

## **Acute Artificial Light Diminishes Central Texas Anuran Calling Behavior**

Author(s): Alexander S. Hall

Source: *The American Midland Naturalist*, 175(2):183-193.

Published By: University of Notre Dame

DOI: <http://dx.doi.org/10.1674/0003-0031-175.2.183>

URL: <http://www.bioone.org/doi/full/10.1674/0003-0031-175.2.183>

---

BioOne ([www.bioone.org](http://www.bioone.org)) is a nonprofit, online aggregation of core research in the biological, ecological, and environmental sciences. BioOne provides a sustainable online platform for over 170 journals and books published by nonprofit societies, associations, museums, institutions, and presses.

Your use of this PDF, the BioOne Web site, and all posted and associated content indicates your acceptance of BioOne's Terms of Use, available at [www.bioone.org/page/terms\\_of\\_use](http://www.bioone.org/page/terms_of_use).

Usage of BioOne content is strictly limited to personal, educational, and non-commercial use. Commercial inquiries or rights and permissions requests should be directed to the individual publisher as copyright holder.

---

# Acute Artificial Light Diminishes Central Texas Anuran Calling Behavior

ALEXANDER S. HALL<sup>1</sup>

*Department of Animal Behavior, Southwestern University, Georgetown, Texas 78626*

**ABSTRACT.**—Male anuran (frog and toad) advertisement calls associate with fitness and can respond to environmental cues such as rain and air temperature. Moonlight is thought to generally decrease call behaviors – perhaps as a response to increased perceived risk of predation – and this study sought to determine if artificial lighting produces a similar pattern. Using a handheld spotlight, light was experimentally introduced to natural anuran communities in ponds and streams. Custom call surveys where then used to measure anuran calls in paired unlit and lit conditions at six locations in central Texas. Among seven species heard, the number of frogs calling and call index declined in response to the acute light input. Local weather conditions could not explain differences between numbers of frogs calling between species, sites, survey order, or lighting order suggesting the main effect on number calling was light treatment. It appears acute artificial light alone can change calling behavior within several species in natural, mixed species assemblages.

## INTRODUCTION

During the breeding season, adult male anurans (frogs and toads) of most species use auditory, species-specific advertisement calls to attract mates (Ryan, 2001). In these species variation in calling behavior – whether in frequency, duration, pitch, or intensity – can be critical to female choice of a mate (Ryan, 2001). Abiotic factors (*e.g.*, air temperature, rainfall, and moonlight) contribute to variation in calling behavior (Oseen and Wassersug, 2002; Saenz *et al.*, 2006; Steelman and Dorcas, 2010). For example during anuran call surveys, male anuran breeding calls are heard less frequently and less reliably under naturally high illumination levels caused by moonlight (Weir *et al.*, 2005; Pierce and Gutzwiller, 2007; Granda *et al.*, 2008). These authors suggest brighter natural illumination may cause decreased anuran calling behavior, perhaps in response to a greater perceived risk of predation (Weir *et al.*, 2005; Pierce and Gutzwiller, 2007; Granda *et al.*, 2008). Bright moonlight increases anti-predatory behavior (*e.g.*, reduces foraging, decreases vocal activity) in several other taxa: snowshoe hares (Griffin *et al.*, 2005), nocturnal rodents (Daly *et al.*, 1992), scorpions (Skutelsky, 1996), and nocturnal seabirds (Mougeot and Bretagnoll, 2000). Following the logic that natural light affects anuran calling behavior, I sought to investigate how an experimentally introduced artificial light source may affect mating behavior in natural populations of frogs in central Texas.

Light pollution (outdoor-oriented artificial illumination modifying the natural light environment) occurs as a side effect of modern human habitation and activity (Riegel, 1973; Verheijen, 1985; Buchanan, 2006). Globally, a substantial proportion of terrestrial surfaces are light polluted; for example, to the effect that one cannot see the Milky Way (Cinzano *et al.*, 2001; Elvidge *et al.*, 2001). In response to the globally increasing coverage and intensity of light pollution, a growing number of conservation biologists are investigating how light pollution affects the environment; specifically, how artificial light modifies natural patterns of

---

<sup>1</sup>Corresponding author present address: Department of Biology, The University of Texas at Arlington, Arlington, Texas 76019; e-mail: allopatty@gmail.com

