CHORUSING PATTERNS OF A DIVERSE ANURAN COMMUNITY, WITH AN EMPHASIS ON SOUTHERN CRAWFISH FROGS (*LITHOBATES AREOLATUS AREOLATUS*)

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ABSTRACT: Wildlife surveys have a critical role in conservation efforts and the collection of life history data. For anuran amphibians these surveys often focus on calling males. In order to further our understanding of anuran ecology, we used automated recording systems to monitor the calling activities of the anuran communities at two beaver-formed lakes and one cattle pond in southeastern Oklahoma. We documented 14 anuran species between 5 February and 28 April 2012. Temperature had a significant effect on the calling patterns of Eastern Narrow-mouthed Toads (*Gastrophryne carolinensis*), Green Treefrogs (*Hyla cinerea*), Gray Treefrogs (*Hyla versicolor*), Southern Crawfish Frogs (*Lithobates areolatus areolatus*), and Cajun Chorus Frogs (*Pseudacris fouquettei*). Temperature did not have a significant effect on the calling patterns of Dwarf American Toads (*Anaxyrus americanus charlesmithi*), American Bullfrogs (*Lithobates catesbeianus*), or Green Frogs (*Lithobates clamitans*). There was not a significant relationship between rainfall and calling for *L. a. areolatus*. The presence of several of these species, including *L. a. areolatus* and Hurter's Spadefoots (*Scaphiopus hurterii*) was unusual because these anurans typically breed in ephemeral, fishless pools, but the beaver lakes are permanent and sustain populations of carnivorous fishes.

Key Words.—amphibian; automated recording system; calling; ecology; Oklahoma; survey; weather

INTRODUCTION

Wildlife surveys have a critical role in many conservation efforts. For anuran amphibians this frequently involves monitoring breeding pools for calling males (Knutson et al. 1999; Corn et al. 2000; Nelson and Graves 2004; Pellet and Schmidt 2005). Monitoring is often accomplished through the use of automated recording systems (ARS) which can collect data throughout the breeding season without the continual presence of a researcher (Peterson and Dorcas 1992, 1994). Although multiple studies have been published on the effects that temperature, rainfall, time of day, and other abiotic factors have on anuran calling behavior, relatively few have reported the calling patterns of large, complex anuran communities throughout the breeding season (Mohr and Dorcas 1999; Bridges and Dorcas 2000; Ossen and Wassersug 2002; Saenz et al. 2006; Steelman and Dorcas 2010). Studying the entire community can, however, reveal a wealth of information about how weather and time of year affect the breeding patterns of different species. Understanding the entire community can also aid conservation efforts because different species may not respond identically to environmental stresses, so understanding community dynamics can be useful for detecting and interpreting declines (Hawley 2010). Therefore, we investigated the calling patterns of 14 species of syntopic anurans from February–April at two beaver-formed lakes in southeastern Oklahoma, a region and habitat type in which such studies have not previously been conducted.

One species, the Southern Crawfish Frog (*Lithobates areolatus areolatus*), is of particular conservation interest. *Lithobates areolatus* is an unusual anuran that is noted for its brief breeding season and extensive use of burrows (Thompson 1915; Smith 1934; Heemeyer and Lannoo 2010; Engbrecht et al. 2011). On rainy nights in early spring, *L. areolatus* migrate up to 1.2 km to fishless pools to breed (McCarley 1970; Heemeyer and Lannoo 2012; Engbrecht et al. 2013). Breeding usually occurs between February and April, but the exact dates vary across the species' range and can be affected by weather (Bragg 1953; Busby and Brecheisen 1997; Williams et al. 2013). Outside of the breeding season, adults live in and forage at the mouths of crawfish burrows (Hoffman et al. 2010; Engbrecht and Lannoo 2012). These burrows

TABLE 1. Results of the Mann-Whitney U tests comparing temperatures at 1900 on nights when each anuran species called with temperatures on nights when they did not call. Dates included in analyses ranged from the first night a species was detected to the last night it was detected (inclusive).

	W	P	Called		Did not call	
			N	Median (ºC)	N	Median (ºC)
Anaxyrus americanus charlesmithi	524	0.6478	35	19.3	28	19.1
Gastrophryne carolinensis	171	0.0016*	17	24.2	12	19.2
Hyla cinerea	200	< 0.0001*	18	24.6	12	19.3
Hyla versicolor	607	< 0.0001*	44	23.3	15	13.7
Lithobates areolatus areolatus	286	0.0299*	12	16.9	31	10.3
Lithobates catesbeianus	173	0.2816	14	21.1	31	23.3
Lithobates clamitans	320	0.5378	32	21.8	18	23.3
Pseudacris fouquettei	603	0.0309*	59	18.0	15	8.7

*statistically significant differences (α = 0.05)

are generally found in fields and grasslands and can be more than 1 m deep (Heemeyer et al. 2012; Williams et al. 2012a). Globally, *L. areolatus* is considered "Near Threatened" and is listed as endangered in several states (IUCN Red List 2012). In Oklahoma, it is a Species of Greatest Conservation Need, but little is known about its present distribution and abundance within the state (ODWC 2005). Therefore, in addition to collecting data on the general anuran community at our site, we focused our efforts especially on monitoring the calling patterns and ecology of *L. areolatus*. This focused effort included monitoring a nearby cattle pond in addition to the two lakes.

