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Social facilitation is a better predictor of frog reproductive activity than environmental factors

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ABSTRACT

Anuran breeding activity is frequently linked to environmental factors, mainly temperature and rainfall. However, a key feature of anuran reproductive behavior—gathering in choruses and producing loud advertisement calls to attract females—generates a conspicuous social cue that may also facilitate reproductive behavior. Here, I examine the relative importance of environmental and social factors in explaining the intensity of reproductive activity in the Neotropical treefrog *Hypsiboas rosenbergi*. I show that social cues generally play an important role, but that there are sex differences: male behavior is associated with a combination of environmental and social factors, while female behavior is associated almost exclusively with social cues. I discuss the potential benefits of using social cues in regulating breeding activity, and suggest that conservation efforts may take advantage of the apparently widespread pattern of social facilitation in anuran reproductive ecology.

Abstract in Spanish is available with online material.

Key words: calling activity; chorus size; Costa Rica; *Hypsiboas rosenbergi*; lunar cycle; lunar illumination; precipitation; temperature.

When to breed is one the most important decisions in the life of any organism. Reproduction is often energetically costly (Ryser 1989, Grafe *et al.* 1992), and in order to maximize fitness, the timing of reproduction should coincide with favorable environmental conditions. Determining the factors that regulate the onset and intensity of reproduction of a given taxon is thus of empirical interest because it informs our understanding of life history evolution, and it has also important practical applications for predicting how populations may respond to global change.

Since anuran amphibians are ectothermic organisms with permeable skin and largely aquatic reproduction (Duellman & Trueb 1994, Wells 2007), it is perhaps not surprising that studies seeking to explain how their reproductive activity is regulated frequently focus on environmental factors. Indeed, temperature and rainfall are common correlates of anuran reproduction (Blankenhorn 1972, Fukuyama & Kusano 1992, Henzi *et al.* 1995, Oseen & Wassersug 2002), as are drops in barometric pressure, humidity, moisture, wind, photoperiod, moonlight intensity, and lunar cycle (Bellis 1962, Heinzmann 1970, FitzGerald & Bider 1974, Obert 1975, Jaeger *et al.* 1976, Henzi *et al.* 1995, Hatano *et al.* 2002, Both *et al.* 2008, Grant *et al.* 2013, Johnson *et al.* 2013, Steen *et al.* 2013).

Males of most anuran species produce loud advertisement calls (Gerhardt & Huber 2002, Wells 2007). This key feature of anuran breeding behavior creates a prominent social cue that in itself has the potential to influence reproductive behavior. For example, hearing conspecific mating calls can change reproductive physiology in frogs (*i.e.*, Burmeister & Wilczynski 2004). Also, when not actively breeding, anurans often disperse into the surrounding terrestrial habitat (Johnson & Semlitsch 2003, Smith & Green 2005), and the sounds of a conspecific chorus may serve as social information on which to base decisions about the current location of the breeding aggregation, the timing of breeding, or both (Gerhardt & Klump 1988, Bee 2007, Swanson *et al.* 2007, Buxton *et al.* 2015, Yasumiba *et al.* 2015). The few studies that have investigated whether social facilitation—in addition to environmental factors—may affect the intensity of anuran reproductive activity indeed found that chorus size is often strongly correlated with increased reproduction (Ritke *et al.* 1992, Henzi *et al.* 1995, Brooke *et al.* 2000, Murphy 2003, Llusia *et al.* 2013).

The relative importance of social and environmental factors in regulating anuran reproductive activity is not only interesting from a behavioral ecology viewpoint, it also has conservation implications. Amphibians are one of the taxa showing the strongest decline during the current biodiversity crisis (Stuart *et al.* 2004), which may at least partly be exacerbated by the effects of global climate change (Pounds *et al.* 2006). While some environmental factors (*i.e.*, lunar cues) will remain constant, weather-related factors (*i.e.*, temperature, rainfall patterns) are predicted to become different as a consequence of global climate change. Indeed, Touchon (2012) has already documented that precipitation patterns in Central Panama have changed over the past 40 years. Knowledge about which factors most strongly affect reproductive activity in anurans may thus help better predict the effects of climate change for this group of organisms. Finding a strong influence of social facilitation would not only suggest that climate change might be less problematic for anurans than

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currently feared, but would also suggest management strategies for existing populations. Buxton *et al.* (2015) recently showed that anurans are attracted to chorus sounds, and suggested that managers could use call playbacks to assist in colonization of mitigation wetlands and other protected sites. If social cues also play a role in regulating the intensity of anuran reproduction, then playbacks might also be useful in fostering reproduction within existing breeding sites.

Another conservation-related topic where knowledge about the factors influencing anuran breeding intensity takes center stage is population monitoring. Anuran populations are declining worldwide, and programs that use calling surveys have been established to monitor their populations (*i.e.*, Weir & Mossman 2005). The availability of automated recording devices allows for the monitoring of more populations than site visits by human observers could accomplish, while at the same time reducing the probability of missing the presence of species because they did not call during the (short) time the observer was present (Bridges & Dorcas 2000). But, how useful are call surveys that focus on calling males for capturing the criterion that is most important for conservation – successful reproduction and thus, population maintenance?