light and dark in ecosystems (*i.e.*, ecological light pollution; Longcore and Rich, 2004). Considering natural lighting may affect nocturnal anuran calling behavior (*e.g.*, Granda *et al.*, 2008), artificial lighting should also emerge as a relevant facet of breeding behavior in natural populations. A recent study by Steelman and Dorcas (2010) incorporated illuminance from a remote detector into a detection probability model of anuran advertisement calls. These authors uncovered a correlation between greater light intensity and decreased probabilities of hearing Spring Peepers (*Pseudacris crucifer*), Upland Chorus Frogs (*Pseudacris feriarum*), and Southern Leopard Frogs (*Lithobates sphenoccephalus*). Despite a handful of reviews discussing how artificial light does or might affect amphibians (Buchanan, 2006; Wise, 2007; Perry *et al.*, 2008), very little has been published on how artificial lighting affects amphibian behavior and ecology. Wise (2007) suggests that by yet-undetermined mechanisms, light pollution exacerbates amphibian declines, perhaps as an additional environmental stressor. Tested more directly, only one published field experiment (Baker and Richardson, 2006) has assessed how artificial light changes anuran calling behavior. Baker and Richardson (2006) observed male Green Frogs (*Lithobates clamitans*) in Ontario, Canada and found that compared to frogs in ambient lighting, a brief stimulus of artificial light from a flashlight decreases the number of detected calls, decreases the occurrence of multi-note calls, and leads to a higher frequency of movement. This study focused on the individual responses of 20 frogs of one species in a single habitat type (swampy bog).

Motivated by the need for further research on how artificial lighting may affect anuran calling behavior in group settings, a field experiment was conducted in Texas to determine how temporary experimentally introduced artificial light affects male anuran breeding calls. The light may have a disrupting affect on calling behavior, as predicted by reviews on the topic (Buchanan, 2006; Wise, 2007). Using a paired design in combination with modified anuran call surveys, I can compare the calling behavior of male frogs within a site and within a species between unlit and lit trials. The following experiment sought to investigate the hypothesis males that in natural populations of anurans call less often in the presence of acute artificial night lighting.

#### METHODS

Six anuran breeding habitats within Williamson County, Texas (30°39'45'' N, 97°42'43'' W) were chosen. Coordinates for each site are available in the supplementary material. Riparian Texas blackland prairie collectively characterizes these sites, though urbanization encroaches upon this ecosystem. Of these six sites, three were human-made ponds and the remaining three sites were flow-managed first- or second-order streams. Between 31 March and 5 June 2010, amphibian call surveys were conducted between 2030 h and 2400 h. Each site was tested once per week and two sites were tested per survey night. Across the duration of this experiment, each site was tested seven times.

To monitor frog behavior without recording equipment, a modified version of the North American Amphibian Monitoring Program (NAAMP) protocol (Weir and Mossman, 2005) was used. An NAAMP survey provides evidence of species presence and allows for a rough index of adult population size (Heyer *et al.*, 1994; Nelson and Graves, 2004; Weir and Mossman, 2005). At each site, I first recorded survey time and then measured air temperature (C) and maximum wind speed (m/s) across 1 min using a Kestrel 4000 Pocket Weather Tracker. I then visually estimated cloud cover (percentage) and visible moonlight (percentage of disk illuminated). During surveys, each species heard, the maximum NAAMP calling intensity index (0, 1, 2, or 3) for individual species, and the estimated maximum number of individuals calling for each species was recorded.

A range was recorded when the precise number of individual anurans calling within a species was indeterminate.

Each night, two different sites were surveyed. I did not survey any site twice in fewer than 48 h (to avoid potential carryover effects). Using a paired sample design, each surveyed site received two lighting conditions in the same evening and each site served as its own control. During surveys, I conducted five 3 min surveys successively, waited 5 min, and conducted another set of five 3 min surveys. Each 15 min block (of five 3 min surveys) comprised one-half of the paired samples. Shirose *et al.* (1997) found that 3 min surveys robustly detect species and that longer surveys do not appreciably increase call detection. More recently, Pierce and Gutzwiller (2004) found 15 min anuran call surveys have a high (>90%) cumulative detection efficiency compared to 30 min surveys. Therefore, all data from the five 3 min surveys were averaged to generate a representative record of what called during the 15 min block. Using a total survey time of 15 min permitted a high probability of detecting species. Splitting the survey time into five 3 min surveys allowed for a representative record of what was calling, on average, during the 15 min survey time (*i.e.*, rather than one 15 min survey, which would only account for the maximum number of anurans and maximum calling intensity heard at any point over 15 min). I randomly determined one of these 15 min survey blocks to be a lit condition and the other 15 min survey block to be an unlit condition. In the lit condition, I slowly swept the beam of a high-powered spotlight back and forth over the entire water surface and surrounding shore of the respective site. Unlit conditions were exactly the same except the experimental light was not turned on (*i.e.*, site disturbance should be the same between conditions). When approaching sites, I parked all vehicles at least 25 m away with the headlights turned off. I sparingly used headlamps covered with red filters to aid data recording.

