding frogs in eastern Texas.

The summer-breeding assemblage of 8 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. woodhouseii*, *H. versicolor*, and *G. carolinensis* were positively associated with rain and lags after rainfall. Risk of desiccation is a known risk to anurans that use ephemeral breeding sites (Dayton and Fitzgerald 2002). Hence, it was not unexpected that rainfall had a very strong positive effect on species that 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 (Wells 1977, Oseen and Wassersug 2002). 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, 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*, a spadefoot toad, is an explosive breeder that depends on highly ephemeral sites and large rain events. My 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 my results on calling intensity over the 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. woodhouseii*, *H. versicolor*, and *G. carolinensis* are all known to use ephemeral breeding sites in eastern Texas (Garrett and Barker 1987, Conant and Collins 1998, personal observations). However, they can also use permanent ponds, such as the ones I monitored during this study, with the exception of

*S. holbrookii* that only used ephemeral sites. My 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 is 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 either winter-breeding species that used permanent or ephemeral breeding sites, or summer-breeding species that used permanent water. The species dependent on permanent ponds in eastern Texas have relatively long larval periods and breed and spend much of their lives in and around sites that are wet year-round (Garrett and Barker 1987, Conant and Collins 1998). These sites are not as dependent on daily rainfall, and I 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, the negative response to rain occurred only during the day of rain; there was no negative association between rainfall lags and calling.

Abiotic factors clearly play an extremely important role in cuing breeding behavior of eastern Texas anurans, and my 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 5 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. 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).

# CHAPTER III

# A SIMULATION MODEL OF ANURAN COMMUNITY SUCCESSION AND COLONIZATION

## INTRODUCTION

The classic theory of succession highlights the consequences of life history traits in structuring communities through time. For example, early colonizing species that invade soon after a disturbance typically have great dispersal ability, and low competitive ability, whereas later colonizers tend to have poorer dispersing ability but tend to out-compete earlier arriving species (McCook 1994).

In freshwater systems, pond drying and predation are important sources of mortality and thereby constrain and regulate community composition (Smith 1983, Banks and Beebee 1988). In these systems, other life history characteristics, such as rates of development and predator avoidance behaviors also affect community structure (Skelly 1997) and should be considered important factors influencing community composition and succession.

The current paradigm about community assembly in freshwater environments is that species distributions are correlated with the environmental gradient of water permanency (Collins and Wilbur 1979, Werner and McPeek 1994, Wellborn et al. 1996, Skelly 1997, Stoks and McPeek 2003) and every species is restricted to some portion of the hydroperiod continuum. As a consequence, each species should have unique natural history traits suited for existence at a particular portion of the gradient that could affect community composition over time.

Anuran species that typically breed in ephemeral sites tend to have short larval stages associated with high activity levels required for rapid development (Skelly 1997). As a consequence of high activity levels they are quite susceptible to predation (Woodard 1983, Lawler 1989, Skelly 1992 Dayton and Fitzgerald 2002). I hypothesize that, as a general rule, these species will likely be more evenly distributed (spatially) than other species, because they are not as strictly constrained by the hydroperiod of a breeding site as species that exclusively use permanent breeding sites. For example, species with extremely short larval periods could breed in puddles found throughout the landscape. As ponds age, the number and density of species that prey on amphibian larvae should increase (Schneider and Frost 1996) and will differentially impact anuran species depending on how resistant each species is to predators (Skelly 1997).

By contrast, species that are associated with permanent water tend to have longer larval periods, lower activity levels, and lower susceptibility to predation than species in ephemeral sites (Woodard 1983, Lawler 1989, Skelly 1992). I hypothesize that species associated with permanent water will have a clumped spatial distribution because they are tied to historically permanent breeding sites that are less common on the landscape than ephemeral sites. However, when species associated with permanent water arrive at a site, they should be able to coexist with predators and become the predominant amphibian species as the ponds age.

A few studies have addressed community succession in anurans; however, they have mainly focused on breeding phenology or seasonal changes instead of long-term changes in community composition (Dixon and Heyer 1968, Wiest 1982). The lack of anuran community succession studies is likely associated with inherent difficulties in working with amphibians, such as identification of species in the larval stage, nocturnal habits, fluctuations in natural populations influenced by weather and human activities, and the time required to follow communities through successional stages (Bragg 1960, Pechmann et al. 1991, Pechmann and Wilbur 1994). However, anuran communities, particularly the larval communities, have the potential to be extremely useful for testing hypotheses related to succession because they can be easily sampled and obtained in large numbers useful in experimentation as long as researchers have adequate skills to identify larvae and time required to obtain a dataset of sufficient duration to overcome the problems of natural population fluctuations.

The piney woods region of eastern Texas has a diverse herpetofauna including 12 common anuran species representing five families of frogs and toads. The anurans in our study system range in size from the small northern cricket frog (*Acris crepitans)* at 2 – 3 cm in length to the bullfrog (*Rana catesbeiana*) at up to 15 cm. In addition to size, the anurans vary greatly in other natural history characteristics that may influence community assembly, such as length of the larval stage, natural population levels, fecundity, colonizing ability, and resistance to predators (Table 14). Variables in Table 14 are explained in the methods.

Table 14. Distribution and abundance rankings, and colonization and predation indices.

| Species | Days to metamorphosis | Clutch size | Breeding months | Distr. rank | Abund. rank | Colon. index | Funct. response |
|---|---|---|---|---|---|---|---|
| *Acris crepitans* | 70 days (Conant and Collins 1998) | Mean = 323 (Burkett 1969) | 3-6 | 4 | 5 | 0.20 | 4 |
| *Bufo valliceps* | 20 days (Garrett and Barker1987) | Mean = 4,100 (Linbaugh and Volpi 1937) | 3-9 | 9 | 4 | 0.36 | 9 |
| *Bufo Woodhousii* | 35 days (Wright and Wright 1949) | Mean = 8,500 (Conant and Collins 1998) | 3-6 | 8 | 10 | 0.80 | 8 |
| *Gastrophryne carolinensis* | 23days (Pechmann 1994) | 598 (Wilbur 1997) | 5-9 | 9 | 8 | 0.72 | 9 |
| *Hyla cinerea* | 55 days (Garrett and Barker1987) | 275-1,160 (Perrill et al. 1982) | 3-8 | 6 | 4 | 0.24 | 6 |
| *Hyla versicolor* | 35 days (Ritke et al. 1990) | 628-4,208 (Ritke et al. 1990) | 4-6 | 8 | 6 | 0.48 | 8 |
| *Pseudacris crucifer* | 90 days (Garrett and Barker1987) | Mean = 900 (Gosner and Rossman 1960) | 3-6 | 2 | 8 | 0.16 | 2 |

Table 14. Continued.

| Species | Days to metamorphosis | Clutch size | Breeding months | Distr. rank | Abund. rank | Colon. index | Funct. response |
|---|---|---|---|---|---|---|---|
| *Pseudacris triseriata* | 55 days (Smith 1983) | 100-1,500 (Conant and Collins 1998) | 2-3 | 6 | 9 | 0.54 | 6 |
| *Rana catesbeiana* | 365 days (Graves and Anderson 1987) | 1,000-10,000 (Wright 1920) | 4-8 | 1 | 4 | 0.04 | 1 |
| *Rana sphenocephala* | 67 days (Wright and Wright 1949) | 3,000-5,000 (Smith 1961) | 2-10 | 5 | 10 | 0.50 | 5 |
| *Rana clamitans* | 90 days (Conant and Collins 1998) | 1,000-7,000 (Wells 1976) | 3-6 | 2 | 4 | 0.08 | 2 |
| *Scaphiopus holbrookii* | 14 days (Garrett and Barker1987) | 2,000 (Wright and Wright 1949) | 3-9 | 10 | 1 | 0.10 | 10 |

Numbers of predators such as fish and odonate larvae (dragonflies) have been correlated with mortality rates in some larval amphibian populations (Brockelman 1969, Skelly and Werner 1990), and are common in ponds in eastern Texas (personal observation). Four families of dragonflies are common in eastern Texas including Aeshnidae, Corduliidae, Gomphidae, and Libellulidae. A common species of fish in ponds in eastern Texas is the green sunfish (*Lepomis cyanellus*), which is known to be a significant predator on larval anurans (Sexton and Phillips 1986).

My goal was to develop a simulation model of anuran community succession based on life-history characters of each species in my study system in eastern Texas. Specifically, my objective was to determine the importance of fecundity and length of larval stage to community assembly over time. Currently, there is a paucity of long-term baseline data available and much of what is known about amphibian population dynamics comes from short duration studies or anecdotal accounts (Blaustein et al. 1994). This model is particularly timely due to the current concerns about the worldwide decline in amphibian populations (Blaustein and Wake 1990, Blaustein et al. 1994, Pechmann and Wilbur 1994). Predictive models are useful for amphibian conservation because they highlight mechanisms that may be operating in the field and orient research toward testable hypotheses about factors that determine species presense or persistence. This model is developed to lead to a better understanding of anuran communities and the development of informed hypotheses on anuran community assembly.

## METHODS

### Model overview

The model simulates anuran community succession over a 10-year period in a newly created pond in the piney woods region of eastern Texas. The model predicts monthly fluctuations in anuran colonization of the ponds and recruitment (individuals that reach metamorphosis) from the ponds. The complete model system consists of 12 independent models for each of the anuran species that are run simultaneously and the results are merged to form the overall anuran community. Predator submodels are the common link between the anuran submodels because our model assumes no interactions among the anuran species.

### Anuran submodels

#### *Colonization*

The anuran submodels are basically the same (see the bullfrog submodel for an example, Figure 29) in that adults of each species may colonize the pond during their specific breeding season where they deposit eggs and then leave. Each anuran species has the potential to colonize the pond, but each species varies in its colonizing ability. I developed a colonization index (Table 14) based on a combination of a species' spatial distribution on the landscape, calculated from length of larval stage, and the relative abundance of that species, based on mostly on personnel and consultation with local

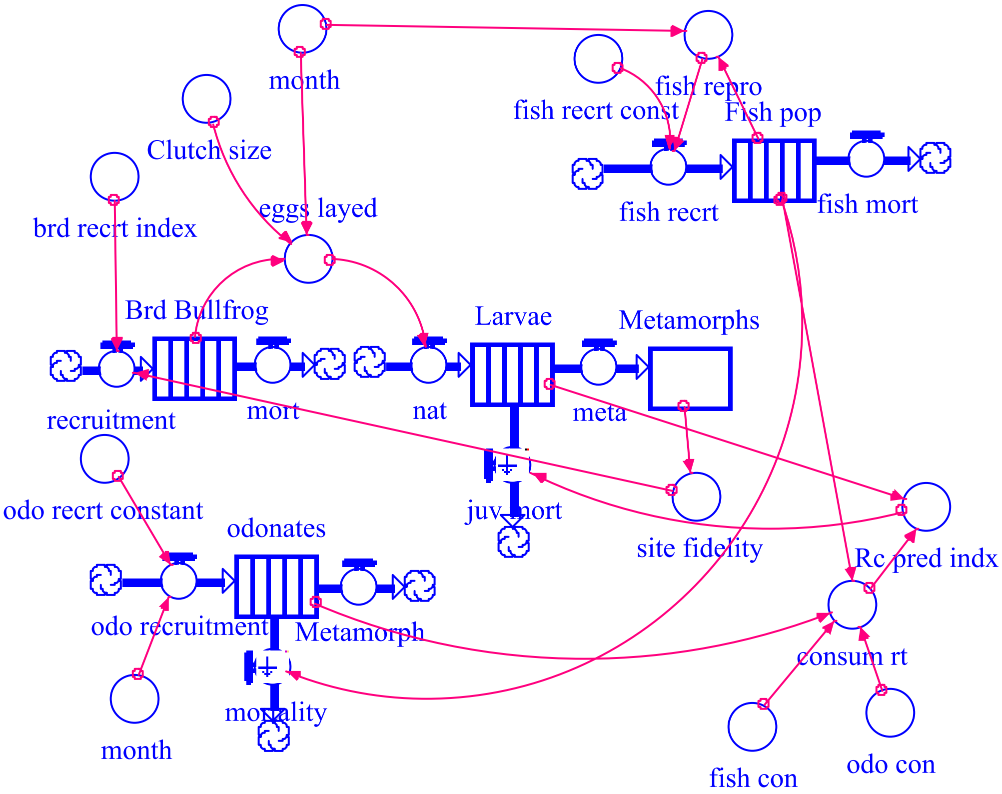


Figure 29. Example of the bullfrog model depicting information and material transfer.

experts. I did not consider species vagility, because of the paucity and subjective nature of those data.

To calculate the colonization index, I ranked the length of the larval stage on a scale from 1 to 10 where the shortest larval stage received a 10 and the longest larval stage received a 1 (Table 15). I ranked the spatial distribution of each species based on the length of the larval stages, because I assumed that as the length of the larval stages decreases the spatial distribution increases. Rank abundance was based on personal observations. The least abundant species received a 1 and the most common species received a 10 (Table 15). The distribution and relative abundance rankings contributed equally to colonization ability and were multiplied to produce a probability of colonization for each species for each timestep (month) that the particular species was known to breed (Table 14). For example, a species with a relative abundance ranking of 10 and a distribution ranking of 8 would have an 80% probability of colonizing the pond each month of its breeding season while a species with an abundance ranking of 3 and a distribution ranking of 8 would have only a 24% probability of colonizing the pond each month of its breeding season.

### *Fecundity*

Upon colonizing a pond, anurans breed, deposit eggs, larvae develop, metamorphose, and disperse. In this model, the number of pairs finding the breeding site was equivalent to the relative abundance ranking. The number of eggs produced can range from 100 to 10,000 eggs per pair and is species specific (Table 14). Variation in clutch-size is also common within a species, therefore, when available; clutch-size was randomly selected from the known range of clutch-sizes for a particular species. For some species, little natural history information was available, and I was limited to using average clutch-sizes or data from a single observation.

### *Larval stage and resistance to predation*

Length of larval stage can vary from as short as two weeks for the *Scaphiopus holbrookii* to over a year for *R. catesbeiana* (Table 14). Because simulations were conducted at one-month intervals, I estimated the nearest number of timesteps a species would remain in the pond as a larvae based on information from the literature (Table 14). For example, *S. holbrookii* larvae would inhabit the pond for one timestep, while *R. catesbeiana* larva would take 12 timesteps to reach metamorphosis.

During the time anurans inhabit a pond as larvae, they are vulnerable to predation by whatever predators may be present. Type and abundance of predators affect anuran prey species' populations. Moreover, a moving tadpole is more vulnerable to a predator than one that is immobile (Lawler 1989, Werner and Anholt 1993, Skelly 1994). Anuran species with short larval stages develop more quickly than species with long larval stages, and also are more active in order to secure enough food to quickly reach metamorphosis (Wassersug 1972, Werner 1991). Resistance to predation is species specific among anurans. As a general rule, the longer the larval stage the lower the susceptibility to predation, and the shorter the larval stage the higher the susceptibility (Dayton and Fitzgerald 2002). This model incorporates this paradigm by using the same ranking system for estimating spatial distributions for estimating a species' susceptibility to predation (Table 14). For example, the *R. catesbeiana* has a very long larval stage and has a ranking of 1 for susceptibility to predators, whereas *S. holbrookii* has an extremely short larval stage and ranks a 10. Other species range from a ranking of 2 to 9 (Table 15).

In this model, the anuran larvae will either reach metamorphosis at the end of their larval stage and recruit into the population or they will be removed from the system by a predator. The susceptibility value will be multiplied by the number of predators in the system to determine the predation index for each species. The predation index will be in constant flux as the predator population is constantly changing. The number of timesteps a species spends in the larval stage will then be divided into the predation index to remove the effect of variable larval stages among species on the predicted amount of predation. This predation value for each species will equal the number of tadpoles removed from the system each timestep.

### *Predation level*

Susceptibility to predation among tadpoles may not follow a linear function. A linear function, for example, based on a scale form 1 to 10, would mean the most susceptible species is ten times more vulnerable than the least susceptible species. This would imply that in this model, susceptibility to predation is a linear function based on the length of the larval stage. However, a linear model of predation susceptibility may be unrealistic. A curvilinear function might provide a better representation of the true

Table 15. Ranking system for distribution and relative abundance rankings.

| Days to metamorphosis | Distribution Rank | Relative abundance | Abundance rank |
|---|---|---|---|
| < 20 | 10 | MOST | 10 |
| 20-29 | 9 | ↓ | 9 |
| 30-39 | 8 | | 8 |
| 40-49 | 7 | | 7 |
| 50-59 | 6 | | 6 |
| 60-69 | 5 | | 5 |
| 70-79 | 4 | | 4 |
| 80-89 | 3 | | 3 |
| 90-99 | 2 | | 2 |
| > 99 | 1 | LEAST | 1 |

range of susceptibilities where the most vulnerable species might be orders of magnitude more sensitive to predation. I evaluated different curvilinear functions where susceptibility rankings were squared, and cubed (Figure 30). I chose the cubed function for anuran susceptibility to predation. Based on studies on susceptibility of anuran larvae to predation, I felt there was too little difference in susceptibility the species in the other models (Werner and Anholt 1993, Skelly 1994, Dayton and Fitzgerald 2001).

### Predator submodels

Predators in this model affect all of the anuran species simultaneously. The presence of multiple predators can result in highly variable affects on the prey species (Relyea 2004). If predators in a system had no affect on another predator's ability to capture prey, the effect of the additional predator would simply be added to the overall effect of predation on the prey species of concern. The addition of a predator species that also preys on other predators may reduce a portion of the predation pressure on the prey species of concern; therefore the addition of this type of predator would have an effect that is less than additive. Several studies demonstrate that fish greatly reduce invertebrate populations, including odonates (McPeek 1990, Skelly 1995, Smith et al. 1999). Smith et al. (1999) showed that a negative effect on invertebrates occurred even at very low fish densities. In our model, the presence of fish in the pond eliminates odonates after one timestep, however odonates are still able to colonize the pond. Because information is lacking for many species in the community, the model does not make assumptions about the role of anuran palatability to predators.

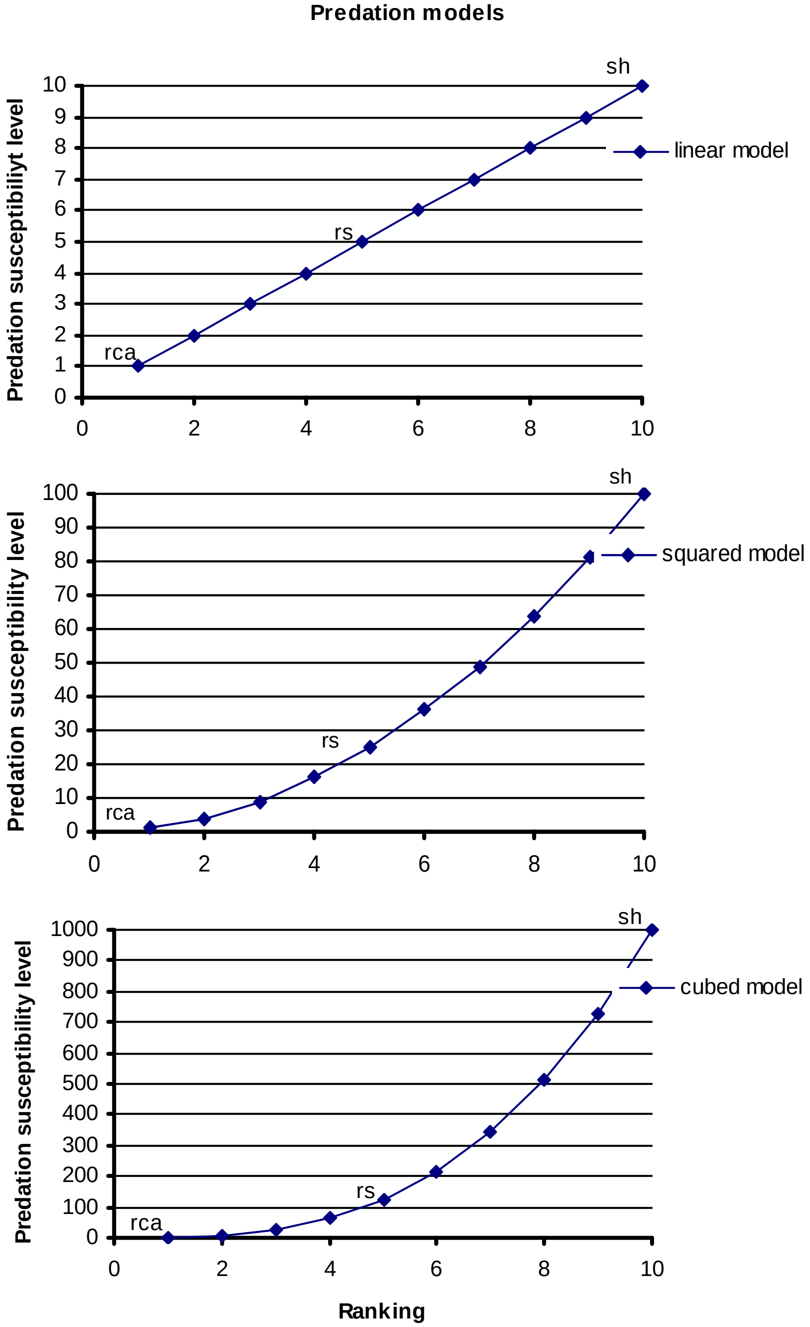


Figure 30. Examples of 3 models depicting different predation susceptibility functions. Susceptibility levels for R. catesbeiana (rca) *R. sphenocephala* (rs) and *S. holbrookii* (sh) are graphed showing relative differences under the different models.

### *Fish.submodel*

Unlike the other predators in the model, fish do not have a life cycle that includes a terrestrial stage, yet they are not uncommon in ponds. The two most likely scenarios in which fish colonize a pond are through flooding or introduction by humans. Based the colonization index on the current rate of occurrence in ponds in eastern Texas (D. Saenz unpublished data), I calculated the probability of colonization per month as 0.004. Once established, sunfish will breed annually in the pond and at some point in time reach a maximum population density. A limit of 500 fish per pond was based on sunfish population density estimates (D. Saenz unpublished data). Fish are voracious predators that cue in on prey by visually detecting movement. In the model, fish will prey on anuran larvae at a rate proportional to their susceptibility to predation.

### *Odonate submodel*

Dragonflies are winged insects and extremely vagile organisms that quickly exploit new water sources for egg deposition. Eggs develop into aquatic larvae that spend up to eight months in a pond before metamorphosis. Dragonfly larvae are highly predaceous on most small moving aquatic animal, including anuran larvae. The predaceous odonate larvae, like sunfish, are visually oriented predators (Pritchard 1965) that key on prey by detecting movement (Avezedo-Ramos et al 1992). Odonate larvae in the model also prey on anuran larvae at a rate proportional to their susceptibility to predation.

## Model evaluation

### *Sensitivity analyses*

Sensitivity analyses were performed to examine the influence of uncertainty of life history parameters (colonizing ability, fecundity, and susceptibility to predation) on anuran community succession. These analyses should provide insight to which parameters are important to produce recruitment to the next generation (successfully producing larvae that escape predation and metamorphose in the pond) and insight to which parameters might influence where a species might occur along the successional timescale.