The above question arises because of an important consideration that is often overlooked when examining determinants of anuran reproductive activity: reproduction has two components that are connected but not necessarily matched: (1) the males that gather at suitable breeding sites and call to attract mates generally participate in the chorus for several consecutive nights; and (2) the females that approach the breeding site only when they are ready to lay eggs, and only do so every few weeks or even only once per season (Perrill & Daniel 1983, Höbel 2000). As a consequence, the ratio of fertilizable females to sexually active males at the site and time when mating occurs, *i.e.*, the operational sex ratio (Emlen & Oring 1977), tends to be heavily male biased in frogs (Kluge 1981, Howard & Kluge 1985, Bourne 1992, Höbel 2000). Thus, calling generally occurs much more often than actual reproduction (Fukuyama & Kusano 1992, Marsh 2000, Van Sluys *et al.* 2006). Yet, call monitoring programs, as well as many studies examining determinants of anuran reproductive activity, do not collect evidence for actual reproduction, but use advertisement calls as a surrogate for breeding activity (*i.e.*, Ospina *et al.* 2013, but see Fukuyama & Kusano 1992, Marsh 2000, Van Sluys *et al.* 2006). Because female arrival, not male calling activity, is the critical factor determining anuran reproduction, using male calling as a surrogate is only warranted if both sexes respond to social and environmental factors in similar ways.

Despite the long-standing interest in the factors that determine anuran reproductive activity and their important practical conservation applications, we know relatively little about whether social or environmental factors play a larger role in determining the intensity of anuran reproductive activity (but see Ritke *et al.* 1992, Brooke *et al.* 2000, Llusia *et al.* 2013), or whether males and females attend to the same factors (but see Henzi *et al.* 1995, Murphy 2003). Here I investigate the determinants of reproductive activity of a Neotropical frog, *Hypiboas rosenbergi*, and test two hypotheses about the relative importance of social and environmental cues. The first hypothesis centers on a key feature of anuran reproduction—male calls. It states that social cues are more important in regulating anuran reproductive activity than environmental ones. This hypothesis makes the predictions that (1) there is a positive relationship between the intensity of the social cue and the magnitude of reproductive activity, and (2) that inclusion of social cues into the predictor model reduces the number of significant environmental variables that explained the intensity of reproductive activity. The second hypothesis deals with how reproductive activity is synchronized between the sexes. This hypothesis makes the prediction that the same cues that influence male calling activity also influence female reproduction.

METHODS

Study Species and Study Site.—I studied the reproductive activity of the gladiator frog *Hypsiboas rosenbergi* at La Gamba Biological Station, Puntarenas Province, Costa Rica. The choruses formed in a cattle pasture, adjacent to a forest (where frogs spent the day). I studied the population for a four-month period (May–August 1995), and sampling effort (about 2 hours/night) was sufficiently intense to yield representative data for 79 nights. All frogs were toe-clipped to facilitate individual identification.

Males only call from within small water-filled basins that they either built themselves, or they find a suitable natural basins to occupy (Höbel 1999). These basins serve as obligatory oviposition sites for the females (Kluge 1981, Höbel 2000). Early embryonic and larval development occurs in the basins, and eventually heavy rains flood the basins and the tadpoles are carried to larger bodies of water where they complete their development.

Sampling of Environmental Factors.—I sampled three categories of environmental factors: Temperature, precipitation, and lunar cues. Every day I collected data on the daily minimum (T_{min}) and maximum (T_{max}) temperature using an analog min-max thermometer, and precipitation data using a rainfall gauge (Prec). This precipitation data represents the cumulative rainfall over the previous 24 hours, *i.e.*, it is a measure of magnitude. The timing of rainfall may be just as important in determining frog activity, but it was logistically not feasible to sample precipitation at a finer scale.

The lunar cycle provides several rhythmic temporal cues that animals could use to time important group events. For example, gravitational forces peak twice per lunar cycle (at new and full moons), and the geomagnetic field peaks during the moon's third quarter (Bell & Defouw 1966). Furthermore, throughout the course of the lunar cycle, light levels can vary by nearly two orders of magnitude (Campbell *et al.* 2009), and the environmental variation in nighttime light levels associated with waning and waxing phases of the moon may also affect the behavior of nocturnal animals. I used two measures to test for moon-related effects on frog breeding activity: (1) to express lunar cycle, I assigned each observation night a value, calculated as the days since full moon divided by 29.5 (where 0 represents the full moon, and the number of days in the lunar cycle is 29.5). Then I multiplied the results obtained by 360° (0° = 360° = full moon; 180° = new moon) (Grant *et al.*, 2009). (2) to obtain an estimate of nocturnal light levels (henceforth 'illumination'), I looked up % lunar disk illumination data for the study area. Here, lunar light is at its peak at full moon and at its minimum at new moon, and this measure also conveys that the first and third quarter are different lunar phases, but equally bright in terms of lunar light provided. Lunar cycle and illumination data for the study area (Golfito, Costa Rica) were obtained from the website http://timeanddate.com.

SAMPLING OF REPRODUCTIVE BEHAVIOR AND SOCIAL CUES.—To quantify male reproductive behavior, I counted the maximum number of calling males that participated in the chorus each night. These data also served as the measure of the social factor (activity of calling conspecifics) incorporated in the predictor models.

To quantify female reproductive behavior, I searched for mated females, taking advantage of the central role the basins play in the reproduction of this species. During the course of the evening when calling activity was high, I marked occupied basins with plastic flags, and later checked the marked basins for the presence of egg-laying females or clutches.

STATISTICAL ANALYSIS.—To investigate the factors affecting reproductive activity in *H. rosenbergi*, I considered the following variables obtained from the same day in which calling and mating data were obtained: T_{min}, T_{max}, Prec, illumination, lunar cycle, and same day chorus size. Because there may be a time lag in the effectiveness of environmental and social factors, I further considered the previous' day measures T_{min}-1, T_{max}-1, Prec-1, chorus size-1.