During the lit condition, one hand-held high-intensity spotlight (Brinkmann model number 800-2605-0), used in combination with a 6 V rechargeable lead acid battery (Brinkmann model number 802-2605-0), illuminated the largest proportion of the site possible from the site's edge using a slow sweeping motion with the beam from the spotlight. On a cloudy night without moonlight, the illuminance of the brightest part of the spotlight's beam at 1 m was 940.5 lux (*i.e.*,  $\text{lumen m}^{-2}$ ; Quantum/LiCor LI1000 photometer; for unit conversions, *see* Meyer-Arendt, 1968). Using the inverse-square law, I estimated the illuminance at 5 m to be 37.6 lux and 9.4 lux at 10 m. This approximates the range of illumination presented to frog communities in natural environments during lit conditions. In unlit conditions the same sweeping motion was used with the same equipment, but the light was not turned on.

#### DATA ANALYSIS

Calls from sites not being analyzed were heard often; therefore, only calling behavior from anurans heard on the site were used (*i.e.*, in the water or on the surrounding shoreline). When the exact number of anuran individuals heard during a survey was difficult to determine and a range was recorded (*e.g.*, 8–10), the median number of that range for data analyses was used. For each 15 min survey block of five 3 min surveys, the five maximum numbers of frogs heard calling and the maximum recorded call indices were averaged. After this point, I refer to average maximum number of frogs heard calling as 'number calling' average maximum call index as 'call index' (each during a 15 minute block), unless otherwise noted.

After surveys, moonlight data recorded in the field were compared against data posted on the U.S. Naval Oceanography (USNO) web site (<http://www.usno.navy.mil/USNO/astronomical-applications>). If moonlight on surveys was noted (*i.e.*, seen despite clouds

and protective vegetation), the USNO percentage was used. This corrected moonlight percentage was used in place of site-recorded estimates for all analyses. As precipitation affects anuran calling behavior (*e.g.*, Oseen and Wassersug, 2002), I tallied the previous 48 h of rainfall for each survey (the survey day and day previous) as monitored daily at the Lake Georgetown U.S. Army Corps of Engineers (USACE) main office (30°40'34.75" N, 97°43'14.79" W). These data were obtained from the USACE Fort Worth District website (<http://www.swf-wc.usace.army.mil/cgi-bin/rcshtml.pl?page=Reports>). The rain monitoring site was within 7.5 km of all six study sites.

To assess correspondence between number calling and call index, regression analyses were used to test simple relationships between the variables. All zero values from the regression analyses were removed to satisfy tests that cannot work with nonpositive integers. Neither call latencies nor call indices distributed normally; therefore, difference scores between the lighting conditions were calculated. The response in unlit conditions minus the response in paired lit conditions comprises dependent variables in following tests. Difference scores for call index and number calling distributed approximately normally. Assuming a parametric response variable, a null distribution centered at zero should correspond to no effect of lighting condition on calling behavior. To uncover differences from the null distribution, I tested if the observed difference score distributions for call index and number calling centered at zero using two one-sample *t*-tests.

Several factors (*e.g.*, weather, study design, social facilitation) could explain differences in calling behavior between lighting conditions other than the light itself. To account for this, the difference in number calling between unlit and lit surveys was modeled using abiotic factors as independent variables and systematic conditions as treatments. Poor fit to this type of model would suggest the difference score was due primarily to the introduced light rather than the factors tested. To avoid statistical issues with multiple inferences when combining several the treatment conditions, an information theoretic approach was used to select best linear mixed models. Linear mixed models accommodate an arbitrary number of experimentally controlled variables called random effects into a model of how one response variable responds to any number of variables outside of experimental control: so-called fixed effects (Grueber *et al.*, 2011). In the models I tested, random effects include species, site number, the survey order (first or second survey in the evening), and lighting order (unlit then lit or lit then unlit) – each experimentally controlled or known *a priori* to correspond to different response conditions. For example species-specific differences in calling behavior were noted by Pierce and Hall (2013) for nearby anuran populations with similar species assemblages. I tested four fixed effects: maximum wind speed (m/s), air temperature (C), percent moonlight, and the previous 48 h of precipitation (mm). These are measures typically recorded or easily extracted from a standard NAAMP survey and may affect the difference score or overall response to calling. Precipitation generally promotes calling (Oseen and Wassersug, 2002), though not always at permanent sites (Saenz *et al.*, 2006; Steen *et al.*, 2013) such as those studied here. Ambient temperature is widely reported to affect anuran behavior (Oseen and Wassersug, 2002; Saenz *et al.*, 2006; Steen *et al.*, 2013). Moonlight, generally stable within a survey night at a given site, may interact with the added light and is thus included. At high speeds, wind may contribute to a perceived risk of desiccation on the part of the frog, and thus this variable is also included.