### *Colonization sensitivity analysis*

Predicted colonization probabilities ranged from a 4 percent chance of colonization per month for *R. catesbeiana* to 80 percent per month for *B. woodhouseii* (Table 15). I developed three different models in which I manipulated the colonization probabilities for all of the species and compared them to each other and to our baseline model. In the low colonization model, I set the colonization probability for each species to 1 percent chance of colonization per month for all species in their respective breeding seasons. In the mid colonization model, the colonization probability was set at 50 percent for each species in their respective breeding season and the high colonization model was set at 100 percent chance of colonization for all species. Finally, in the baseline model of colonization, I assigned each species its predicted colonization probability (see Table 14). All other parameters were set to baseline levels (see baseline simulations below), and I ran 30 simulations of the four models. Mean monthly recruitment for each model was compared for all species with an analysis of variance at the $\alpha \leq 0.05$ significance level.

### *Fecundity sensitivity analysis*

I modeled and compared four levels of fecundity for all of the anuran species in our community at baseline colonization and predation levels. In the low-level fecundity model, we changed clutch-size to 100 eggs for all species. The mid-level fecundity model was run with all species producing 1,000 eggs per breeding effort. In the high-level model of fecundity all species produced 10,000 eggs per breeding attempt. Finally, the artificial fecundity level models above were compared to the baseline fecundity model where fecundity levels of the 12 species were taken from actual life-history data (see Table 14). All other parameters were set to baseline levels (see baseline simulations below). The four models were run 30 times for each species and mean monthly recruitment was compared with an analysis of variance at the $\alpha \leq 0.05$ significance level.

## Experimental design for simulations

We ran 100 iterations of our baseline model at monthly time steps for 120 months. In our baseline model we used our predicted colonization probabilities, natural fecundity levels (Table 14), and the cubed function of predation (Figure 14). Anuran mean recruitment rates among species and within species were graphed and compared over time. Predator population levels also were graphed over the 10-year period. The probability of producing recruitment each year was calculated and comparisons were made between anuran species.

## RESULTS

### Colonization sensitivity analysis

All the species in our model were sensitive to changes in colonizing ability (Figure 31). Differences in the amount of recruitment produced between models with 1 percent probability of colonization for each species and models with 50 percent probability were much greater than the differences between models with 50 percent probability and 100 percent probability of colonization. Only in the two *Hyla* species did I fail to detect a difference between low and mid levels of colonization, which may be due in part to the extremely low recruitment rates observed under baseline conditions for these two species. By contrast, in comparisons between mid and high levels of colonization I detected a significant difference in nine of 12 species. Differences between the low and the high levels were always significant (Figure 31).

### Fecundity sensitivity analysis

Mean anuran recruitment rates did not differ significantly between low and mid-level fecundity models for any species (Figure 32). Mean recruitment rates were significantly higher in the high-level fecundity model than either the low or mid-level models for all species except *G. carolinensis*, which was probably due to the overall low recruitment rates for this species. Mean recruitment in the baseline fecundity model was significantly lower than the high-level model for most species except *B. woodhouseii*, *R.catesbeiana*, and *G. carolinensis*. *Bufo woodhouseii* and *R. catesbeiana* have naturally high fecundity levels that help explain the observed patterns and *G. carolinensis* has very low recruitment. In general, in this model, higher fecundity was related to higher recruitment rates for all the species. Due to the simplistic nature of the model, the more anuran larvae produced by a species the more larvae escaped predation.

### Baseline simulations

Mean odonate population levels were highest early in succession due to their high colonizing ability but showed an overall decline over the ten-year period in our model due to predation pressure from rising fish population levels (Figure 33). Odonate population levels cycled seasonally as a result of the larvae leaving the ponds to metamorphose into adults. Mean fish population levels steadily increased throughout the simulation (Figure 33). In this system fish have a very poor colonizing ability, therefore they are not common in new ponds. Once established, fish persist and increase in density in this model becoming the principle predator.

At baseline levels of colonization ability, fecundity, and predation sensitivity, *Acris crepitans*, *Hyla cinerea*, *H. versicolor*, *P. triseriata*, and *S. holbrookii* appear to be early successional species (Figures 34, 35). *Acris crepitans* does not have a high colonization index, meaning it should not be an effective colonizer, nor should it be very susceptible to predators based on the predation index (see Table 14). These parameters suggest *A. crepitans* is a late successional species, however the fecundity is extremely

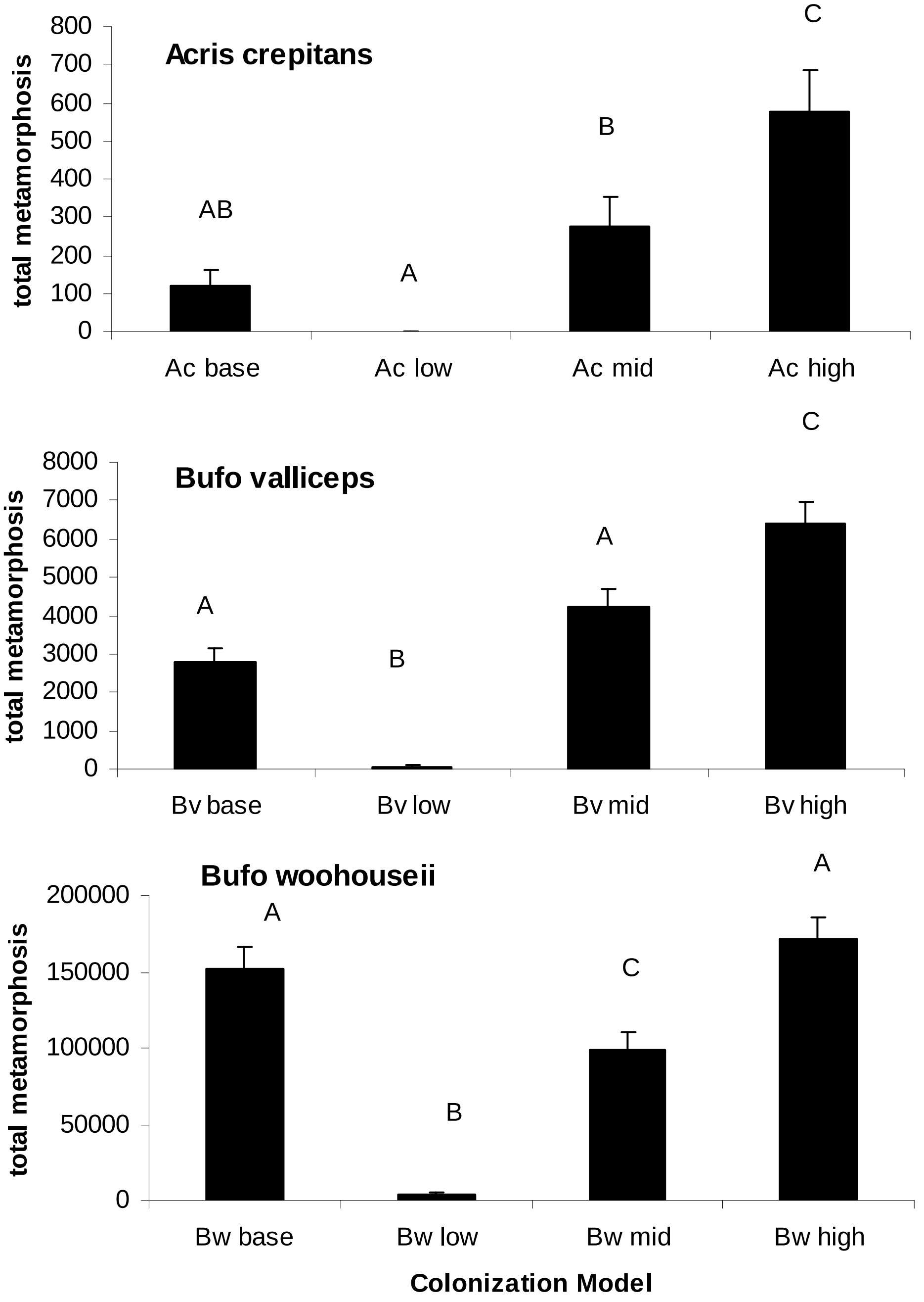
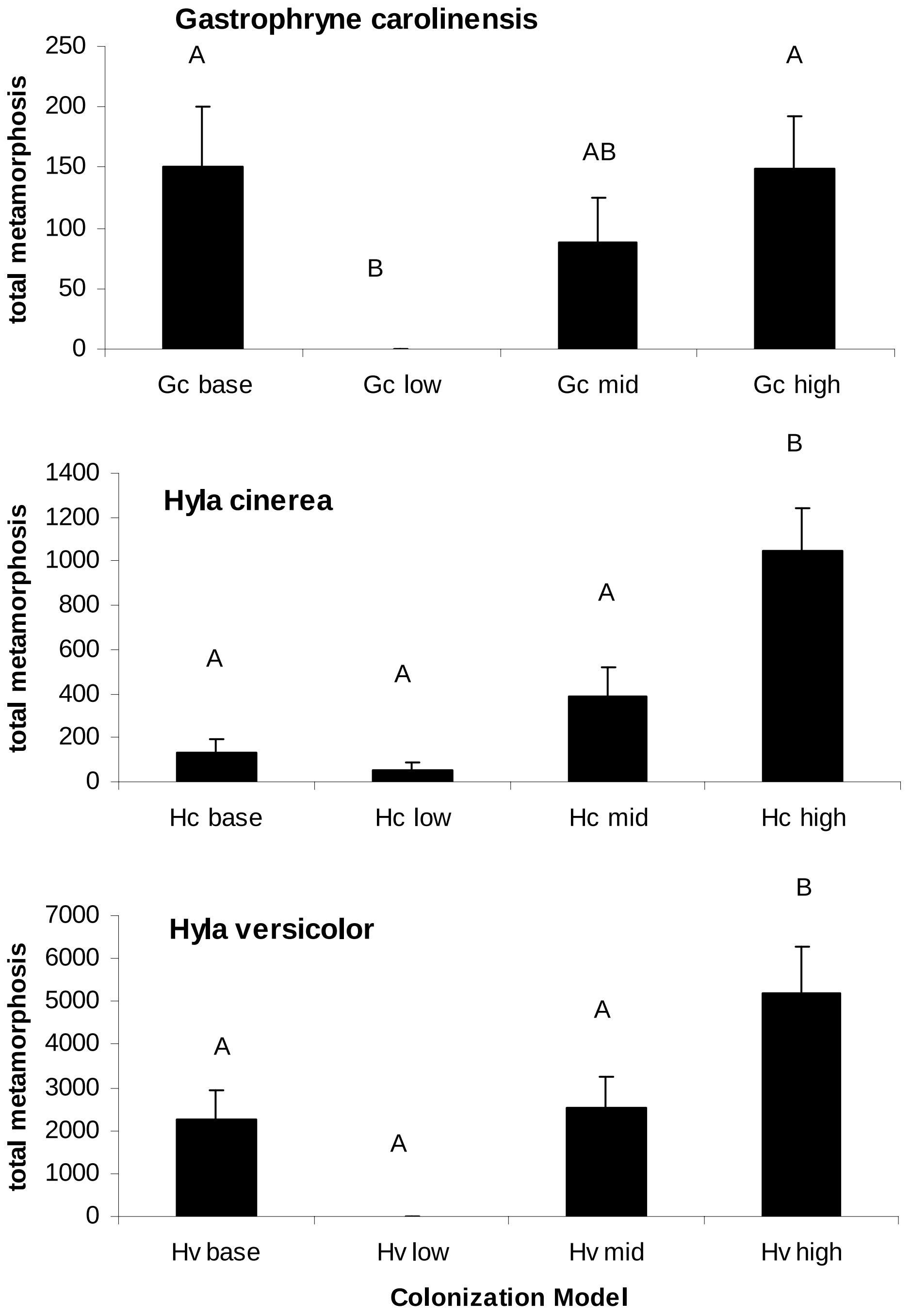


Figure 31. Results from colonization sensitivity analyses for species models. Bars show the mean number of individual that reach metamorphosis at baseline and each colonization level for a given species. Different letters over the bars represent significantly different means at the $\alpha \leq 0.05$ significance level.



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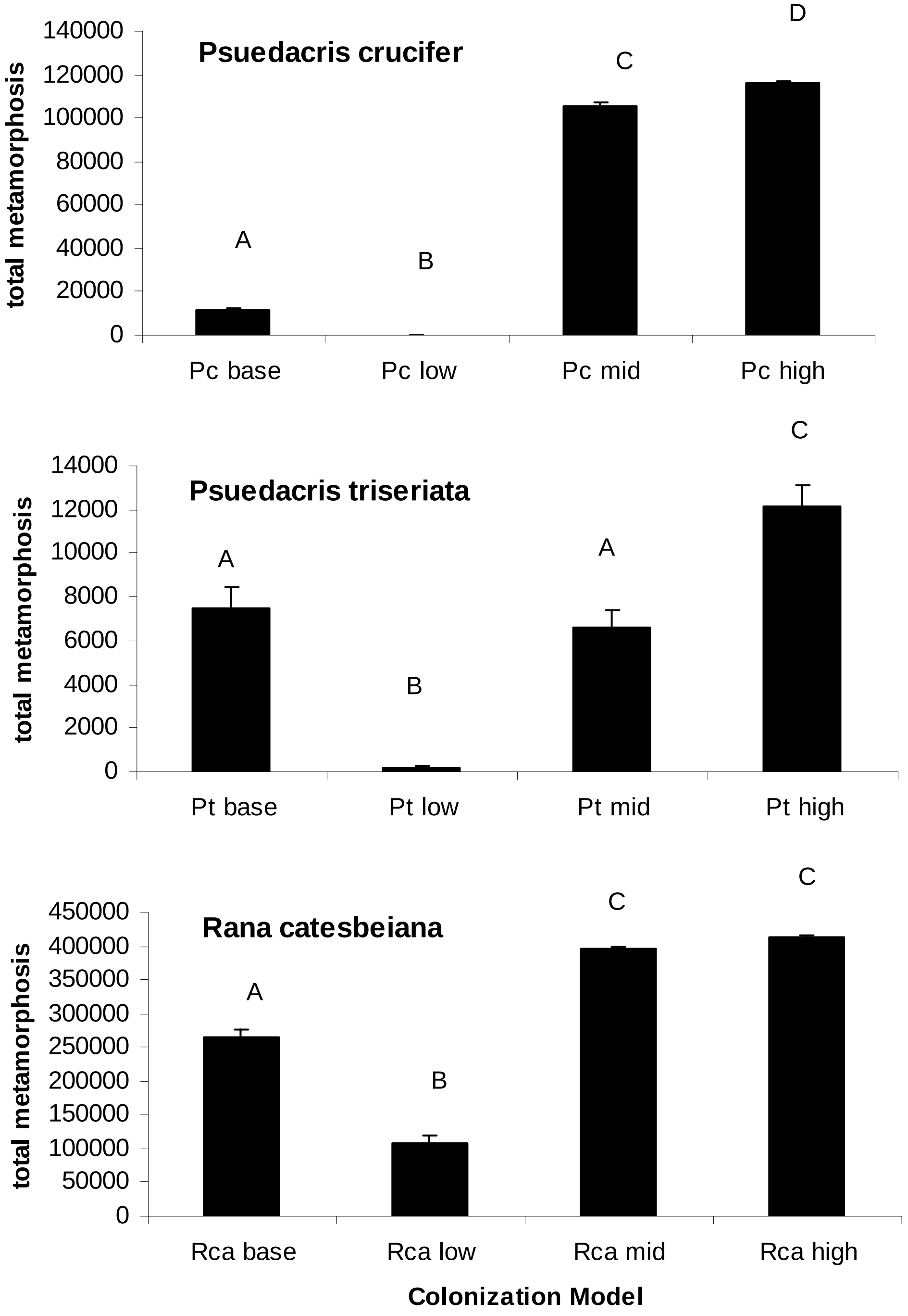

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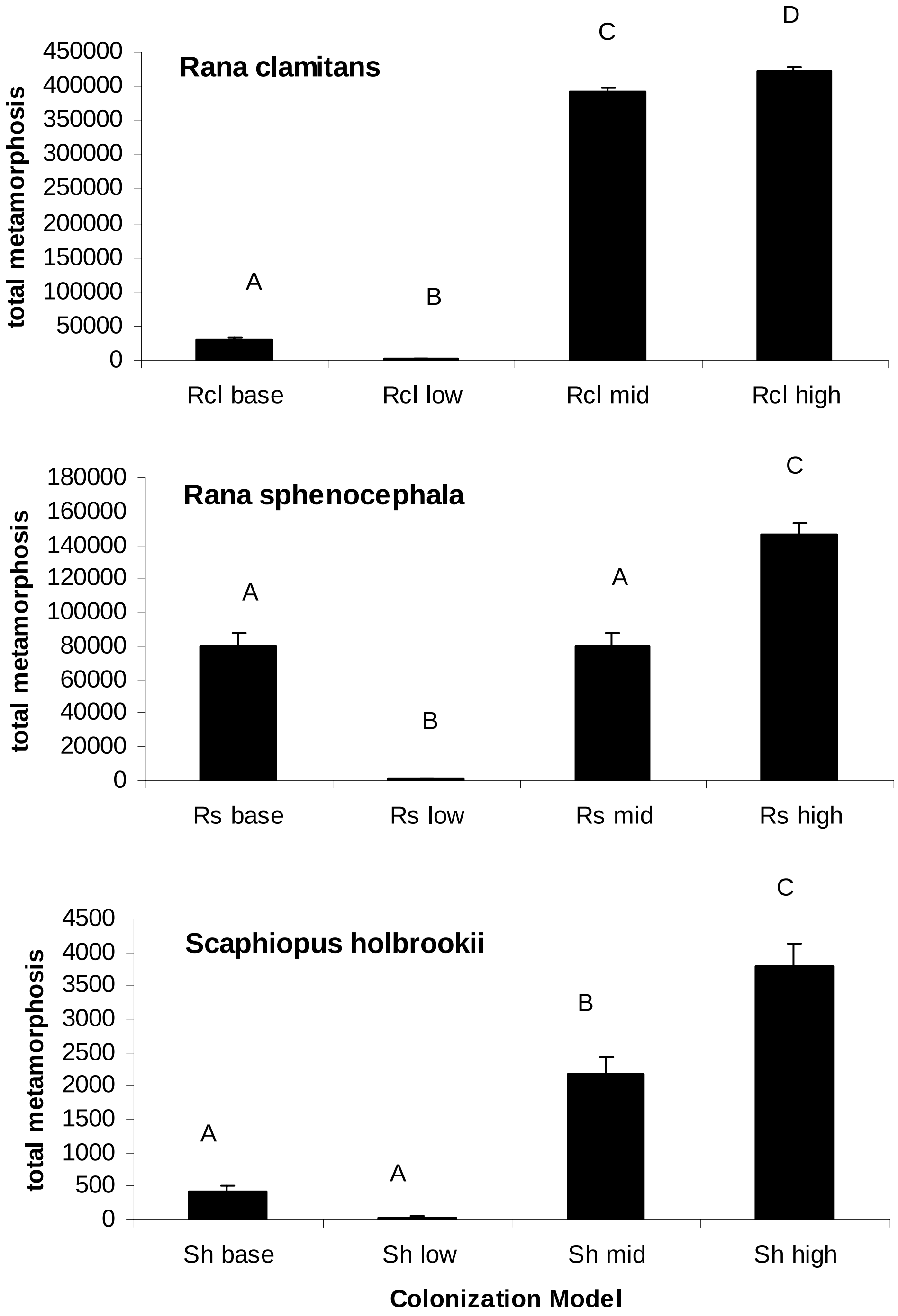


Figure 31. Continued.

low for *A. crepitans*. Low fecundity does not allow *A crepitans* to persist with high levels of predators that are common during late succession in our model (Figure 34).

The two *Hyla* species and *S. holbrookii* have relatively high predation indices and do not persist in high numbers during late succession in our model when predation pressure is high. *Pseudacris triseriata* is a good colonizer but is relatively susceptible to predation (see Table 14) making it a good example of an early successional species.

*Rana catesbeiana* and *G. carolinensis* were the only species that had greater recruitment during later stages of succession in our model (Figures 33, 34). *Rana catesbeiana* is a late succession species with poor colonizing ability and high resistance to predation. *Gastrophryne carolinensis*, however, has a very high colonization index and is very susceptible to predators, which is not consistent with a late succession species. Closer examination reveals that *G. carolinensis* only produced recruitment in extremely low numbers, likely due to low fecundity, and the patterns observed (more recruitment later in successional sequence) may have occurred merely by chance.