Some factors were highly correlated (*i.e.*, present and previous day illumination, or present and previous day lunar cycle). Whenever factors were statistically significantly correlated at P <0.05, I removed one from the model (the previous day measure). The exception was chorus size. Although present and previous day chorus sizes were correlated (r = 0.49, P < 0.0001), I consider them discrete data sets because of (1) the low chorus tenure in *H. rosenbergi* (Höbel 2000), and (2) the observation that even males that participate in the chorus for several nights generally did not do so in consecutive nights; in 67 percent of the times a male was observed in the chorus, he did not return the following night. Thus, the majority of males making up the chorus in consecutive nights are males that newly joined the chorus, not males that remained in the chorus from the previous day.

I analysed the effect of environmental and social cues on frog breeding activity in a two-step process. First, I used the Akaike Information Criterion (Akaike 1973) to select the best of several candidate models (below). Then I used these best-supported models to evaluate the effect that particular environmental and social factors had on frog activity. In all models, the measure of frog activity (male chorus size or number of mating female, respectively) was entered as the dependent variable, and up to 10 factors (environmental: T_{min}, T_{max}, Prec, illumination, lunar cycle, T_{min}-1, T_{max}-1, Prec-1; social: chorus size and chorus size-1) were entered as predictor variables (see Table 1). All models were implemented in JMP 12.1.0 (SAS Institute, Cary, NC, USA).

Using an information-theoretic approach, I assessed mixed models via AIC (Akaike Information Criterion; Akaike 1973) after correcting for small sample size by using AIC$_C$ (Burnham & Anderson 2002). Following initial global model analyses, I selected nine candidate models that focused on present versus previous day data, or environmental factors versus social cues respectively (see Table 1). Candidate models with the greatest Akaike weight (ω), which determines the probability of that model being the best among the candidate models, were considered supported (Mazerolle 2006). Models within 2 AIC units from the best model also suggest substantial evidence for the model, while models within 3–7 AIC units from the best model have considerable less support, and models > 10 AIC units removed are very unlikely to be true (Mazerolle 2006).

TABLE 1. *Nine candidate models including environmental and social factors used to evaluate determinants of reproductive activity in* Hypsiboas rosenbergi *frogs (−1 denotes previous day values).*

Model type		Model	Parameters
Global	1	Global$_{\text{(environ. \& social)}}$	T_{min} T_{max} Prec Illumination Lunar Cycle $T_{min}-1$ $T_{max}-1$ Prec-1 Chorus size Chorus size-1
Global	2	Global$_{\text{(same day)}}$	T_{min} T_{max} Prec Illumination Lunar Cycle Chorus size
Global	3	Global$_{\text{(prev. day)}}$	T_{min}-1 $T_{max}-1$ Prec-1 Illumination-1 Lunar Cycle -1 Chorus size-1
Environ.	4	Environ.$_{\text{(same \& prev. day)}}$	T_{min} T_{max} Prec Illumination Lunar Cycle $T_{min}-1$ $T_{max}-1$ Prec-1
Environ.	5	Environ.$_{\text{(same day)}}$	T_{min} T_{max} Prec Illumination Lunar Cycle
Environ.	6	Environ.$_{\text{(prev. day)}}$	$T_{min}-1$ $T_{max}-1$ Prec-1 Illumination-1 Lunar Cycle-1
Social	7	Social$_{\text{(same \& prev. day)}}$	Chorus size Chorus size-1
Social	8	Social$_{\text{(same day)}}$	Chorus size
Social	9	Social$_{\text{(prev. day)}}$	Chorus size-1

I calculated separate models to describe male reproductive behavior (calling in a chorus) and female reproductive activity (amplexus and mating). Because male frogs generally arrive at the chorus before females (*i.e.*, Henzi *et al.* 1995, Murphy 2003, pers. obs), it seems unlikely that males can assess the number of females that will arrive at the breeding site; by contrast, male advertisement calls allow females to assess the number of males in the chorus. Consequently, I included the male chorus size term in the female models, but did not include a female term in the male models.

Finally, I also evaluated the effect of the lunar cycle on male and female reproductive activity using circular statistics (Oriana v. 3.21; Kovach Computing Services, Anglesey, Wales, UK). I tested the null hypothesis that frog reproductive activity was uniformly distributed over the lunar cycle using Rao's spacing tests.

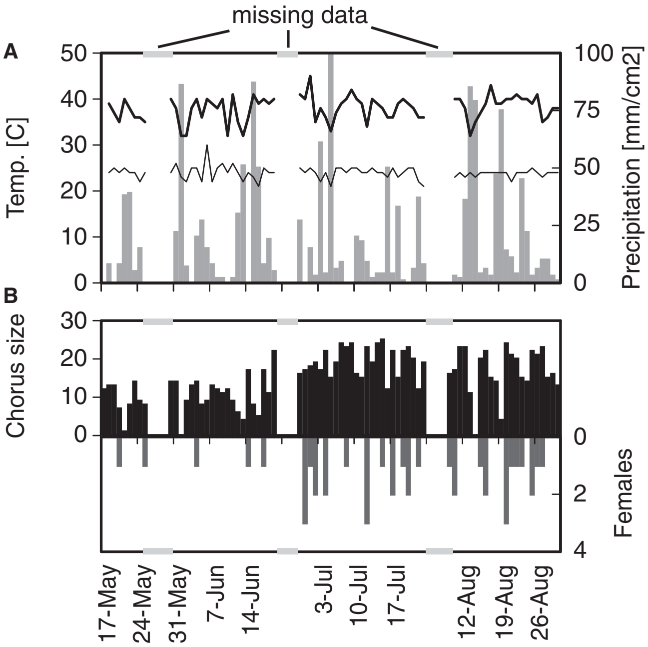

FIGURE 1. Variation in daily rainfall (Prec; light gray bars) and temperature ($T_{\min}$, $T_{\max}$; thin and thick black line, respectively) during the study period (A). Variation in reproductive activity of male (black bars) and female (dark gray bars) *Hypsiboas rosenbergi;* note that chorusing occurred much more frequently than breeding (B). Three gaps in the timeline indicate periods where no / too little sampling occurred.

