Journal of Herpetology, Vol. 55, No. 2, 137–150, 2021

Confirmation Bias Perpetuates Century-Old Ecological Misconception: Evidence Against 'Secretive' Behavior of Eastern Spadefoots

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Abstract.—Despite a 1944 publication questioning the misconception that Eastern Spadefoots (*Scaphiopus holbrookii*) and other Scaphiopodidae are 'secretive' outside of rain-induced migration and breeding aggregations, confirmation bias has perpetuated this fallacy. As a result, *S. holbrookii* is one of the least studied frogs in the United States. Amassing a large postmetamorphic dataset, we examined the misconception that *S. holbrookii* are secretive outside of breeding aggregates or optimal environmental conditions. Using eyeshine spotlighting, we conducted transect, mark–recapture, and haphazard spotlighting surveys in Virginia and Rhode Island forests. Although no breeding events or migration occurred during this study, we detected thousands of postmetamorphic *S. holbrookii* in Virginia and dozens in Rhode Island, the majority of which were subadults—a demographic category severely overlooked in the literature. These results are in direct contradiction with historical surveys of our sites. Spotlighting was an efficient method of detecting *S. holbrookii* eyeshine in forests, which were easily differentiated from arthropod eyeshine. Minimal effort was needed to detect the presence of *S. holbrookii* in Virginia and Rhode Island, even though both states have different climates and *S. holbrookii* densities. We also discovered a previously undetected population in Rhode Island. *Scaphiopus holbrookii* of all postmetamorphic size classes emerged regularly from burrows, even with no precipitation. We discuss how confirmation bias and lack of appropriate field methods for nonbreeding life history stages has fueled the misconception that *S. holbrookii* are difficult to find outside of optimal weather conditions, which has hindered progress studying the ecology and conservation of this species.

Even when presented with evidence to the contrary, scientific misconceptions are perpetuated for many cases. Examples such as the link between vaccines and autism are almost unanimously panned by experts (Flaherty, 2011), yet science is permeated with persistent misconceptions despite contradictory research (Scudellari, 2015). Even with lofty ambitions for objectivity (Ziman, 1996) and self-correction (Alberts et al., 2015), the iterative testing and eventual rectifying nature of collective knowledge and research over centuries may operate on timescales far longer than the average scientist's lifetime, if at all (Ioannidis, 2012). Reasons why hypotheses may become dogma without sufficient evidence include confirmation bias—interpreting evidence as supporting one's beliefs (Munafò, et al. 2017).

An example of a century-old misconception in naturalist communities involves the Eastern Spadefoot (*Scaphiopus holbrookii*), a frog that ranges widely through the eastern United States (Powell et al., 2016). *Scaphiopus holbrookii* has an explosive or xeric breeding strategy (Gosner and Black, 1955) in which breeding adults migrate from their preferred forested habitats (Baughman and Todd, 2007) to highly ephemeral breeding ponds in optimal weather conditions (Hansen, 1958; Wells, 1977). This may only be a few days a year (Palis, 2012) from spring through fall (Bragg, 1945; Neill, 1957; Cook et al., 2011) or, in years of suboptimal precipitation, individuals in a population may not breed at all (Cook et al., 2011; Timm et al., 2014). Prevailing wisdom indicates that *S. holbrookii* is 'secretive,' which we define as 1) evading detection by erratic nocturnal activity (Dodd, 2013; International Union for Conservation of Nature Species Survival Commission [IUCN-SSC] Amphibian Specialist Group, 2015; Powell et al., 2016); 2) individuals are usually only detectable under specific weather conditions (Palis, 2005; Beane et al., 2010; Dodd, 2013; Gibson and Anthony, 2019); or 3) their presence in a site is difficult to detect outside of breeding and migration events (Palis, 2005; Gibson and Anthony, 2019). The lack of population data about this species, and lack of data from postmetamorphic subadults, also suggests that we may not have the supporting data to categorize threats against this species and their current listing status.

In an issue of American Naturalist, Arthur N. Bragg (1944) wrote an essay attempting to dispel inaccurate notions surrounding spadefoots, a small family of frogs of the genera *Scaphiopus* and *Spea*. Bragg detailed the uncritical acceptance of the perception that spadefoot species spend most of their time underground, and that the misconception that they rarely emerge from burrows was "without foundation in fact." In spite of this article, this misconception has continued to shape the breadth of work surrounding this species. Perceptions that *S. holbrookii* are difficult to find outside of these rain-led events have limited most in situ research to the very short duration when eggs, larvae, and breeding individuals are present at breeding pools. Postmetamorphic subadults are almost completely overlooked in the scientific literature. Nonmigratory upland aspects of life history and ecology of adult *S. holbrookii* are also largely unknown. The purported secretive nature of this species has resulted in it being one of the poorest known amphibians in the United States (Ryan et al., 2015), despite its abundance in some habitats and broad geographic distribution (Powell et al., 2016).

Interestingly, there is evidence in addition to Bragg's (1944) pronouncement that the notion of *S. holbrookii* as secretive is simply untrue. Pike (1886) described this species as not

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DOI: 10.1670/20-044

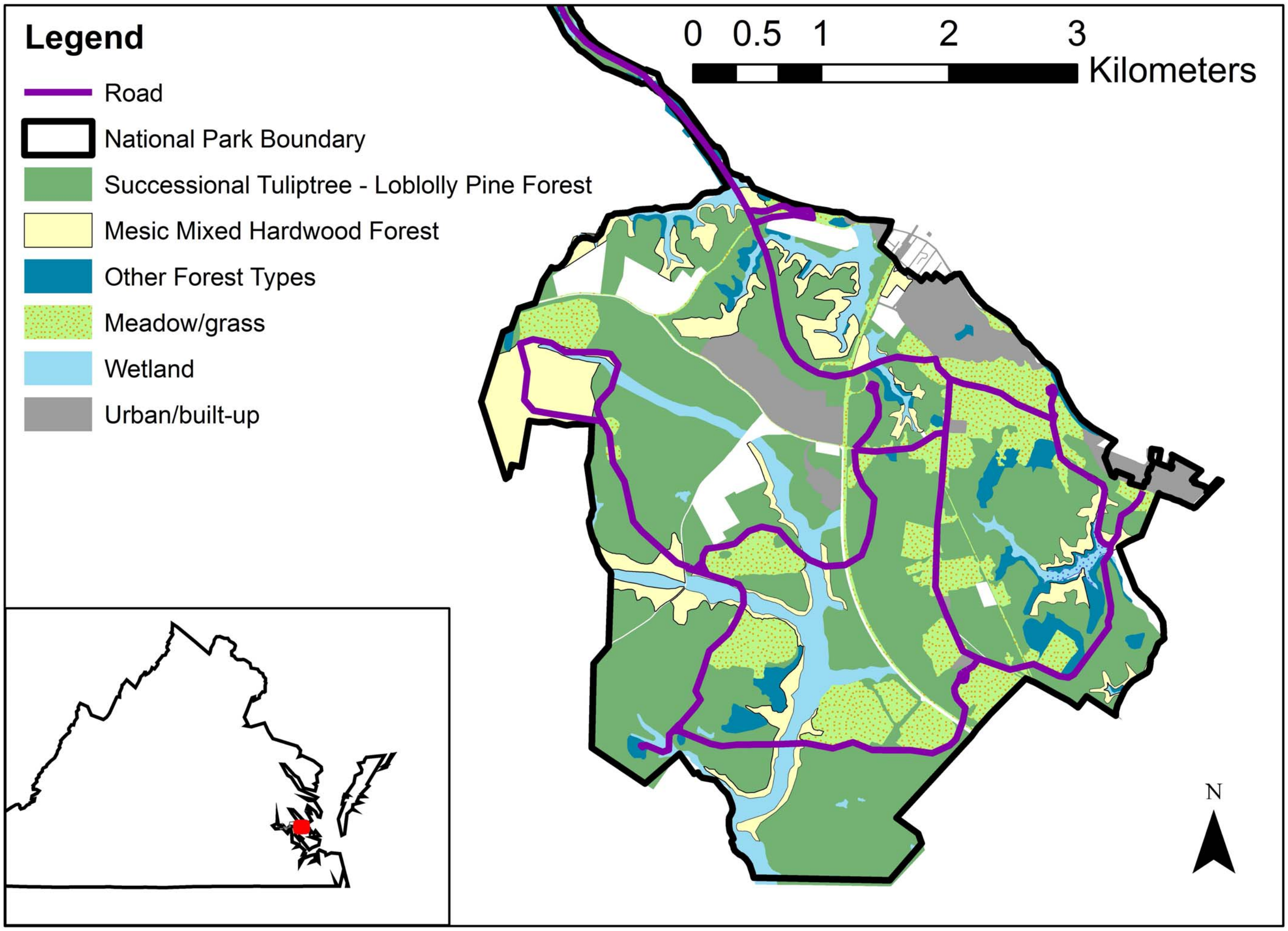

FIG. 1. Map of the Yorktown Battlefield unit of Colonial National Historical Park in the York–James Peninsula, southeast Virginia, USA, in 2016 and 2017. Surveys for Eastern Spadefoots (*Scaphiopus holbrookii*) were conducted in successional tuliptree–loblolly pine forest.