The remaining five species produced a fairly consistent amount of recruitment throughout the 10-year period (Figures 33, 34). The two *Bufo* species and *R. sphenocephala* all have high colonization indices and moderate to high susceptibility to predation which would appear to be traits common to early successional species. However, these species have very high fecundity that may overwhelm predators in our model. *Psuedacris crucifer* and *R. clamitans* both have extremely low susceptibility to

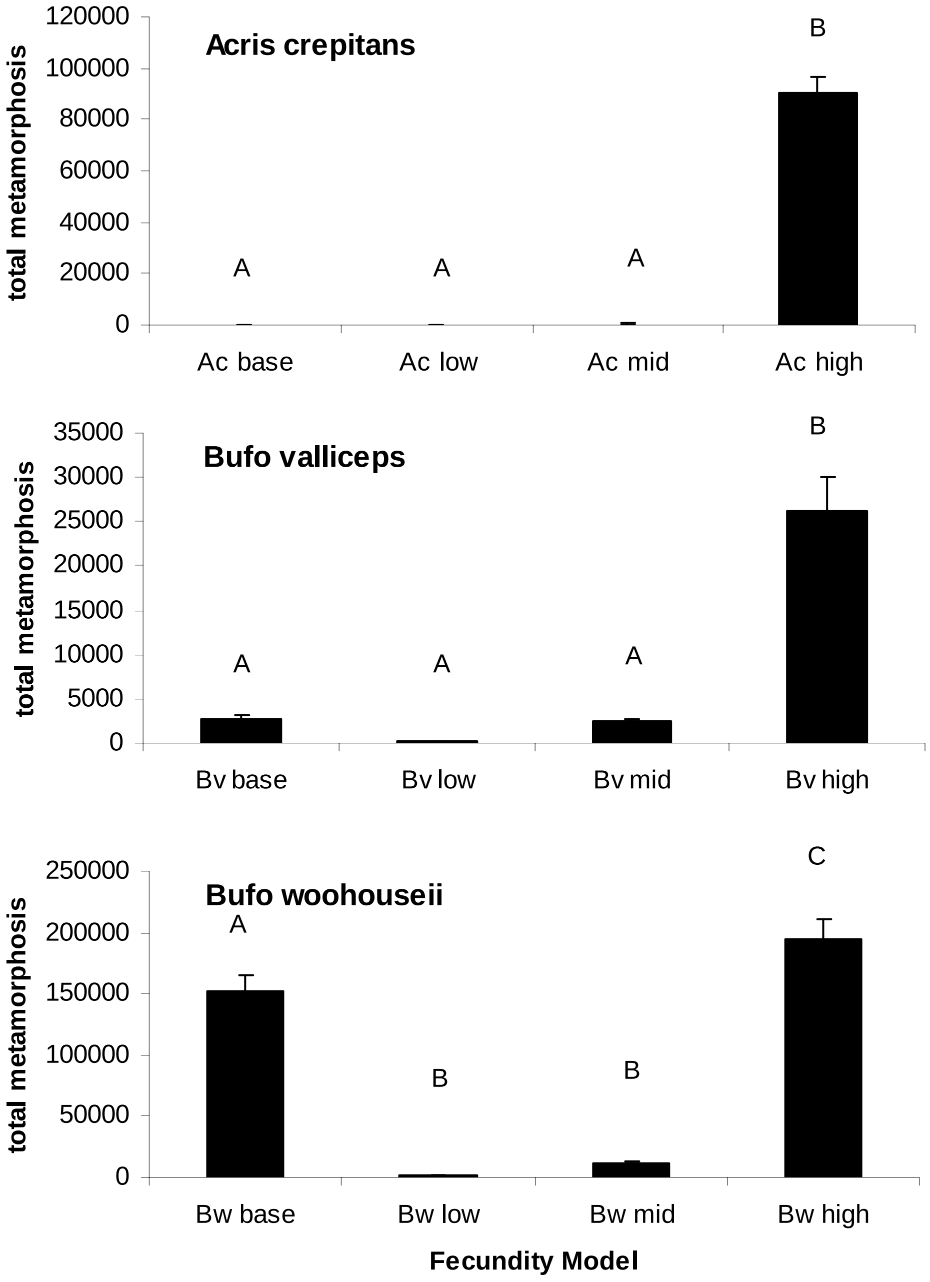
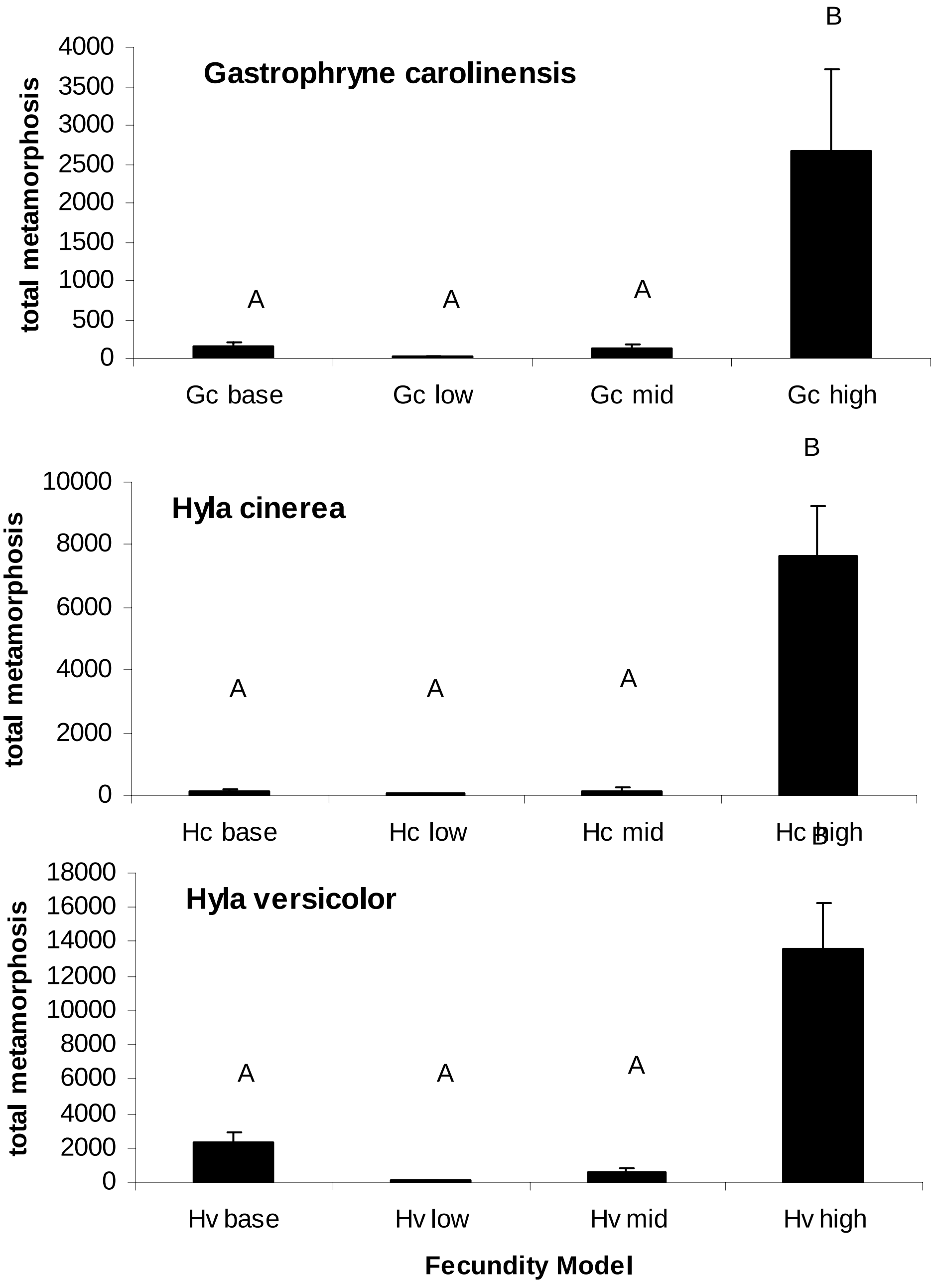


Figure 32. Results from fecundity sensitivity analyses for species models. Bars show the mean number of individual that reach metamorphosis at baseline and each fecundity level for a given species. Different letters over the bars represent significantly different means at the $\alpha \leq 0.05$ significance level.



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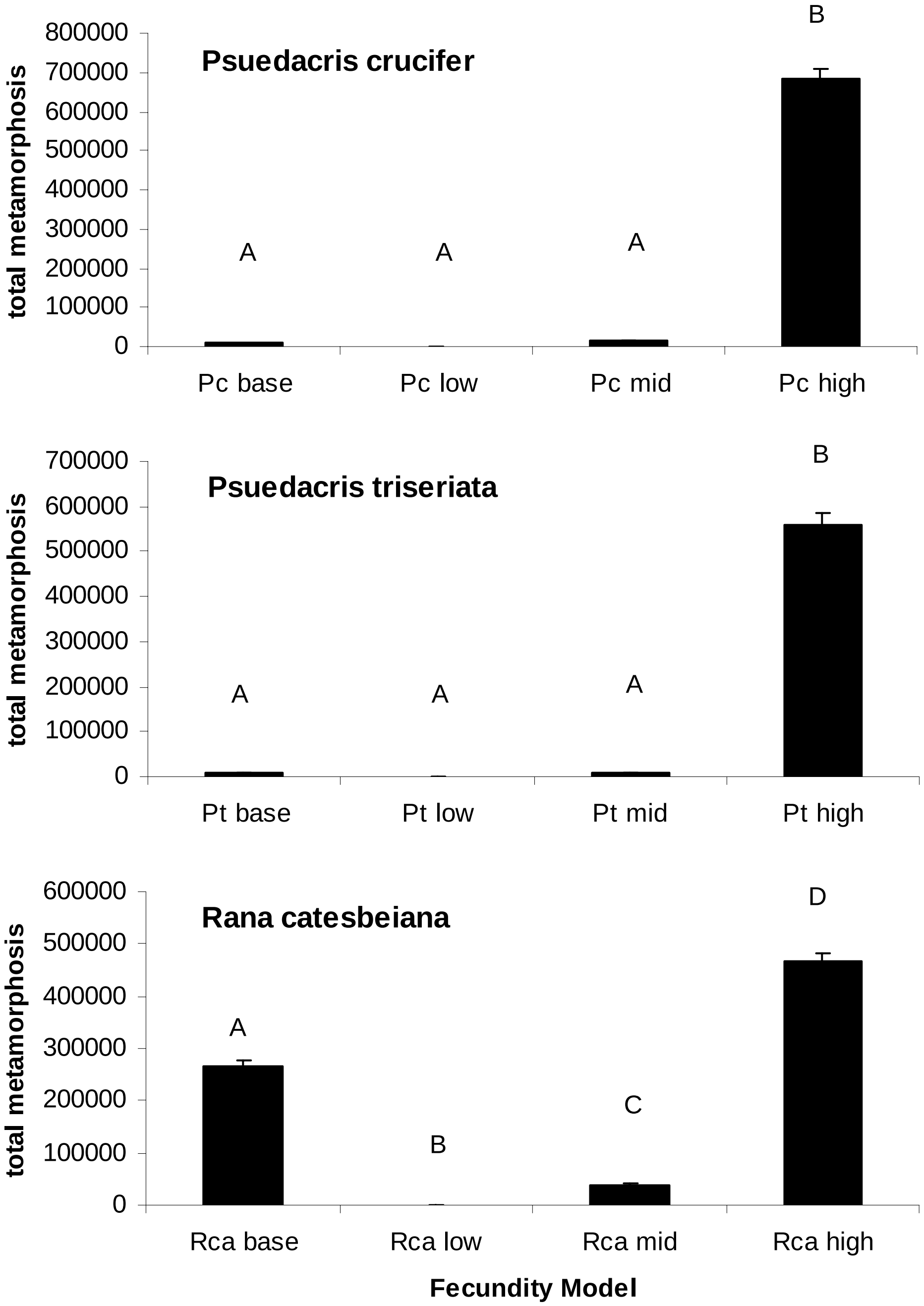

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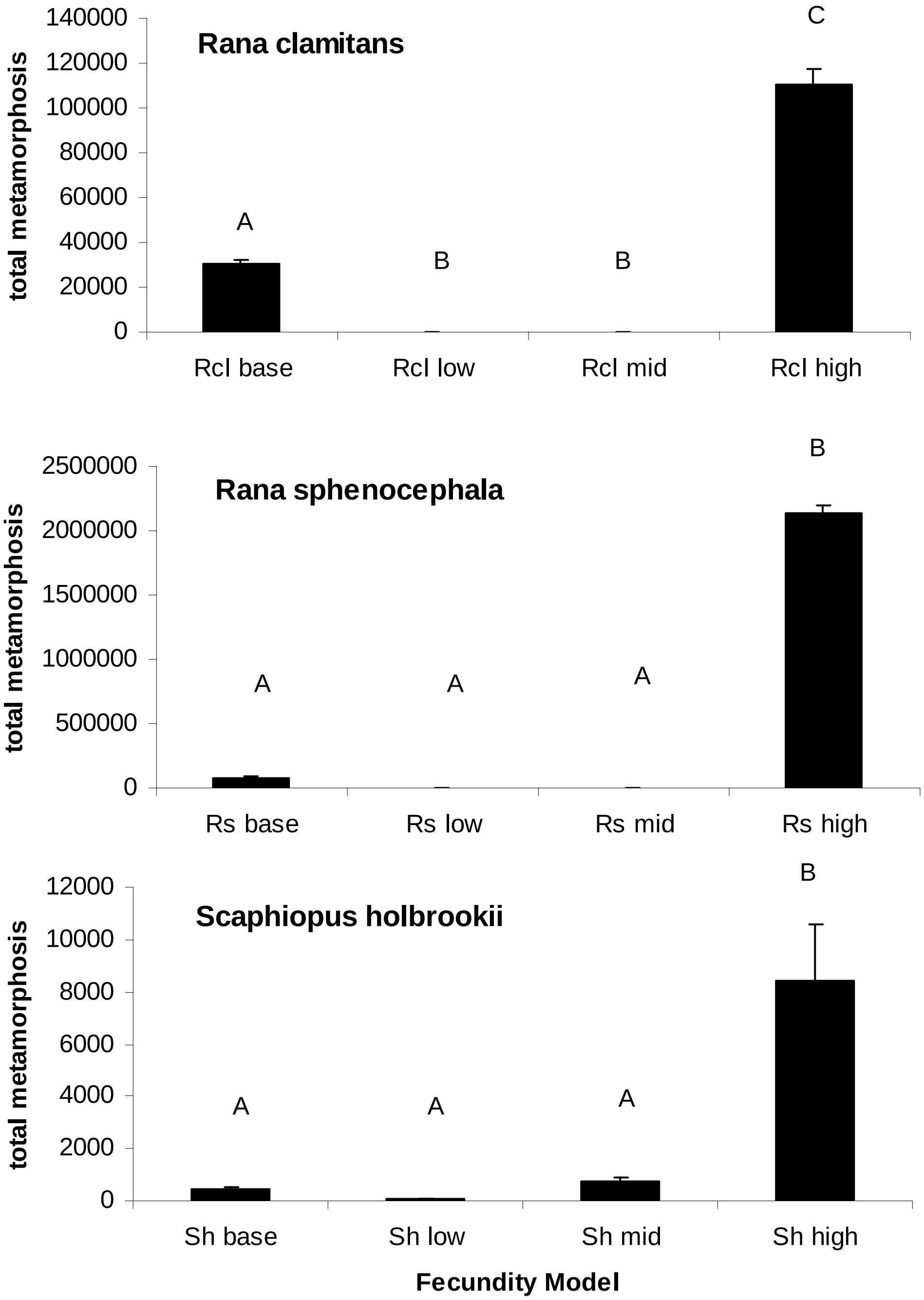

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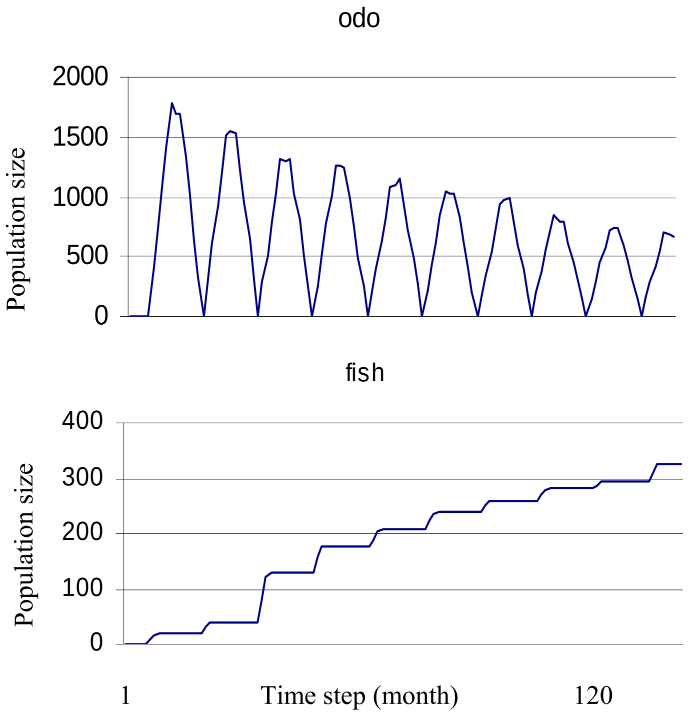
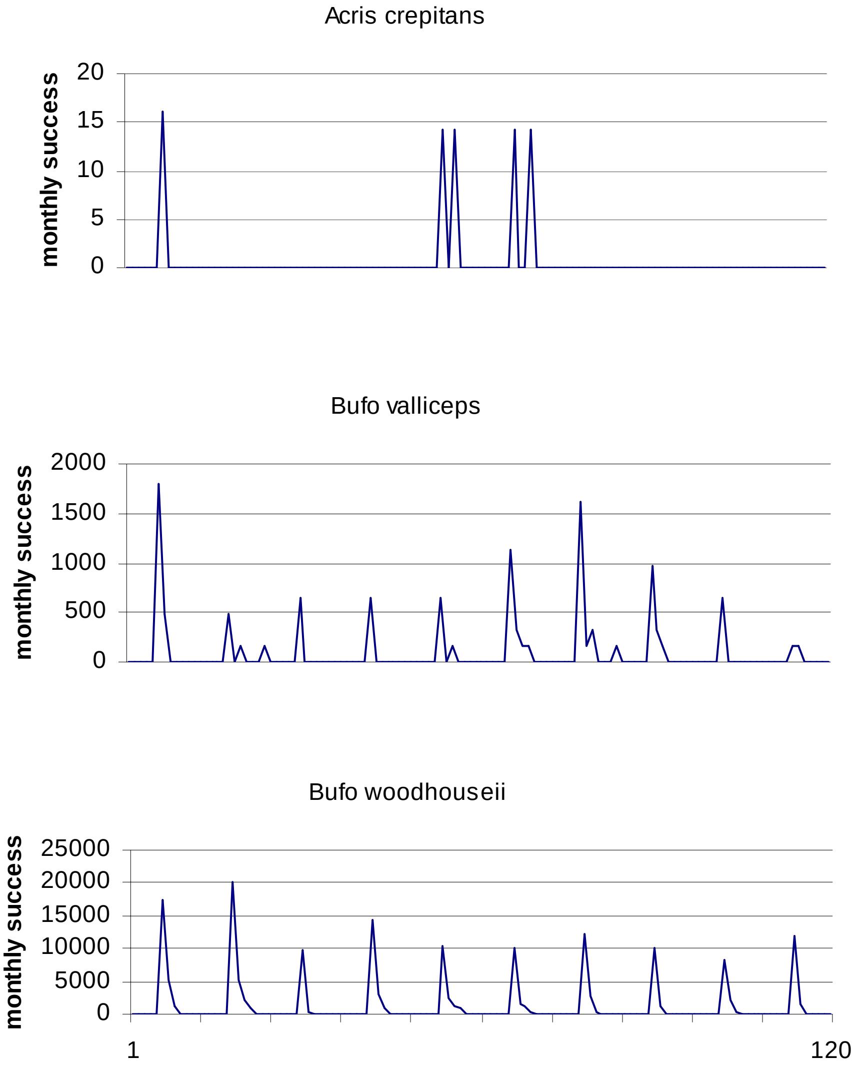


Figure 33. Simulated predator population trends over a ten year period. The lines on the graphs represent the mean population size over the 120 month period.

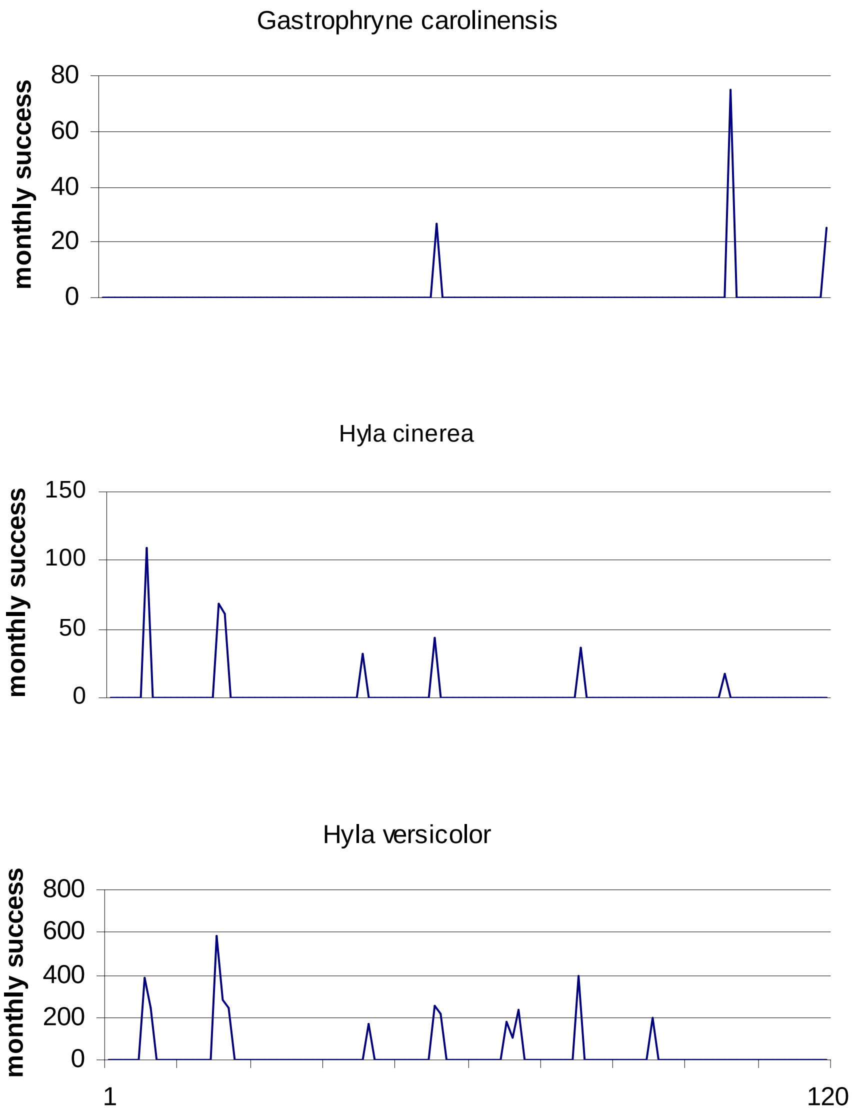


Acris crepitans

Bufo valliceps

Bufo woodhouseii

Figure 34. Simulated anuran population trends over a ten year period. The lines on the graphs represent the mean number of tadpoles that reach metamorphosis over the 120 month period.