MATERIALS AND METHODS

Study site — Boehler Seeps and Sandhills Preserve is a 196-ha nature preserve located in Atoka County, Oklahoma. This site contains two beaver-formed lakes (Hassell Lake and Boehler Lake) which are fed from a series of seeps and small streams (Figure 1). Hassell Lake has a surface area of 2.05 ha, and Boehler Lake has a surface area of 2.82 ha. Both lakes are shallow (1.5 m at their deepest, and usually < 1 m), and large sections of the lakes consist of thick mats of floating soil and vegetation. These mats support numerous plants, including some shrubs and saplings. The lakes and the edges of the floating mats are choked with thick emergent vegetation (emergent vegetation is also scattered throughout the mats). The emergent plant community is dominated by Common Rush (*Juncus effusus*), Giant Cutgrass (*Zizaniopsis miliacea*), and Broadleaf Cattail (*Typha latifolia*). Both lakes also contain a few sections of comparatively open water, which frequently contains Yellow Water-lilies (*Nuphar lutea*) and several species of submerged aquatic vegetation.

There are a few small clearings adjacent to each lake that contain dense ground cover (no soil was showing) with vegetation up to 1.5 m tall, but no trees. Both the clearings beside Hassell Lake and the lake itself are heavily trafficked by cattle. With the exception of these small clearings, both of the lakes are surrounded by upland deciduous forest. There are no fields in the preserve, but there are several cattle fields on adjacent properties. Some of these fields contain cattle ponds that have little emergent vegetation.

Both lakes support a variety of predators, including multiple species of carnivorous fish such as Redfin Pickerel (*Esox americanus*), Black Bullhead Catfish (*Ameiurus melas*), Yellow Bullhead Catfish (*Ameiurus natalis*), Blue-gill (*Lepomis macrochirus*), Green Sunfish (*Lepomis cyanellus*), and Largemouth Bass (*Micropterus salmoides*)(J. Tucker, pers. comm.; McKnight, pers. obs.). Additionally, Western Cottonmouths (*Agkistrodon piscivorus leucostoma*), Western Mud Snakes (*Farancia abacura*), three species of watersnake (*Nerodia* spp.), and several species of omnivorous turtles inhabit the lakes (Patton and Wood 2009; McKnight et al. 2014; McKnight et al. 2015). Finally, various species of herons, egrets, and bitterns are usually present (McKnight, pers. obs.). Despite the thick vegetation and floating mats, no section of the lake appeared to be isolated from the predators, and fish, snakes, and turtles have been captured all throughout both lakes (McKnight pers. obs.).

Overall, the ecology of this site is unusual for Oklahoma, and the habitat more closely resembles sites in Gulf Coast states such as Louisiana than it does most other sites in Oklahoma (the exceptions being several sites in extreme SE Oklahoma)(Blair and Hubbell 1938). This site is also of interest because of the general loss of wetlands in southeastern Oklahoma. Although other natural wetlands still exist, many have been drained for agriculture, and the habitat has become fragmented. The ecology of this site is, therefore, both interesting and important not only because of the high species richness, but also because it is one of the few pristine, natural wetlands that remains in the area.

Anuran call survey — We used automated recording systems (ARS; Wildlife Acoustics, Concord, MA, USA) to document the presence of breeding amphibians (Peterson and Dorcas 1992, 1994). We placed two ARS (#5 and #6) at Hassell Lake, and three (#2–4) at Boehler Lake. They recorded daily for three minute intervals at 1900, 2000, 2100, 2200, 2300, and 0000 (Shirose et al. 1997; de Solla et al. 2005). They were deployed from 5 February–28 April 2012 (ARS #3 stopped working on 14 March and was not used again, ARS #4 stopped working on 31 March and was not used again, and on 24 March ARS #2 started only recording at 1900 and 2000 and continued doing so for the remainder of the study). For most nights we only analyzed three recordings from each ARS. From 5 February–24 March we analyzed the recordings at 1900, 2100, and 2300, and starting on 25 March we only analyzed the recordings at 2000, 2200, and 0000. The shift was made to compensate for increasing day length. These time ranges were expected to encompass the peak calling times for most species (Bridges and Dorcas 2000). For each recording that we

analyzed, we determined which species were calling, but we did not attempt to quantify the number of individuals that were calling. To increase the accuracy of the results, we listened to the recordings manually rather than using call recognition software (Waddle et al. 2009). In order to hear particular calls clearly, it was sometimes necessary to amplify a section of a recording and remove background noise using audio editing software (Audacity® 2.0.2).

We placed a temperature data logger (iButton 1922L, Maxim Integrated, Sunnyvale, CA, USA) at each lake. These loggers recorded the air temperature hourly throughout the study. We acquired daily rainfall data from a weather station located 17.5 km from the site (Oklahoma Mesonet).

For each species we used a Mann-Whitney U test (α = 0.05) to compare the air temperature (mean from both lakes) at 1900 on days when it was detected with the temperature at 1900 on days when it was not detected (a species was scored as "detected" if it was identified on any of the ARS units). To reduce seasonal biases, only the days from the first day that a species was detected to the last day that it was detected (inclusive) were used. We only analyzed species for which more than 10 days were available for each category. We used the exactRankTests package in R (version 3.0.2) to perform the tests.

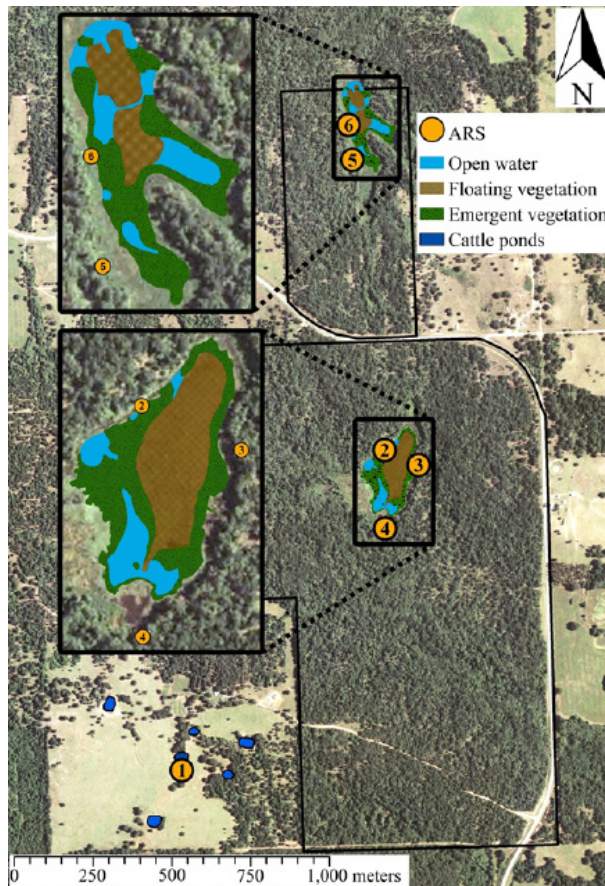*Southern Crawfish Frogs* — Because of the conservation