RESULTS

Variation in Environmental Factors.—Rainfall and temperature was typical for a tropical rainy season. Precipitation was frequent (on 87% of observation days). Average (±SD) daily precipitation was 19.4 ± 25.4 mm (range 0–100 mm), and several major rainfall events (>50 mm/cm^2/day) occurred at regular intervals (Fig. 1A). Daily minimum and maximum temperature was also quite regular (Fig. 1A). Average (±SD) $T_{\min}$ was 24 ± 1.3°C (range 21–30°C), $T_{\max}$ was 38.1 ± 2.7°C (range 32–46°C).

Variation in Reproductive Activity.—There was within-season variation in both chorusing activity and breeding activity, and chorusing occurred more frequently than breeding (Fig. 1B). Chorus size varied between 0–25 males (mean ± SD = 16 ± 6 males), but nights without chorusing activity were very rare. Male chorus tenure was generally short (mean: 3 ± 2.6 nights; mode = 2), and males never called more than two consecutive nights in a row; females were never observed more than once. The operational sex ratio across the breeding season was male biased 2.2:1 (see also Höbel 2000). Breeding activity varied between 0–3 breeding pairs per night, and in 54 percent of observation nights no breeding took place.

Effect of Environmental and Social Factors on Reproductive Activity.—Within the candidate model set for male chorusing activity (Table 2), the model that garnered the highest support was the global model that included both present and previous day environmental and social factors. All other models were poorly supported. Closer examination of the global model (Fig. 2, Table 3) revealed that chorusing activity was mainly correlated with same day precipitation (with heavy rainfall decreasing chorusing activity; Fig. 2E), and previous day chorus size (with larger choruses increasing chorusing activity; Fig. 2I).

TABLE 2. *Reproductive activity of male* Hypsiboas rosenbergi *assessed using mixed models and AICc. Models in bold gained the most support.*

Model no.	Model type	No. parameters	AIC$_C$	Δ AIC$_C$	Akaike weight (ω)
1	**Global$_{\text{(environ. \& social)}}$**	**10**	**171.25**	**0**	**0.99**
2	Global$_{\text{(same day)}}$	NA – same as model 5			
3	Global$_{\text{(prev. day)}}$	6	196.04	24.39	5.1 e-6
4	Environ.$_{\text{(same \& prev. day)}}$	8	207.86	36.21	1.4 e-8
5	Environ.$_{\text{(same day)}}$	5	223.44	51.78	5.7 e-12
6	Environ.$_{\text{(prev. day)}}$	5	230.53	58.87	1.6 e-13
7	Social$_{\text{(same \& prev. day)}}$	1	201.61	29.95	3.1 e-7
8	Social$_{\text{(same day)}}$	NA – same as model 7			
9	Social$_{\text{(prev. day)}}$	NA – same as model 7			

Within the candidate model set for female breeding activity (Table 4), the model that garnered the highest support was the global social model, which included both present and previous day chorus size. Closer examination of the global social model (Fig. 3; Table 5) revealed that female breeding activity was mainly correlated with present day chorus size (Fig. 3I). None of the models involving environmental factors were supported (Table 4).