Recommendations by Grueber *et al.* (2011) were followed in constructing a best fit model. In brief, a global model was constructed consisting of all fixed effects and their

first-order interactions. By iteratively removing variables and recording the Akaike's Information Criterion corrected for small sample size ( $\Delta\text{AIC}_C$ ; Hurvich and Tsai, 1989) the most informative models can be recovered. This approach will return a best model, though biologically relevant information may still be contained in less informative models. To account for this, I averaged models with  $\Delta\text{AIC}_C$  of  $<4$  from the best models. A  $\Delta\text{AIC}_C$  of  $<2$  corresponds with highly informative models and  $\Delta\text{AIC}_C$  of  $<4$  corresponds to moderately informative models (Burnham and Anderson, 2002). Models with  $\Delta\text{AIC}_C > 4$  poorly describe the response variable as measured (Burnham and Anderson, 2002; Grueber *et al.*, 2011). To allow meaningful coefficient comparisons after model averaging, I standardized averaged model coefficients by 2 SD following Gelman (2008). Data were deposited in the Dryad repository://doi.org/10.5061/dryad.cd62n. I used R (R Core Team 2015) and the R packages *lme4* (Bates *et al.*, 2015), *arm* (Gelman and Su, 2015), and *MuMIn* (Bartoń, 2015) to conduct linear mixed model analyses. All other statistical tests were performed in SPSS (IBM Corp, 2013).

## RESULTS

In total seven surveys were conducted at all six sites for a total of 42 paired surveys. Frogs called during all surveys. Six species called across these surveys: Northern Cricket Frogs (*Acris crepitans*), Gulf Coast Toads (*Inciilius nebulifer*), Cliff Chirping Frogs (*Eleutherodactylus marnockii*), Spotted Chorus Frogs (*Pseudacris clarkii*), American Bullfrogs (*Lithobates catesbeianus*), and Rio Grande Leopard Frogs (*Lithobates berlandieri*).

Overall, fewer frogs called when illuminated than when kept dark ( $t = -6.574$ ,  $df = 88$ ,  $P < 0.001$ ; Fig. 1; Table 1). Additionally, frogs called less intensely during lit conditions than paired unlit conditions ( $t = -5.077$ ,  $df = 88$ ,  $P < 0.001$ ; Table 1). Correspondence between these results did not surprise as the call index strongly correlated with number of frogs heard calling in a natural log relationship (adjusted  $r^2 = 0.913$ ,  $F_{1,166} = 1758.9$ ,  $P < 0.001$ ; call index =  $0.784 \cdot \ln(\text{number calling}) + 1.036$ ).

Since call index and number of frogs calling strongly correlated, linear modeling was limited to the number of frogs calling difference score as a dependent variable. The tested linear mixed models contained four random effect variables: species (six levels), site number (six levels), site order (first or second site within an evening), and lighting order (unlit then lit or lit then unlit). A global model consisted of an intercept, four environmental (fixed effect) variables, and all first order interactions between the fixed effects. After iterative testing of all model parameter combinations in an information theory framework, the null model emerged as the best predictor of the difference in number of frogs heard calling between unlit and lit conditions (Table 2). No models other than the null model returned a  $\Delta\text{AIC}_C$  of  $<2$  (Table 2). All four single fixed effect models returned  $\Delta\text{AIC}_C$ s of  $<4$  from the null model (Table 2). For the five models (including the null model), standardizing effect sizes and model averaging produced a best fitting model (Table 3). When assessing the significance of coefficients in linear and generalized linear mixed models, it is generally assumed that not including zero in the confidence interval indicates a significant explanatory coefficient (Grueber *et al.*, 2011). In the best fit model, each coefficient estimates' confidence intervals include zero except wind speed. In combination with the null model being the best supported model and no other models returning a  $\Delta\text{AIC}_C$  of  $<2$ , the best fit model does not appear to show strong support for the effect of measured environmental variables on the difference in number of frogs calling between unlit and lit surveys.