FIGURE 1. Boehler Seeps and Sandhills Preserve. Locations of the automated recording systems (ARS) and the approximate boundaries of the habitats of each lake are shown. Hassell Lake is in the north, Boehler Lake is in the middle, and the cattle ponds are in the south.

status of *L. a. areolatus*, we collected additional data for this species. First, in addition to the ARS units at the lakes, we placed an ARS (#1) and temperature data logger at a cattle pond on an adjacent property (because of overlapping calls from neighboring ponds, the presence or absence of species other than *L. a. areolatus* was not noted)(Figure 1). This ARS was set to record on the same schedule as the other ARS units. All six recordings from each of the ARS units were analyzed for the presence of *L. a. areolatus* on all nights that *L. a. areolatus* was detected on any of the ARS units.

We used a Mann-Whitney U test to compare the temperature at 1900 on nights when *L. a. areolatus* did and did not call exactly as we did for the other species. Additionally, we calculated the mean air temperature at each body of water using the temperatures recorded at the times that *L. a. areolatus* were actually calling instead of the temperature at 1900. When *L. a. areolatus* were heard simultaneously on two or more ARS units deployed at a single site, we scored it as one detection. Thus, the means are per lake not per ARS. Comparing these means statistically was not possible because of a lack of independence resulting from multiple recordings on the same night.

For the entire *L. a. areolatus* breeding season (defined as the first night that they were detected to the last night that they were detected), we recorded the number of days since the last rainfall event for each night that *L. a. areolatus* were detected (N = 20), for each night that they were not detected (N = 24), and for 20 randomly selected nights. Days when it rained were scored as 0 for their respective category. We used a Kruskal-Wallis test (α = 0.05) in R to compare the mean ranks of these three categories.

RESULTS

Anuran call survey — The ARS units documented 14 anuran species at each lake. The temperature data, timing, and duration of the breeding seasons are summarized in Figure 2. The results from the two lakes were generally consistent, but there were a few differences. For example, Cajun Chorus Frogs (*Pseudacris fouquettei*) began calling eight days earlier at Boehler Lake than at Hassell Lake, and they continued to call for 20 days after the *P. fouquettei* in Hassell Lake had stopped. Similarly, Eastern Narrow-mouthed Toads (*Gastrophryne carolinensis*) started calling in Boehler Lake 25 days before they were first detected in Hassell Lake. Conversely, Pickerel Frogs (*Lithobates palustris*) began calling nine days earlier in Hassell Lake than Boehler Lake, and they continued to call for 15 days after the *L. palustris* in Boehler Lake had stopped calling. Both *L. palustris* and Dwarf American Toads (*Anaxyrus americanus charlesmithi*) were detected more frequently in Hassell Lake than Boehler Lake.

There was a significant difference in the mean ranks of temperatures on nights when the following species did and did not call: *G. carolinensis*, Green Treefrogs (*Hyla cinerea*), Gray Treefrogs (*Hyla versicolor*), *L. a. areolatus*, and *P. fouquettei* (Table 1). The majority of calling for these species occurred on relatively warmer nights. There was not a significant effect of temperature for *A. a. charlesmithi*, American Bullfrogs (*Lithobates catesbeianus*), or Green Frogs (*Lithobates clamitans*). The remaining species could not be analyzed statistically because of small sample sizes.

Although limited habitat data can be gleaned from ARS units, different parts of the lakes appeared to be preferred by different species. This was most apparent for

L. palustris. In Hassell Lake, *L. palustris* was detected by ARS #6 on 45 nights and was only detected by ARS #5 on 12 nights. Similarly, in Boehler Lake it was detected by ARS #4 on 21 nights, by ARS #2 on three nights, and never by ARS #3. In both lakes, it was heard predominately in association with the larger expanses of open water and was less prevalent in areas that were dominated by either emergent or floating vegetation (Figure 1).

Southern Crawfish Frogs — Lithobates areolatus areolatus were recorded by all six ARS units (Figure 3). They were detected 14 times (nine nights) at Hassell Lake, 23 times (nine nights) at Boehler Lake, and 51 times (17 nights) at the nearby cattle pond. Based on the amplitude of the calls, some of the males detected at the cattle pond were probably calling from at least one neighboring pond (60 m away). In Boehler Lake, *L. a. areolatus* were detected most frequently on ARS #4, and least frequently on ARS #3. In Hassell Lake, they were detected on ARS #5 more often than on ARS #6. *L. a. areolatus* called most frequently at 2200 (Figure 4).

On average, *L. a. areolatus* called at Hassell Lake when it was 11.7 °C, at Boehler Lake when it was 16.9 °C, and at the cattle pond when it was 16.0 °C (Figure 5). The mean ranks of the temperatures on nights when they were detected were significantly higher than the mean ranks on nights when they were not detected (Table 1). There was not a significant difference ($\chi^2 = 0.9601$, df $= 2$, $P = 0.6187$) in the mean ranks of the number of days since the last rainfall event among nights when *L. a. areolatus* called, nights when they did not call, and 20 randomly selected nights (Figure 6).