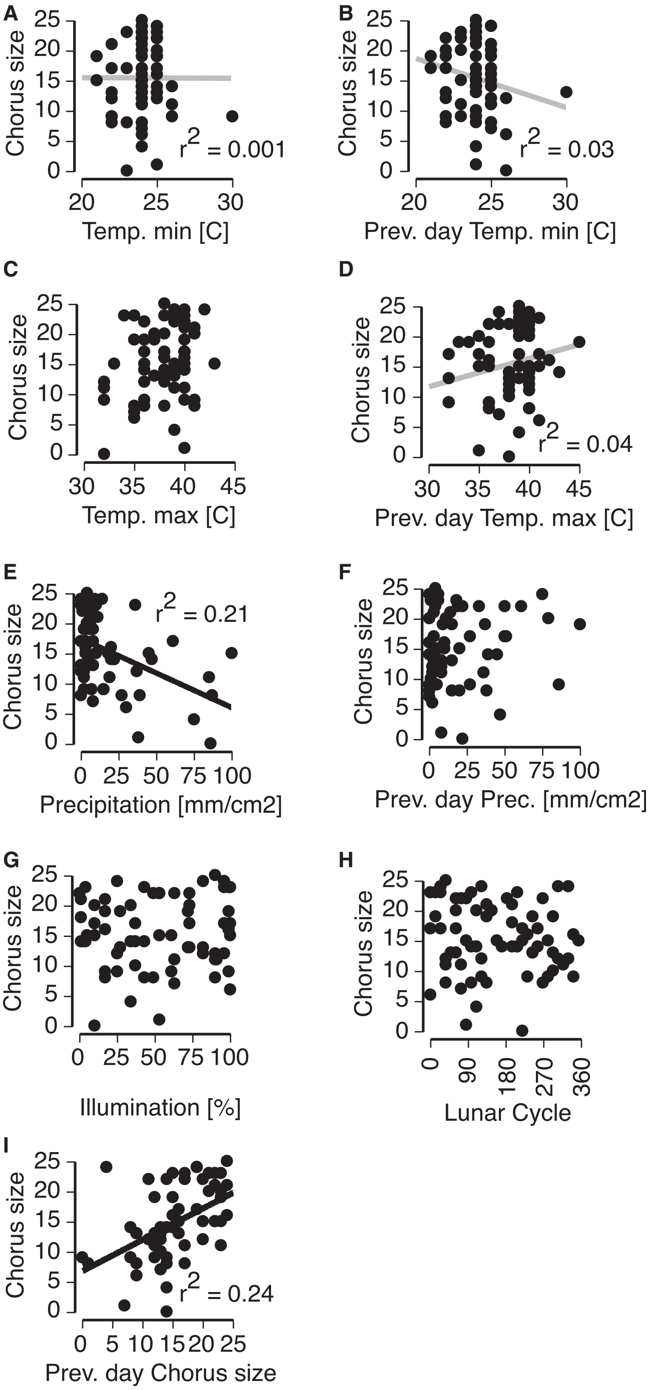

FIGURE 2. Influence of environmental (A–H) and social (I) factors on calling activity of male *Hypsiboas rosenbergi*. Significant factors are indicated by the addition of a linear regression line (and r^2 value) in the panels. Black line indicates significant effect in the best supported model (see Table 3), gray lines indicate significant effects in the reduced (environmental only; Table 6) model.

Since many studies investigating anuran reproductive activity only focus on environmental factors (but see Ritke *et al.* 1992, Henzi *et al.* 1995, Brooke *et al.* 2000, Murphy 2003, Llusia *et al.* 2013), I searched the model set for the most strongly supported model containing only environmental factors. For males, this was the global environmental model. Closer examination of this model (Fig. 2; Table 6) showed that chorusing activity was mainly correlated with Prec, T_{max}-1, T_{min} and T_{min}-1 (Fig. 2A,B,D). For females, the best-supported environmental model was the one containing only previous day data. Closer examination of this model (Fig. 3, Table 7) revealed that female breeding activity was only correlated with T_{max}-1 (Fig. 3D). Thus, if analysis is limited to environmental factors, only one factor affects both sexes: T_{max}-1 is positively related to both male chorusing activity and female breeding activity.

TABLE 3. *Environmental (E) and social (S) factors affecting male chorusing activity; shown are details for Model 1, the model that garnered the highest support during model selection (see Table 2). Significant factors are set in bold.*

Type	Source	df	*F*	*P*
E	T_{min}	1, 43	2.96	0.09
E	T_{max}	1, 43	1.59	0.21
E	**Prec**	**1, 43**	**24.47**	**<0.0001**
E	Illumination	1, 43	1.53	0.22
E	Lunar Cycle	1, 43	0.08	0.78
E	T_{min} −1d	1, 43	1.47	0.23
E	T_{max} −1d	1, 43	3.47	0.07
E	Prec −1d	1, 43	3.93	0.054
S	**Chorus size −1d**	**1, 43**	**18.55**	**<0.0001**

TABLE 4. *Reproductive activity of female* Hypsiboas rosenbergi *assessed using mixed models and AICc. Models in bold gained the most support.*

Model no.	Model	No. parameters	$\mathrm{AIC_C}$	$\Delta\ \mathrm{AIC_C}$	Akaike weight (ω)
1	$\mathrm{Global}_{\text{(environ. \& social)}}$	10	−7.40	13.90	0.001
2	$\mathrm{Global}_{\text{(same day)}}$	6	−3.19	18.11	0.0001
3	$\mathrm{Global}_{\text{(prev. day)}}$	6	−10.53	10.77	0.005
4	$\mathrm{Environ.}_{\text{(same \& prev. day)}}$	8	−0.57	20.73	3.2 e-5
5	$\mathrm{Environ.}_{\text{(same day)}}$	5	−1.02	20.28	4.0 e-5
6	$\mathrm{Environ.}_{\text{(prev. day)}}$	5	−7.57	13.73	0.001
7	$\mathbf{Social}_{\textbf{(same \& prev. day)}}$	**2**	**−21.30**	**0**	1.0
8	$\mathrm{Social}_{\text{(same day)}}$	1	−16.29	5.01	0.08
9	$\mathrm{Social}_{\text{(prev. day)}}$	1	−14.88	6.42	0.04