uncommon in New York, even with snow on the ground, and Pearson (1955) reported the species to be far less secretive in Florida, USA than commonly believed. Recent research has further challenged the notion that *S. holbrookii* is subterranean for most of its life by quantifying surprisingly high above-ground activity in Massachusetts (Timm et al., 2014) and Connecticut (Ryan et al., 2015). *Scaphiopus holbrookii* should then be easy to detect above the surface across multiple seasons in areas where they are known to occur, at least in their coastal habitat range, and in habitat where the forest floor can be seen. Their relatively long lifespans and high site fidelity (Pearson, 1957) also make them ideal candidates for upland mark–recapture studies, life table reconstruction, and quantification of growth rates, few of which have been published since Pearson (1955). Despite these published articles indicating that *S. holbrookii* is more active on the surface than previously thought, articles continue to describe this species as difficult to detect outside of breeding bouts.

Misconceptions about the frequency of surface activity in *S. holbrookii* are not trivial. Twelve of the 25 states making up the distribution of *S. holbrookii* list it as vulnerable or imperiled, and the species is vulnerable to disease (Hoverman et al., 2011; Kirschman et al., 2017), habitat loss (Delis et al., 1996; Jansen et al., 2001), and climate change (Greenberg et al., 2017). In the oft-cited global amphibian crisis (Houlahan et al., 2000), it is ever more imperative for accurate monitoring and forecasting of amphibian population trajectories, including for species considered to be common and widespread (Karraker et al., 2018).

The aims of this study were to 1) empirically determine if *Scaphiopus holbrookii* do indeed emerge regularly from burrows and are easily detected by spotlighting for eyeshine in upland habitats on nonbreeding nights, even on nights with environmental conditions perceived to be suboptimal for this species; 2) evaluate the efficacy of eyeshine spotlighting in detecting all postmetamorphic categories of *S. holbrookii*, and differentiating anuran eyeshine from arthropod eyeshine, in a range of weather conditions across multiple seasons in a field site in Virginia; and 3) determine if our methods and findings could be generalized in Rhode Island, a northern and less hospitable portion of the species range where *S. holbrookii* is endangered and detected extremely rarely.

MATERIALS AND METHODS

Study Sites.—Our first study area was the Yorktown Battlefield unit of Colonial National Historical Park in southeastern Virginia, USA (Fig. 1). This site is dominated by tuliptree (*Liriodendron tulipifera*) and loblolly pine (*Pinus taeda*) forest (Appendices 1, 2). Our second study area consisted of five sites in Washington and Kent Counties, Rhode Island, USA. The sites (Appendix 3) were

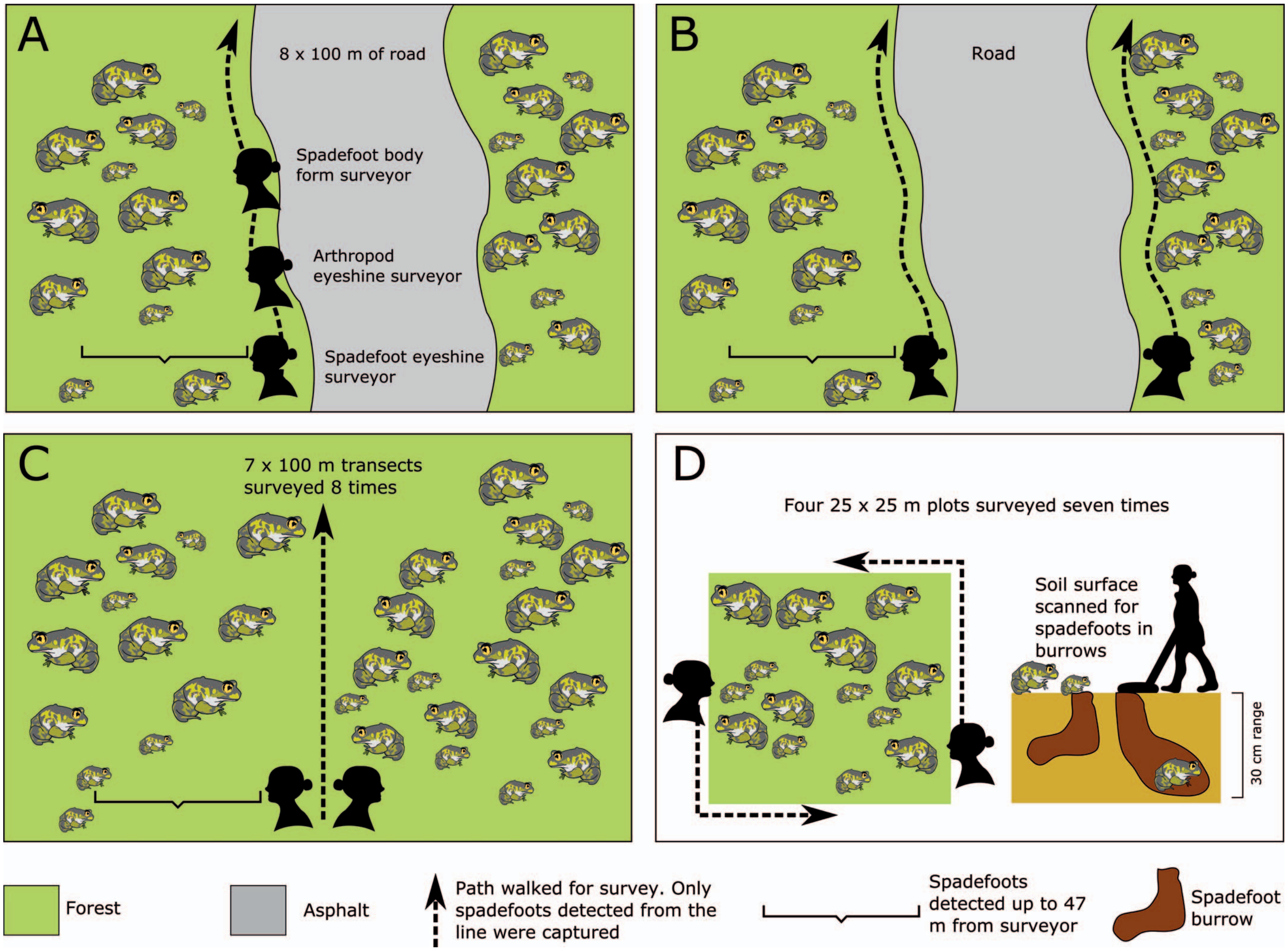

FIG. 2. Diagrams of the four different Eastern Spadefoot (*Scaphiopus holbrookii*) surveys conducted in Yorktown Battlefield in Colonial National Historical Park, Virginia, USA, in 2016. Comparative bodyform-arthropod-eyeshine surveys were: (A) used to compare efficacy of spotlighting for eyeshine and searching for body form of *S. holbrookii* and also to determine if arthropod eyeshine was distinguishable from frog eyeshine, over 16 km of road surveys; and (B) used to calculate the mean number of *S. holbrookii* captured per unit effort. Seven, 100-m transects were surveyed eight times over the course of 6 mo; (C) to calculate detection probability using eyeshine spotlighting. Mark–recapture surveys were used to quantify seasonal variation in burrow emergence (D). Figures not drawn to scale.

selected as those most likely to contain *S. holbrookii* based on historic records of *S. holbrookii* and presence of well-drained soils (Raithel, 2019).