DISCUSSION

Anuran call survey — Our results on the timing of the breeding seasons of different species are generally consistent with the results of other studies (Bragg 1940; Weir et al. 2005; Saenz et al. 2006). The cause of the temporal differences between the lakes that some species (most notably *P. fouquettei* and *G. carolinensis*) exhibited is unknown, but we speculate that they resulted from some subtle environmental difference between the two lakes. Five of the eight species that were examined statistically called on nights that were significantly warmer than the nights when they did not call (Table 1). The two *Hyla* species (*H. versicolor* and *H. cinerea*) showed the most obvious relationships with temperature, with their calling noticeably interrupted by cold nights (Figure 2). Most of the species for which we did not have sufficiently large datasets to analyze statistically appeared to be tolerant of a wide range of temperatures (Figure 2). Nevertheless, Southern Leopard Frogs (*Litho-*
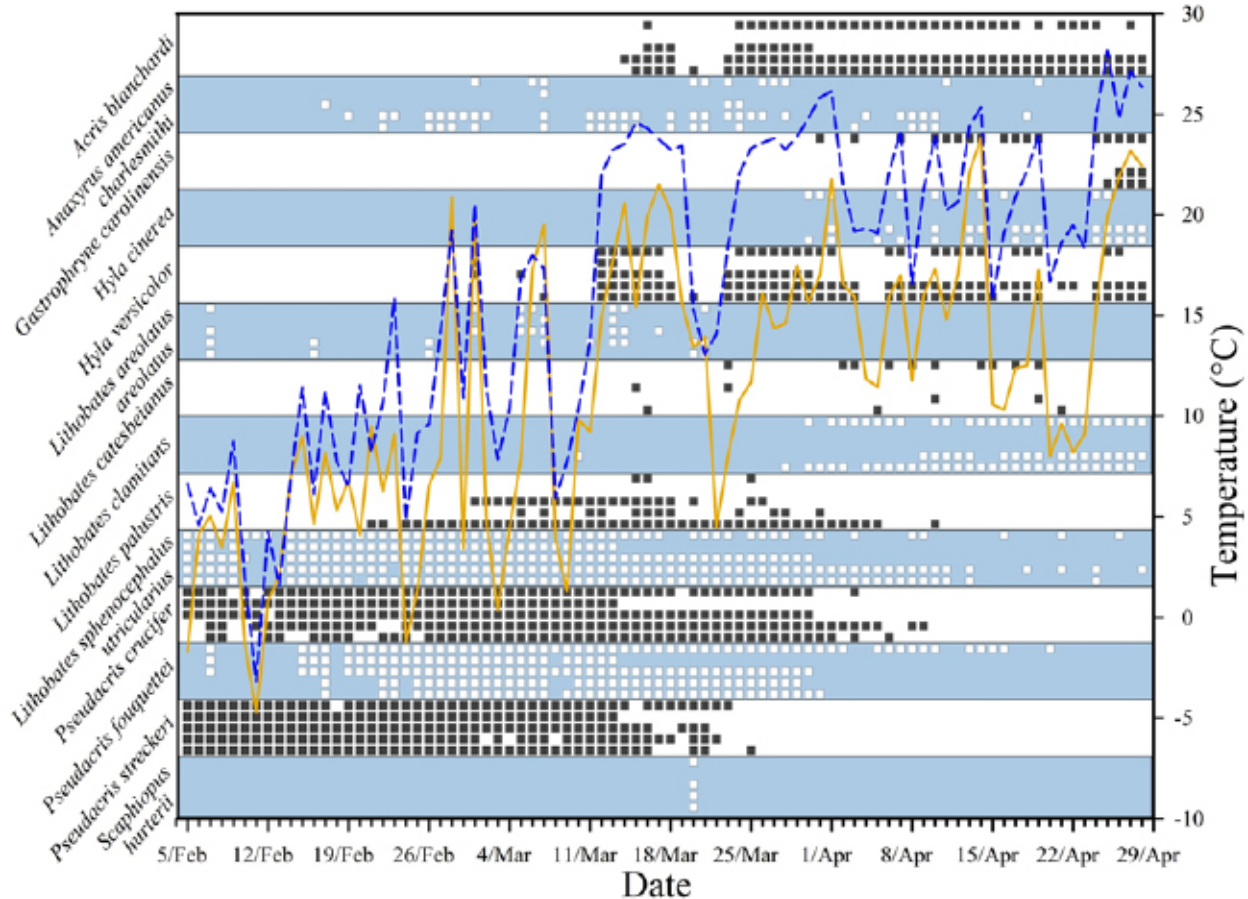

FIGURE 2. Results of the anuran call survey. Each alternating white and light-blue band contains data for a single species. Within each band, the topmost row is automated recording system (ARS) #2, the second row is ARS #3, the third row is ARS #4, the fourth row is ARS #5, and the fifth row is ARS #6. ARS #2–4 were positioned near Boehler Lake. ARS #5 and #6 were near Hassell Lake. Squares indicate nights when a species was detected on any of the three recordings taken by a single ARS. The dashed blue line is the mean air temperature for both lakes at 1900, and the solid yellow line is the mean air temperature for both lakes at 0000. Data collected from the additional recordings that were analyzed when listening for Southern Crawfish Frogs (*Lithobates areolatus areolatus*) are not included.

bates sphenocephalus utricularius) still reduced calling at temperatures < 4 °C, and Blanchard's Cricket Frogs (*Acris blanchardi*) stopped calling at temperatures < 16 °C. Hurter's Spadefoot Toads (*Scaphiopus hurterii*) only called on one night in each lake and, as is typical of *S. hurterii*, that night was preceded by rainfall (9.7 cm) within the previous 48 hours (Bragg 1944).