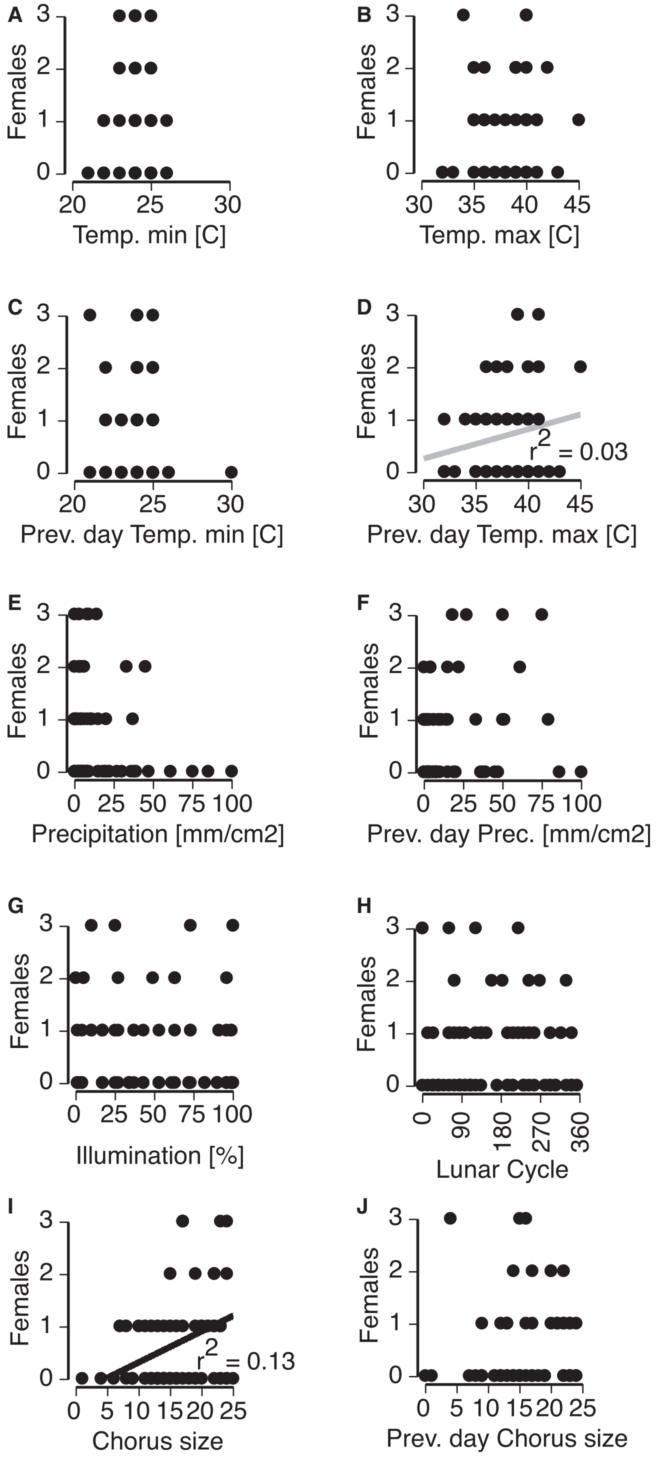

FIGURE 3. Influence of environmental (A–H) and social (I, J) factors on breeding activity of female *Hypsiboas rosenbergi*. Significant factors are indicated by the addition of a linear regression line (and r^2 value) in the panels. Black line indicates significant effect in the best supported model (Table 5), gray lines indicate significant effects in the reduced (environmental only, Table 7) model.

TABLE 5. *Social cues affecting female reproductive activity; shown are details for Model 7, the model that garnered the highest support during model selection (see Table 4). Significant factors are set in bold.*

Type	Source	df	*F*	*P*
S	**Chorus size**	**1, 52**	**7.21**	**0.0097**
S	Chorus size −1d	1, 52	0.87	0.35

TABLE 6. *Environmental factors affecting male calling activity; shown are details for model 4, the model focusing on only environmental factors that garnered the highest support during model selection (see Table 2). Significant factors are set in bold.*

Type	Source	df	*F*	*P*
E	$\mathbf{T_{min}}$	**1, 52**	**7.36**	**0.009**
E	$T_{\max}$	1, 52	3.12	0.083
E	**Prec**	**1, 52**	**18.34**	**<0.0001**
E	Illumination	1, 52	4.02	0.051
E	Lunar Cycle	1, 52	0.02	0.90
E	$\mathbf{T_{min}}$ **−1d**	**1, 52**	**5.32**	**0.025**
E	$\mathbf{T_{max}}$ **−1d**	**1, 52**	**8.75**	**0.005**
E	Prec −1d	1, 52	0.04	0.84

TABLE 7. *Environmental factors affecting female reproductive activity; shown are details for model 6, the model focusing on only environmental factors that garnered the highest support during model selection (see Table 4). Significant factors are set in bold.*

Type	Source	df	*F*	*P*
E	$T_{\min}$ −1d	1, 55	2.19	0.14
E	$\mathbf{T_{max}}$ **−1d**	**1, 55**	**4.86**	**0.032**
E	$\text{Prec}_{24\ \text{hours}}$ −1d	1, 55	0.88	0.35
E	Illumination −1d	1, 55	0.80	0.37
E	Lunar Cycle −1d	1, 55	0.45	0.50

The moon had at best a weak effect on reproductive activity of gladiator frogs. Illumination never had an effect on male or female reproductive activity (Tables 3 and 6), suggesting that variation in light levels associated with the lunar phases did not affect reproduction in the frogs. Lunar cycle, when included in models with other factors (Tables 3, 6–7), was not correlated with reproductive behavior. However, when using circular statistics, i.e., focusing only on this single factor, then a relationship became apparent: Both male chorusing activity (Rao's spacing test: U = 349.0, $P < 0.01$) and female breeding activity (U = 171, $P < 0.01$) were not randomly distributed across the lunar cycle; both peaked around the waning moon (chorusing activity: mean vector $\mu = 61°$; oviposition: $\mu = 110°$) (Fig. 4).

SEX DIFFERENCES IN THE EFFECT OF ENVIRONMENTAL AND SOCIAL FACTORS ON REPRODUCTIVE ACTIVITY.—There were some stark differences as well as similarities in the factors regulating reproductive activity in male and female *H. rosenbergi*. Sex differences

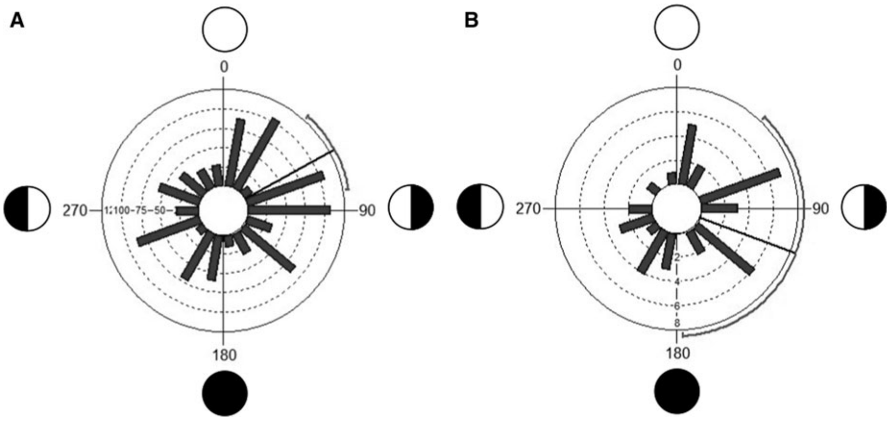

FIGURE 4. Circular diagrams showing male calling activity (A) and female reproductive activity (B) as a function of the lunar cycle. Bars indicate the number of males or females respectively; the black line indicates the mean vector (μ) and the external black curved line represents 95% confidence intervals. 0° = full moon; 180° = new moon.