Overview.—We used spotlighting for eyeshine (hereafter abbreviated to SES) to detect *S. holbrookii*. Spotlighting involves using a bright light to detect the eyeshine of animals and has been widely used to locate nocturnal vertebrates (Van Rossem, 1927; Setchell and Curtis, 2011; Andrew, 2015), including amphibians (Fellers and Freel, 1995; Corben and Fellers, 2001). Pearson (1955) used spotlighting to detect very large numbers of *S. holbrookii* in Florida, but this technique has not since been widely used for this species.

We conducted four different types of surveys in Yorktown Battlefield between April and September 2016, and in May 2017, and one type of survey in multiple sites in Southern Rhode Island between June and October 2020: 1) comparative SES/body form/arthropod surveys to compare the efficacy of SES vs. searching for *S. holbrookii* body form, 2) road SES surveys to detect *S. holbrookii* in forests adjacent to paved roads to demonstrate the large sample size that can be obtained with relatively little effort, 3) repeated surveys of transects within forests to calculate occupancy and detection probabilities using SES, 4) mark–recapture plot surveys to quantify nightly variation in burrow emergence, and 5) ground truthing of spotlighting methods and effort needed to detect spadefoots in occupied sites in Rhode Island.

On each survey night, we commenced surveys at least half an hour after sunset and ended surveys by 0300 h. We used 340–500-lumen (lm) headlamps on the brightest spotlight setting, positioned on surveyors' foreheads, directly between the eyebrows but not impeding vision. When an *S. holbrookii* was detected, we captured it by hand and recorded snout–vent length (SVL) using digital handheld calipers (with the spadefoot gently flattened against our fingers with light pressure on the dorsal region using a thumb) and presence or absence of nuptial pads or eggs. We classified an individual as female if it had eggs, male it if it had nuptial pads, and subadult/nonbreeding adult if it had neither. All individuals were released at the original point of capture.

Survey Method 1: SES/Body Form/Arthropod.—We surveyed forest adjacent to eight, 100-m stretches of road (Fig. 2A) in August 2016. Three surveyors, in single file, walked along the

TABLE 1. Single season occupancy models for Eastern Spadefoots (*Scaphiopus holbrookii*) detected on seven random transects surveyed eight times in Yorktown Battlefield in Colonial National Historical Park, Virginia, USA in 2016. Note: Occupancy probability (ψ) was held constant (.) across all surveys, while detection probability (p) was allowed to vary by air temperature (°C), relative humidity (RH), daily precipitation total (precip), or number of days since January 1 (date). Models are ranked by AIC; models in bold are within two AIC values of the lowest AIC value. Air temperature and relative humidity were missing for two surveys on the first sampling occasion; we substituted air temperature and relative humidity from the Newport News International Airport weather station (11 km from site, the closest station with relative humidity data; NOAA-NCEI 2019).

Model	Parameters	AIC	ΔAIC	AIC weight	*LL*
ψ (.) p (date)	**3**	**53.4**	**0**	**0.31**	**−23.699**
ψ (.) p (date + °C)	**4**	**54.53**	**1.14**	**0.48**	**−23.267**
ψ (.) p (date + precip)	**4**	**54.92**	**1.52**	**0.62**	**−23.460**
ψ (.) p (date + RH)	**4**	**55.39**	**2**	**0.73**	**−23.697**
ψ (.) p (date + °C + precip))	5	55.67	2.28	0.83	−22.837
ψ (.) p (date + °C + RH)	5	56.49	3.1	0.9	−23.247
ψ (.) p (date + RH + precip)	5	56.93	3.53	0.95	−23.466
ψ (.) p (date + °C + RH + precip)	6	57.65	4.25	0.99	−22.825
ψ (.) p (precip)	3	61.3	7.9	0.99	−27.651
ψ (.) p (RH + precip)	4	62.87	9.47	0.99	−27.433
ψ (.) p (°C + precip)	4	63.16	9.77	1	−27.582
ψ (.) p (.)	2	64.69	11.29	1	−30.344
ψ (.) p (°C + RH + precip)	5	64.73	11.34	1	−27.367
ψ (.) p (°C)	3	66.44	13.04	1	−30.219
ψ (.) p (RH)	3	66.48	13.08	1	−30.239
ψ (.) p (°C + RH)	4	68.18	14.78	1	−30.090

edge of the road. The first surveyor looked for *S. holbrookii* only by body form. The second surveyor followed behind and counted the numbers of arthropod eyeshine observed, which are distinguished from anuran eyeshine from the 'twinkling' of compound eyes. The last surveyor followed about 20 m behind in order not to be influenced by *S. holbrookii* detections made by the first surveyor and searched for *S. holbrookii* only by eyeshine.

Survey Method 2: Road SES.—We surveyed forest adjacent to either side of a nonoverlapping 12.13 km of roads on 13 nights between 11 April–20 July 2016 and on nonoverlapping 9.31 km of road on eight nights between 11–19 May 2017. Two researchers walked along opposite edges of paved tour roads, scanning the ground for anuran eyeshine to the distance the headlamp allowed (approximately 47 m) (Fig. 2B).

Survey Method 3: Forest Transects.—We established seven randomly located, 100-m transects in loblolly pine and mesic hardwood forest habitat. We surveyed each transect eight times between May and September 2016. Two surveyors walked the transect surveying opposite sides of the transect using SES (Fig. 2C). In order to understand the effort required to detect occupancy of a site using spotlighting, we developed a single species, single season model for occupancy using the unmarked (1.0.1) library (Fiske and Chandler 2011) based on our transect detection data. We included four survey-specific covariates to explain variation in detection probability between sampling occasions: air temperature and relative humidity at 1 m above ground using a weather meter (Kestrel 3000, Nielsen-Kellerman Co, Pennsylvania, USA), Julian date, and the daily precipitation total. Four models fell within two Akaike information criterion (AIC) values of the lowest AIC (Table 1); we performed model averaging among these four models to determine the predicted occupancy and detection probabilities across the range of observed data.

Next, we used simulations to determine the power to estimate occupancy at different transect and survey numbers. We set occupancy probability at 0.20, 0.50, and 0.95, and detection probability was set at either 0.30, 0.75, or 0.95. When the site was correctly identified as occupied, the iteration received a score of one. Simulations were iterated 1,000 times for a given number of transects and surveys, and all 1,000 iteration scores were then averaged to determine power.

Survey Method 4: Mark–Recapture Plots.—We marked the perimeter of four, 25 × 25-m plots in Yorktown Battlefield, chosen in areas known to have high *S. holbrookii* densities. We surveyed each plot seven times between April and August 2016. Starting from the same point, two surveyors walked in opposite directions around the entire perimeter of the plot, spotlighting for anuran eyeshine throughout the plot (Fig. 2D). When an individual was detected, we captured it, marked its location with a flag, placed it in a plastic bucket, and removed it from the plot. In addition to obtaining SVL and sex, we subcutaneously implanted a passive integrated transponder (PIT) tag (HPT8-10 mm, Biomark, Boise, Idaho) following the methods of Christy (1996). If *S. holbrookii* were <30 mm in SVL, we clipped the distal one quarter of their toes with unique combinations using sterilized surgical scissors following the methods of Donnelly et al. (1994). To determine detection probabilities for *S. holbrookii* above the ground surface, we scanned the surface of the plots after removing all *S. holbrookii* detected with spotlighting, using an HPR Plus reader and BP Plus Antenna (Biomark, Boise, Idaho). This antenna detected tagged *S. holbrookii* up to 30 cm below the ground surface (Fig. 2D). When the antenna detected an individual, we checked if it was on the surface (hence, missed by spotlighting) or underground. We returned all captured surface *S. holbrookii* to their original locations after completing the scan.

We used capture histories for individuals found above ground to estimate plot abundance at each sampling occasion using the POPAN parameterization of the Jolly-Seber model in the RMark (2.2.7) library (Laake, 2013). Each plot was modeled separately because of nonrandom site selection and unequal time intervals between capture occasions. We set survival probability and probability of entrance as time-invariant and allowed capture probability to vary with time. We also monitored all 12 known *S. holbrookii* breeding pools in our field site for hydroperiod and breeding activity from February to September 2016 and in May 2017.

Survey Method 5: 2020 Rhode Island Surveys to Test the Efficacy of Spotlighting.—We conducted SES for *S. holbrookii* in Rhode Island

TABLE 2. Sample size and demographic categories of Eastern Spadefoots (*Scaphiopus holbrookii*) from survey Method 2 (road spotlight eyeshine surveys) for surveys conducted in Yorktown Battlefield in Colonial National Historical Park, Virginia, USA in 2016.