The calling pattern of *L. catesbeianus* is interesting. Most species either called almost continually regardless of temperature (with a few exceptions on particularly cold nights), or called continually on warm nights, but ceased calling on cold nights. In contrast, *L. catesbeianus* called sporadically, with no apparent association between nights that it called and temperature (Table 1; Figure 2). This was likely because the breeding season of *L. catesbeianus* is typically later in the year than most of the other species at our site, and many males do not establish territories until late April/early May (Willis et al. 1956; Ryan 1980).

One unusual result of our study was that several species that usually breed in ephemeral bodies of water were heard calling at Hassell Lake and Boehler Lake, both of which retain water year-round and support multiple carnivorous fish species. *Scaphiopus hurterii* is one of the most striking examples. While several species of spadefoots have occasionally been reported breeding in permanent bodies of water, to our knowledge this is the first documented case of *S. hurterii* doing so (Bragg 1944, 1967; Morey and Reznick 2004; Adams et al. 2011).

Southern Crawfish Frogs — Our study presents a number of novel results concerning *L. a. areolatus*. First, this study has added the following species to the list of anurans that *L. areolatus* will breed syntopically with: *H. cinerea*, *L. catesbeianus*, *L. palustris*, *P. fouquettei*, Strecker's Chorus Frogs (*Pseudacris streckeri*), and *S. hurterii* (see Parris and Redmer 2005). It is interesting that *L. a. areolatus* chose to breed in bodies of water with so many other anurans. Although they will inhabit sites with high anuran diversities (Lannoo et al. 2009), breeding in bodies of water with such a large number of anuran species has not been previously reported, and *L. areolatus* tadpoles are poor competitors that exhibit decreased physical fitness in high densities (Parris and Semlitsch 1998; Williams et al. 2012b).

Also, to our knowledge this is the first report of *L. areolatus* breeding in natural, permanent, fish-filled bodies of water (Smith 1934; Bragg 1953; Busby and Brecheisen 1997). Palis (2009) reported them breeding in a pond that was stocked with predatory fish, but in that case the pond was drained and restocked annually, and the size of the fish at the time when *L. areolatus* tadpoles were developing prevented the fish from feeding on them. Engbrecht et al. (2013) also noted a *L. areolatus* breeding pool that is now stocked with fish, but whether or not this population will survive the presence of the fish is currently unknown. In interviews, longtime residents living near Boehler Seeps and Sandhills Preserve stated that the beaver dams have been present at least since the 1960s,
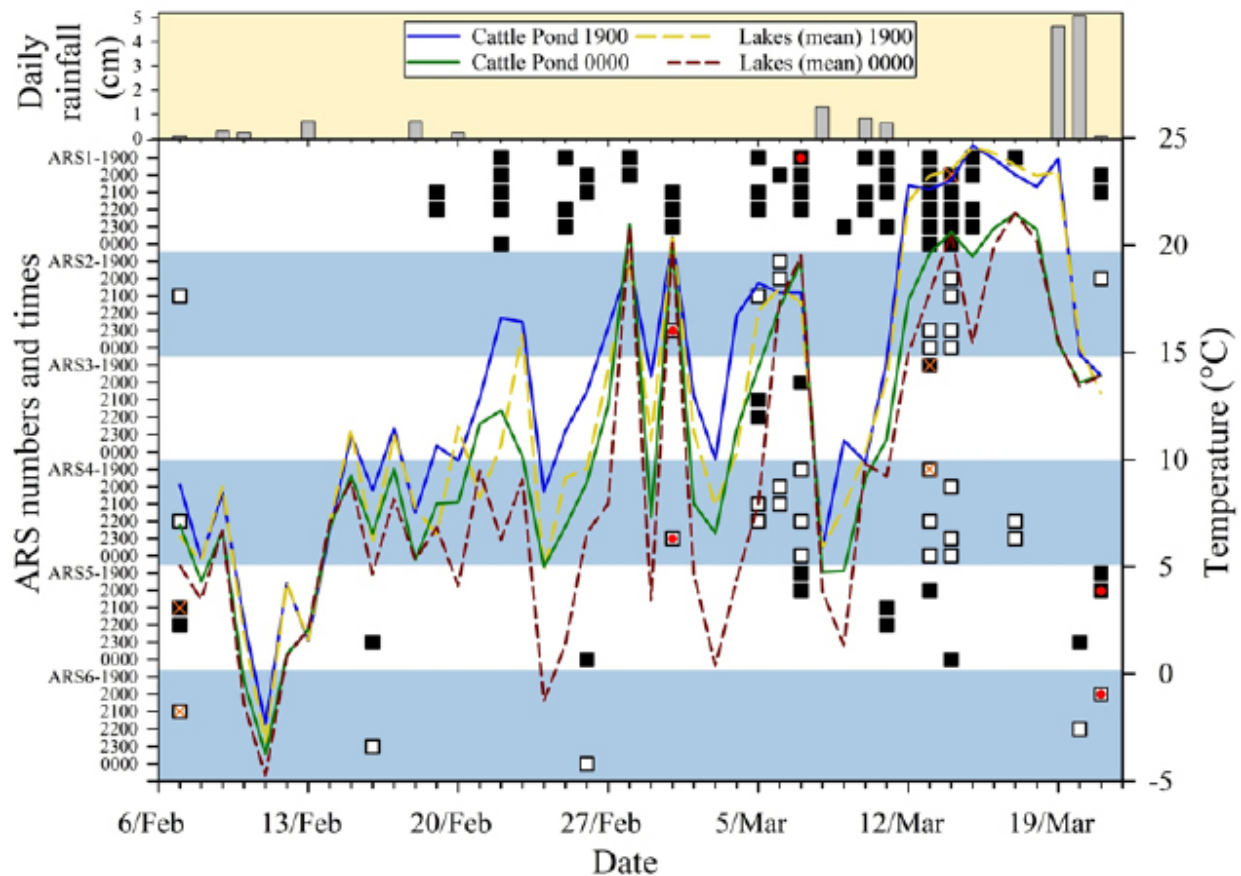

