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BREEDING FREQUENCY AND SUCCESS OF EASTERN SPADEFOOTS, *SCAPHIOPUS HOLBROOKII*, IN SOUTHERN ILLINOIS

John G. Palis: Palis Environmental Consulting, P.O. Box 387, Jonesboro, IL 62952

ABSTRACT. The Eastern Spadefoot, *Scaphiopus holbrookii*, an anuran that ranges widely across eastern North America, exhibits latitudinal variation in breeding activity. In the southern United States, Eastern Spadefoots breed any time of year, whereas further north breeding activity is restricted to the warmer months. In the Midwest, Eastern Spadefoots are described as breeding any time meteorological conditions are favorable between March and September. I examined this commonly held belief at a southern Illinois sinkhole from 1996 to 2012. Eastern Spadefoots bred (oviposited) 26 times, up to three times per year, during 12 of 17 years (70.5%). Breeding occurred from March through July, but most frequently (69.2%) during April and May. Most (92.3%) breeding events occurred during months of above-average precipitation. Recruitment of juveniles followed seven breeding events (in April and May only) in 5 of 17 years and was dependent upon rainfall subsequent to breeding activity. Observations of breeding activity suggest that Eastern Spadefoots in the Midwest breed most often in spring, coincident with favorable meteorological conditions, and that breeding success may be reliant on rainfall subsequent to breeding.

Keywords: Breeding frequency, breeding season, breeding success, Eastern Spadefoot, Illinois, *Scaphiopus holbrookii*

INTRODUCTION

Temperate-zone anuran breeding activity is typically cyclic, occurring annually in late-winter/spring or summer, depending upon the species (Duellman and Trueb 1986; Stebbins and Cohen 1995). Seasonal variation in breeding activity of temperate-zone anurans is strongly influenced by latitude. For example, the breeding season of wide-ranging anurans is typically abbreviated at higher latitudes and prolonged at lower latitudes (Bury and Whelan 1984; Ritke et al. 1990; Redmer and Brandon 2003; Green 2005; Mitchell and Lannoo 2005). The latitudinal variation in length of breeding season may be the result of species-specific responses to temperature and rainfall thresholds.

Eastern Spadefoots (*Scaphiopus holbrookii*) range widely across eastern North America (approx. 26–43° latitude) and exhibit latitudinal variation in breeding activity. They are explosive breeders (Wells 1977) and breeding activity is generally more closely correlated with heavy rainfall than with season (Palis 2005). At the southern end of the range (Florida), Eastern Spadefoots can breed anytime during the year when suitable meteorological conditions occur (Hansen 1958; Greenburg and Tanner 2005). In the northern portion of the range (New England), however, breeding activity is restricted to rainy periods occurring only during warmer months (Hansen 1958; Klemens 1993). In southern Illinois, which is intermediate in latitude between the southern and northern range limits of Eastern Spadefoots, the exogenous cues of heavy rains and warm temperatures that stimulate Eastern Spadefoot breeding activity (Hansen 1958) may occur year-round, and Eastern Spadefoots become surface-active during warm, wet periods, even in winter (pers. obs.). Nonetheless, Eastern Spadefoots are only known to breed between March and September in Illinois (Smith 1961; Phillips et al. 1999), which suggests a temperature threshold below which Eastern Spadefoots will not breed (Bragg 1945; Gosner and Black 1955; Hansen 1958).

The proximal cue that stimulates Eastern Spadefoot emergence from subterranean burrows and movement to breeding sites is thought to be soil moisture. Hansen (1958) suggested that physiological uptake of water activates gametogenesis in Eastern Spadefoots and that soil saturation resulting from heavy rainfall stimulates reproductive behavior. In southern Illinois, soil moisture and rainfall are higher in

E-mail: jpalis@yahoo.com, 618-833-3227

spring than at any other time of year (Hollinger and Isard 1994; NOAA 2002). Thus, combined with rising air and soil temperatures, ample rainfall and soil moisture in spring may provide a greater likelihood of stimulating Eastern Spadefoot breeding activity than at any other time of year. I examined this assumption at a breeding site in southern Illinois. Specifically, my goals were to (1) determine whether Eastern Spadefoots in southern Illinois breed any time suitable meteorological conditions occur from March through September and (2) determine the annual frequency of breeding activity and the frequency of occurrence of successful juvenile recruitment.