	2016	2017	Total
Number of survey nights	13	8	21
Search effort (person-meters)	24,252	18,612	42,864
Number unsexed *S. holbrookii*	332	0	332
Number adult *S. holbrookii*	217	474	691
Number subadult/nonbreeding *S. holbrookii*	346	590	936
Proportion subadult/nonbreeding *S. holbrookii*	0.61	0.56	0.58

to explore the generalizability of the method to lower density populations. Surveys were conducted by 2–5 surveyors a night between June and September 2020. Surveys were conducted in such a way that the search area would slightly overlap between adjacent surveyors, spaced 10–20 m apart. Survey nights were chosen haphazardly by surveyor availability, not by weather conditions. Each of the five sites was surveyed between three and six times. We have withheld more-detailed geographic information because *S. holbrookii* is listed as an endangered species in Rhode Island.

RESULTS

We detected postmetamorphic *S. holbrookii* on 88.5% of 78 unique survey nights and captured 3,065 postmetamorphic individuals by hand in Virginia, despite observing no breeding activity or migration in any of our field sites. In Rhode Island we detected *S. holbrookii* on 90% of 10 survey nights and captured 42 individuals. The majority of these individuals were subadults. *Scaphiopus holbrookii* were detected by SES in a variety of environmental conditions. New surveyors took no more than three survey nights to develop a highly accurate search image for anuran eyeshine amidst a forest of arthropods.

Survey Method 1: Eyeshine/Body Form/Arthropod Surveys.—In the eight, 100-m transect surveys, we detected on average 6.50 (±1.71 SE) *S. holbrookii* per transect via spotlighting, walking an average 15.4 person-m to detect one *S. holbrookii*. Alternatively, only one *S. holbrookii* was found using detection by body form. We detected arthropod eyeshine that numerically surpassed *S. holbrookii* by orders of magnitude (601.1 mean, ±80.85 SE). Arthropod eyeshine was easily distinguished from anuran eyeshine. Only once did an SES surveyor mistake arthropod eyeshine for anuran. No precipitation occurred on either night when survey Method 1 took place.

Survey Method 2: Road SES.—We captured 1,959 *S. holbrookii* in 21 survey nights in 2016 and 2017, most of which were rainless nights, walking an average of 21.9 person-m to detect one *S. holbrookii*. Mean precipitation across survey nights was 0.26 cm (±0.15 SE). Of the 1,959 *S. holbrookii* detected, we did not determine the breeding status of 332 individuals captured during the first three surveys (Table 2). Of the remaining 1,627 individuals, 57.5% were subadults or nonbreeding adults. We detected very small subadults (22 mm SVL and <2 g in mass) as well as very large subadults/nonbreeding adults (up to 66 mm SVL without nuptial pads or eggs).

Survey Method 3: Forest Transects.—In eight repeated surveys of seven transects, we detected 825 *S. holbrookii*, the majority of which were subadults or nonbreeding adults (Fig. 3). We walked an average of 6.8 person-m to detect one *S. holbrookii*. Mean precipitation across survey occasions was 0.07 cm (±0.03 SE). Predicted occupancy of our site was 99.9%, and mean predicted detection probability over the sampling occasions was 76.8% (range 31.1–97.4%). In order to correctly identify a site as occupied at 0.80 power, very few surveys are needed for

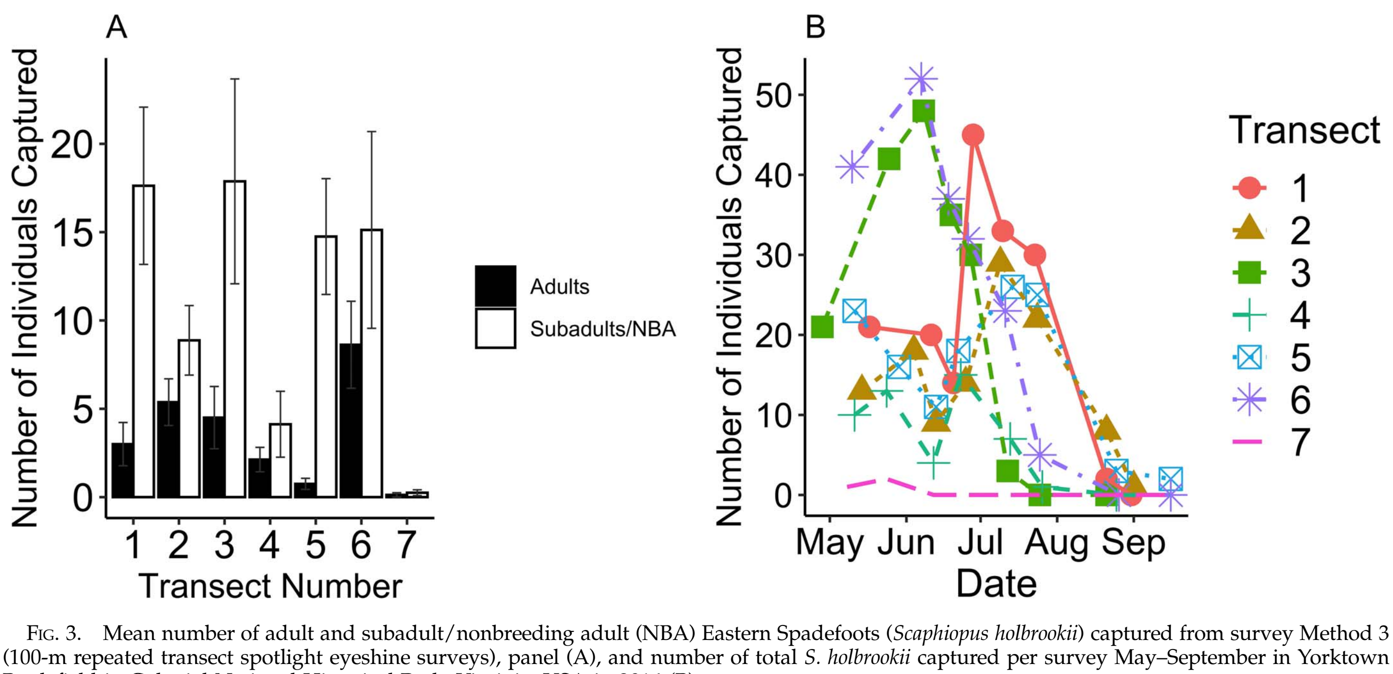

FIG. 3. Mean number of adult and subadult/nonbreeding adult (NBA) Eastern Spadefoots (*Scaphiopus holbrookii*) captured from survey Method 3 (100-m repeated transect spotlight eyeshine surveys), panel (A), and number of total *S. holbrookii* captured per survey May–September in Yorktown Battlefield in Colonial National Historical Park, Virginia, USA in 2016 (B).