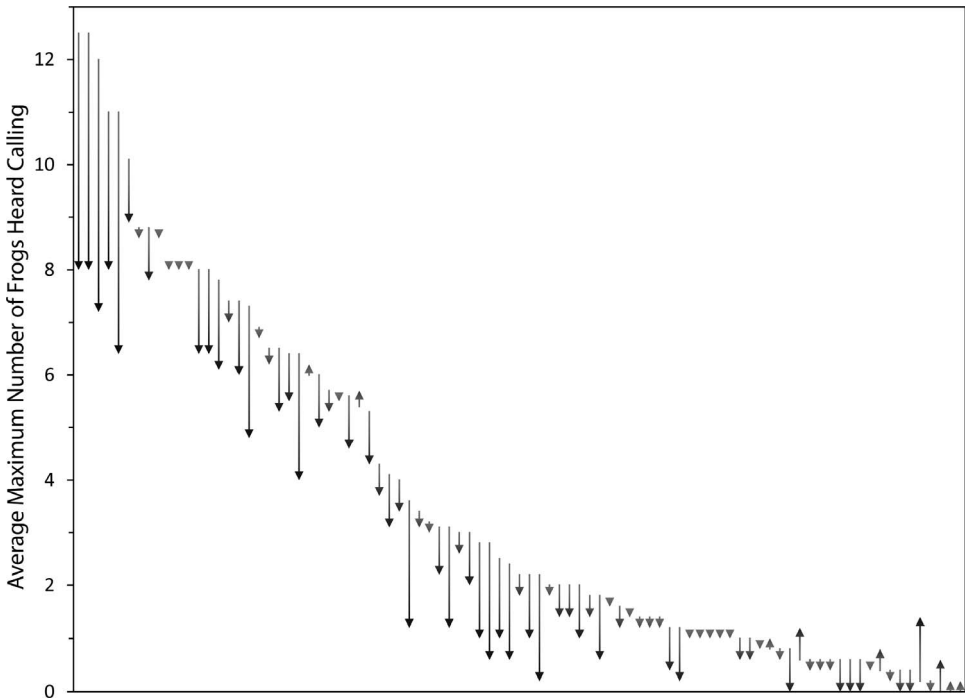


FIG. 1.—Adding artificial light to natural frog populations decreased the number of frogs heard calling. Each line represents a paired survey and surveys are ordered by decreasing number of frogs heard calling in the unlit condition. Arrowheads point towards the lit survey record

TABLE 1.—Nocturnal male anuran calling behavior at ponds in central Texas. Statistics are reported for paired surveys in artificially lit and naturally unlit conditions

Measure and species*	Average unlit (SD)	Average lit (SD)	N
<b>Number Calling</b>			
All Species	3.696 (3.391)	2.910 (2.826)	89
<i>Acris crepitans</i>	6.500 (2.931)	5.248 (2.474)	42
<i>Incilius nebulifer</i>	1.706 (1.039)	1.100 (0.748)	16
<i>Eleutherodactylus marnockii</i>	0.900 (0.622)	0.600 (0.589)	4
<i>Lithobates catesbeianus</i>	0.720 (0.477)	0.573 (0.406)	15
<i>Lithobates berlandieri</i>	1.218 (0.724)	0.836 (0.543)	11
<b>Call Index</b>			
All Species	1.647 (0.928)	1.418 (0.970)	89
<i>Acris crepitans</i>	2.376 (0.640)	2.195 (0.748)	42
<i>Incilius nebulifer</i>	1.350 (0.663)	0.950 (0.618)	16
<i>Eleutherodactylus marnockii</i>	0.700 (0.383)	0.500 (0.416)	4
<i>Lithobates catesbeianus</i>	0.693 (0.453)	0.560 (0.408)	15
<i>Lithobates berlandieri</i>	1.018 (0.555)	0.691 (0.423)	11

\* *Pseudacris clarkii* not listed due to being heard only once

TABLE 2.—Comparison of linear mixed models and associated likelihoods for the best five models ( $\Delta AIC_C < 4$ ). The models predict difference in number of frogs calling between paired unlit and lit surveys. Species number, site number, site order, and lighting order were random effects. The models shown below represent fixed effects

Model	df	Log likelihood	AIC <sub>C</sub>	$\Delta AIC_C$	Weight
(Intercept Only)	6	-132.35	277.73	0.00	0.49
Wind (m/s)	7	-132.33	280.04	2.31	0.15
Precipitation (mm)	7	-132.46	280.30	2.57	0.14
Air Temperature (°C)	7	-132.49	280.36	2.63	0.13
Moonlight (%)	7	-132.89	281.16	3.43	0.09

DISCUSSION

Overall, the acute artificial lighting introduced to natural populations of anurans in central Texas reduced number of frogs heard calling and call index calling across all detected species (Fig. 1). Frogs did not stop calling entirely, a pattern that surely would have been previously uncovered. Instead, the decrease was more subtle, and in this study corresponded to just under one less frog calling per species on average during call surveys (Fig. 1; Table 1). The direct biological relevance of this slight decrease is unclear; however, these findings may be biologically meaningful because here I demonstrated that discrete artificial lighting affected frog breeding behavior in an urban anuran community. This observation agrees with previous studies (e.g., Buchanan, 1993; Baker and Richardson, 2006) which demonstrated that, in other species, artificial lighting affects nocturnal anuran behavior.

The regression test may have indirectly measured social facilitation whereby when more frogs called, noncalling frogs may have begun to call at a rate in a nonlinear relationship. Conspecific social facilitation would not be expected when individuals are tested on their own, such as in Baker and Richardson (2006). Controlling for social facilitation in a field experiment would require modifying chorus size, and since the goals of this study were to examine natural populations, facilitation could explain the degree of change or variance in calling behavior (i.e., heteroscedasticity). Social aspects of behavioral responses to artificial light warrant additional investigation (Kurvers and Hölker, 2015). Nevertheless, by using a difference scores in calling behaviors between paired experimental conditions, I have minimized within-site differences between responses to lighting conditions.