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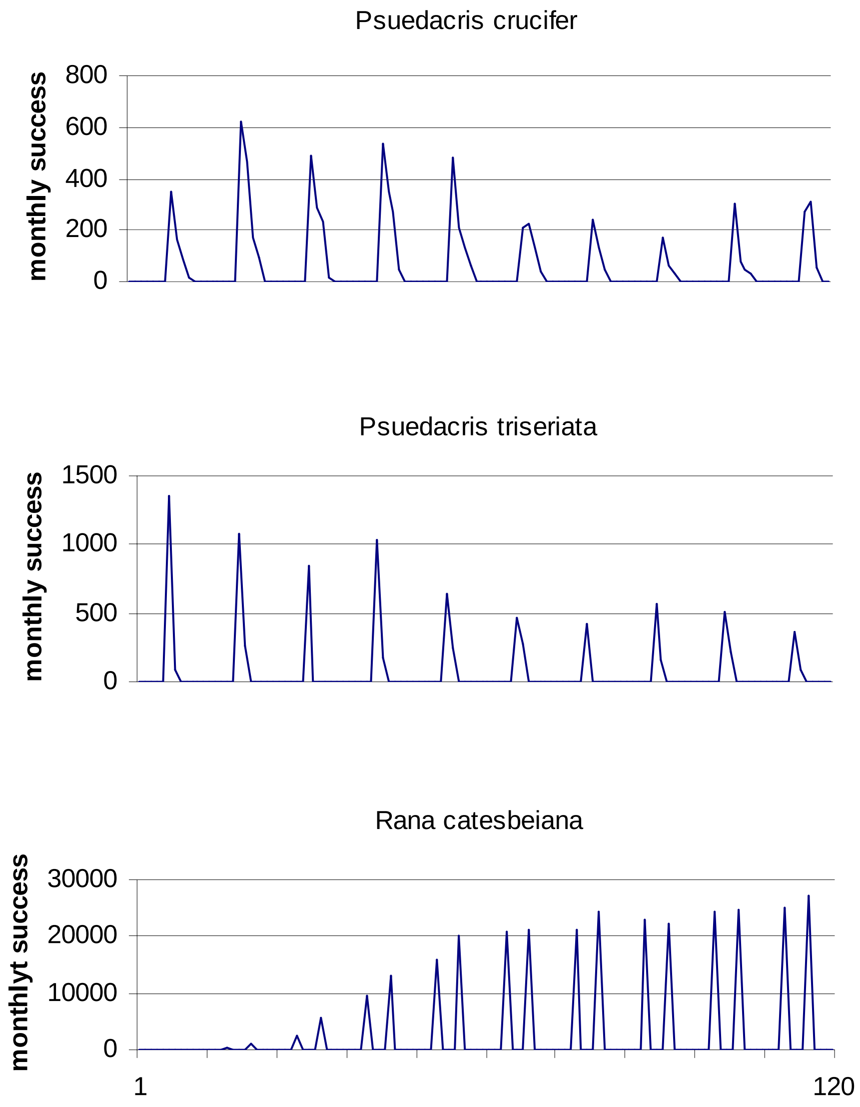

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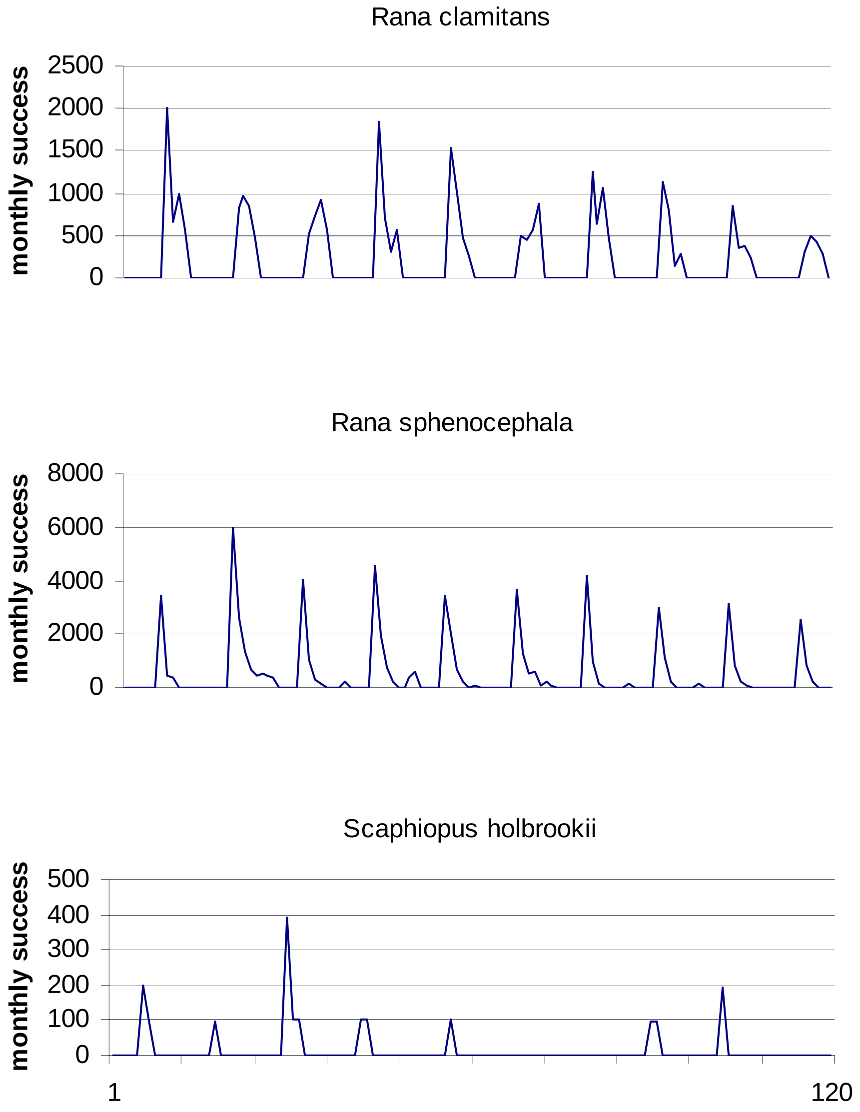

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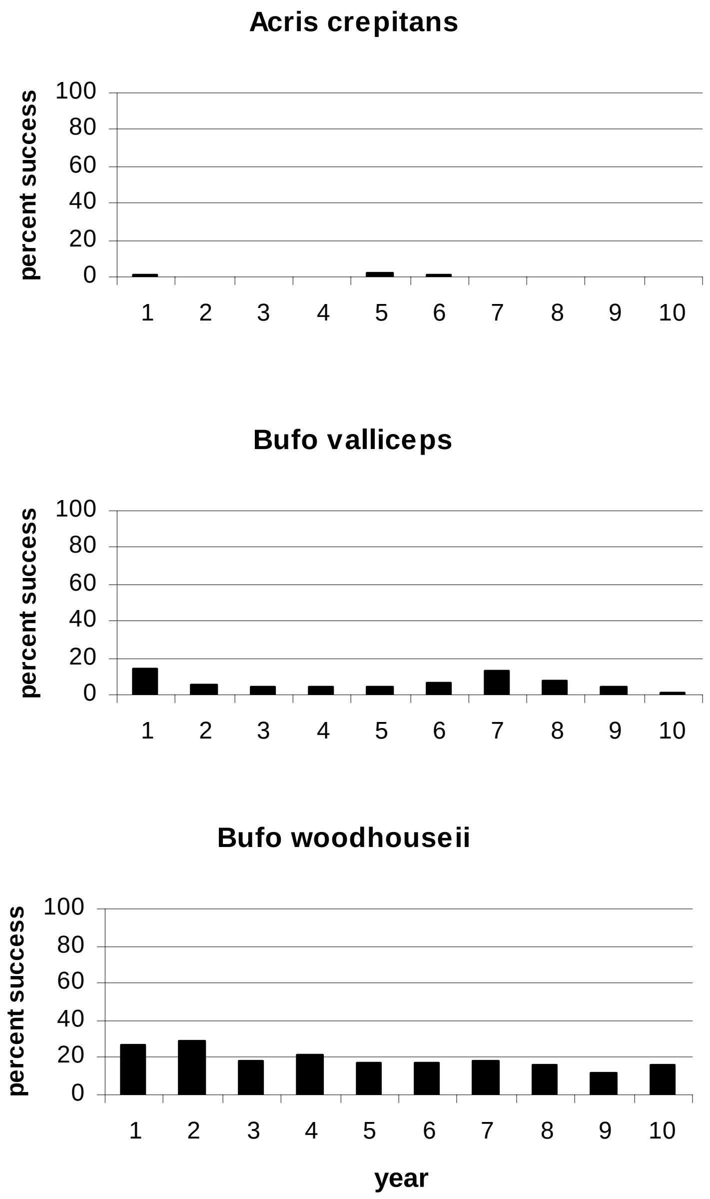
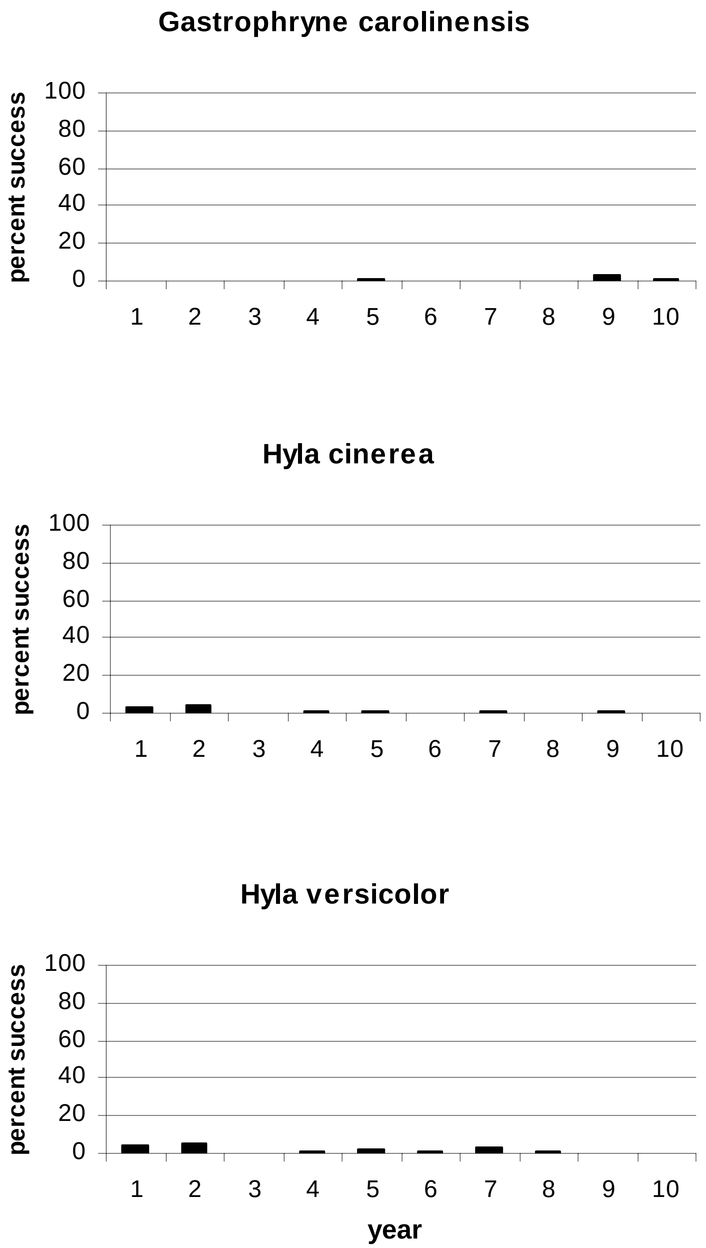


Figure 35. Probability of successfully reaching metamorphosis. The bars on the graphs represent the probability that a given species will produce tadpoles that reach metamorphosis in a given year.



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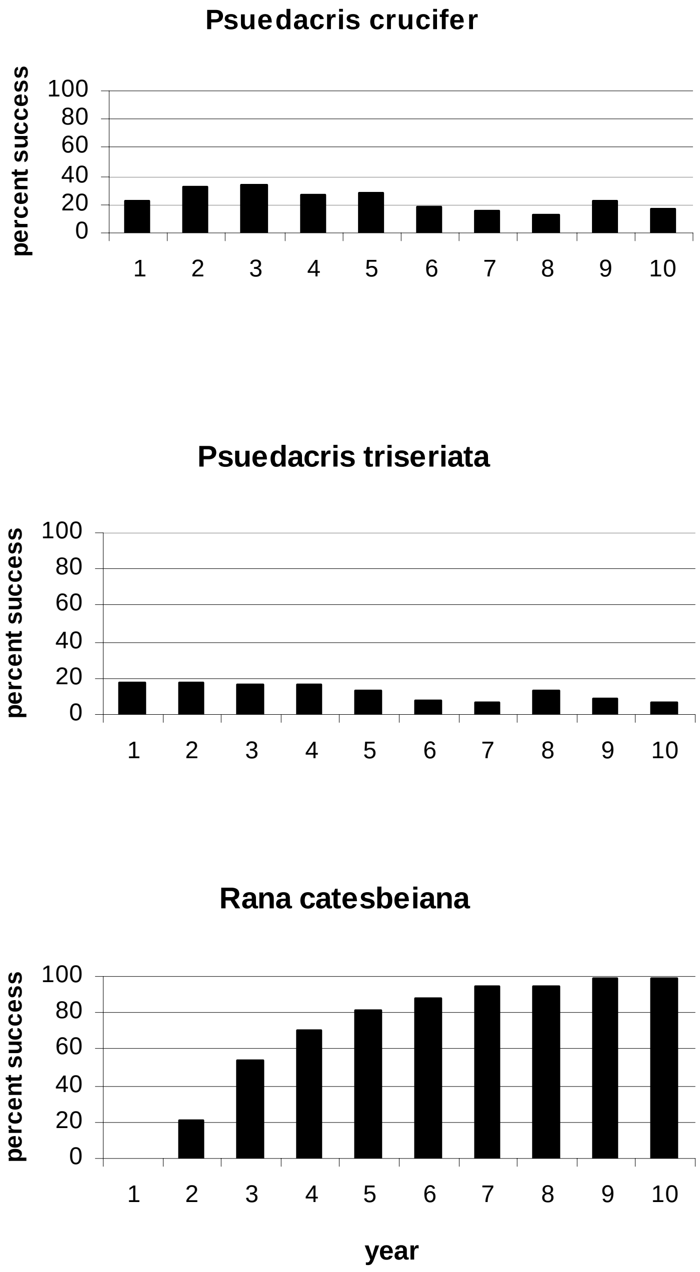

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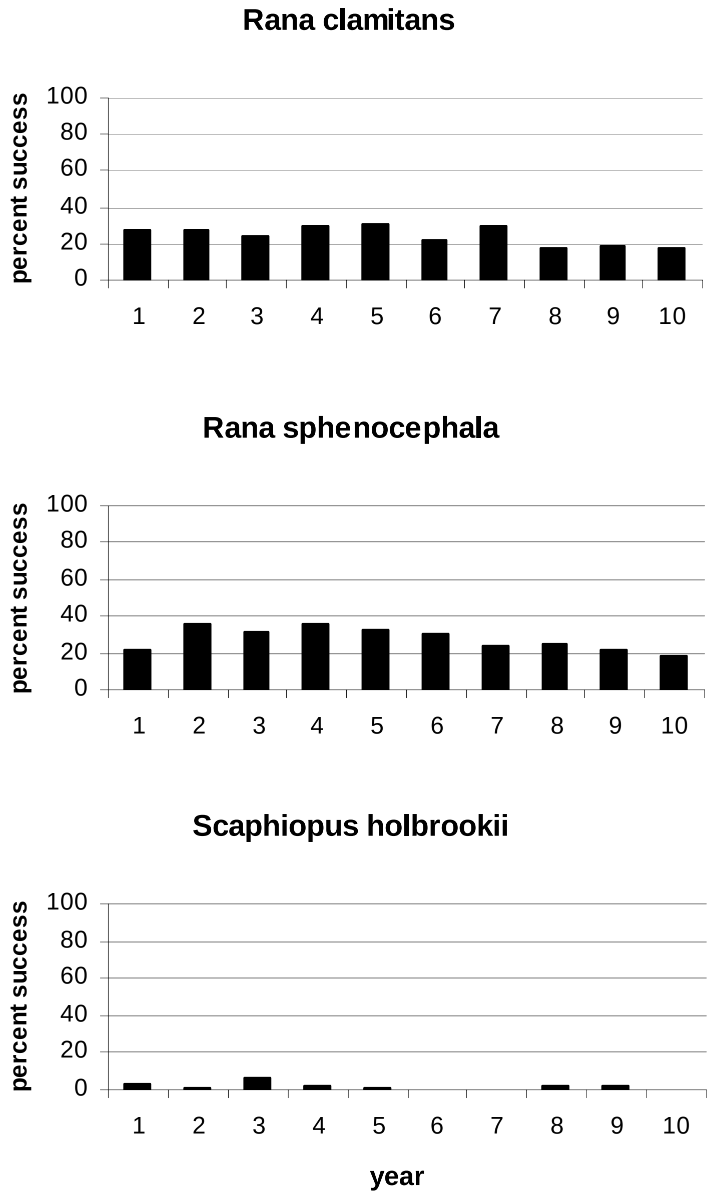


Figure 35. Continued

predation, therefore they likely produce recruitment each time they colonize the breeding pond in this model which may explain the uniform recruitment throughout succession.

## DISCUSSION

Ecological succession is a concept that is important to understanding ecological systems and patterns of successional change and can be identified for almost any natural system (McCook 1994). However, succession can be considered individualistic or stochastic in nature (Gleason 1927). Each sucessional process can be unique depending on timing, initial conditions, and other factors (Sousa 1984).

Each iteration of this model was unique due to the probabilistic nature of colonization of a new site and the within species variation in fecundity. Sensitivity analyses, in this model, suggested colonizing ability, fecundity, and susceptibility to predation greatly influence a species' ability to colonize and successfully reproduce in a pond and determine species occurrence during successional stages. Colonizing ability was important for species with low fecundity and high susceptibility to predation. These early succession species are typically species that use ephemeral breeding habitats and tend to be constrained from later stages of succession by predators (Woodard 1983, Lawler 1989, Richards and Bull 1990, Skelly 1994, 1995, Smith and Van Buskirk 1995). Species that are resistant to predators are generally poor colonizers that tend to arrive late in succession, but once they colonize a pond they tend to persist and produce recruitment. These species are not constrained from producing recruitment early in succession but the probability of reaching the pond quickly is low.

Early succession species have been characterized as typically having vagile offspring that are more likely to colonize an area quickly because of their mobility, while late succession species tend to have offspring that are not as vagile and less likely to colonize an area quickly (Salisbury 1929, Keever 1950, Horn 1974). However, in this model, the importance of vagility was not tested; rather a species' distribution on the landscape is considered an important factor for predicting the probability of colonization. If mobility doesn't differ, this model dictated that species that are more evenly spatially distributed on the landscape would have a higher probability of finding a new site to colonize and were the early colonizers.

High fecundity has been associated with early succession species in plants (McCook 1994, Lichter 1998). However, high fecundity appears to be associated with the late succession anuran species in this model. This is consistent with Winemiller and Rose's (1992) model for an adaptive surface of fish life-history strategies based on fundamental demographic trade-offs and selection in response to different kinds of environmental variation. In their conceptual model, they characterize species that use ephemeral or opportunistic environments as having low fecundity while species that use habitats with seasonal or with large scale patches tend to have higher fecundity. While early succession species tend to have lower clutch sizes they still might have high reproductive output via frequent reproduction.

The idea that predation on anuran larvae is the most important constraint in late succession stages where some proportion of the population is lost to predation is a central theme in anuran community ecology (Woodard 1983, Lawler 1989, Richards and Bull 1990, Skelly 1994, 1995, Werner and McPeek 1994, Smith and Van Buskirk 1995, Wellborn et al. 1996). The early succession species are mainly species that might be expected to use ephemeral aquatic habitats for breeding. These sites generally have relatively low predator populations and the greatest danger to the larvae is desiccation of the breeding site (Woodward 1983).

Although sensitivity analyses in this model identified natural history traits, fecundity, colonizing ability, and resistance to predation, as important factors affecting community assembly and succession, other factors may also be important in structuring anuran communities over time. Species' vagility should also be factored into the model. Species that are more mobile should be better colonizers (McCook 1994). A measure of each species' ability to move over specified distances might prove difficult to attain because in addition to the physical ability of an anuran to move, resistance to desiccation should affect the distance an individual will travel over land.

Other factors, not included in this model should also affect predation rates. Palatability of tadpoles to predators will affect predation (Formaniwicz and Brodie 1982). Currently little information in known for relative palatabilities of whole anuran communities, however this information could be attained for the model community and applied to the simulation. Also, in the current model, only a species susceptibility to predation, in the absence of density dependent responses, is factored into the simulation.

Functional responses to predation could also be incorporated to improve the model (Holling 1959). It is unclear how species within this community respond under different density levels.

Although this model and any other future models provide predictions on anuran community succession; the models can be evaluated with experiments and actual field data. Predicted patterns of community assembly over time should be tested with natural community succession to assure that the actual causal mechanisms that are important to amphibian conservation and that drive community structure in the simulation model are the same as in nature. This can be done by trapping animals over time and documenting species turnover to compare simulated and actual patterns of succession. Multiple trapping arrays over a large spatial scale can be used to determine encounter rates of different species to evaluate a species' distribution over the landscape. Finally, predator prey experiments can be conducted to test for relative susceptibility to predation among the anuran species

# CHAPTER IV

# MECHANISMS FOR COMMUNITY ASSEMBLY

## INTRODUCTION

The current paradigm for community assembly in freshwater habitats suggests species distributions are correlated with environmental gradients of water permanency (Collins and Wilbur 1979, Dale et al. 1985, Werner and McPeek 1994, Anholt and Werner 1995, Wellborn et al. 1996, Skelly 1995, 1997, Stoks and McPeek 2003). Virtually every animal population that lives in freshwater habitats is affected either by the amount of time water is available or the distribution of predators (Wellborn et al. 1996).

Constraints posed by drying aquatic habitats are an important cause of mortality in many freshwater systems (Smith 1983, Banks and Beebee 1988) and have profound effects on ecological communities. Amphibious vertebrates that develop relatively slowly with long larval stages are constrained from using ponds that dry quickly, whereas completely aquatic forms, like most fish, are constrained from sites that dry with any frequency over long time scales. However, some vertebrates, in particular amphibians, possess life-history traits that allow them to thrive in ephemeral environments. Tadpoles of many anuran species that live in ephemeral habitats, for example, are relatively more active, grow faster, and metamorphose sooner, thus enabling them to survive by escaping drying ponds (Woodard 1983, Lawler 1989, Skelly

1992). However, there is a trade-off. Although species with high activity levels appear to have high fitness in temporary ponds (Ludwig and Rowe 1990, Werner and Anholt 1993), they are also at greater risk of predation by visually cued predators (Woodard 1983, Lawler 1989, Richards and Bull 1990, Skelly 1994, 1995, Smith and Van Buskirk 1995; Figure 36).

Predation is therefore widely recognized as another mechanism driving the structure of ecological communities (Paine 1966, Sih et al. 1985, Morin 1986). In freshwater environments, a gradient of predator species is typically correlated with water permanency (Werner and McPeek 1994). Woodward (1983) found more predator species and more individual aquatic predators per cubic meter in permanent ponds than in temporary ponds. Moreover, experiments demonstrated the predators in these systems affect the local distribution of prey species (Wilbur 1972, Morin 1981, Dayton and Fitzgerald 2001).

An interesting link between predation and water permanency exists in the complex behavioral and life-history trade-offs among prey communities in freshwater systems. Faster development rates in temporary pond species presumably require high energy intake that in turn leads to higher activity levels during foraging, which would lower anti-predator defenses (the ability to avoid being detected by predators) in these species (Low 1976, Woodward 1983, Lawler 1989, Richards and Bull 1990, Skelly 1994).