manifested mainly in the importance of social facilitation. First, while male reproductive activity was correlated with environmental factors in addition to social cues (see Tables 2, 3 and 6), female reproductive activity was dominated by social cues (Tables 4–5). Second, the social cue that was most strongly attended to differed between the sexes: male chorusing activity was influenced by previous day chorus size (Table 3; Fig. 2I), while female breeding activity was influence by same day chorus size (Table 5, Fig. 3I).

There were also some similarities between the sexes, namely that higher previous day maximum temperatures ($T_{\max}$-1) increasing reproductive activity in both sexes (Figs. 2D and 3D), and that both chorusing and breeding activity peaked around the waning moon (Fig. 4). It is important to keep in mind, however, that these similarities only become apparent when social cues are removed from the analysis.

DISCUSSION

The intensity of reproductive activity in *H. rosenbergi* frogs varied across the breeding season, and was correlated with social cues, and to a lesser degree, with environmental factors. Male behavior is affected by both environmental and social factors, while female behavior is dominated by social cues, with environmental factors playing a secondary role. Since this was a correlational study, one might wonder that if male activity is correlated with environmental factors, and female activity is correlated with social cues (i.e., males), then how can one be sure that females are not simply affected by the same environmental factors as males? The results of the reduced models (environmental factors only) help settle this question: When social cues are removed, male behavior is still correlated with several environmental factors, while female behavior is still only correlated with one environmental factor. Thus, females are likely not unaffected by environmental factors, but any small, or indirect, effects are simply overshadowed by the stronger influence of social cues.

IMPORTANCE OF SOCIAL CUES.—Data from *H. rosenbergi* matches a pattern that is emerging from the anuran literature: Chorus noise may act as a social cue that affects chorus visitation rates, and whenever social facilitation is taken into account, it is always found to play a role in regulating anuran reproductive activity. The degree to which social cues matter, however, can vary. In some species social cues do play a role in determining reproductive activity, but environmental factors are more important (Henzi *et al.* 1995). In others, social cues have a greater predictive ability in terms of calling activity than environmental factors (Brooke *et al.* 2000, Murphy 2003, Llusia *et al.* 2013, this study). And in some, the only significant predictor of the intensity of male and female reproductive activity was the number of individuals of the opposite sex (Ritke *et al.* 1992).

EFFECT OF ENVIRONMENTAL VARIABLES.—Calling activity in *H. rosenbergi* frogs was negatively influenced by strong same day precipitation, and positively influenced by previous-day $T_{\max}$. This is a rather typical pattern for tropical frogs. While reproductive activity is usually influenced by both temperature and rainfall in temperate anurans (*e.g.*, Blankenhorn 1972, Sinsch 1988, Murphy 2003), in the tropics temperatures are amenable for anuran development year-round and breeding activity is mainly influenced by rainfall (i.e., Gottsberger & Gruber 2004). While moderate rainfall is generally beneficial for breeding, it is quite common for excessive same-day rainfall to suppress calling activity (Kluge 1981, Henzi *et al.* 1995; this study). Late afternoon/early evening rainfall often coincides with the start of male calling activity, and acoustic interference from storm noise that reduces the efficacy of advertisement calls, or the mechanical disturbance associated with strong tropical rainstorms may curb calling in males. That previous-day $T_{\max}$ facilitated reproductive activity may suggest that very high same day temperatures suppressed breeding activity during that night, which is then compensated by increased activity the following night. Note however that the effect of temperature was weak, since it was only apparent once social cues were excluded.

There are considerable species differences in how amphibians respond to the moon (Grant *et al.* 2013). Some species show increased activity under full moon (Tuttle & Ryan 1982, Johnson *et al.* 2013), others decrease activity under full moon (FitzGerald & Bider 1974, Vignoli & Luiselli 2013, this study), and some species show no apparent influence at all (Hauselberger & Alford 2005). Few studies have tried to disentangle whether these patterns are due to variation in moonlight intensity, or result from the actual lunar cycle, which is associated with other changes beyond variation in light intensity (Grant *et al.* 2013). For example, Vignoli and Luiselli (2013) found that depressed reproductive activity in *Rana dalmatina* and *Hyla intermedia* during full moon was not merely regulated by light avoidance. Rather, reproduction was concentrated immediately after the new moon, suggesting an influence of the actual lunar cycle. The reproductive activity of *H. rosenbergi* studied here showed a similar pattern: no effect of light availability (*i.e.*, illumination), but increased reproductive activity during the waning period of the lunar cycle. Note however, that this effect was only apparent in the circular statistic analysis, i.e., when other environmental or social factors were not included in the analysis.