FIGURE 3. Results of the call survey for Southern Crawfish Frogs (*Lithobates areolatus areolatus*). Temperature data were averaged for Boehler Lake and Hassell Lake (there was little variation between them). There was no rainfall in the days preceding the interval displayed. Red dots indicate the recording with the greatest activity for that body of water, and orange × symbols identify the recordings with the second greatest activity for that body of water.

and the area generally retained some water even before the dams were built. One man reported that his father hunted ducks at the site that is now Boehler Lake at least as far back as the 1930s. Therefore, it seems likely that fish have been present at these sites for many years.

In addition to the presence of predators and anuran competitors, Boehler and Hassell lakes are also somewhat unusual habitat for *L. a. areolatus* because of the extensive hardwood forest habitat surrounding them. *Lithobates areolatus* have been reported to utilize wetlands in wooded habitat (Bragg 1953), but they more typically breed in pools surrounded by grasslands, and they generally use primary burrows that are in open habitat (Busby and Brecheisen 1997; Heemeyer et al. 2012; Heemeyer and Lannoo 2012; Williams et al. 2012a,c). The burrow locations of this population were not determined, and individuals might be migrating long distances to fields on neighboring properties. Alternatively, there may be adequate burrows present in the small clearings beside each lake (Heemeyer and Lannoo 2012; Williams et al. 2012a).

Although we were not present at the study site to locate *L. a. areolatus* and *S. hurterii* during their mating season, a preponderance of evidence supports our conclusion that *L. a. areolatus* and *S. hurterii* were calling from the lakes themselves and not from nearby ephemeral pools. First, Patton and Wood (2009) reported hearing *L. a. areolatus* calling from these lakes during manual calling surveys. Second, the closest ephemeral pools were 0.4–0.5 km from the ARS units (there were several seeps that were closer to the lakes, but all of these also contained predatory fish, so the presence of *L. a. areolatus* or *S. hurterii* in them would have been equally atypical). Under good acoustic conditions, *L. areolatus* calls can be detected up to 1 km away. However, at Boehler Seeps and Sandhills Preserve, anuran calls did not carry long distances because of the forest and dense understory vegetation, and it was generally not possible to distinguish the calls
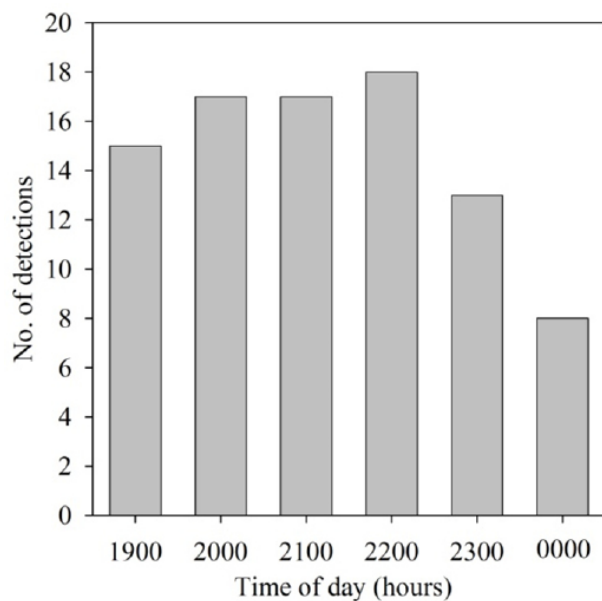

FIGURE 4. The number of recordings that detected Southern Crawfish Frogs (*Lithobates areolatus areolatus*) at each of the sampled time periods. Data from all automated recording systems were combined, but if *L. a. areolatus* was heard on multiple simultaneous recordings at a given body of water they were scored as a single detection.

of other boisterous species at 0.5 km (McKnight, pers. obs.). Also, during the recordings with *L. a. areolatus* or *S. hurterii*, there was nearly always a strong chorus of other species that would have obscured any *L. a. areolatus* or *S. hurterii* calls that did not originate from a proximate location. Further, Engbrecht (2010) reported that *L. areolatus* calls are detected more readily when the ARS is uphill from the breeding pool, but all of our ARS units were downhill from the ephemeral pools. Additionally, most of the ARS units were mounted to large trees such that the trunks acted as soundboards, greatly dampening any sounds except for those coming from the direction of the lakes. Therefore, it appears that these anurans were, in fact, calling from the lakes themselves.

An additional explanation for the unusual presence of *L. a. areolatus* and *S. hurterii* in these lakes is that the lakes were simply acting as satellite sites, and no actual breeding was taking place. However, there are several reasons why this explanation is not likely. First, we captured recent metamorphs of both *S. hurterii* and *L. a. areolatus* in drift fences alongside Boehler Lake (McKnight et al. 2013). Also, in 2013, a large chorus of *L. a. areolatus* (too many to accurately count calls per minute) was observed at a permanent pond 14 km from the preserve that we also observed to have predatory fish. The extraordinary number of individuals at this pond, and the presence of both males and gravid females make it highly likely that breeding was occurring, despite the fact that predatory fish were seen in the same parts of the pond where the frogs were calling (McKnight, pers. obs.). This observation strongly supports the conclusion that *L. a. areolatus* will sometimes breed in the presence of predatory fish. Second, although male *L. a. areolatus* will call from satellite pools, these pools are generally proximate to primary breeding pools, and they only contain one or two males (McKnight, pers. obs.). However, neither Boehler Lake nor Hassell Lake were proximate to breeding pools (the closest known *L. a. areolatus* breeding pools were 1 km away), and both lakes contained multiple males that called throughout the spring of 2012. Therefore, given the presence of males in 2008 (Patton and Wood 2009), the presence of multiple males throughout the breeding season in 2012, the distance to the nearest breeding pool, the presence of recent metamorphs in drift fences, and the confirmation of *L. a. areolatus* breeding syntopically with fish at a nearby pond, we conclude that the most reasonable explanation of these observations is that breeding was taking place despite the presence of predatory fish.