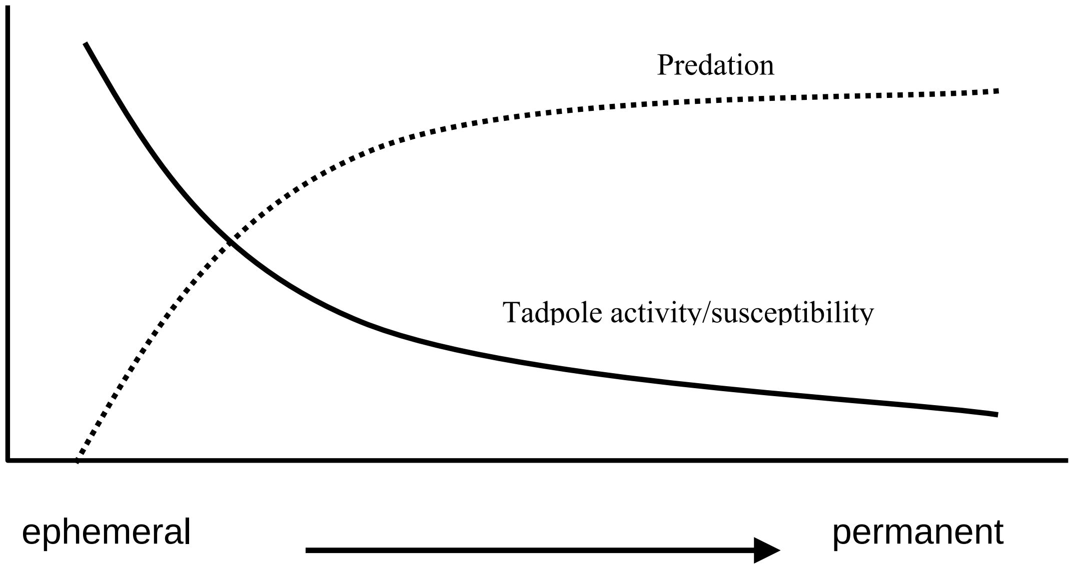


Figure 36. Representation of the activity/predation trade-off for tadpoles in a hydroperiod continuum from ephemeral to permanent. The solid curve represents decreasing tadpole activity and susceptibility to predation along the hydroperiod gradient, while the dashed line represents changes in predator populations and predation rates as water sources become more permanent.

Conversely, species that inhabit more permanent aquatic environments spend less time foraging, and consequently less time in motion (Skelly 1994).

Larval anuran distributions are frequently nonoverlapping and existing distributions among breeding ponds appear to be correlated to both biotic (predation and competition) and abiotic (hydroperiod) factors (Skelly 1996; Chapter II). These two major sources of mortality and the predation gradient defines the generally accepted paradigm of assembly rules for tadpole communities used to explain anuran larval distributions (Figure 36). Under this predation-hydroperiod paradigm, segregated distributions of tadpole species are due to differential abilities to cope with predation, desiccation, and perhaps interspecific competition (Heyer et al. 1975, Werner and McPeek 1994, Smith and Van Buskirk 1995, Dayton and Fitzgerald 2001). However, the predation-hydroperiod paradigm may not fully explain traits and behaviors exhibited by all species of anuran larvae present in a community. Historical contingency (Schluter and Ricklefs 1993) and phylogenetic effects must also influence the kinds of tadpoles that may be present in a community, and it would be interesting to disentangle the role of phylogenetic history in community assembly of anurans (Richardson 2001)

Herein, I take a comprehensive approach to testing the central hypothesis that the predation-hydroperiod paradigm drives community assembly of a winter-breeding guild of four anuran species in eastern Texas. By determining breeding site associations for the four species, I test the prediction of habitat segregation among species according to the hydroperiod gradient. The paradigm predicts that species in ephemeral habitats should have high activity levels, and be more susceptible to predation than their counterpart species that occupy permanent water. I test this by comparing tadpole activity levels and susceptibility to predation in controlled laboratory trials. Finally, to place the results in a historical perspective, I use phylogenetic character mapping (Miles and Dunham 1993) of species' habitat affinities onto published anuran phylogenies. This comprehensive approach to community assembly of the entire guild is valuable for identifying mechanisms that explain membership of species in the community, including those that with traits that may not necessarily fit the classic paradigm.

## METHODS

I collected field data of larvae of four winter breeding anuran species that commonly occur in eastern Texas: two hylids, *Pseudacris crucifer* and *P. triseriata*, one ranid, *Rana sphenocephala*, and one pelobatid, *Scaphiopus hurterii*. Egg masses and tadpoles were collected within Houston, Nacogdoches, and San Augustine Counties in eastern Texas and maintained in the lab until used in experiments. Tadpoles not immediately used were kept in dechlorinated aged tap water and fed tropical fish food flakes (48% crude protein). One ration was roughly equivalent to 10% of a tadpole's body weight (Alford and Harris 1988).

### Breeding site associations

All anurans that occur in eastern Texas lay their eggs in an aquatic environment where they hatch into tadpoles and live as larvae until metamorphosis (Conant and Collins 1998). This allowed me to quickly sample several locations for the presence of tadpoles and to determine use by anurans. I surveyed 75 aquatic sites in Houston, Nacogdoches, and San Augustine Counties in eastern Texas for evidence of anuran breeding from 15 January 2001 through 15 March 2001. When I located a site, I used a either a long-handled dip net or a fine-meshed aquarium net to sample for tadpoles. At smaller sites with little or no vegetation structure, I was able to completely sample the site in one sweep of the net, but at larger deeper sites I would regularly spend up to 30 minutes sampling (up to 50 net sweeps) the littoral zone (see Diaz-Paniagua 1987) until I was satisfied I had collected at least one of each species of tadpoles present in the pond. Once tadpoles were captured, they were identified to species then released. I also estimated pond length, width, and depth for each site, and estimated length of time the pond would hold water.

### Tadpole movement

I conducted independent movement trials for each of four tadpole species which included a range of tadpole sizes and developmental stages (Gosner 1960) for each species. Seventy-five 3-liter plastic tubs (19 x 19 x 33.5 cm) were filled with 2 liters of dechlorinated tap water at room temperature (21 ºC). Four conspecific tadpoles were placed into each of the 75 tubs where they were allowed to acclimate for 30 minutes. There was a range of sizes among tubs, but equal sized tadpoles within tubs. No food was provided during trials. After acclimatization, each tub was sampled by closing my eyes and upon opening them, counting the number of tadpoles moving in each tub the instant the tub was first viewed (Skelly 1995). Each tub was observed every 30 minutes for a total of 5 replicates. I preserved all tadpoles in 10% formalin immediately following the trials, measured them, and determined developmental stage (Gosner 1960). This protocol was repeated for all four species. I calculated the mean proportion of tadpoles moving per tub. I arc-sine square root transformed the data and used ANOVA followed by Tukey's multiple range test ($\alpha \leq 0.05$) to test the hypothesis that the mean number of moving tadpoles would differ among species. I also used Pearson's correlation analysis ($\alpha \leq 0.05$) to determine if developmental stage was correlated to total length or activity levels in the four species of tadpoles.

### Susceptibility to predation

#### *Multiple species predation trials*

*Anax junius* (Odonata) larvae, the focal predator in this study, are sit-and-wait predators (Brockelman 1969, Skelly and Werner 1990) that generally require movement to detect prey and elicit a strike (Oakley and Palka 1967, Kanou and Shimozawa 1983). Several authors have noted that *A. junius* larvae can reduce or eliminate tadpoles from ponds (Heyer and Muedeking 1976, Smith 1983, Van Buskirk 1988, Werner and McPeek 1994). Werner (1991) found *A. junius* can have a large impact on absolute and relative abundances of *R. catesbeiana* and *R. clamitans* tadpoles.

On 20 March 2001, I placed one tadpole of each of the four species and an *A. junius* naiad in a 3-l tub filled with dechlorinated water (21 C°) under fluorescent light in the laboratory. Tadpoles used in the experiment ranged in size from 20 mm to 30 mm in total length, and I took extreme to assure tadpoles in a given tub did not differ by more than 2 mm total length. Dragonfly larvae varied greatly in size (30 mm - 60 mm total length) and developmental stage (third through fifth instar), but all sizes of naiads were competent tadpole predators. The four tadpoles were placed into the water before introducing the naiad. Care was taken to gently release the naiad into the tub to minimize the amount of disturbance to the tadpoles and the dragonfly naiad. Disturbing the tadpoles could alter their behavior, which in turn could affect their susceptibility to predation, and disturbance to the naiad could affect its motivation to feed.

The experiment lasted until one tadpole in a given tub was captured and eaten by the dragonfly naiad. The tadpole was then identified to species and that species was assigned a value of one and the other three species were assigned a value of zero. The experiment was replicated 129 times. I used a logistic regression model (SAS 1996) with species as a categorical predictor, to model the probability of being eaten first in order to compare the susceptibility of the four species while in the presence of each other.

### *Relationship between activity levels (stimulus) and susceptibility to predation*

I calculated cumulative total movement for all four species in my movement experiment, which I predict should equal the total amount of stimulus that the tadpoles give to potential predators. I then calculated the proportion of the total stimulus contributed by each species. I predict the proportion of the stimulus or movement should reflect the relative susceptibility of each species in the multiple species predation trials. I tested the null hypothesis that the proportion of stimulus (tadpole movement) and predation did not differ (Chi-square analysis for specified proportions $\alpha \leq 0.05$.

### *Single species predation trials*

From 19 March 2001 to 25 March 2001, I tested for differences in the relative abilities of the four tadpole species to escape predation. I did this by placing four randomly selected tadpoles of a single species and an *A. junius* naiad in a 3-l tub filled with dechlorinated water (21° C) under fluorescent light in the laboratory. I determined the ratio of the total number of dragonfly larvae attacks to successful attacks by visual observation. The experiment was repeated for each of the four species; *R. sphenocephala* (N = 30 replications), *P. crucifer* (N = 29 replications), *P. triseriata* (N = 33 replications) and *S. holbrookii* (N = 33 replications).

In each tub, I counted the total number of predation attempts by the naiad in pursuit of a tadpole until a tadpole was captured in that tub or until 30 minutes had expired. Dragonfly naiads of the family Ashneidae have a feeding apparatus that allows them to be successful at capturing tadpoles. The spiny labium can be extended in a quick strike manner to ensnare a prey item (Pritchard 1965). Recording of a predation attempts started when a naiad extended its labium in an attempt to capture a tadpole; however, the attempt was not complete until the naiad became motionless and had obviously abandoned pursuit of the tadpole. Therefore, a single attempt could have included several strikes with the labium in a single pursuit, but a chase was not counted if a strike was not made with the labium. I used a Chi-square analysis ($\alpha \leq 0.05$) to compare the mean number of attacks made by naiads to capture a tadpole of each of the four anuran species. The mean length of different species of tadpoles used in this experiment did not differ significantly and ranged in size from 23 – 27mm in total length.

### Escape behavior

Individual tadpoles were placed in approximately 10-l of water in a 100 cm x 40 cm glass arena and allowed to habituate for one minute. Sprint speed, net and total distance traveled, time spent during escape move, and complexity of escape trajectories were measured for each species by simulating an attack in which I probed the proximal end of the tail of each tadpole with a sharp dissecting probe. Responses were recorded using a Sony® digital camcorder placed 2 m above the enclosure. Trials were replicated 30 times for each species and all tadpoles were preserved in 10% formalin and measured. Each tadpole was filmed from the time at which the predation attempt was simulated until the tadpole stopped moving. On several occasions in the trials, tadpoles moved out of the field of view of the camera and were excluded from analyses.

I calculated sprint speed (m/sec) by measuring distance traveled by each individual tadpole during the first 0.20 (6 frames of film) and 0.40 (12 frames of film) second periods immediately after a simulated attack. I used one-way ANOVA followed by a Tukey’s multiple range test ($\alpha \leq 0.05$) to test the hypotheses that sprint speeds differ among species. I used linear regression analyses ($\alpha \leq 0.05$) to test the hypotheses that tadpole total length would predict tadpole sprint speed in the four species.

Duration of the escape moves were calculated three different ways. First, the length of time a tadpole spent moving after a simulated attack was measured to the nearest 0.01 second. Then total distance traveled was measured to the nearest 0.01 mm for the entire escape move. Finally, the net escape distance (the straight-line distance from the point where the tadpole started its escape move to the point where it stopped) was measured to the nearest 0.01 mm. All trials started when the tadpole was first prodded and ended when the tadpole came to rest. I used one-way ANOVAs followed by Tukey's multiple range tests ($\alpha \leq 0.05$) to test the hypotheses that the duration of evasive movements (length of time moving, total escape distance, net escape distance) differed among species.

Escape patterns were analyzed by viewing the escape trials on a 27-inch television monitor and tracing movements onto a 5 mm x 5 mm grid. I estimated the complexity of each escape path using the fractal dimension (D) calculated by the basic dividers method (Dicke and Burrough 1988). Values range from 1 for a straight path to 2 for a plane-filling path. To calculate the D for each escape path, I converted the paths into a series of x, y coordinates using the 5 mm grid. Coordinates were recorded every time the path crossed a grid line or turned and the fractal dimension was calculated numerous times (1000 repetitions) by randomly selecting a starting point (Nams 1996). Once D values were obtained for all of the escape moves, I used a one-way ANOVA followed by a Tukey's multiple range test ($\alpha \leq 0.05$) to test the hypothesis that the complexity of escape maneuvers differs among species.

## Phylogenetic relationships

To asses whether current observations in breeding site associations are pliesiomorphic or derived character states in the four anuran species in this study, I needed to explore phylogenetic relationships between the species and their most closely related extant relatives. First, I determined from several field guides and other literature (Stebbins 1985, Garrett and Barker 1987, Behler and King 1988, Conant and Collins 1998, Leenders 2001) whether each species in my study and their close relatives used permanent or ephemeral water sources for breeding. I used existing phylogenies of two of the families of anurans in my study, Hylidae (Hedges 1986), Pelobatidae (Buchholtz and Hayes 2002), and the Genus *Rana* (Hillis and Davis 1986), and mapped the characters of permanent or ephemeral breeding site use for all of the species in the clades. For each phylogeny, I selected the most closely related species or family to serve as an outgroup to root the clade to better decide if the ancestral state for the group was associated with permanent or ephemeral water for breeding sites. The family Bufonidae was used as the outgroup for the family Hylidae (Richardson 2001), the Old World Pelobatidae were used as the outgroup for the New World Pelobatidae (Buchholtz and Hayes 2002), and the genus *Pyxicephalus* was the outgroup for the *Rana* clade (Hillis and Davis 1986).

## RESULTS

### Breeding site association

I classified 75 surveyed sites according to three major types of ponds used by the four winter-breeding species. Species used different parts of the hydroperiod gradient; however, no tadpoles of the four species were collected from permanent water sites (Figure 37). The first and the rarest type of site was one “extremely short” duration site. It was on well-drained soil and did not hold water for more than a few days except for instances of flood-level rain events. The next type was the “short duration” site. This was the most common type of site comprising 66 of the 75 total sites. The short duration sites were small, extremely abundant, and very unpredictable. Many were tree tip-overs, road ruts, or roadside ditches. These would fill with a single rain event and could appear rapidly by some random event such as a tree fall. Clay-rich soils allowed them to hold water for several weeks to months. The final type was the “seasonal site”. The 8 seasonal sites were large, ranging from 500 $m^2$ to 2 ha in surface area. They were on poorly drained soils and held water for at least half of the year. Often these sites required several rain events to collect a sufficient amount of water for successful anuran breeding.

*Scaphiopus holbrookii* tadpoles were observed only in the single extremely short duration breeding site. The pond had approximately 600 $m^2$ surface area with a maximum depth of 0.5 m. No other species of tadpoles occurred in the same pond with *S. holbrookii* tadpoles.

*Pseudacris crucifer* tadpoles were observed only at the 8 seasonal sites. *Pseudacris crucifer* tadpoles co-occurred with *P. triseriata* tadpoles in two of the seasonal sites and co-occurred in all 8 sites with *R. sphenocephala* tadpoles. *Pseudacris triseriata* was found in 39 sites, 37 of which were short duration sites and 2 seasonal sites. It co-occurred in 2 seasonal sites with *P. crucifer* and *R. sphenocephala*. In the short duration sites, *P. triseriata* co-occurred with *R. sphenocephala* in 19 of 37 sites. The lack of complete overlap between the *P. triseriata* and *R. sphenocephala* was probably due to chance. I found *R. sphenocephala* tadpoles at 48 sites. This species occurred in all types of sites with the exception of sites with extremely short hydroperiods such as the one used by *S. holbrookii*. In fact this species overlapped with 100% of the sites used by *P. crucifer* and in more than 50% of the sites used by *P. triseriata*.

### Tadpole activity

As predicted by species segregation along the hydroperiod gradient, I found significant differences in activity levels among the four species of tadpoles ($F_{3,296} = 113.33$, $P \leq 0.001$). *Scaphiopus holbrookii* tadpoles moved more than three times as much, on average, as either *P. triseriata* or *R. sphenocephala*. *Pseudacris crucifer* moved less than 5 percent of time during this experiment, significantly less ($p < 0.05$) than all other species (Figure 38). *Pseudacris triseriata* used sites intermediate in permanency relative to *P. crucifer* and *S. holbrookii*, reflecting the same pattern as their intermediate activity levels. However, results of *R. sphenocephala* activity experiments

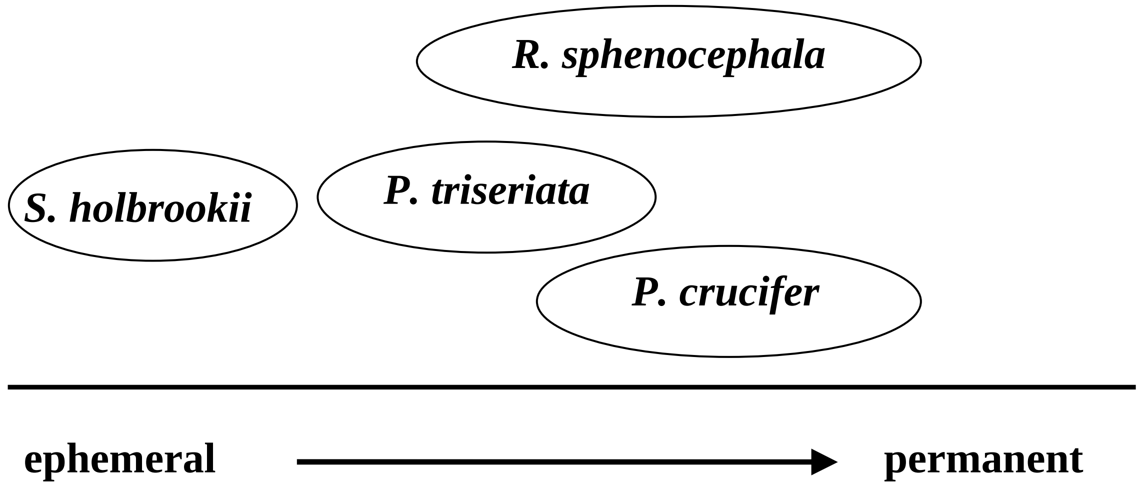


Figure 37. A schematic of the hydroperiod from ephemeral to permanent and breeding sites used by 4 species of winter-breeding anurans in eastern Texas, USA. The ellipses represent idealized breeding based on the portion of the hydro-period gradient the species used at field sites in eastern Texas. Overlap in site use by the different species was evident for *R. sphenocephala*, *P. triseriata*, and *P. crucifer.*

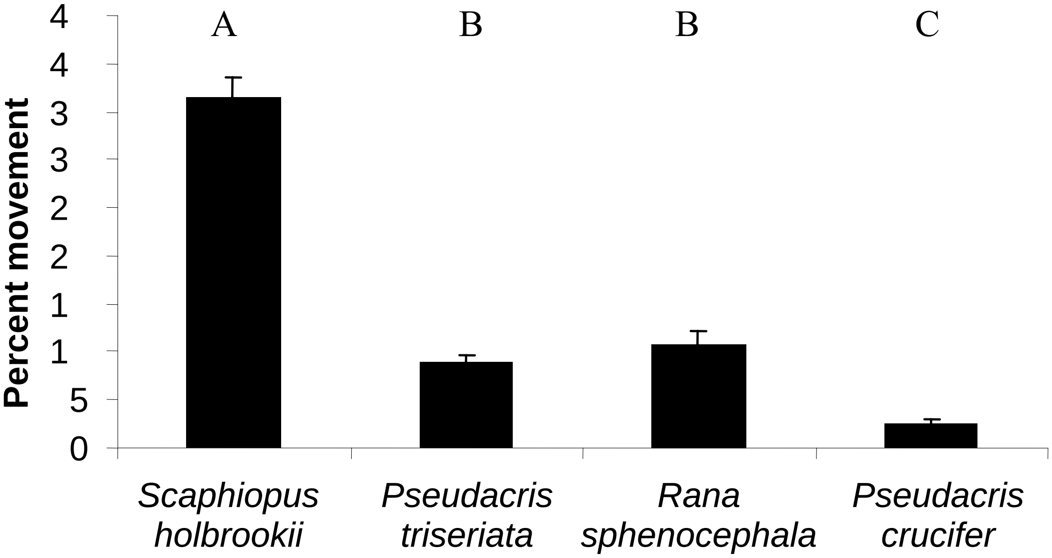


Figure 38. The proportion of time each species spent in motion during movement trials. Letters above bars indicate significantly different subgroups ($P < 0.05$) according to Tukey's post hoc tests.