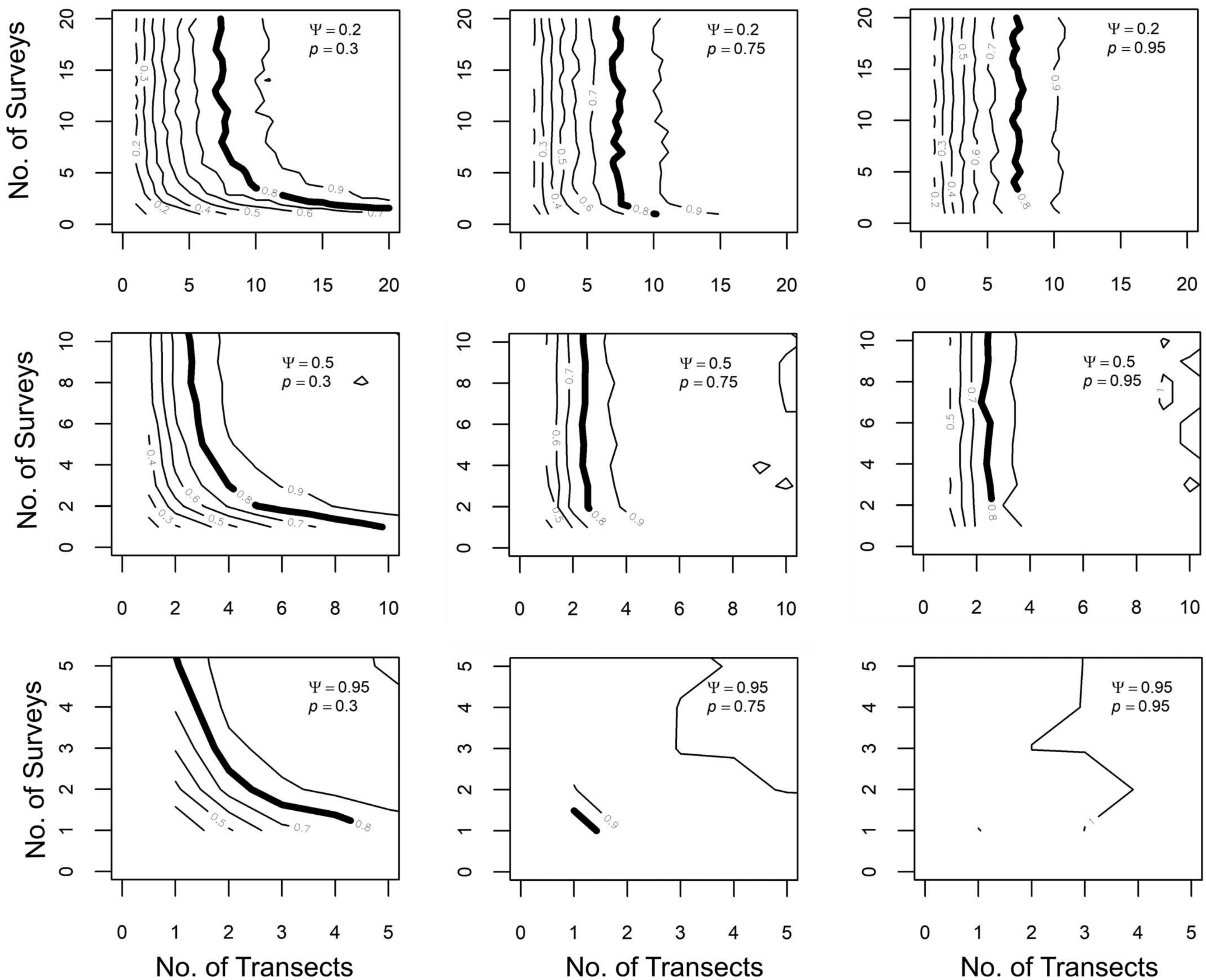

FIG. 4. Power analysis for identifying whether a site is occupied by Eastern Spadefoots (*Scaphiopus holbrookii*) based on models of empirical surveys using spotlighting of eyeshine conducted in Yorktown Battlefield in Colonial National Historical Park, Virginia, USA in 2016. Varying combinations of occupancy (ψ) and detection probabilities (p) determine the different combinations of transect and survey numbers needed to identify if a site is occupied at a power threshold (bold black line) of 0.80.

occupied sites (Fig. 4). Precipitation, relative humidity, temperature (Appendix 4), and distance to nearest breeding pool (Appendix 5) had no effect on detection or abundance.

Survey Method 4: Mark–Recapture Plots.—In seven repeated surveys of four plots conducted between April to September 2016, we detected and recaptured 183 unique *S. holbrookii* 416 times (271 above ground, 145 below ground). Mean precipitation for the 25 survey nights was 0.60 cm (0.22 SE). We found *S. holbrookii* on the surface of plots on 86% of surveys for two plots and on 71% of surveys for the other two plots (Appendix 6). Population sizes estimated for each plot survey ranged from 5 to 167 individuals (Appendix 6). All *S. holbrookii* detected with the antenna were underground and not on the surface of the plot, indicating that we captured all individuals on the surface by spotlighting. Percentage of *S. holbrookii* on the ground surface varied, with lowest surface activity in August (Fig. 5). Mean observed densities of *S. holbrookii* on the surface for each plot ranged between 2.74–14.13 individuals per 100 m^2 (Appendix 6).

TABLE 3. Results of spotlight eyeshine surveys for Eastern Spadefoots (*Scaphiopus holbrookii*) in Rhode Island, USA in 2020.

Location name	No. of surveys conducted (no. of surveys with *S. holbrookii* detected)	No. of *S. holbrookii* detections	No. of other anuran detections
Charlestown	6 (6)	18	56
Richmond 1	4 (0)	0	70
Richmond 2	3 (0)	0	40
West Greenwich	3 (0)	0	25
Westerly	4 (3)	24	40

Survey Method 5: 2020 Rhode Island Surveys to Test the Efficacy of Spotlighting in Sites where S. Holbrookii is Endangered and Rarely Encountered.—We detected *S. holbrookii* at two out of five sites, one of which was previously known to be occupied by *S. holbrookii* (Table 3). For these two sites, surveys yielded *S. holbrookii* detections in all of six surveys of the first site and in three out of four surveys of the second site (Table 3 and Appendix 7). Of the two occupied sites, the first site (Charles-

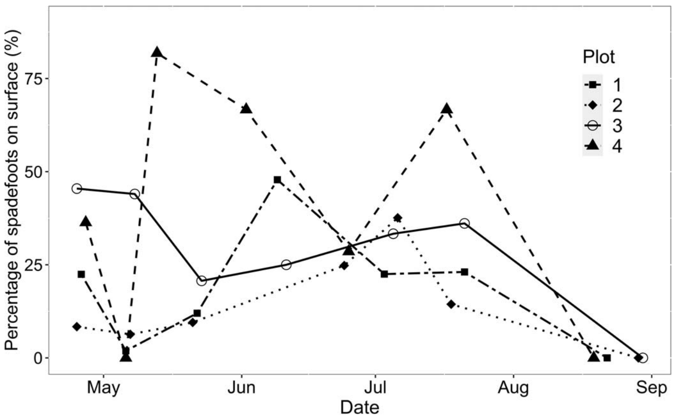

FIG. 5. Proportion of Eastern Spadefoots (*Scaphiopus holbrookii*) found above ground out of population estimates from mark–recapture surveys in four, 25 × 25-m forest plots in Yorktown Battlefield in Colonial National Historical Park, Virginia, USA in 2016.

town; Table 3) is one of two locations statewide that has yielded contemporary (i.e., since 2014) observations of *S. holbrookii*. This observation occurred incidentally in 2019 during a breeding event. The second occupied site (Westerly, Rhode Island; Table 3) was heretofore unknown to contain *S. holbrookii*.

DISCUSSION

Our study provides evidence that *S. holbrookii* of all postmetamorphic demographic categories 1) emerge from burrows regularly throughout the active season, even on dry and nonbreeding nights, 2) are easy to detect by spotlighting for eyeshine if a surveyor's view of the ground is largely unobstructed, and 3) have eyeshine that is easily distinguishable from that of arthropods. With relatively little effort, we amassed one of the largest in situ datasets on postmetamorphic *S. holbrookii* of which we are aware, with numbers that are orders of magnitude higher than most previous research. In addition to detecting large numbers of *S. holbrookii*, the majority of our captures were of subadults and nonbreeding adults, capturing demographic groups that are consistently underestimated or entirely undetected by survey methods focused on breeding pools. The efficacy of our approach stands in contrast to a 3-yr inventory of the same field site (Colonial National Historical Park), during which only two individuals were detected between 2001 and 2003 (Mitchell, 2004). Our detection models using spotlighting in Virginia are also corroborated by our 2020 surveys in Rhode Island, even though *S. holbrookii* is endangered there and not known to be abundant. We documented 42 sightings of *S. holbrookii* via spotlighting in 2020. By comparison, approximately 50 historic records of *S. holbrookii* exist for the entire state of Rhode Island between 1935 and 2014 (Raithel, 2019; NEK, pers. obs.).

We acknowledge that labor intensive field methods are necessary to answer specific questions about recruitment and migration to and from breeding pools (Greenberg and Tanner, 2004, 2005; Todd and Winne, 2006). We also recognize that many in situ studies with primary data on postmetamorphic anurans were not specifically focused on *S. holbrookii* (Owens et al., 2008), and our study does not intend to critique study designs of prior studies that included data on *S. holbrookii*. However, our results demonstrate the enormous amounts of data that can be collected on this species with the use of spotlighting, if the aim is to detect postmetamorphic individuals within a population across all demographic categories in a variety of environmental conditions. As long-term monitoring at wetlands lacks the power to detect population trends (Greenberg et al., 2017), *S. holbrookii* researchers with access to suitable habitat should utilize spotlighting to quantify population trends of this species.

