

# Visual cues elicit courtship signals in a nocturnal anuran

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**Abstract** In lekking species, the allocation of effort into mate attraction signals is not uniform over time, and signalers may expend the greatest effort when potential mates are nearby. Close-range courtship interactions are critical determinants of male fitness and the study of these interactions can therefore answer important questions in sexual selection. In anurans, attention has largely focused on long-range mate attraction mediated by acoustic signaling. However, many species also engage in courtship behaviors at close range, and the cues that elicit these behaviors are unknown but likely to be non-acoustic. I performed an experiment in which I assessed the role of female visual cues in eliciting courtship calls by males of the nocturnal treefrog *Hyla versicolor*. Males that could see an approaching female were more likely to give courtship calls than those that could not. These results provide some of the first evidence for an effect of vision on calling behavior in a nocturnal anuran and demonstrate that multiple sensory modalities are involved in the final stages of mate attraction.

**Keywords** Nocturnal vision · Courtship · Anuran · Phonotaxis

## Introduction

Animal courtship involves intense behavioral displays, and animals may regulate the expression of these often costly displays based on cues associated with the likelihood of

mating (Patricelli et al. 2002). For example, displaying males may increase the expression of a costly display when receptive females are nearby (Kelso and Verrell 2002; Byrne 2008; Patricelli and Krakauer 2010). These close-range courtship interactions likely are critical determinants of male fitness and it is therefore of interest to determine the cues that lead males to increase their investment in signaling during courtship. In nocturnal anurans, this problem is not straightforward because most social interactions take place in the acoustic modality, yet females in most species do not advertise their presence by producing vocalizations of their own (Gerhardt and Huber 2002). Nonetheless, male anurans exhibit unique behaviors when females are at close range such as producing distinctive vocalizations (courtship calls) and grasping females in amplexus, implying that cues from other sensory modalities elicit these behaviors (Fellers 1979; Wells 1988). Anurans are sensitive to stimuli in multiple modalities, but little is known about how these cues are used by males in courtship (Taylor et al. 2008; Caldwell et al. 2010; Akre and Ryan 2011). Close-range courtship interactions likely have a strong impact on male fitness, and therefore, studies of sexual selection in anurans should consider the possibility that other sensory modalities, in addition to sound, play important roles in mediating these processes. Here, I describe an experiment in which I tested the role of vision on the production of courtship calls in the grey treefrog, *Hyla versicolor*.

The primary call type given by males in most anuran species, and thus the focus of most studies of anuran communication, is the advertisement call. Males' advertisement calls attract females and are often involved in mediating interactions with neighboring males as well (Wells 1977; Wells and Schwartz 2006; Wells 2007). Advertisement calls generally are broadcast irrespective of cues indicating that a female is nearby. In contrast, courtship calls are a vocalization type that males typically produce only when a female is approaching at close range (Wells and Schwartz 2006; Wells 2007). The courtship calls of many anurans are modifications of the advertisement call such that calling performance reaches an extreme level (Rosen and Lemon 1974; Wells 1980; Owen and Tucker 2006). Courtship calls in *H.*

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*versicolor* have the same spectral and fine-temporal structure as advertisement calls but are substantially longer in duration (Fellers 1979; Wells and Taigen 1986; Klump and Gerhardt 1987). In fact, calling efforts during courtship calling approach the upper limits on acoustic signal performance measured for *H. versicolor* (Reichert and Gerhardt 2012). The increase in call duration during courtship calls corresponds to female preferences for longer duration calls (Klump and Gerhardt 1987; Gerhardt et al. 1996). However, the substantial energetic costs that are likely to be associated with courtship calling render long-term production of courtship calls unsustainable (Wells and Taigen 1986). Thus, individuals are expected to limit production of courtship calls to contexts in which they are especially likely to be effective; that is, when there are cues indicating the presence of a receptive female.

Previous studies of anurans demonstrated that males increase vocal production in the presence of females, although the particular cues used by males to detect female presence are rarely described (Morris and Yoon 1989; Byrne 2008; Akre and Ryan 2011). Visual cues are an especially likely candidate because females make conspicuous movements during phonotaxis (Rheinlaender et al. 1979), frogs are highly sensitive to motion (Ewert 2004), and several studies have demonstrated the importance of vision in mate choice in nocturnal anurans (Taylor et al. 2008; Gomez et al. 2009; Gomez et al. 2010; Sztatecsny et al. 2010). I tested whether vision plays a role in eliciting courtship calls in male *H. versicolor* by recording their vocal behavior in an experiment in which I manipulated their ability to see an approaching female. This experiment is one of the first tests of the importance of nocturnal vision on male mating behaviors in an anuran and provides important information on the cues used in the critical final stages of courtship.

## Methods

Subject males and females were captured from local ponds in Boone County, Missouri (USA). Gravid females were captured in amplexus and maintained at 4 °C to prevent oviposition prior to testing. On testing days, I released 20–80 males at approximately 1,600 h from a temporary animal-care facility into an artificial pond located within a greenhouse (details on the artificial pond facility are given by Schwartz et al. 2001; Reichert and Gerhardt 2011). I stimulated males with an artificial rainstorm and broadcasts of synthetic chorus noise, which generally resulted in strong nightly choruses. I chose test subject males from among these chorusing individuals. I performed experiments between 2100 and 0100 hours from May to July of 2011.