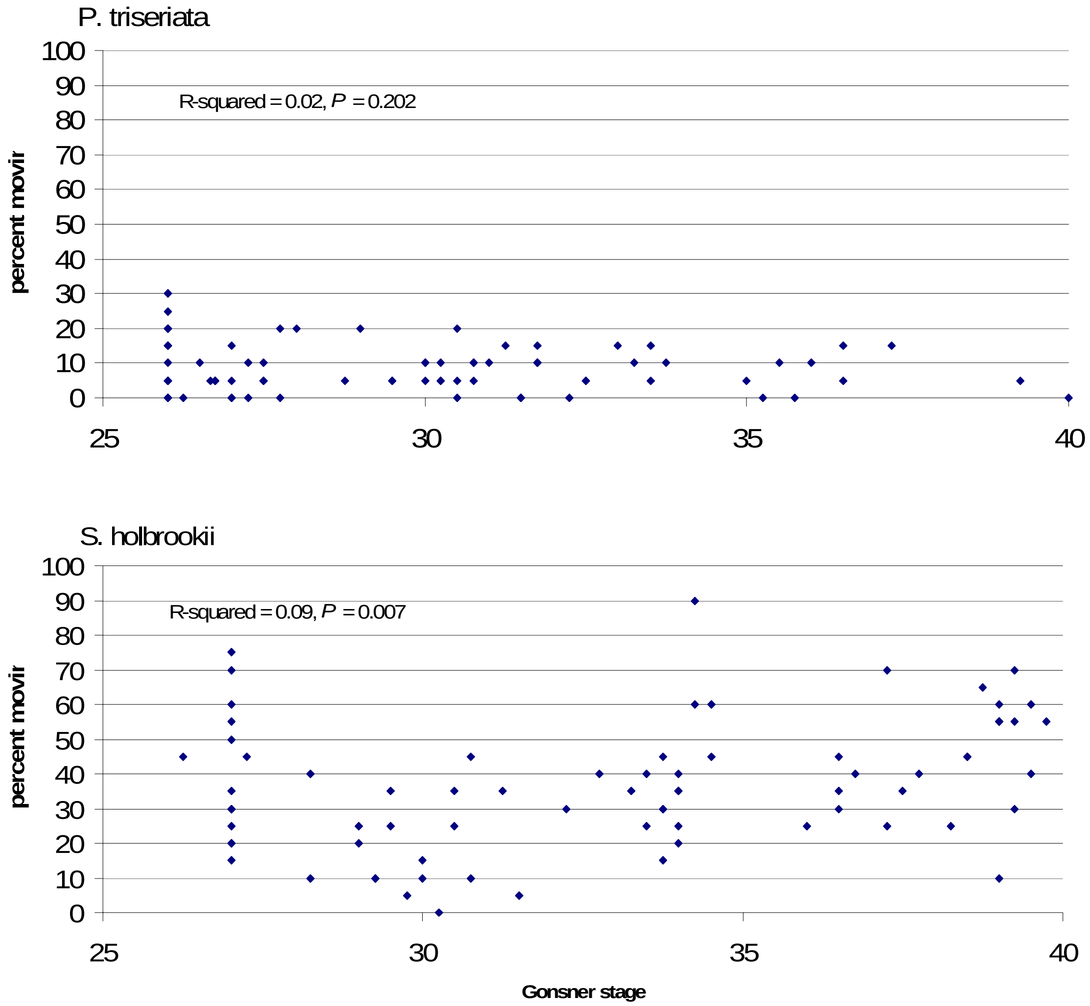
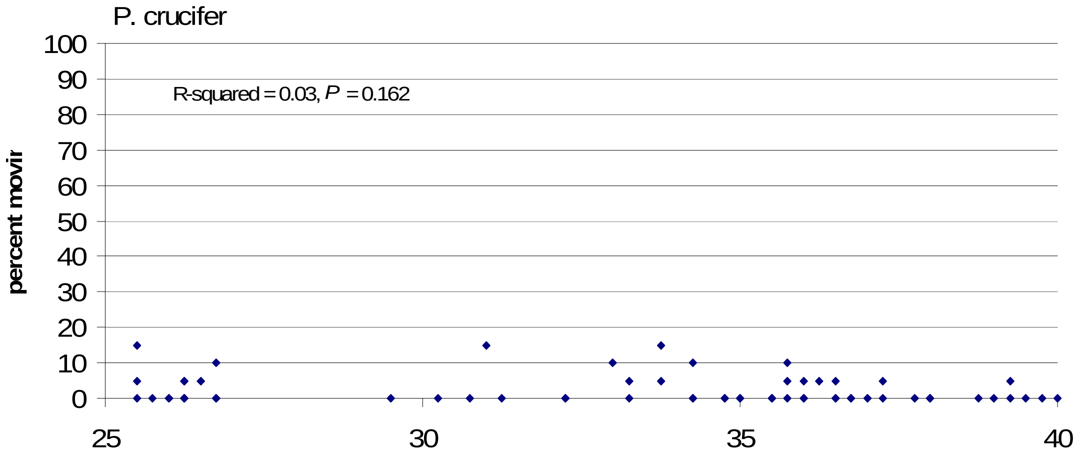


Figure 39. Percent tadpoles moving and Gosner (1960) stage in tubs in the movement trials. Results of Pearson's correlation analyses are on each graph.



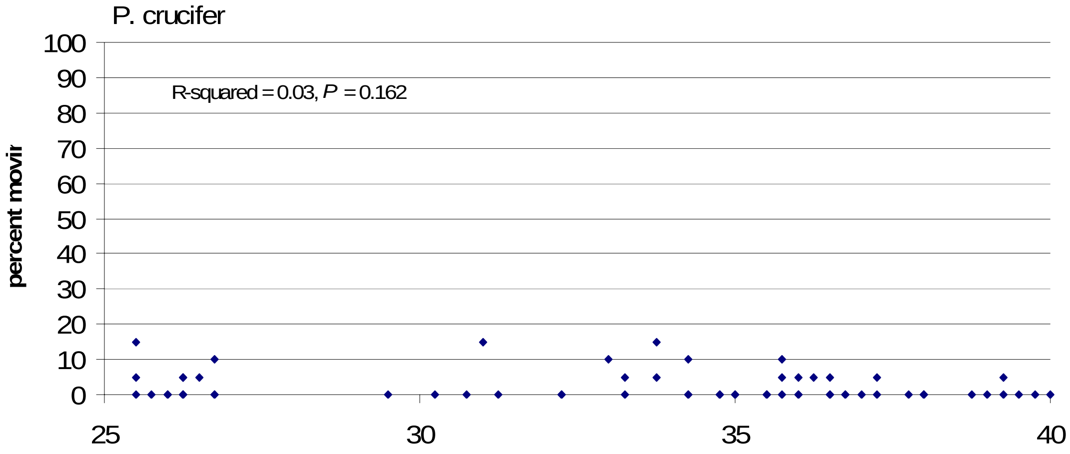


Figure 39. Continued.

were not as simple to interpret. This species exhibited intermediate movement, but also occurred in sites near both ends of the hydroperiod continuum. No relationship was found between developmental stage and activity levels in *P. crucifer (*$R^2 = 0.02$, $P = 0.202$), *P. triseriata* ($R^2 = 0.03$, $P = 0.162$), or *R. sphenocephala* tadpoles ($R^2 = 0.02$, $P = 0.224$) whereas *S. holbrookii* activity ($R^2 = 0.09$, $P = 0.007$) appeared to increase with increasing developmental stage (Figure 39). However, low $R^2$ values indicated Gosner (1960) stage was not a very good predictor of activity levels for any species.

Gosner (1960) stage was a good predictor of total length in all four species in this study, but *R. sphenocephala* tadpoles grew three times as much per developmental stage than the three other species ($Y = -86.10 + 4.08$, $R^2 = 0.80$, $P < 0.001$). Therefore, at later developmental stages, *R. sphenocephala* tadpoles were much larger than the other three species. *Scaphiopus holbrookii* ($Y = -26.12 + 1.41$, $R^2 = 0.92$, $P = 0.001$), *P. triseriata* ($Y = -24.59 + 1.36$, $R^2 = 0.94$, $P = 0.001$), and *P. crucifer* ($Y = -27.31 + 1.43$, $R^2 = 0.83$, $P = 0.001$) had very similar growth rates (as defined as growth per developmental stage) and did not differ in size (Figure 40).

## Susceptibility to predation

### *Multiple species predation trials*

The odds of a dragonfly naiad capturing and eating a *S. holbrookii* tadpole first were greater than the other three species, as predicted, and in concordance with the high activity levels of this species. Independent contrasts showed the odds of being eaten first were greater for *P. triseriata* tadpoles (intermediate activity levels) than *P. crucifer*

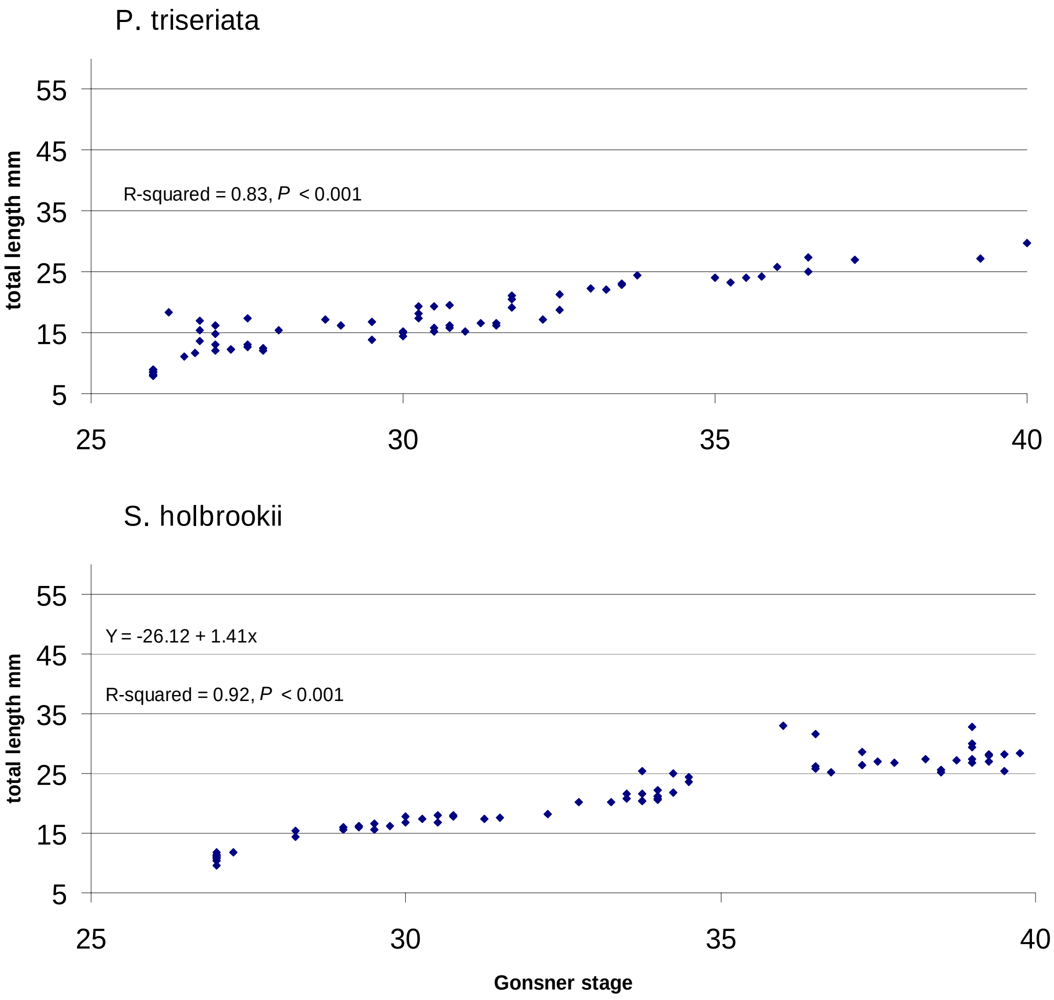
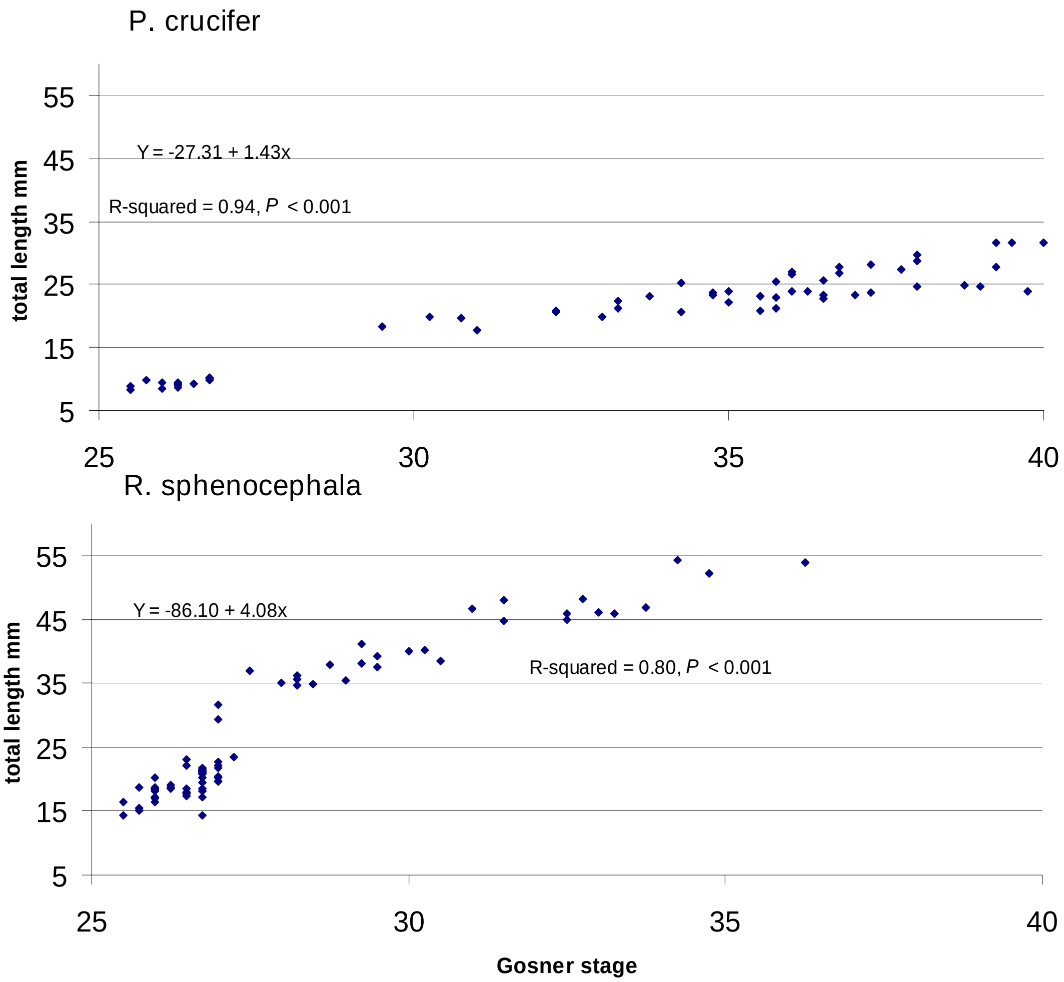


Figure 40. Size and Gosner (1960) stage of tadpoles used in movement trials. Rregression statistics are shown on each graph.



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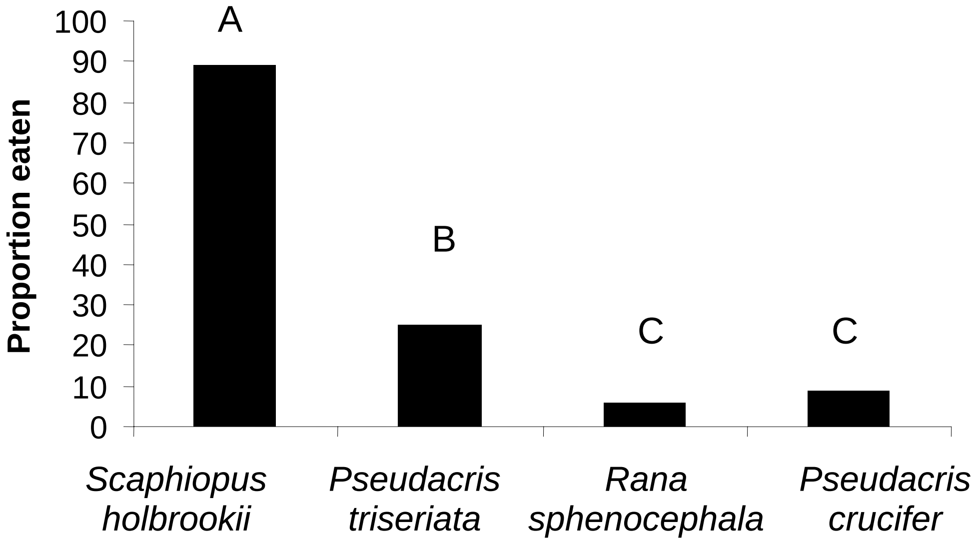


Figure 41. The number of individuals of each species captured and eaten first out of 129 trials. Letters over the bars indicate significantly different odds of being eaten first ($P < 0.05$) while like letters indicate that the odds do not differ.

(lowest activity levels) or *R. sphenocephala* tadpoles. However, the odds of being eaten first were similar for *P. crucifer* and *R. sphenocephala* tadpoles (Figure 41).

### *Relationship between activity levels and susceptibility to predation*

Chi-square analysis for specified proportions ($X^2 = 18.1$, $P < 0.001$) indicate the proportion of movement contributed by each species was not a good predictor of predation. However, upon closer inspection, it was apparent *R. sphenocephala* showed the unique combination of high activity levels and low susceptibility to predation (Figure 42). When *R. sphenocephala* data were omitted, the results were quite different ($X^2 = 1.4$, $P = 0.496$), indicating that with the exception of *R. sphenocephala*, movement was indeed a good predictor of susceptibility to predation (Figure 43).

### *Single species predation trials*

Tadpoles showed marked differences in their ability to escape a predation attack from *Anax junius* naiads ($X^2 = 7.5$ , $P < 0.001$). Dragonfly naiads made on average over four attacks before successfully capturing a *R. sphenocephala* tadpole. *Rana sphenocephala* also escaped predation significantly more often than the other three species of tadpoles. Dragonfly naiads were most efficient at capturing *S. holbrookii* tadpoles. Over one half of all attempts on *S. holbrookii* tadpoles resulted in a successful predation event. The ability to escape predation was intermediate for the *P. crucifer* and *P. triseriata* tadpoles (Figure 44).

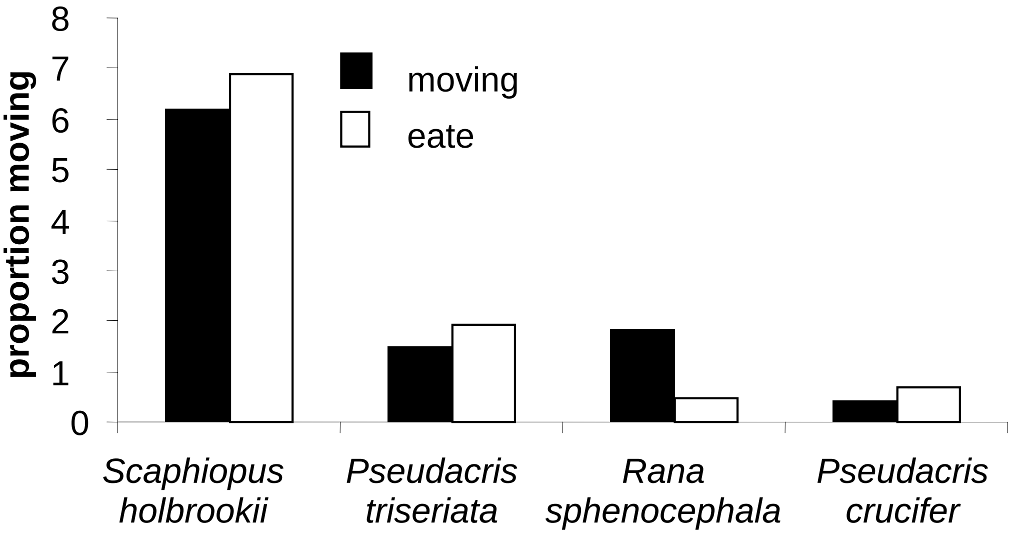


Figure 42. Total movement contributed by all four species during movement trials compared to the proportion of total tadpoles eaten first in the multiple species predation experiment.

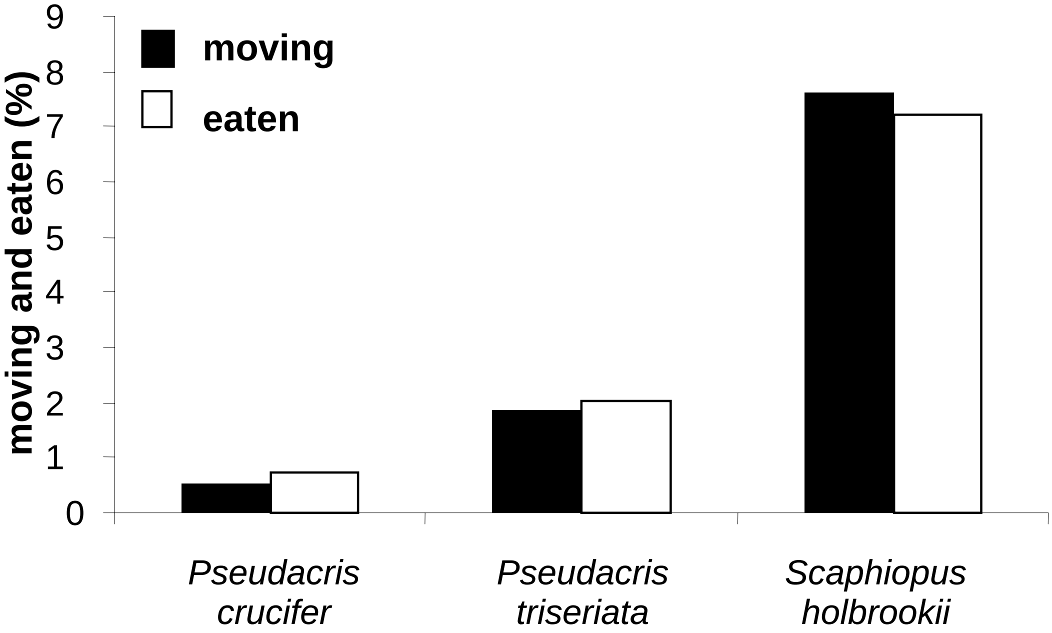


Figure 43. Total movement contributed by a given species during movement trials compared to the proportion of total tadpoles eaten first in the multiple species predation experiment.

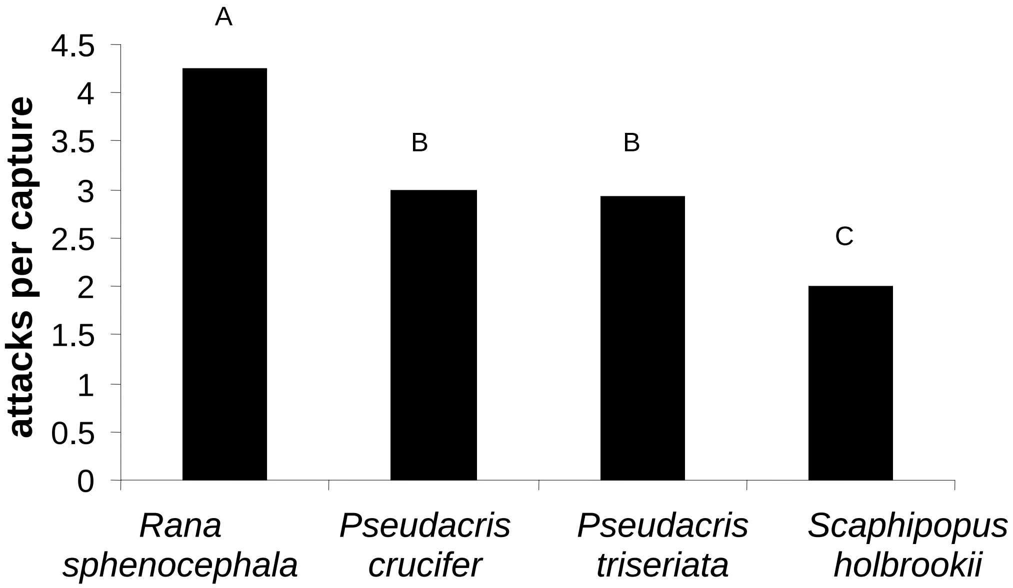


Figure 44. Number of individual attacks by a dragonfly naiad per successful capture of a tadpole. Different letters over the bars represent significantly different subgroups based on Tukey's post hoc tests (P < 0.05).