One or more factors or their interactions could yield the difference in calling scores observed between lit and unlit surveys. Therefore, four weather variables and their

TABLE 3.—Estimated coefficients and  $\pm 1.96$  SE confidence intervals for the best model after model averaging. The model relates the difference in number of frogs calling between paired unlit and lit surveys to environmental conditions

Variable	Estimate*	Unconditional SE	Confidence interval	Relative importance
(Intercept)	-0.303	0.366	(-1.02, 0.414)	-
Wind (m/s)	-0.039	0.013	(-0.064, -0.014)	0.15
Precipitation (mm)	0.030	0.111	(-0.187, 0.247)	0.14
Air Temperature (°C)	0.028	0.110	(-0.187, 0.243)	0.13
Moonlight (%)	0.005	0.069	(-0.130, 0.141)	0.09

\* Standardized using two SD (Gelman, 2008)



interactions between several systematic treatment conditions were modeled. Using a linear mixed modeling approach, marginal effects of environmental variables on the difference scores when accounting for differences between species, sites, survey order, and lighting order were found (Table 3). Confidence intervals for the average model's standardized coefficients include zero with one exception. Increased maximum wind speed corresponded to a slight decline in the difference between conditions. However, the null model enjoyed the most support as measured by  $AIC_C$  and no other models exhibited a  $\Delta AIC_C$  of  $< 2$  (Table 2). Therefore, it appears the experimental condition best predicted the difference in number of frogs calling between paired unlit and lit conditions.

By choosing to use difference scores as response variables, rather than the raw data across all species, it is difficult to infer from my data how environmental variables affect calling behavior in the broadest sense. Therefore, despite recovering linear mixed models with little influence of environmental variables affecting the difference between conditions, I cannot simultaneously explain how these environmental variables should change frog calling behavior. Assuming a field experiment, a more appropriate study design for testing these questions would involve covering greater geographic area, sampling more species, and measuring across more variable environmental conditions and ranges. Nevertheless, by testing the difference scores against environmental variables, it is clear that lighting condition constitutes the major determinant of calling behavior in this experiment.

Certainly, the decision to use a moving point light source as a stimulus probably affects the change in calling behavior when compared to a stationary point source or ambient lighting. For instance Baker and Richardson (2006) did not move their light source, nor did they need to as they measured responses of individual frogs of one species. By moving the light source in this study, I attempted to provide equivalent light saturation across the entire study site during a lit condition as opposed to a strongly illuminated point at the center of the beam and diffuse lighting along its periphery. By moving similarly in unlit trials, I hoped to eliminate the possibility for a change in calling behavior due to my movement alone, though it is not possible to rule this out entirely in this study. The introduced light likely adjusts the animal's photoperiod or disrupts dark adaptation (*sensu* Warrant, 1999). By including survey order (essentially earlier or later in the evening) and lighting order (potential dark adaptation disruption) as random effects in the linear mixed models, I have accounted for the effects of light other than the acute experimental addition of artificial light.

The decrease in number of calling anurans in lit conditions could have a detrimental impact to a population's reproductive efficiency, at least in the short term. Though not under investigation in this study, the link between calling effort and reproductive outcome is well supported (*e.g.*, Greer and Wells, 1980; Arak, 1983; Welch *et al.*, 1998). Although the relationship between calling variability and relative fitness remains untested in most anuran species, research focused on this relationship generally demonstrates that better male advertisement calls yield better individual reproductive outcomes (*e.g.*, greater female mate preference, more offspring sired, increased offspring phenotypic performance). Implicit to this observation is the hypothesis that if advertisement call quality worsens, individual reproductive outcomes also worsen. Anurans exhibit a great diversity of alternative mating strategies (Roberts, 1994; Greene and Funk, 2009; Meuche and Pröhl, 2011; Zhang *et al.*, 2012; Laufer *et al.*, 2014), and such species might deviate from this call-fitness pattern. Future experiments could investigate the link between changes in individual reproductive outcomes due to artificially imposed environmental stimuli (such as artificial light). Given the increasing global prevalence of artificial lighting (Cinzano *et al.*, 2001), natural anuran populations warrant increased focus on behavioral responses to artificial lighting.

*Acknowledgments.*—I thank B. Pierce for suggesting this research topic and thoughtful, helpful advice throughout the experiment and manuscript preparation. This project would not have been possible without his ever-present wisdom and charm. M. Cramer, N. Gordon, R. Burks, F. Guarraci, L. Hobgood-Oster and J. Hellmann provided key experimental design and manuscript advice. K. Rudd, G. Giuffre, S. Henderson, A. Schumacher, and K. McEntire assisted in the field. Financial support for this study was provided through the Bernard J. Hank Family Endowment, Fleming Funds, and Southwestern University.