In additional to the unusual breeding habitat, *Lithobates areolatus areolatus* in our study exhibited a tendency to chorus at temperatures that were notably lower than those previously reported. Busby and Brecheisen (1997) and Engbrecht (2010) both reported that *L. areolatus* typically called when temperatures were ≥ 13 °C, and Busby and Brecheisen (1997) noted that no calls were heard below 8 °C. In contrast, Williams et al. (2013) found that detection probabilities were highest when temperatures were ≥ 9 °C. In our study, 15 / 88 detections of *L. a. areolatus* occurred at temperatures < 9 °C, and 31 detections occurred at temperatures < 13 °C (Figure 5). While many of these occurrences consisted of only one or two frogs, there were some noteworthy exceptions. For example, the second largest chorus at Hassell Lake was recorded at the coldest temperature at which any *L. a. areolatus* were documented (4.1 °C). Also, the strongest chorus at Hassell Lake occurred at 9.6 °C, which is well below the optimal temperature reported

by Busby and Brecheisen (1997) and Engbrecht (2010) (Figure 3).

  Several studies have reported a strong association between rainfall and *L. areolatus* breeding activity (Bragg 1953; McCarley 1970; Busby and Brecheisen 1997), but Engbrecht (2010) found that rainfall reduced detection probabilities. Williams et al. (2012b) suggested that rainfall has a greater positive effect on frogs migrating to the pools than it does on calling activity, and it is rain in the previous 24 hours that is important. In contrast,

Williams et al. (2013) found that there was a negative relationship between detection probabilities and rainfall in the previous 24 hours. In our study, there was no apparent association between rainfall and nights on which *L. a. areolatus* called. Forty percent of the nights during which they called were within 48 hours of a rainfall event, but we interpret this to be an artifact of having many nights of rain rather than a behavioral trait of the frogs (Figure 6). The reasons for these discrepancies among studies are not entirely clear. One possibility is that the
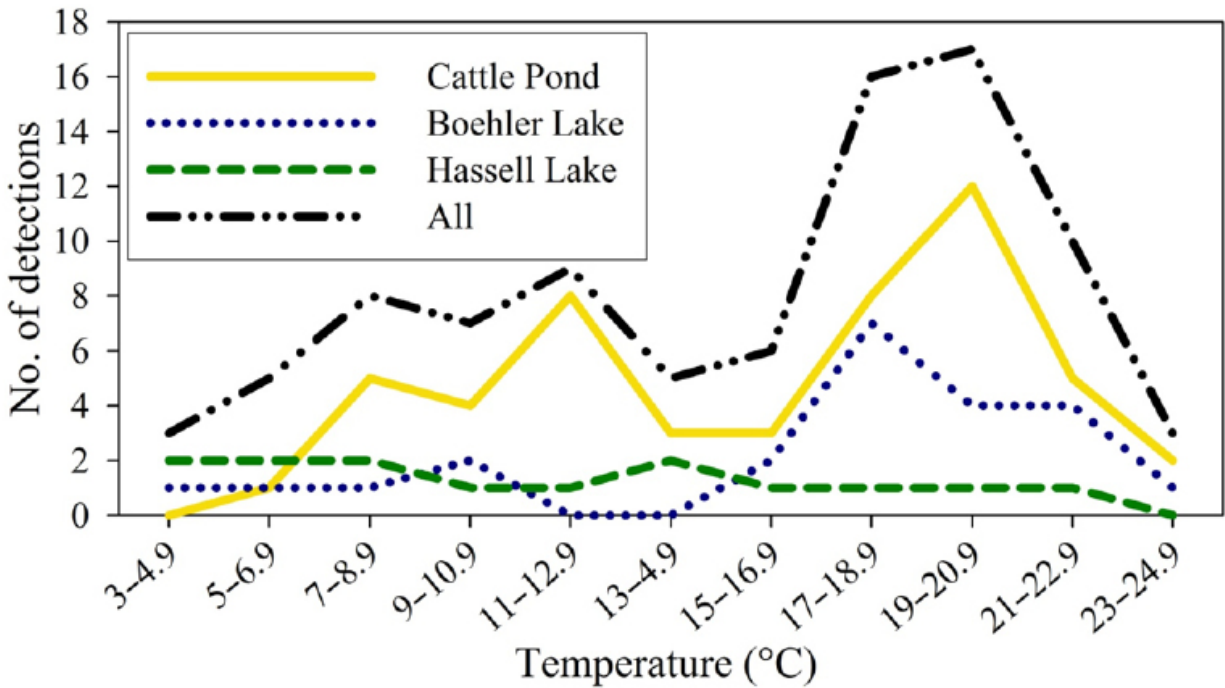