Using spotlighting to detect upland *S. holbrookii* is a highly efficient method in habitat where the forest floor is visible to a certain degree. Spotlighting is a low-cost, low-effort method that causes minimal habitat disturbance and yields high sample sizes in areas where the target species is abundant. Individuals can be consistently detected up to >40 m from the surveyor. Relatively inexperienced researchers learn quickly to detect anurans by eyeshine and differentiate their eyeshine from that of arthropods. There is no 'by-catch,' unlike pitfall trapping (Karraker, 2001). Surveys need not be weather-sensitive or dependent on migration and breeding patterns, researchers do not need prior knowledge of breeding pool locations, and this method permits detection of all postmetamorphic stages. While the high densities of *S. holbrookii* we observed in southeast Virginia are probably region-specific, we obtained similar detection results from our surveys in Rhode Island (Table 3), where the climate and spadefoot abundance differ greatly.

We acknowledge that our methods may be less effective in other study sites. The York–James Peninsula has high deer-browsing levels (Lookingbill, et al. 2012), allowing a far range of visual detection from the transects. This method may not be as effective in areas with extremely dense understory or grasses where eyeshine will be obscured by very thick vegetation. As can be seen from the habitat descriptions of our Virginia and Rhode Island sites (Appendix 1, 3), at least some proportion of the leaf litter was visible from a distance. One of our transects (number 6) had high densities of Japanese stiltgrass (*Microstegium vimineum*), but this still did not impede us from finding at least some individuals during surveys. Potential critiques of our survey methods, built from multiple conversations about our datasets, and our counter arguments (and associated primary data) are detailed in Table 4. Even with eyeshine spotlighting caveats in mind, however, our data demonstrate clearly that the notion of *S. holbrookii* as a secretive species is simply untrue.

From a reproductive biology and physiological perspective, the perception that *S. holbrookii* remain underground most of their lives is illogical. Physiological cues for prolonged torpor or estivation are triggered by high temperatures, lack of food availability, and aridity (Storey, 2002), none of which dominate the mesic habitats of *S. holbrookii*. While it has been demonstrated that rains trigger physiological changes to gonads in sexually mature individuals (Hansen, 1958), mature male *S. holbrookii* maintain breeding condition year round and mature females across various states maintain spawning conditions from April to December (Goldberg, 2018). *Scaphiopus holbrookii* feed primarily on terrestrial insects (Jamieson and Trauth, 1996) on the surface, and not underground (Whitaker et al., 1977). They would therefore need to emerge and feed regularly to maintain breeding condition.

We believe the persistent myth that *S. holbrookii* is secretive and difficult to find is the result of two factors. First, individuals rely on camouflage as a primary defense strategy, and males only call during rare explosive breeding events. These characteristics lead to individuals being easily overlooked by observers in upland habitats without the aid of intensive trapping methods. Second, there is little precedence for locating upland *S. holbrookii* using eyeshine spotlighting (but see

TABLE 4. List of criticisms gathered from communications with herpetologists about the findings of this study regarding eyeshine spotlighting of Eastern Spadefoots (*Scaphiopus holbrookii*) in Virginia (2016–2017) and Rhode Island (2020), USA and respective counterarguments and supporting primary data.

Criticism	Counterargument	Data
Arthropod eyeshine impedes anuran eyeshine detection	Very large numbers of 'twinkly' compound eyes of arthropods are easily distinguishable from duller, round anuran eyeshine	Corben and Fellers (2001); Survey 1 of this study
	Surveyors should make sure that light sources, of appropriate luminous flux and focus, are placed as close to the eyes as possible. Headlamps placed too high on the forehead are able to pick up arthropod eyeshine, but not that of anurans	
Detecting migrating individuals in large numbers is not unusual	All spadefoots in this study were found sedentary in forests, not migrating to and from wetlands. No breeding events were known to have occurred during this study	Surveys 1–5 of this study
	More subadults/nonbreeding adults than breeding adults detected via SES	
High level of burrow emergence behavior is unique to this site	We found similar results in Jamestown Island and Green Spring in the York–James Peninsula, Virginia	Appendix 8; Pearson (1955); Timm et al. (2014); Ryan et al (2015); Survey 5 of this study
	High burrow emergence rates have been recorded in Massachusetts, Connecticut, Florida, and Rhode Island	
Weather conditions at this site in this particular time period were unusually ideal (e.g., high rainfall to trigger migration)	2016 was a drought year with relatively little rain compared to other years, and survey nights had low or no precipitation	Surveys 1–4 of this study
	No mass breeding events took place between February–September 2016 and in May 2017, when this study took place	
	Both Virginia and Rhode Island survey nights had low or no precipitation	
S. holbrookii are easy to detect near breeding pools	Road and transect surveys in Yorktown Battlefield were established irrespective of breeding pool locations	Appendix 5
	Many incidental *S. holbrookii* were spotlighted across the York–James Peninsula in 2015, not just at our Yorktown Battlefield site, despite the fact that we do not know the breeding pool locations in Jamestown and Green Spring in Virginia or the Westerley site in Rhode Island.	Appendix 8

Pearson, 1955), hence studies rely on methods known to yield high sample sizes such as trapping migrating individuals or waiting for breeding aggregations. A lack of data on individuals in upland habitats, combined with the relative ease with which researchers can find large numbers of individuals in breeding aggregations, has fueled the confirmation bias (interpreting new evidence as supporting previous beliefs) that *S. holbrookii* is secretive. With the exception of a few contemporary studies such as Timm et al. (2014) and Ryan et al. (2015), we believe this persistent, century-long misconception has hindered progress in understanding the ecology of *S. holbrookii* and has severely impeded research on and conservation of this species.

Acknowledgments.—We thank L. Corcoran for field assistance and data management. We thank the following for field assistance: A. O'Malley, K. Nicastro, B. Nissen, F. Woods, L. Tirrell, R. Healey, A. Cojocaru, J. Lord, and H. Woo. We thank T. Christensen for providing information on site locations. We thank C.A. Kruse, R.S. Mostow, and A. O'Malley for vegetation identification. This manuscript benefited from discussions with B. Buffum. We are grateful to D. Geyer and the law enforcement and dispatch staff at Colonial National Historical Park and S. Stevens of the National Park Service Inventory and Monitoring Program. Animal care and welfare protocols were approved by the University of Rhode Island Institutional Animal Care and Use Committee (IACUC protocol no. AN1415-004). Funding provided by National Park Service Cooperative Agreement P09AC00212 with the University of Rhode Island. Research permits were approved by the National Park Service (permit COLO-2015-SCI-0004) and the Virginia Department of Game and Inland Fisheries (SCP 053129).