Escape behavior

After a simulated attack, species differed in escape speed at both the first 0.2 seconds of the escape move (6 video frames) ($F_{4,103} = 18.1$, $P < 0.001$), and the first 0.4 seconds of the escape move (12 video frames) ($F_{4,103} = 20.22$, $P < 0.001$). *Rana sphenocephala*, *P. triseriata*, and *P. crucifer* tadpoles exhibited greater escape speed than *S. holbrookii* tadpoles but did not differ from each other (Figure 45). Additionally, regression analyses indicated statistically significant relationships (between tadpole length and sprint speed in the *R. sphenocephala* ($R^2 = 0.24$; $P = 0.009$) and *P. crucifer* ($R^2 = 0.20$; $P = 0.017$), while a marginal, nonsignificant relationship existed between sprint speed and total length in *P. triseriata* and no relationship was observed in *S. holbrookii* (Figure 46). Within-species variation in sprint speed was high for all species, resulting in low predictive power (see $R^2$ values in Figure 46).

The duration of escape moves differed significantly between the species ($F_{4,103} = 6.39$, $P < 0.001$). *Scaphiopus holbrookii* tadpoles moved significantly longer after the simulated predation attempts than the other three species. *Rana sphenocephala*, *P. crucifer* and *P. triseriata* tadpoles did not differ in the length of time spent during the escape move (Figure 47).

Total distances traveled from the point of the simulated attack also differed significantly between the species ($F_{4,103} = 5.08$, $P = 0.002$). *Pseudacris triseriata* and *S. holbrookii* tadpoles moved significantly farther after being attacked than did the other two species but

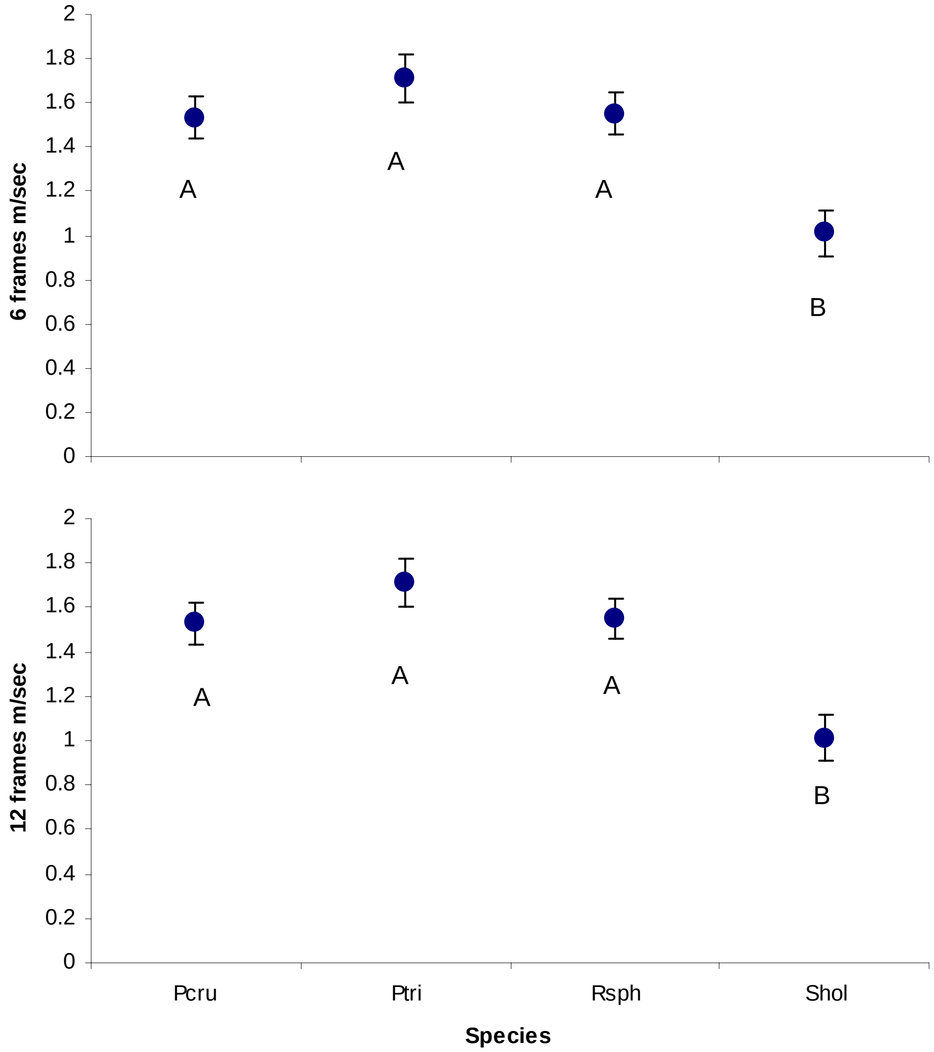


Figure 45. Mean speed (m/sec ± SE) swam by different tadpole species. Different letters over the bars represent significantly different subsets in sprint speed according to Tukey's post hoc tests.

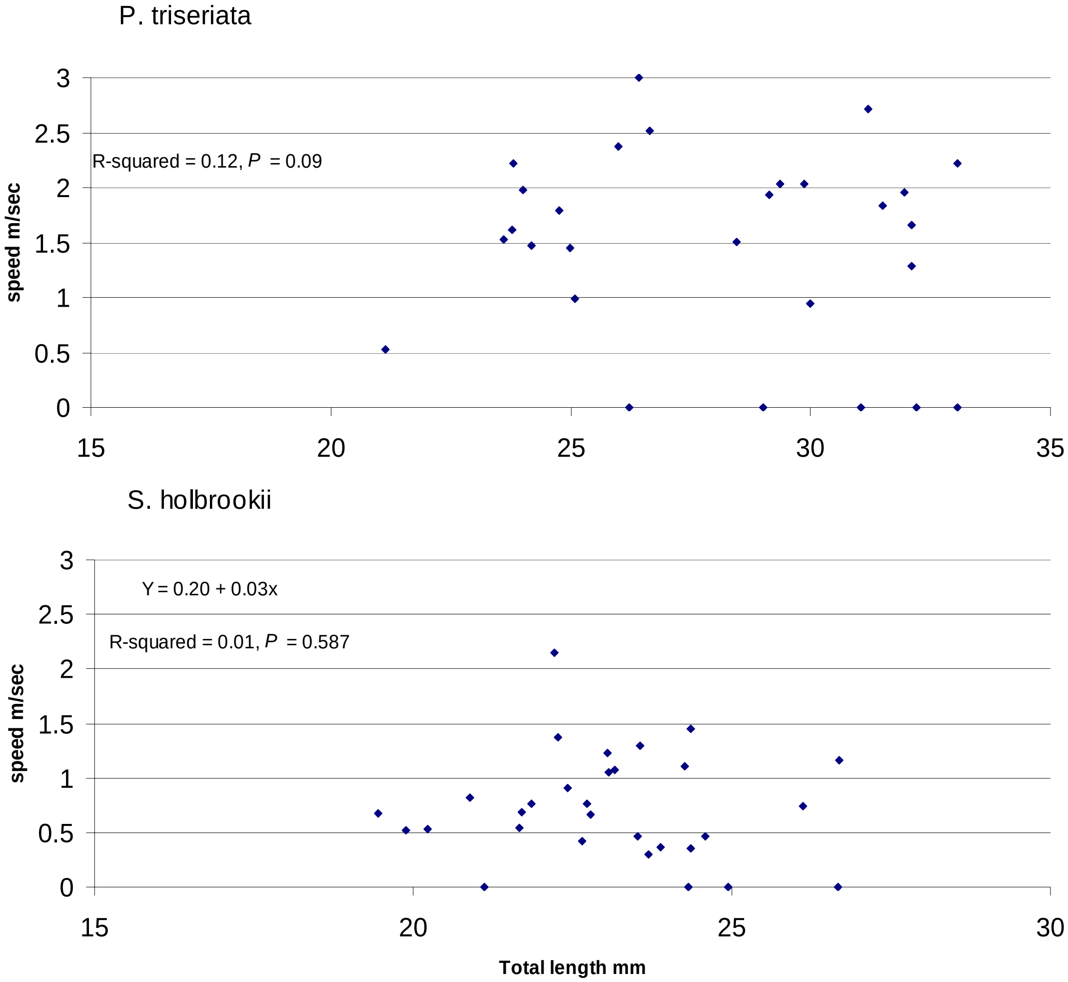
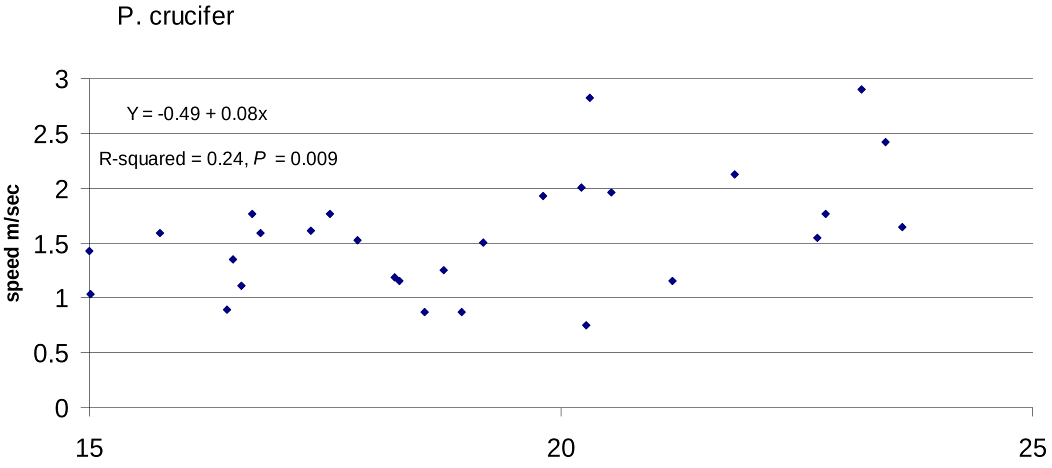


Figure 46. Tadpole sprint speed (m/sec) versus total tadpole length in the escape behavior trials. Results of regression analyses are shown on each graph.



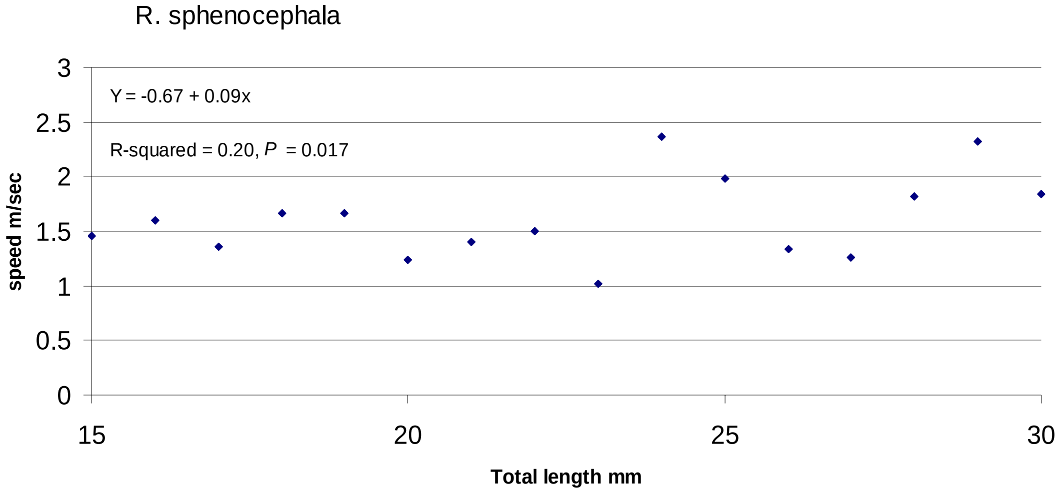


Figure 46. Continued.

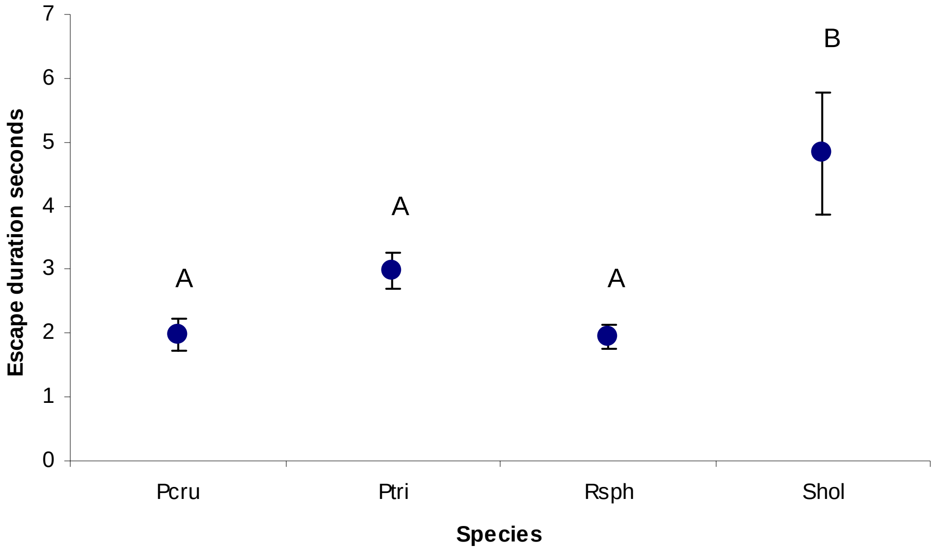


Figure 47. Mean duration in seconds (± SE) of the escape move by each tadpole of each species during the escape behavior experiment. Letters over the bars represent significantly different subsets identified by Tukey’s post hoc tests.

did not differ from each other. *Pseudacris crucifer* and *R. sphenocephala* tadpoles moved the shortest distance and did not differ from each other (Figure 48).

The straight-line distance from the point of the simulated attack to the point where the tadpole stopped moving differed significantly among species ($F = 7.90$, $P < 0.001$). Results for straight-line differences were similar to the results from the total escape difference comparisons. *Pseudacris triseriata* ended its escape move farther from the point of the simulated attack than the *R. sphenocephala* or the *P. crucifer* but did not differ from *S. holbrookii*. *Pseudacris crucifer*, *R. sphenocephala*, and *S. holbrookii* tadpoles did not differ from each other in net distances traveled in their escape move (Figure 49).

Patterns of the path taken during escape moves varied markedly among the species ($F_{4,103} = 4.94$, $P = 0.003$). *Scaphiopus holbrookii* took significantly more tortuous paths than the other three species of tadpoles. *Pseudacris crucifer*, *P. triseriata*, and *R. sphenocephala* did not differ significantly in the tortuosity of their escape paths. However, there was relatively little variation in the escape paths taken by the *P. crucifer* and *R. sphenocephala* tadpoles (Figure 50).

### Phylogenetic relationships

The Hylidae includes species that use permanent and ephemeral breeding sites (Figure 51). Use of ephemeral sites for breeding appears to be ancestral among hylids. A majority of the species in the Hylidae use ephemeral sites for breeding and the most closely related group, the family Bufonidae, are mostly ephemeral site breeders.

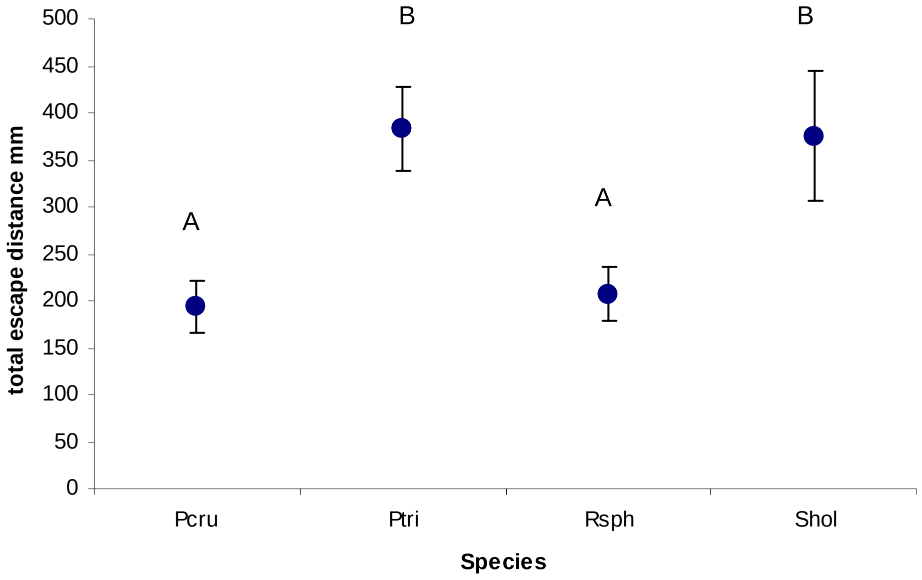


Figure 48. Mean total distance in millimeters (± SE) of the escape move by each tadpole of each species during the escape behavior experiment. Letters over the bars represent significantly different subsets in the total distance of escape moves identified by Tukey's tests.

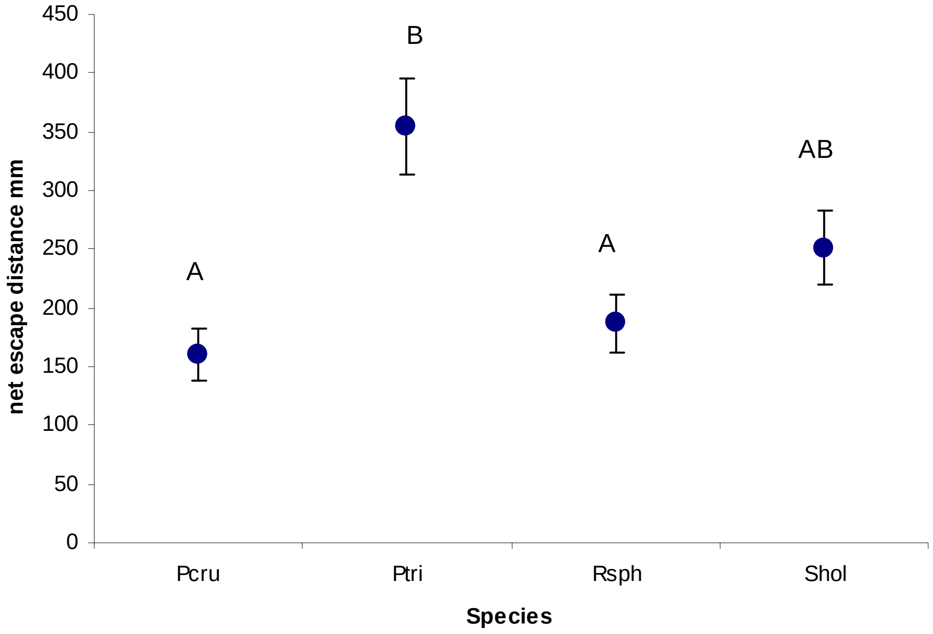


Figure 49. Mean net distance in millimeters (± SE) of the escape move by each tadpole of each species during the escape behavior experiment. Letters over the bars represent significantly different subsets in the net distance of escape moves identified by Tukey's tests.

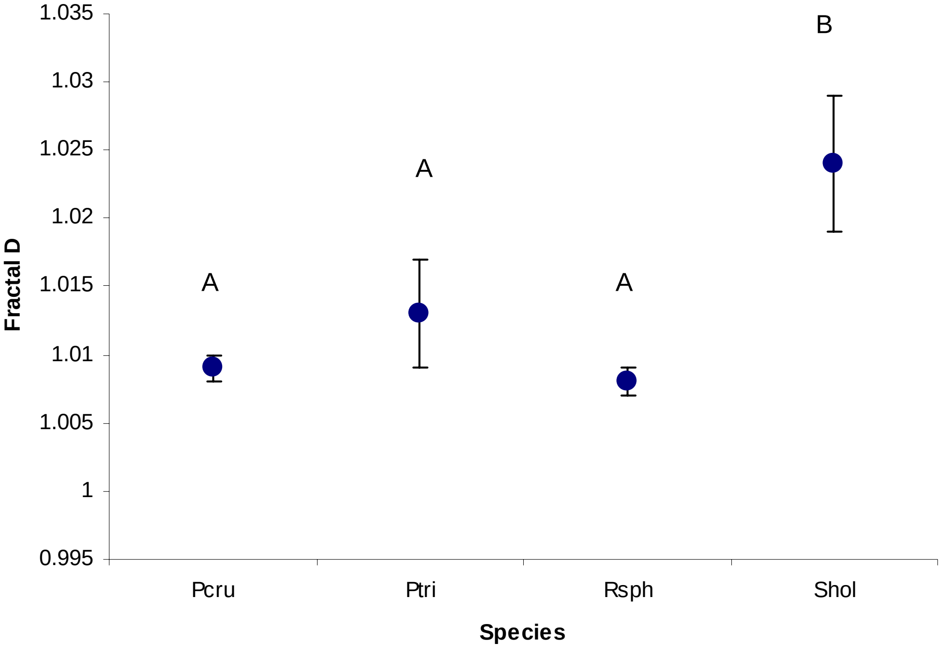


Figure 50. Mean fractal dimension (D) values (± SE) of the escape move by each tadpole of each species during the escape behavior experiment. Letters over the bars represent significantly different subsets of mean D identified by Tukey's tests.

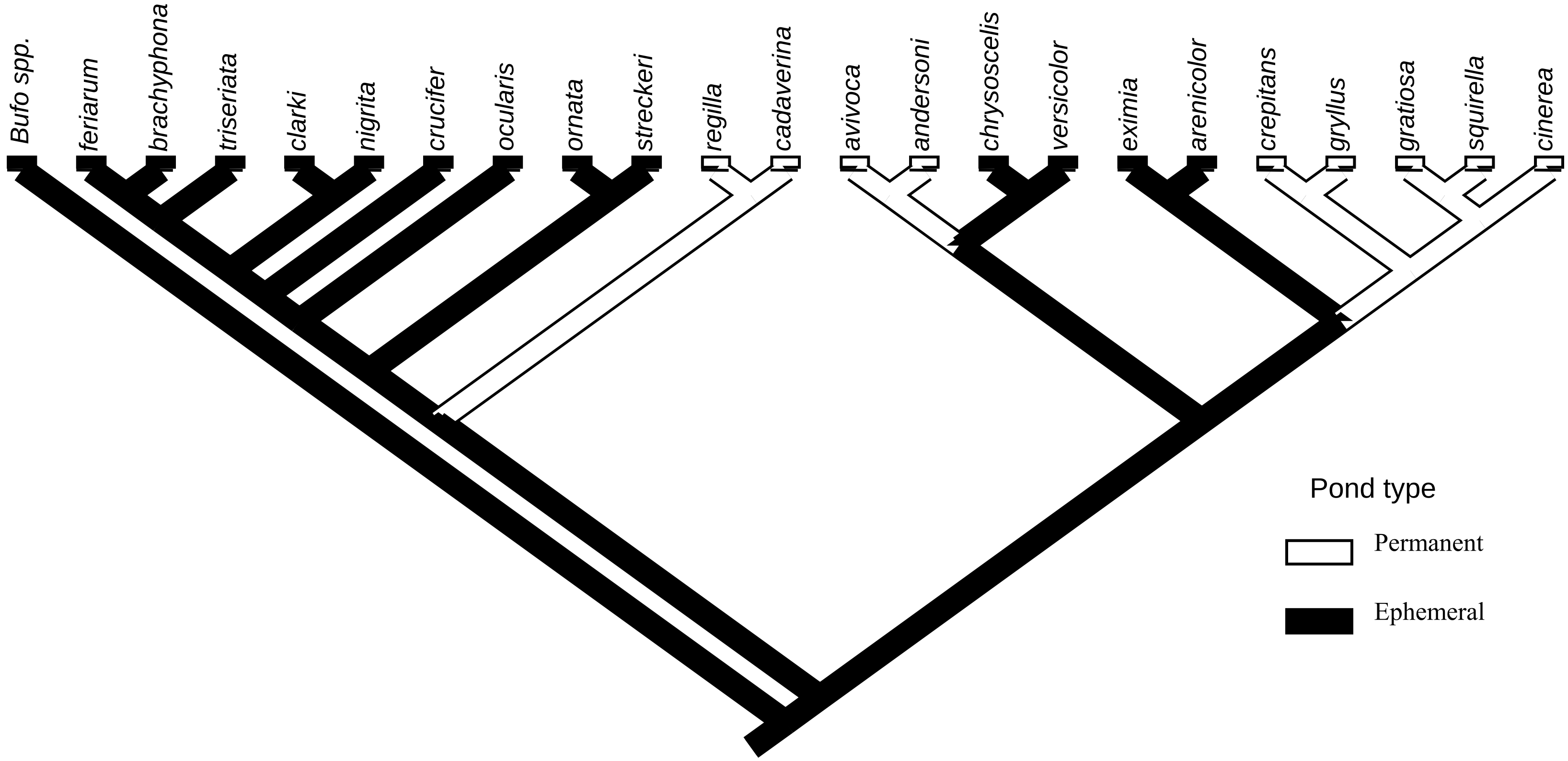


Figure 51. Phylogenetic tree of the Family Hylidae with the Genus *Bufo* as the outgroup (modified from Hedges 1986). Character states of permanent water use are mapped in white and species that use ephemeral water sources for breeding are mapped in black.