FIGURE 5. The number of detections of Southern Crawfish Frogs (*Lithobates areolatus areolatus*) at each temperature. *Lithobates a. areolatus* that were heard on multiple simultaneous recordings at a given body of water were scored as a single detection.
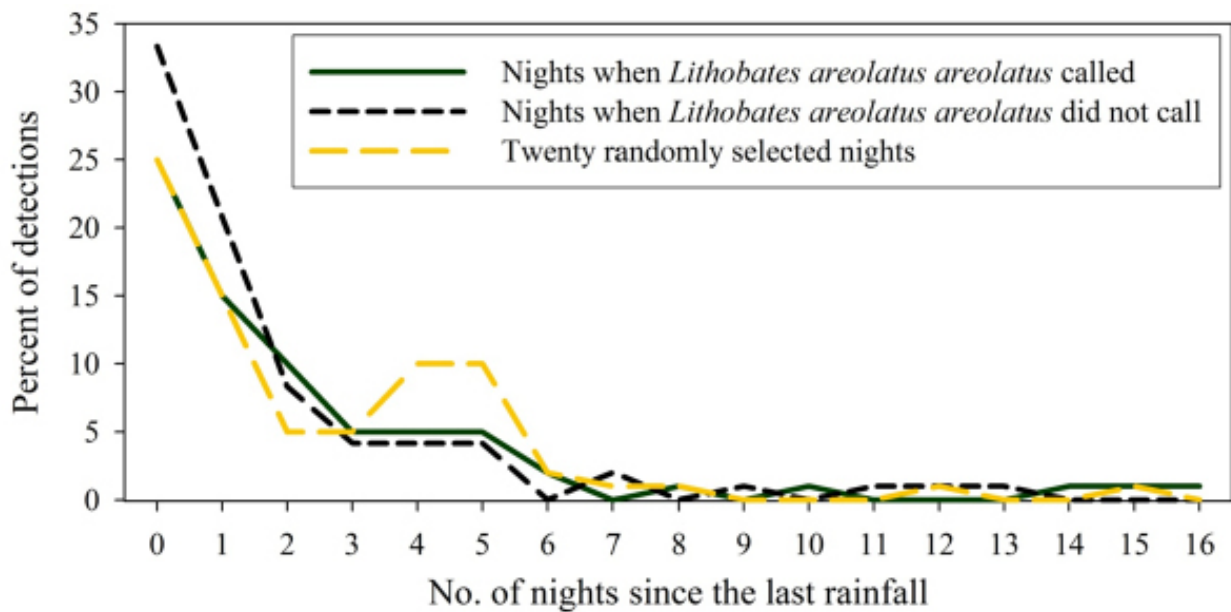

FIGURE 6. The number of days since the last rainfall event for nights when Southern Crawfish Frogs (*Lithobates areolatus areolatus*) called, nights when they did not call, and 20 randomly selected nights. Results are displayed as percentages of all nights in a given category.

first warm rains of the year trigger the initial migration to breeding pools, and as Williams et al. (2013) suggested, subsequent rainfall events result in the immigration of new males that increase detection probabilities in small populations (such as those reported by Williams et al. [2012b]) but have little effect on the detection probabilities in larger populations. Thus in many populations, after the initial rainfall event calling will occur continuously irrespective of additional rainfall unless conditions become unfavorable.

The times of day at which *L. a. areolatus* called were consistent with results from Northern Crawfish Frogs (*L. a. circulosus*) in Indiana where calling intensity increased from 1900–2045 and decreased thereafter (Williams et al. 2013). Although we recorded the number of detections, not calling intensity, our results show a similar pattern with the number of detections increasing from 1900–2200 then decreasing after 2200 (Figure 4). Therefore, the interval of 1900–2300 suggested by Williams et al. (2013) should be optimal for surveying for *L. a. areolatus* in Oklahoma.

In both lakes, *L. a. areolatus* seemed to associate with some habitats more than others. In Hassell Lake we detected more calling in the section of the lake characterized by extensive emergent vegetation, little open water, and little floating vegetation (ARS #5)(Figs. 1, 3). In Boehler Lake, on the other hand, they were predominantly heard in the area characterized by extensive open water with smaller amounts of emergent and floating vegetation (ARS #4), but they were also frequently detected by ARS #2, which recorded calls in an area with a lot of emergent vegetation, little open water, and some floating vegetation. Based on the relative strengths of the calls, it is likely that they were scattered throughout the area of emergent vegetation that stretched between ARS #2 and #4. In both lakes, it appears that they avoided the areas with thick mats of floating vegetation.

The fact that males were frequently heard on one ARS but were absent from simultaneous recordings from other ARS units has important implications for survey efforts. Because male *L. a. areolatus* have very loud calls, one ARS at each lake could, in concept, have detected all of the *L. a. areolatus* that called. In practice however, *L. a. areolatus* calls were often masked by loud choruses of other anuran species, wind, and other background noises. Therefore we recommend that surveys at large bodies of water use several ARS units to maximize detection.

Southern Crawfish Frogs: conservation implications — The result that *L. a. areolatus* appears to be breeding in bodies of water that contain predatory fish has several interesting conservation implications. On the one hand, this expands the range of habitats that this species will utilize, and future survey efforts should not overlook these wetlands. On the other hand, these ponds are likely not ideal for this species, and our results should not diminish the importance of conserving fishless breeding pools. It would be useful for future researchers to determine both how widespread the use of fish-filled ponds is, and what level of recruitment occurs at these ponds. The presence of recent metamorphs at Boehler Seeps and Sandhills Preserve supports the conclusion that some recruitment does take place, but the amount of recruitment may be very low, and *L. a. areolatus* may only be using these lakes because so few natural wetlands remain. Man-made cattle ponds currently dominate the landscape around the preserve, and nearly all of these

contain predatory fish (McKnight pers. obs.). Therefore, this may be a regional phenomenon that has resulted from a lack of ideal breeding sites. Finally, it is possible that paucity of fishless wetlands in this part of Oklahoma has driven the evolution of anti-predatory mechanisms that allow *L. a. areolatus* to survive the presence of predatory fish and maintain high recruitment rates. The current data do not allow us to distinguish among these possibilities, but future studies should examine them so that we can maximize the efficiency of our conservation efforts.

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