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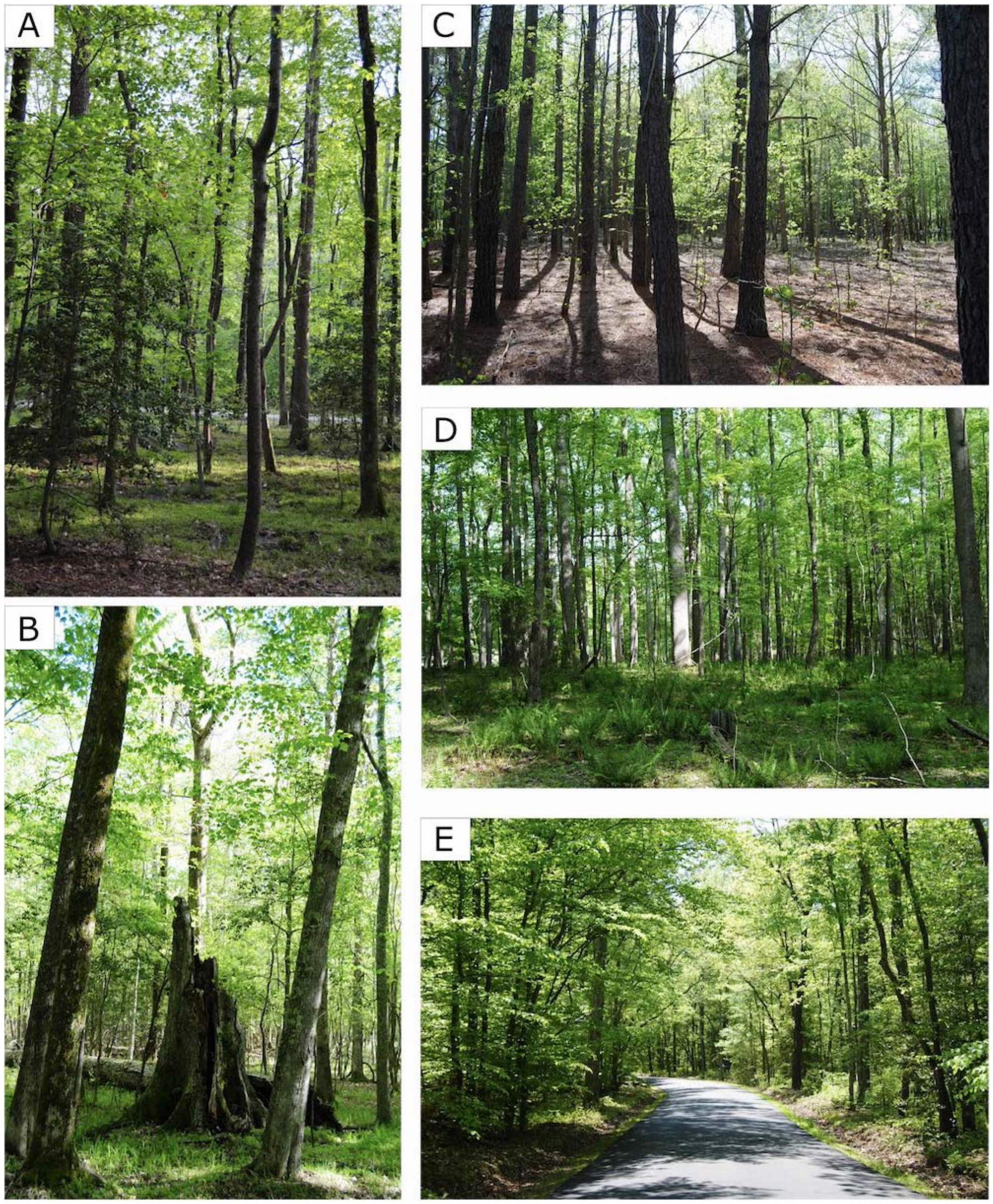
Accepted: 1 February 2021.
Published online: 11 June 2021.

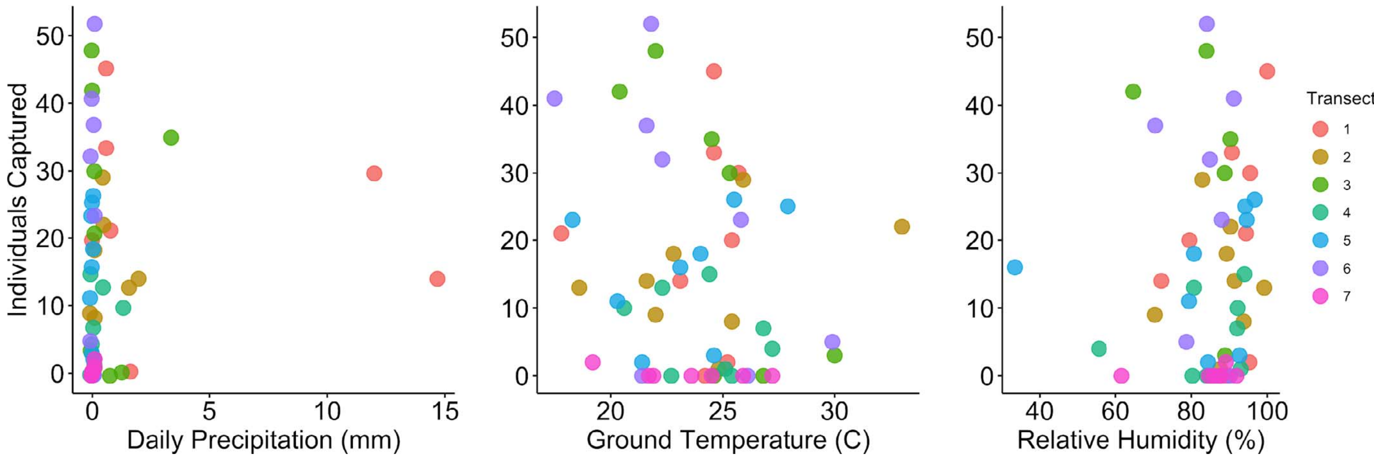


APPENDIX 1. Photographs of the variety of canopy and understory vegetation where Eastern Spadefoots (*Scaphiopus holbrookii*) were found in Colonial National Historical Park, Virginia, USA between 2015–2017, ranging from: (A, C) very sparse understory, (B) areas with higher grass, to (D, E) areas with higher densities of shrub and sapling cover. All photographs by Anna O'Malley.

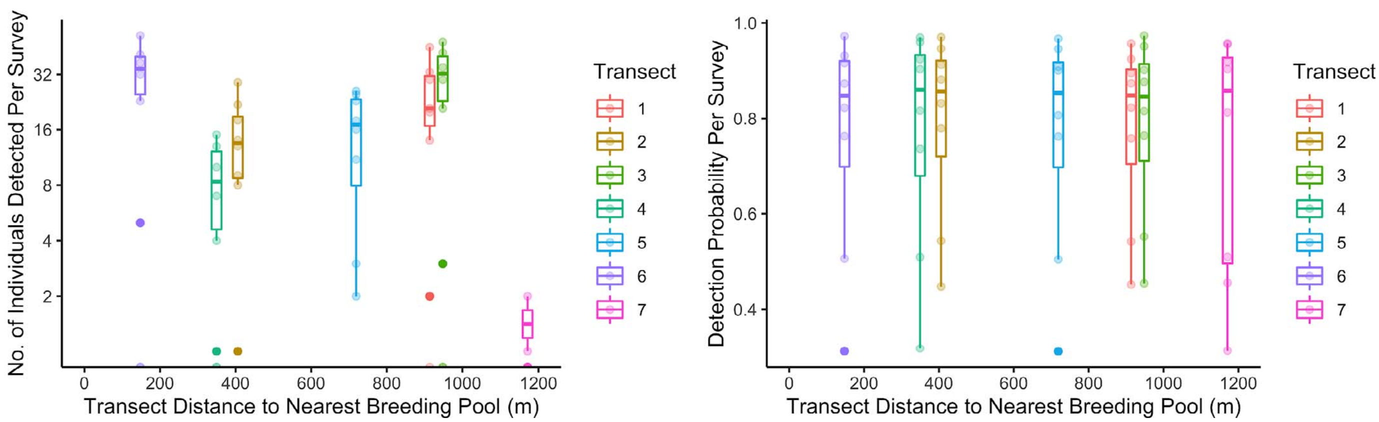
Appendix 2. Habitat types and vegetation descriptions for sites where Eastern Spadefoots (*Scaphiopus holbrookii*) were detected in Colonial National Historical Park, Virginia, USA from 2015–2017.

Unit	Habitat	Vegetation community	Additional associated species
Green Spring	Disturbed depressional wetland	Disturbed depressional wetland	—
Jamestown	Grass	—	—
Jamestown	Coastal plain loblolly pine–oak forest	*Pinus taeda* – *Quercus* spp. (*alba, falcata, stellata*)	—
Jamestown	Tidal oligohaline marsh	—	—
Parkway	Tidal bald cypress forest–woodland	*Taxodium distichum* tidal woodland	*Carex hyalinolepis*
Yorktown Battlefield	Successional tuliptree–loblolly pine forest	*Liriodendron tulipifera*	*Pinus taeda*
Yorktown Battlefield	Coastal plain mesic calcareous ravine forest	*Fagus grandifolia* – *Quercus alba*	*Acer barbatum*, *Quercus muehlenbergii*, *Sanguinaria canadensis*
Yorktown Battlefield	Cultural meadow	*Dactylis glomerata* – *Rumex acetosella*	*Dactylis glomerata*, *Phleum pratense*, *Festuca* spp., *Solidago* spp.
Yorktown Battlefield	Loblolly pine plantation	*Pinus taeda* planted forest	*Pinus taeda* planted forest
Yorktown Battlefield	Mesic mixed hardwood forest	*Fagus grandifolia* –*Quercus rubra* – *Quercus alba*	*Fagus grandifolis*, *Quercus* spp. (*alba, rubra*), *Liriodendron tulipifera*, *Ilex opaca*, *Polystichum acrostichoides*
Yorktown Battlefield	Successional black walnut forest	*Juglans nigra*	*Verbesina alternifolia*
Yorktown Battlefield	Successional tuliptree – loblolly pine forest	*Liriodendron tulipifera*	*Pinus taeda*

Appendix 3. Photographs showing variation in understory vegetation at sites where Eastern Spadefoots (*Scaphiopus holbrookii*) were found in Rhode Island, USA in 2020. Survey sites were composed primarily of mixed oak (*Quercus velutina*, *Quercus alba*) and pine (*Pinus rigida*, *Pinus strobus*) forests with variable understory. All photographs by Liam Corcoran.