METHODS

Study site.—I studied the breeding activity of Eastern Spadefoots at a naturally-formed sinkhole in Union County, Illinois (37°27″N, 89°16″W) annually from March through September 1996–2012. The sinkhole is dry except following heavy rains or extended periods of rain. Ponding of water is possible because the bottom of the sinkhole is overlain with soil and does not have a direct connection to subterranean karst features. During this study, maximum surface area of water in the sinkhole was 0.16 ha, maximum depth was 2 m, and maximum hydroperiod was 53 successive days. The sinkhole is in a residential area bordered by mowed lawn to the east, north, and west, and a 0.15 ha woodland to the south. Predominant tree species of the woodland include loblolly pine (*Pinus taeda*), tuliptree (*Liriodendron tulipifera*), sweetgum (*Liquidambar styraciflua*), black walnut (*Juglans nigra*), white oak (*Quercus alba*), northern red oak (*Quercus rubra*), and hackberry (*Celtis occidentalis*). The central portion of the sinkhole is enclosed by a wood-rail fence. At the initiation of this study, the slopes of the sinkhole were mowed to the perimeter of the fence. Beginning in June 1996, the outside perimeter of the fence was no longer mowed, resulting in a flush of weedy herbaceous growth that was followed by encroachment of woody vegetation dominated by boxelder (*Acer negundo*). The sinkhole is surrounded by well-drained and friable Alford silt loam (USDA 1979).

Data collection.—During or following heavy or extended rain events occurring from March through September each year, I examined the sinkhole for evidence of Eastern Spadefoot breeding activity. Visitation varied considerably, corresponding to annual differences in rainfall. I visited the sinkhole at night to listen and look for the presence of adults and/or examined the sinkhole during the day for the presence of eggs or tadpoles. I recorded air and water temperatures (to the nearest 0.5°C) at the sinkhole using a pocket thermometer when adults were present, and recorded rainfall daily (to the nearest 0.5 mm) throughout the year in a rain gauge. Groundwater and soil moisture, which could affect hydrology, were not measured. Following breeding events, I returned to the sinkhole every 1–3 d to monitor tadpole development through metamorphosis or until tadpole mortality resulted from premature drying of the pond. I considered breeding events successful when they resulted in metamorphosis of tadpoles.

Statistical analyses.—I analyzed data using Statistix 8.0 software (Analytical Software, Tallahassee, Florida, USA). Prior to analyses, I examined data for assumptions of normality using Shapiro-Wilk Tests. I made pairwise comparisons of rainfall and hydroperiod between successful and unsuccessful breeding events using t-tests. I present data as mean ± 1 SE and consider $P < 0.05$ statistically significant.

RESULTS

Eastern Spadefoots bred (oviposited) 26 times, 1–3 times per year, during 12 of 17 years (70.6%; Table 1). There was no Eastern Spadefoot breeding activity (calling or calling and oviposition) in 5 of the 17 years (Table 1). Of these 5 years, rainfall was below average in 2004, 2005, and 2012; below average during the first half of 2001; and near-normal in 2000.

Breeding activity occurred from 11 March through 27 August, whereas oviposition was more limited, occurring from 11 March through 14 July. Egg-laying occurred most frequently (69.2%) during April and May. Most breeding events ($N = 24$; 92.3%) occurred during months when precipitation was above the 17-year average (Fig. 1). The two exceptions included a single breeding event each in April 1997 and May 2007 that occurred during below-average monthly rainfall. Above-average monthly precipitation occurred 33 times in spring (March through June), eliciting breeding by Eastern Spadefoots 23 times (69.7%); above-average precipitation occurred 14 times in

Table 1.—Monthly summary of Eastern Spadefoot breeding activity at a Jonesboro, Illinois sinkhole, March–August 1996–2012. B = breeding (oviposition by females following calling by males), C = calling males only, no oviposition, M = newly metamorphed juveniles produced following breeding. The number preceding each letter indicates number of events.