## LITERATURE CITED

- ARAK, A. 1983. Sexual selection by male-male competition in natterjack toad choruses. *Nature*, **306**:261–262.
- BAKER, B. J. AND J. M. L. RICHARDSON. 2006. The effect of artificial light on male breeding-season behaviour in green frogs, *Rana clamitans melanota*. *Can. J. Zoolog.*, **84**:1528–1532.
- BARTOŃ, K. 2015. MuMIn: multi-model inference. R package version 1.13.4. <http://CRAN.R-project.org/package=MuMIn>.
- BATES, D., M. MAECHLER, B. BOLKER, AND S. WALKER. 2015. lme4: linear mixed-effects models using Eigen and S4. R package version 1.1-8. <http://CRAN.R-project.org/package=lme4>.
- BUCHANAN, B. W. 1993. Effects of enhanced lighting on the behaviour of nocturnal frogs. *Anim. Behav.*, **45**:893–899.
- . 2006. Observed and potential effects of artificial night lighting on anuran amphibians. p. 192–220. *In*: C. Rich and T. Longcore (eds.). *Ecological consequences of artificial night lighting*. Island Press, USA, 458 p.
- BURNHAM, K. P. AND D. R. ANDERSON. 2002. Model selection and multimodel inference: a practical information-theoretic approach, 2<sup>nd</sup> edn. Springer, Berlin. 488 p.
- CINZANO, P., F. FALCHI, AND C. D. ELVIDGE. 2001. The first world atlas of the artificial night sky brightness. *Mon. Not. R. Astron. Soc.*, **328**:689–707.
- DALY, M., P. R. BEHRENDIS, M. I. WILSON, AND L. F. JACOBS. 1992. Behavioral modulation of predation risk: moonlight avoidance and crepuscular compensation in a nocturnal desert rodent, *Dipodomys merriami*. *Anim. Behav.*, **44**:1–9.
- ELVIDGE, C. D., M. L. IMHOFF, K. E. BAUGH, V. R. HOBSON, I. NELSON, AND J. B. DIETZ. 2001. Nighttime lights of the world: 1994–95. *ISPRS J. Photogramm.*, **56**:81–99.
- GELMAN, A. 2008. Scaling regression inputs by dividing by two standard deviations. *Stat. Med.*, **27**:2865–2873.
- AND Y.-S. SU. 2015. arm: data analysis using regression and multilevel/hierarchical models. R package version 1.8-6. <http://CRAN.R-project.org/package=arm>.
- GRANDA, J. R., R. M. PENA, AND B. A. PIERCE. 2008. Effects of disturbance, position of observer, and moonlight on efficiency of anuran call surveys. *Appl. Herpetol.*, **5**:253–263.
- GREENE, A. E. AND W. C. FUNK. 2009. Sexual selection on morphology in an explosive breeding amphibian, the Columbia spotted frog (*Rana luteiventris*). *J. Herpetol.*, **43**:244–251.
- GREER, B. J. AND K. D. WELLS. 1980. Territorial and reproductive behavior of the tropical American frog *Centrolenella fleischmanni*. *Herpetologica*, **36**:318–326.
- GRIFFIN, P. C., S. C. GRIFFIN, C. WAROQUIERS, AND L. S. MILLS. 2005. Mortality by moonlight: predation risk and the snowshoe hare. *Behav. Ecol.*, **16**:938–944.
- GRUEBER, C. E., S. NAKAGAWA, R. J. LAWS, AND I. G. JAMIESON. 2011. Multimodel inference in ecology and evolution: challenges and solutions. *J. Evol. Bio.*, **24**:699–711.
- HEYER, W. R., M. A. DONNELLY, R. W. MCDIARMID, L. C. HAYEK AND M. S. FOSTER (eds.). 1994. *Measuring and monitoring biological diversity: standard methods for amphibians*. Smithsonian Institution Press, USA. 384 p.
- HURVICH, C. M. AND C.-L. TSAI. 1989. Regression and time series model selection in small samples. *Biometrika*, **76**:297–307.
- IBM CORP. 2013. IBM SPSS statistics for windows. Version 21.0.0.1. IBM Corp, Armonk, NY: IBM Corp.
- KURVERS, R. H. J. M. AND F. HÖLKER. 2015. Bright nights and social interactions: a neglected issue. *Behav. Ecol.*, **26**:334–339.