APPENDIX 4. Number of individual Eastern Spadefoots (*Scaphiopus holbrookii*) captured per transect in relation to precipitation, temperature, and relative humidity, in Yorktown Battlefield in Colonial National Historical Park, Virginia, USA (2016) surveys.



APPENDIX 5. Relationship between transect distance to nearest pond and number of individual Eastern Spadefoots (*Scaphiopus holbrookii*) captured (left), and to detection probability per survey in Yorktown Battlefield in Colonial National Historical Park, Virginia, USA in 2016.

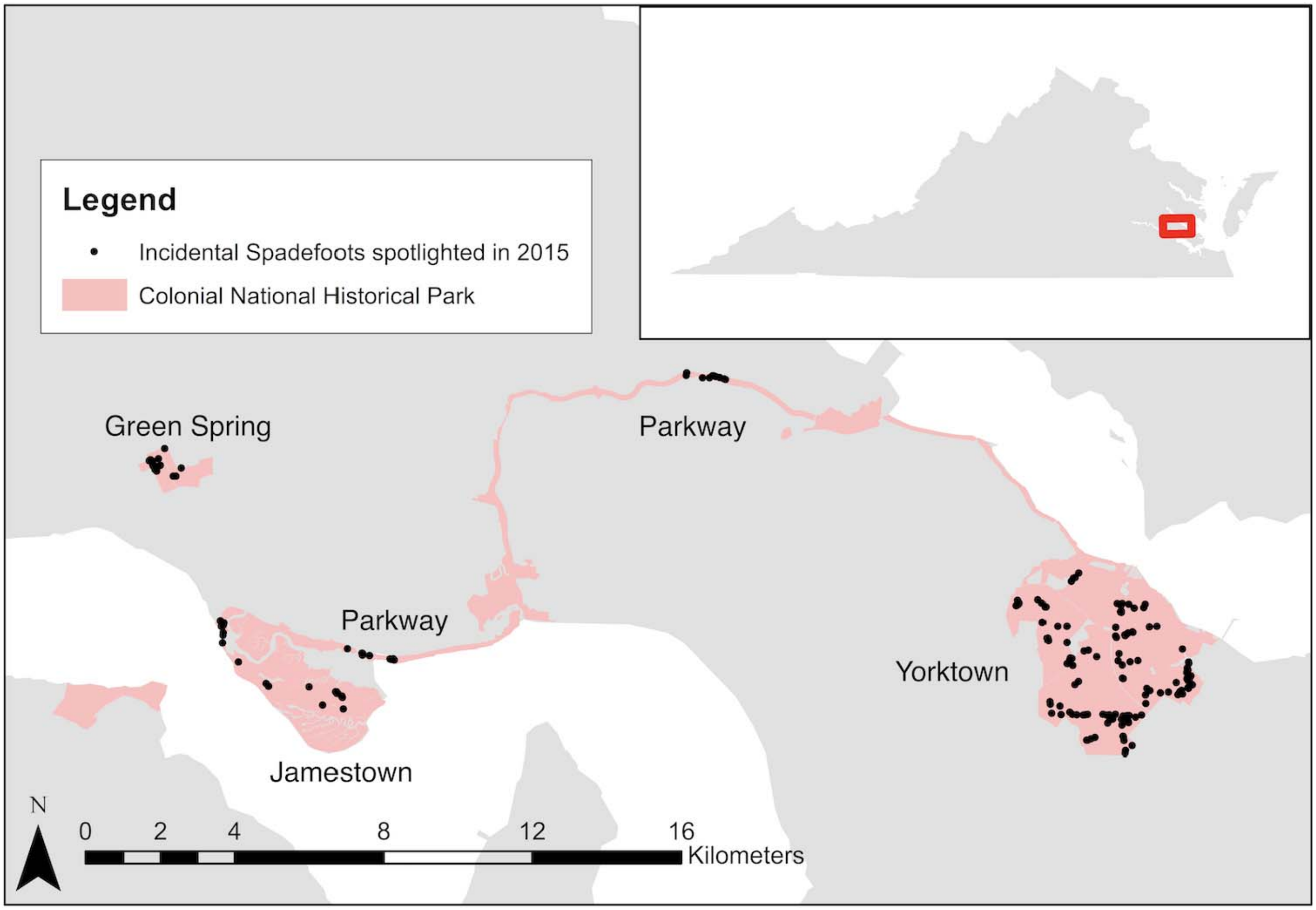
APPENDIX 6. Population estimates and number of Eastern Spadefoots (*Scaphiopus holbrookii*) detected on the surface on each survey night for forest plot surveys in Yorktown Battlefield in Colonial National Historical Park, Virginia, USA in 2016.

Plot	Survey	Abundance estimate	Lower bound 95% CI[a]	Upper bound 95% CI	No. captured on surface	No. detected underground
1	1	49	−38	135	11	0
1	2	53	−15	121	1	0
1	3	50	0	100	6	1
1	4	46	1	92	22	4
1	5	40	−9	89	9	7
1	6	39	−13	92	9	11
1	7	32	−21	85	0	17
2	1	167	112	222	14	0
2	2	158	114	201	10	1
2	3	147	113	181	14	2
2	4	125	91	158	31	6
2	5	117	80	155	44	7
2	6	111	69	152	16	17
2	7	90	34	146	0	27
3	1	22	5	38	10	0
3	2	25	12	38	11	0
3	3	29	17	41	6	2
3	4	32	16	47	8	3
3	5	33	12	55	11	2
3	6	36	9	63	13	2
3	7	36	−2	73	0	13
4	1	11	−3	24	4	0
4	2	11	3	19	0	0
4	3	11	5	17	9	2
4	4	9	0	18	6	2
4	5	7	4	19	2	4
4	6	6	6	19	4	4
4	7	5	7	16	0	10

[a] CI = confidence interval.

APPENDIX 7. Survey data for locations where Eastern Spadefoots (*Scaphiopus holbrookii*) were detected in Rhode Island, USA in 2020. Rainfall obtained from Westerly State Airport, Rhode Island, USA (GHCND:USW00014794) and Charlestown 3.0 WSW, Rhode Island, USA (GHCND:US1RIWS0036) (National Oceanic and Atmospheric Administration, National Centers for Environmental Information [NOAA-NCEI], 2020).

Date (start time)	No. of observers	Total search time (min)	No. of *S. holbrooki*i detections	Temperature (C°) at start of survey	Relative humidity (% at start of survey) [daily rainfall (mm)]
Charlestown					
6/24 (2122 h)	3	180	1	17.5	84.6 [0]
7/3 (2335 h)	2	140	1	19.2	88.6 [0]
7/9 (2122 h)	4	524	2	25.3	82.7 [0]
8/5 (2148 h)	2	100	5	22.7	82.6 [0.5]
8/26 (2300 h)	4	156	1	17.5	63.2 [0]
9/9 (2005 h)	2	294	8	23.4	82.6 [0]
Westerly					
7/23 (2055 h)	4	468	6	24.6	87.2 [1.5]
8/26 (2030 h)	4	348	0	21.0	50.6 [0]
9/2 (2150 h)	4	376	13	22.4	90.9 [3]
9/30 (2022 h)	3	162	5	19.1	70.1 [4.3]



Appendix 8. Incidental Eastern Spadefoot (*Scaphiopus holbrookii*) capture locations in all units of Colonial National Historical Park in the York–James Peninsula, Virginia, USA during herpetofauna surveys in 2015. Breeding pool locations are unknown for the Green Spring and Jamestown sites, either from this study or from historical accounts.