These two pieces of evidence provide good support for an ancestor that used ephemeral breeding sites and the use of permanent sites likely evolved independently in some lineages within this clade.

*Scaphiopus holbrookii* uses ephemeral breeding sites as do all the members of the New World Pelobatidae and their sister clade, the Old World Pelobatids (Figure 52). In this case, all evidence gives strong support for ephemeral breeding site use as the ancestral state for the New World Pelobatids.

Finally, although *R. sphenocephala* uses ephemeral breeding sites, it is likely this is a derived behavior. Most members of the genus *Rana* and the closely related Genus *Pyxicephalus* use permanent water breeding sites (Figure 53). The use of permanent water breeding sites is the ancestral state in this group and it appears that the use of ephemeral breeding sites is derived in the clade to which *R. sphenocephala* belongs. Closely related species are not known to use ephemeral breeding sites, for example, *R. pipiens* and *R. berlandieri*.

## DISCUSSION

The idea that the distribution of populations across the hydroperiod continuum is limited by tolerances to pond drying and predator-prey interactions are commonly accepted paradigms in freshwater community assembly. Evidence from this study suggests that these paradigms are applicable to the winter breeding anurans in eastern Texas; however there are some notable inconsistencies in this guild.

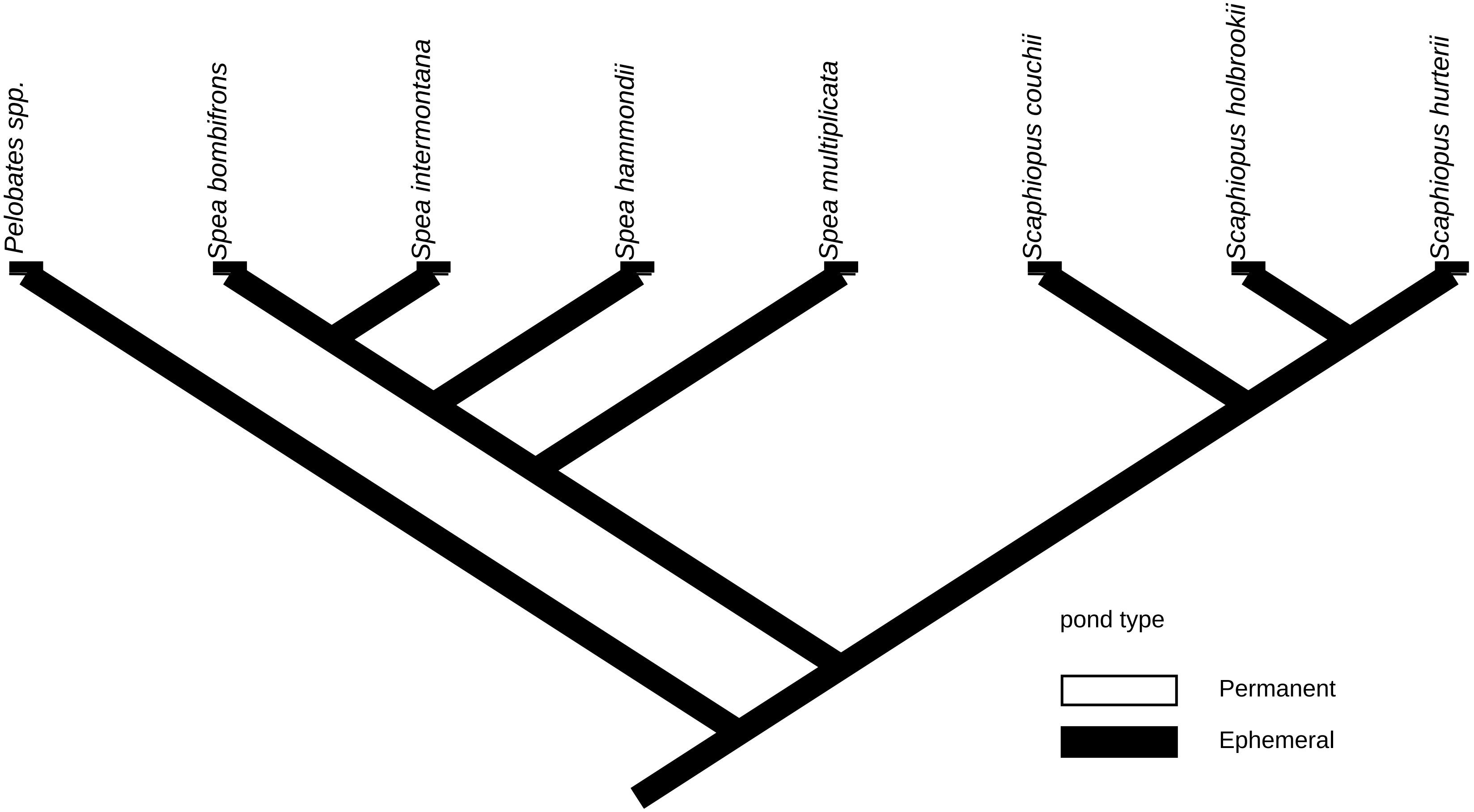


Figure 52. Phylogenetic tree of the New World Pelobatids with the Old World genus *Pelobates* as the outgroup modified from Buchholz and Hayes (2002). All new world Pelobatids use ephemeral breeding sites.

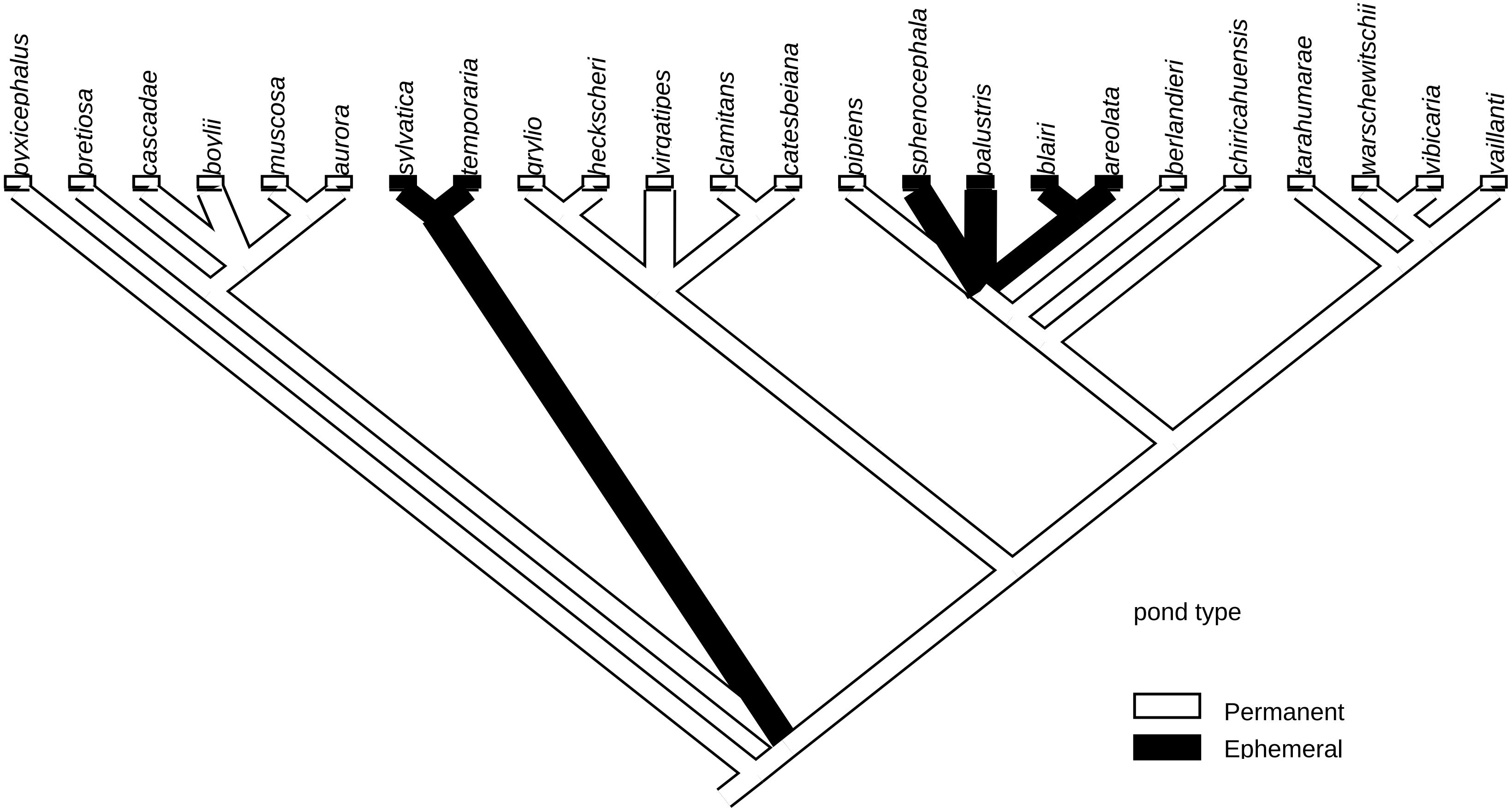


Figure 53. Phylogenetic tree of the Genus *Rana* with *Pyxicephalus* as the outgroup modified from Hillis and Davis (1986). Character states of permanent water use are mapped in white and species that use ephemeral water sources for breeding are mapped in black. *Rana sphenocephala* is in an unresolved polytomy of species that use ephemeral breeding sites.

The four species differentially used ranges of the gradient of water permanency with some overlap in pond use. This was not unexpected since Skelly (1996) found a high frequency of co-occurrence between *P. crucifer* and *P. triseriata* in southeastern Michigan. However, he found a large amount of variation in their relative abundances over a range of pond types suggesting these two species differed in their ability to cope with pond drying and predators. Several other studies also demonstrated segregation in tadpole species along the hydroperiod gradient, and pond drying and predation were attributed as the major mechanisms controlling community assembly (Heyer et al. 1975, Werner and McPeek 1994, Skelly 1995, Smith and Van Buskirk 1995).

Activity rates of tadpoles inhabiting different portions of the hydroperiod continuum have been correlated to the duration of ponds, with increasing activity levels corresponding to decreasing permanency (Morin 1983, Woodward 1983, Dayton and Fitzgerald 2001, Bridges 2002). Higher activity levels may be due to selection for positive benefits of higher growth rates, greater competitive ability, and faster development leading to a decreased susceptibility to mortality due to pond drying (Skelly and Werner 1990, Werner 1991, 1992, Skelly 1995). Activity levels among the four species in the winter-breeding guild in eastern Texas followed the expected pattern, with more ephemerally-associated species moving a greater proportion of the time.

*Rana sphenocephala* tadpoles inhabited a very wide range of habitats with regard to water permanency. However, it makes sense they had higher activity levels than spring peepers, with whom they overlapped in pond use in more permanent sites and similar activity levels to *Pseudacris triseriata* tadpoles that overlapped in site use with them in more ephemeral ponds. It is possible that pond drying may be a more strict constraint than risk of predation because a dry pond means certain death while the presence of predators does not. Therefore, *R. sphenocephala* tadpoles must conform to ephemeral pond activity levels by moving more so that they can more quickly acquire energy for rapid development.

Several studies have described the trade-offs between activity levels and susceptibility to predation, in which high activity allows existence in ephemeral ponds with few predators while low activity allows coexistence with predators in permanent ponds (Skelly 1996, Dayton and Fitzgerald 2001, Bridges 2002). Encounter rates with predators are likely to increase with increased activity and play a major role in a species' susceptibility to predators (Abrams 1991, Werner and Anholt 1993). The means by which prey might be detected are either visual (Mc Peek 1990) or via mechanosensory stimulation (Kanou and Shimozawa 1983, Richards and Bull 1990).

I expected activity rates of East Texas anurans to more accurately predict relative susceptibility to predation by *A. junius* larvae than I observed. *Rana sphenocephala* tadpoles did not fit the expected pattern (Figure 42) because they exhibited greater secondary antipredator abilities (i.e., ability to escape predation post-attack) than the other species. Considering that ephemeral site use is probably derived in *R. sphenocephala*, it is intriguing to speculate maneuvering escape behavior is possibly due to ancestral adaptations to permanent sites (Figure 44). This hypothesis is testable by comparing escape maneuvering in the Ranidae and controlling for phylogenetic effects.

*Rana sphenocephala* tadpoles have activity levels similar to *P. triseriata* that are high enough to allow rapid grow and development sufficient for successful metamorphosis in more ephemeral sites. However, *R. sphenocephala* tadpoles have low susceptibility to predation by *A. junius* naiads, similar to *P. crucifer* that allows them also to exist in the more permanent sites. However, the anti-predator mechanisms that allow *R. sphenocephala* and *P. crucifer* tadpoles to coexist with predators in the more permanent sites are quite different. *Pseudacris crucifer* tadpoles seem to rely on primary antipredator mechanisms to escape predation (e.g., crypsis). Their activity levels are low compared to the other species in this guild; therefore, they should have fewer encounters with predators. But their ability to escape predation subsequent to an attack is not better than *P. triseriata* tadpoles that inhabit more ephemeral sites. Secondary antipredator abilities, by contrast, seem to be the mechanisms that allow *R. sphenocephala* to exist in the more permanent sites because they have high activity rates compared to *P. crucifer* that should increase encounters with predators but are not more susceptible to predation due to their greater ability to escape.

In addition to activity levels, differential abilities to escape predation attempts are known to be important factors determining distributional differences in some anurans (Werner and McPeek 1994). Caldwell et al. (1980) conducted escape behavior experiments with *Hyla gratiosa* and found that upon being prodded the tadpoles moved away quickly then became immobile shortly thereafter. They concluded it would be advantageous to a tadpole to escape quickly then stop when pursued by an *Anax* predator because they hunt visually and might not be able to relocate their prey. *Rana* *sphenocephala* tadpoles seemed to employ the same strategy in this study. This "run and freeze" strategy may be quite prevalent and effective in amphibians. Brodie et al. (1974) and Dodd and Brodie (1976) found terrestrial salamanders became immobile when uncovered from retreats or prodded.

This study does not take into account the natural size differences between the species in the guild (Figure 40), where *R. sphenocephala* tadpoles attain much greater size than the other species in the winter-breeding clade, because I standardized all the experiments by using tadpoles of equal size for all of the predation trials. Several researchers have suggested that risk of predation to tadpoles decreases with increases in size (Caldwell et al. 1980, Smith 1983, Travis et al. 1985, Cronin and Travis 1986, Werner and McPeek 1994). Caldwell et al. (1980) found the most vulnerable tadpoles in their study were the smallest ones used in their experiments, less than 30 mm total length. Pritchard (1965) demonstrated that *Aeshna interrupta* would not attack a disc that was greater than 20 $mm^2$ which is greatly exceeded by *R. sphenocephala* (Figure 40). Had all sizes of *R. sphenocephala* tadpoles been used in this study or had I standardized trials by tadpole developmental stage, the likely outcome would have been an even greater disparity in the abilities of the tadpoles to escape predation because larger *R. sphenocephala* tadpoles would undoubtedly been stronger and faster making them less vulnerable to *Anax junius*. Understanding the effects of body size on community composition of tadpoles would be an interesting and achievable avenue of future research.

*Rana sphenocephala* is part of a clade of anurans associated primarily with permanent breeding sites (Figure 53). These sites are known to have a greater variety and density of predators, and the increased diversity of predators may require a more diversified system of tadpole defenses (Woodard 1983). The large size and greater escape ability are likely two consequences of phylogeny, meaning that most species in this clade are large and likely possess a diversity of defenses. Furthermore, ephemeral pond use in *R. sphenocephala* appears to be a recently derived behavior in the clade. I suggest *R. sphenocephala* are recent members of the ephemeral pond breeding community and the secondary antipredator mechanisms the species possesses are pleisiomorphic traits inherited from its ancestors. Given their phylogenetic history, it is little surprise *R. sphenocephala* posses secondary antipredator abilities that are more developed than in the rest of the winter breeding guild.

The other three species in this study belong to taxonomic groups that are associated primarily with ephemeral breeding sites (Figures 51, 52) that tend to have fewer predators. Their predator defenses tend to be simpler than that of *R. sphenocephala* where primary antipredator mechanisms accurately explain the observed patterns of habitat association and predator vulnerability. While habitat associations most certainly play a part in determining functional relationships among species, they alone are not adequate to make predictions about membership in ecological communities. This study demonstrated through rigorous testing of the predation-hydroperiod paradigm the probable mechanisms responsible for structuring the winter-breeding community of anurans in eastern Texas. In addition to the complex interplay among both primary antipredatory and secondary antipredatory behaviors and susceptibility to predation, it is clear that evolutionary history also plays a major role in determining tadpole performance and life-history traits.

# CHAPTER V

# CONCLUSIONS

The goal of my dissertation was to identify biotic, abiotic, and time correlates of anuran breeding activity and community assembly and to test current paradigms in anuran community ecology that suggest a link between water permanency and life-history trade-offs among the prey communities in freshwater systems.

In chapter II, abiotic mechanisms that regulate breeding activity in an anuran community were examined using automated recording devices, termed frogloggers. Initially, seasonal patterns of anuran calling behavior were determined. Then, each species in the anuran assemblage was assigned to 5 different functional groups or breeding strategy categories based on their calling phenology and response to environmental variables. Enormous variation was found among species calling activity and response to changes in weather and season and I placed the species in the following categories.

1). YEAR-ROUND CALLERS (*R. sphenocephala*). This species is dependent on local temperature and rain in the cool months and only local rainfall in the summer. This species has the widest range of temperatures where it could be observed calling of any of the species in eastern Texas, therefore it is able to call and breed year-round.

2). WINTER/SPRING CALLERS (pickerel frog, spring peeper, chorus frog). These species call opportunistically within a predictable breeding season, in the cooler months, and depend mainly on local temperature. Rainfall was of lesser importance. More research may reveal that in dry years daily local rainfall might play a more important role in calling behavior.

3). SUMMER CALLERS INDEPENDENT OF WEATHER (bullfrog, bronze frog, cricket frog, green treefrog). These species call within a predictable breeding season, in the warmer months, largely independent of local weather patterns. Temperature might be important early in the breeding season but once temperatures reach 22° C further increases have no effect. Local rainfall actually had a negative effect on some species on the day of the rainfall event possibly due to acoustic interference caused by the sound of the falling rain that could reduce the range of anuran calls

4). SUMMER CALLERS DEPENDENT ON LOCAL RAINFALL (gray treefrog, eastern narrowmouth toad, Gulf Coast toad, Woodhouse'e toad). These species call opportunistically within a predictable breeding season, in the warmer months and are dependent on local rainfall. As with the other summer breeders, local temperature is not very important later in the summer when air temperatures are consistently warm. However, local daily rainfall is a good predictor of calling activity in these species.

5). FLOOD LEVEL CALLERS (Hurter's spadefoot). This species breeds only during or soon after very large rainfall events, a minimum of 10 cm.

To examine the influence of the uncertainty in various life history parameters (colonizing ability, fecundity, and susceptibility to predation) in anuran community succession I performed sensitivity analyses that suggested these parameters may greatly influence a species' ability to colonize and successfully reproduce in a pond and determine which stages of succession a species would occur. Colonizing ability was important for species with low fecundity and high susceptibility to predation. These early succession species tend to be constrained from later stages of succession by predators. Species that are resistant to predators are generally poor colonizers and tend to arrive late in succession, but once they colonize a pond they tend to persist and produce recruitment. These species are not constrained from producing recruitment early in succession but the probability of reaching the pond quickly is low.

High fecundity has been associated with early succession species in other studies, particularly in plants. However, high fecundity appears to be associated with the late succession species in the model. This is consistent with the idea that predation on anuran larvae is the most important constraint in the late succession stages where some proportion of the population is lost to predation. The early succession species are mainly species that might be expected to use ephemeral aquatic habitats for breeding. These sites generally have relatively low predator populations and the greatest danger to the larvae is desiccation of the breeding site where all of the larvae are lost at once. It appears to be more or less an all or nothing effort when these species breed making clutch size less important to the survival of the individual.

The idea that the distribution of populations across the hydroperiod continuum is limited by tolerances to pond drying and predator-prey interactions are commonly accepted paradigms in freshwater community assembly. Evidence from this study suggests that these larval anurans use habitats that vary in hydroperiod from permanent water with high predator densities to ephemeral sites with low predator densities that hold water for only a few weeks. Length of larval stage also varies greatly between species. Species with long larval periods tend to inhabit permanent water and are less susceptible to predators, compared to species with short larval periods that tend to inhabit ephemeral water and are more susceptible to predators. I studied four winter breeding anuran species in eastern Texas: *Pseudacris crucifer*, *P. triseriata*, *Rana sphenocephala*, and *Scaphiopus holbrookii*, and compared habitat use, activity rates, and susceptibility to predation by dragonfly larvae (*Anax junius*). Although all the species used ephemeral habitats, I found that species occupying sites with shorter hydroperiods had higher activity rates and were more susceptible to predation with the exception of *R. sphenocephala*. *Rana sphenocephala* appeared to be better at escaping predation than the other species despite a relatively high activity rate. Examination of published phylogenies indicates *R. sphenocephala* is derived from a species group that uses permanent water. I suggest *R. sphenocephala* has retained many anti-predator defenses inherited from its ancestors, even though the species now exploits sites with low predator densities.

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# VITA

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