- LAUFER, G., N. GOBEL, J. M. MAUTONE, M. GALAN, AND R. O. DE SÁ. 2014. First report of satellite males during breeding in *Leptodactylus latrans* (Amphibia, Anura). *Cuad. Herpetol.*, **28**:1–2.
- LONGCORE, T. AND C. RICH. 2004. Ecological light pollution. *Front. Ecol. Environ.*, **2**:191–198.
- MEUCHE, I. AND H. PRÖHL. 2011. Alternative mating tactics in the strawberry poison frog (*Oophaga pumilio*). *Herpetol. J.*, **21**:275–277.
- MEYER-ARENDE, J. R. 1968. Radiometry and photometry: units and conversion factors. *J. Appl. Opt.*, **7**:2081–2084.
- MOUGEOT, F. AND V. BRETAGNOLLE. 2000. Predation risk and moonlight avoidance in nocturnal seabirds. *J. Avian Biol.*, **31**:376–386.
- NELSON, G. L. AND B. M. GRAVES. 2004. Anuran population monitoring: comparison of the North American Amphibian Monitoring Program's calling index with mark-recapture estimates. *J. Herpetol.*, **38**:355–359.
- OSEEN, K. L. AND R. J. WASSERSUG. 2002. Environmental factors influencing calling in sympatric anurans. *Oecologia*, **133**:616–625.
- PERRY, G., B. W. BUCHANAN, R. N. FISHER, M. SALMON, AND S. E. WISE. 2008. Effects of artificial night lighting on amphibians and reptiles in urban environments. p. 239–256. *In*: J. C. Mitchell, R. E. Jung Brown and B. Bartholomew (eds.). Urban herpetology. Society for the Study of Amphibians and Reptiles, USA. 608 p.
- PIERCE, B. A. AND K. J. GUTZWILLER. 2004. Auditory sampling of frogs: detection efficiency in relation to survey duration. *J. Herpetol.*, **38**:495–500.
- AND ———. 2007. Interobserver variation in frog call surveys. *J. Herpetol.*, **41**:424–429.
- PIERCE, B. A. AND A. S. HALL. 2013. Call latency as a measure of calling intensity in anuran auditory surveys. *Herp. Con. Bio.*, **8**:199–206.
- R CORE TEAM (2015). R: A language and environment for statistical computing. R Foundation for Statistical Computing, Vienna, Austria. <http://www.R-project.org/>
- RIEGEL, K. W. 1973. Light pollution. *Science*, **179**:1285–1291.
- ROBERTS, W. W. 1994. Explosive breeding aggregations and parachuting in a neotropical frog, *Agalychnis saltator* (Hylidae). *J. Herpetol.*, **28**:193–199.
- RYAN, M. J. (ed.). 2001. Anuran communication. Smithsonian Institution Press, USA. 252 p.
- SAENZ, D., L. A. FITZGERALD, K. A. BAUM, AND R. N. CONNER. 2006. Abiotic correlates of anuran calling phenology: the importance of rain, temperature, and season. *Herpetol. Monogr.*, **20**: 64–82.
- SHIROSE, L. J., C. A. BISHOP, D. M. GREEN, C. J. MACDONALD, R. J. BROOKS, AND H. J. HELFERTY. 1997. Validation tests of an amphibian call count survey technique in Ontario, Canada. *Herpetologica*, **53**:312–320.
- SKUTELSKY, O. 1996. Predation risk and state-dependent foraging in scorpions: effects of moonlight on foraging in the scorpion *Buthus occitanus*. *Anim. Behav.*, **52**:49–57.
- STEELMAN, C. K. AND M. E. DORCAS. 2010. Anuran calling survey optimization: developing and testing predictive models of anuran calling activity. *J. Herpetol.*, **44**:61–68.
- STEEN, D. A., C. J. W. McCLURE, AND S. P. GRAHAM. 2013. Relative influence of weather and season on anuran calling activity. *Can. J. Zoolog.*, **91**:462–467.
- VERHEIJEN, F. J. 1985. Photopollution: artificial light optic spatial control systems fail to cope with. Incidents, causations, remedies. *Exp. Biol.*, **44**:1–18.
- WARRANT, E. J. 1999. Seeing better at night: life style, eye design and the optimum strategy of spatial and temporal summation. *Vision Res.*, **39**:1611–1630.
- WEIR, L. A. AND M. J. MOSSMAN. 2005. North American Amphibian Monitoring Program (NAAMP). p. 307–313. *In*: M. LANNOO (ed.). Amphibian declines: conservation status of United States species. University of California Press, Berkeley, C. 1115. A.
- , J. A. ROYLE, P. N. NANJAPPA, AND R. E. JUNG. 2005. Modeling anuran detection and site occupancy on North American Amphibian Monitoring Program (NAAMP) routes in Maryland. *J. of Herpetol.*, **39**:627–639.
- WELCH, A. M., R. D. SEMLITSCH, AND H. C. GERHARDT. 1998. Call duration as an indicator of genetic quality in male gray tree frogs. *Science*, **280**:1928–1930.

- WISE, S. 2007. Studying the ecological impacts of light pollution on wildlife: amphibians as models. p. 209–218. *In*: C. Marín and J. Jafari (eds.). *Starlight: a common heritage*. Available from <http://www.starlight2007.net/pdf/StarlightCommonHeritage.pdf> (accessed November 2011). 497 p. Archived by WebCite at <http://www.webcitation.org/66Pw0fNNC> on 23 March 2012.
- ZHANG, L., J. YANG, Y. LU, X. LU, AND X. CHEN. 2012. Aquatic eggs are fertilized by multiple males not engaged in amplexus in a stream-breeding frog. *Behav. Process.*, **91**:304–307.

SUBMITTED 19 MAY 2015

ACCEPTED 19 DECEMBER 2015