	Mar	Apr	May	Jun	Jul	Aug
1996		2M				
1997		1B	2M			
1998		2B		1B		
1999		1B				
2000						
2001						
2002		1B	1M			
2003			2B	1B		
2004						
2005						
2006	1B				1B	1C
2007			1B	1B		
2008	2B		1M			
2009			1B	1B		
2010		1B	1B			
2011		1M				
2012						

summer (July and August), stimulating breeding activity twice (14.3%) in only one year (2006). Summer 2006 breeding activity included oviposition by females on 14 July but was limited to vocalization by males without response by females (i.e., no females present) on 27 August.

Rainfall totals 24 hours prior to breeding and one week prior to breeding (N = 25 each) averaged 56.5 ± 8.5 mm (range = 3.0–209.0 mm) and 97.0 ± 9.5 mm (range = 3.0–228.0 mm), respectively. Air and water temperatures (N = 22 each) averaged 19.0 ± 1.0°C (range = 13.0–26.0°C) and 17.0 ± 0.5°C (range = 12.0–24.0°C), respectively, during breeding events.

Recruitment of juveniles followed seven breeding events (26.9%), twice in 1996 and 1997, and once each in 2002, 2008, and 2011 (Table 1). Although the sinkhole held water longer (mean = 27 ± 2.5 d, range = 18–39 d) when breeding was successful than when it was not (mean = 19 ± 3 d, range = 4–53 d) the difference was not statistically significant (t = 1.48, df = 24, P = 0.1512). The lack of statistical difference is due to inclusion of the three March breeding events that, despite relatively long hydroperiods of 44, 45, and 53 days, were unsuccessful (i.e., no juvenile recruitment). When limiting the comparison of hydroperiod between successful and unsuccessful (mean = 14 ± 1 d, range = 4–21 d) breeding events to warmer months (i.e., April through July), the difference between the two is highly significant (t = 5.26, df = 21. $P < 0.0001$). The length of hydroperiod was influenced by amount of rainfall subsequent to breeding. There was no difference in the amount of rainfall received 24hours prior or one week prior to successful or unsuccessful breeding events (Table 2). However, rainfall totals fol-

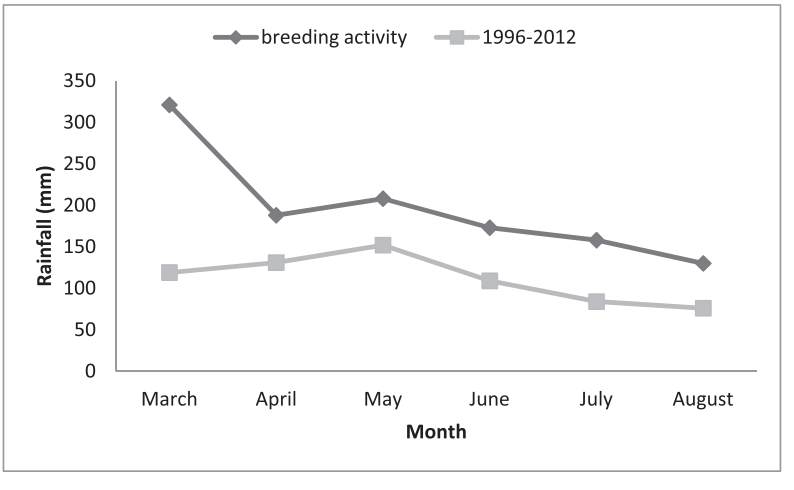

Figure 1.—Monthly mean rainfall and monthly mean rainfall that resulted in breeding activity by Eastern Spadefoots at a Jonesboro, Illinois sinkhole pond, March–August 1996–2012.

Table 2.—Comparison of rainfall (mm) received 24-h before, one week before, and after successful and unsuccessful Eastern Spadefoot breeding activity at a Jonesboro, Illinois sinkhole, March–August 1996–2012. Post-breeding rainfall was recorded until tadpole metamorphosis or until the pond dried and tadpoles died. Data are expressed as mean ± SE and range.