Relative Importance of Environmental and Social Cues.—The origin of species-differences in the relative importance that environmental and social cues play in determining breeding activity may be found in differences in their breeding ecology. Explosive breeders, with short breeding seasons that last only a few days may rely more on environmental cues to synchronize the sexes before the short breeding event (Gottsberger & Gruber 2004, Van Sluys *et al.* 2006), while prolonged breeders that breed for several weeks and in stable environments may require less precise reproductive synchronization by climatic factors. Alternatively, the factors determining the occurrence of breeding activity may not be the same as those determining the intensity of breeding activity. Both explosive and prolonged breeders may benefit from attending to environmental factors for determining the onset of the breeding season, but switch to attending more to social cues once reproduction has started. In fact, because many explosive breeders reproduce in ephemeral pools generated by heavy rains, which may be short lived and form in unpredictable locations, switching from environmental to social cues after the onset of reproductive activity might be particularly beneficial (Swanson *et al.* 2007, Buxton *et al.* 2015). It is also possible that differences in the absolute duration of the breeding season between explosive and prolonged breeders may bias our ability to determine the most influential factors. Imagine that environmental factors determine the onset of reproduction, and social cues determine its intensity across the season. The uniformly high reproductive activity that is a necessary consequence of the short breeding season of explosive breeders may obscure the importance of social cues mediating the within-season intensity of reproductive activity. By contrast, the greater abundance of samples taken after reproduction has commenced in prolonged breeders may overestimate the importance of social cues at the expense of environmental effects. To my knowledge, only prolonged breeders have been examined in terms of the relative importance of social and environmental cues affecting breeding activity, so more explosive breeders need to be sampled before the above hypothesis can be tested.

Difference between the Sexes.—In order to facilitate successful reproduction, physiology and behavior of males and females should be synchronized, which could be achieved by both sexes attending to the same environmental or social cues. Yet, sex differences seem to be common in anurans. In túngara frogs, *Physalaemus pustulosus* (Marsh 2000), painted reed frogs, *Hyperolius marmoratus* (Henzi *et al.* 1995), and the treefrog *Scinax trapicheroi* (Van Sluys *et al.* 2006), females are more sensitive to environmental factors than males. By contrast, females of the rhacophorid frog *Buergeria buergeri* (Fukuyama & Kusano 1992), as well as the female *H. rosenbergi* in the present study, were less sensitive to environmental factors than males.

Sex differences seem to be even more prevalent when it comes to the importance of social facilitation. Here, females seem to be more strongly attuned to social cues than males (Henzi *et al.* 1995, Murphy 2003, this study; but see Ritke *et al.* 1992). Males start to call early in the evening, before females arrive, and choruses generally only form at sites that are suitable for breeding. This pre-selection of appropriate environmental conditions by males may allow females to rely more heavily on social cues. Moreover, since female frogs have to lay eggs within 1–2 days once they have committed to breed, social cues indicating the presence of sexually active males may also reduce the risk of reproductive failure. Social cues indicating the presence of suitable breeding conditions may also explain why female *H. rosenbergi* are unusually inattentive to environmental factors (above): The specialized breeding behavior of gladiator frogs centers around basins as calling and oviposition sites. Female gladiator frogs will generally only lay eggs inside basins, and male gladiator frogs will only call once they have acquired a basin. Consequently, the social cue may be a much more relevant indicator of favorable breeding conditions than environmental factors.

Conservation and Management Implications.—The emerging pattern of social cues playing a larger role in regulating anuran reproductive activity than environmental factors suggests that global climate change may not disrupt patterns of anuran reproduction as much as commonly feared. Unless conditions become completely unsuitable for breeding, social facilitation may be sufficient to synchronize breeding. Nevertheless, other aspects of anuran reproduction besides reproductive synchronization may still be negatively impacted by climate change. In particular, a species' reproductive mode may determine its vulnerability to climate change. Altered rainfall patterns, particularly rainfall becoming more sporadic and the dry gaps between rainfall events increasing in duration, may not have major effects on species that lay their eggs in water, yet may severely impact egg development and survival in terrestrial or arboreal breeders (see Touchon 2012).

The importance of social cues for regulating the intensity of anuran reproduction also underscores the potential usefulness of playback systems as productive and cheap management tools. Recent documentation that playbacks can attract anurans to unoccupied suitable breeding sites (Buxton *et al.* 2015) already suggested playbacks as tools for improving the colonization of mitigation wetlands or for shifting reproduction to better protected areas. Widespread social facilitation of the intensity of reproductive activity further suggests that playback systems may be employed to foster reproduction within existing breeding sites, or to induce higher breeding intensity when environmental conditions are particularly conducive for successful reproduction.

Another management tool that may benefit from improved information about the role of social facilitation for anuran reproductive behavior are call surveys. Programs that use call surveys have been established to monitor anuran populations in many countries. But how well do call surveys capture the criterion that is most important for conservation—successful reproduction and thus, population maintenance? In the present study, breeding activity occurred in about half the nights during which calling activity was registered. This is in line with other studies that also found that breeding only takes place in 40 percent to (rarely up to) 80 percent of nights with calling activity (Fukuyama & Kusano 1992, Ritke *et al.* 1992, Wagner & Sullivan 1992, Martins 1993, Bastos & Haddad 1999, Marsh 2000). However, in the present study the number of breeding females was positively correlated with chorus size, a result mirrored by many other studies (Ryan *et al.* 1981, Dyson *et al.* 1992, Ritke *et al.* 1992, Wagner & Sullivan 1992, Tejedo 1993, Murphy 2003, Stevens & Paszkowski 2004, but see Bastos & Haddad 1996, Marsh 2000). Consequently, mere presence/absence data of calling males is not necessarily a good predictor of successful reproduction. However, estimates of chorus size, such as the three-point calling index advocated by the North American Amphibian Monitoring Program (NAAMP) (Weir & Mossman 2005), or relative call intensity data obtained from recordings gather by passive acoustic monitoring devices, are likely more useful to pinpoint the times when successful reproductive activity occurred.

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DATA AVAILABILITY

Data deposited in the Dryad Repository: https://doi.org/10.5061/dryad.r10d0 (Höbel 2017).

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