	24 h before breeding	1 week before breeding	Post breeding
Successful breeding	66.5 ± 14.5 (4.0–115.0)	110.0 ± 21.0 (58.0–228.0	199.0 ± 56.0 (28.0–481.0
Unsuccessful breeding	53.0 ± 10.5 (3.0–209.5)	92.0 ± 10.5 (3.0–222.5)	64.5 ± 18.0 (0–290.0)
t-test result	$t = 0.71$, P = 0.4867	$t = 0.86$, P = 0.3972	$t = 3.00$, P = 0.0061

lowing successful breeding events (recorded until metamorphosis) were significantly greater than rainfall totals following unsuccessful breeding events (recorded until the pond dried and tadpoles died [Table 2]).

DISCUSSION

Eastern Spadefoot breeding activity in the Midwestern United States is described as episodic and closely correlated with heavy precipitation "any time during spring or summer" (Minton 2001) or "any time between March and September" (Smith 1961). The results of my study generally agree with these descriptions: Eastern Spadefoot breeding activity occurred during relatively warm weather (air temperatures ≥ 13°C) during spring and summer and after rainfall sufficiently heavy or of sufficient duration to cause ponding of water in the sinkhole. However, my observations suggest that at the latitude of southern Illinois, Eastern Spadefoots have a definable period when breeding is most likely to occur: spring. All but one breeding event (96.1%) during the 17-year period occurred between 11 March and 14 June. These dates correlate well with calendar spring (20 March–20 June) and meteorological spring (1 March–30 May).

A spring-breeding tendency also occurs in other states at or near the latitude of southern Illinois. In Kentucky, 83.8% of observed Eastern Spadefoot choruses occurred from March through June (J.R. MacGregor, pers. comm.), and in a summary of five mid-latitude states (Indiana, Kentucky, Ohio, Virginia, and West Virginia), 81.1% of observed Eastern Spadefoot breeding choruses were recorded from March through June (Hansen 1958). In addition, 80.0% of published observations of Eastern Spadefoot breeding activity in Indiana made after Hansen's (1958) summary occurred from March through June (Rubin 1968; Minton 2001; Geboy et al. 2008; Engbrecht et al. 2009; Klueh and Mirtl 2011).

Spring is a time of rising air temperatures and plentiful rainfall. In southern Illinois, precipitation and soil moisture is higher in spring than at any other time of year, and rain storms are more frequent in spring than any other season (Hollinger and Isard 1994; Huff and Angel 1989; NOAA 2002). These precipitation patterns correlate well with the Eastern Spadefoot requirement of enough moisture to fill breeding wetlands and stimulate breeding activity. Although Eastern Spadefoots may be capable of breeding "any time" from March through September in the Midwest, they appear to be more likely to breed in spring than summer.

Breeding at the southern Illinois sinkhole was successful (i.e., resulted in juvenile recruitment) seven times in 5 of 17 years. Years of successful reproduction were separated by up to five years without successful reproduction and without breeding (Table 1). Breeding success was strongly influenced by amount of precipitation following breeding and month of breeding. Breeding was successful only if enough rainfall followed the breeding event to retain water in the sinkhole long enough for successful metamorphosis of tadpoles. This requirement was best met from March through June. There was risk, however, in breeding too early in the season. For example, despite receiving enough precipitation after three March breeding events to generate three of the longest hydroperiods observed during the study (44, 45 and 53 d), tadpoles were unable to metamorphose before the pond dried. This is likely due to low water temperature, which slows larval growth and development (Richmond 1947; Gosner and Black 1955), prolonging the larval period. Autumn breeding could risk a similar fate.

Abundant rainfall subsequent to breeding is critical to providing the hydroperiod needed to ensure Eastern Spadefoot breeding success. Eastern Spadefoots bred most frequently

(69.5%) in April and May, and tadpole metamorphosis occurred only after April and May breeding events. May is, on average, the wettest month of the year in southern Illinois (NOAA 2002) and was the wettest month, on average, during my 17-year study (Fig 1). Thus, at the latitude of southern Illinois, there appears to be a strong correlation between Eastern Spadefoot breeding activity and breeding success and the wettest time of the year.

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