Male test subjects were placed into a wire-mesh cage and transported to an arena located 2 m outside of the artificial pond. The pond was surrounded by opaque cloth that prevented test subjects from obtaining visual cues from any frog in the pond. The arena itself consisted of a PVC pipe skeleton surrounded by a dark cloth screen (2 m in length by 0.5 m in width). I placed the male at one end of the arena, on a platform elevated 10 cm above the ground. Female test subjects were acclimated to the testing temperature for at least 30 min. At the time of testing I placed the female beneath a cup at the opposite end of the arena from the male.

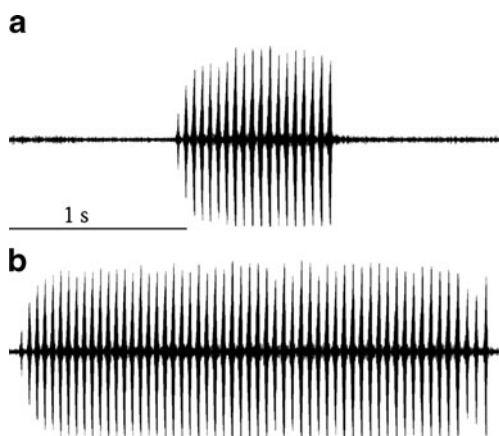
Subjects were divided randomly into two treatment groups. In the opaque treatment, a glass screen (0.5 m wide, 0.3 m tall) was placed immediately next to the male's platform in between the platform and the female release point. The screen had an opaque backing that effectively blocked the male's view of the runway and thus removed any potential visual cues from the female, and prevented the two from contacting one another. In the clear treatment, I removed the opaque backing from the screen so that only the transparent glass remained. In this treatment physical contact was again prevented, but the male could potentially see the female as she approached. Only visual cues were manipulated, thus a difference between the treatment groups indicates that vision played a role in eliciting courtship calling, irrespective of any contribution of other sensory modalities. Tests were performed at night under ambient light levels within the clear-roofed greenhouse. I did not control for irradiance and these tests were performed across nights with different ambient light conditions ranging from full moon to completely overcast; therefore, I do not attempt to specify the range of light levels at which visual detection of females may be possible. Nevertheless, the experimental light levels were likely within the range of those expected to be experienced in the field, and this experimental design is sufficient to demonstrate that males can use visual cues when ambient conditions allow.

While the female was restrained in the arena, I recorded 10 calls from the subject male to serve as a baseline of its calling behavior using a Tascam DR-680 digital-audio recorder (16-bit PCM files, 44.1 kHz sampling rate) and a Sennheiser ME-67 directional microphone mounted on a boom above the male. I then released the female by pulling on a rope attached to her container, allowing her to move freely about the arena. I recorded male calls until the female had spent 30 s at the barrier that separated her from the male. I observed female movements from a position immediately adjacent to the arena using the night-vision feature of a Sony DCR-SR85 camcorder positioned so that the entire arena floor was visible on the video display. I only included tests in the dataset for which the female showed robust phonotaxis (i.e., directed movements towards the calling male including head and body scanning; Rheinlaender et al.

1979) and the male continued calling throughout (3 of 43 experimental trials were excluded because males did not call consistently). Individual males were only tested in one of the two treatment groups ( $N=19$  males in the opaque treatment and  $N=21$  males in the clear treatment) and were only tested once within a treatment group. Some females were used in tests with multiple males, but I randomized male treatment to ensure that female identity did not bias the results.

### Call analyses

To examine courtship calling, I used Raven Pro 1.3 software (Cornell Laboratory of Ornithology) to measure the number of pulses per call in each recording. I used pulse number as a proxy for call duration because call duration itself is heavily affected by individual body temperature (Gerhardt 1978). Thus, comparisons between males recorded at different temperatures, and the development of standard criteria to define courtship calling (see below), are facilitated by using the more temperature-independent pulse numbers. I compiled these data separately for the baseline and experimental periods. Courtship calls in *H. versicolor* differ only quantitatively from advertisement calls (Fig. 1) and thus there is no objective criterion to differentiate the two. To ensure robust results, I used two different criteria that were both based on the observation from previous studies that courtship calls are longer in duration than normal advertisement calls (e.g., Fellers 1979). (a) For the relative threshold criterion, I defined a courtship call as any call given during the experimental period with a pulse number at least 50 % greater than the average pulse number of advertisement calls given during that same individual's baseline calling period. (b) For the absolute threshold criterion, I defined a courtship call as any call that had a pulse number of 30 or greater. Such calls are approximately 3 standard deviations longer than average advertisement calls measured in the field (Gerhardt et al. 1996).



**Fig. 1** **a** Waveform of a typical *H. versicolor* advertisement call (pulse number=19). **b** Waveform of a courtship call given by the same male (pulse number=56)

In addition to examining differences in the propensity to give courtship calls, I also examined whether males in the opaque and clear treatments differed in overall calling output. Thus, in addition to measuring pulse numbers, I analyzed each male's recordings to measure two temporal call characteristics related to calling effort: (a) call duration, here measured as the time from the start to the end of the call and (b) call period, defined as the amount of time between the onsets of two consecutive calls. I averaged these call characteristics separately for each male's baseline and experimental recordings. I performed a mixed MANOVA to examine the effects of treatment (opaque or clear, a between-subjects variable), time period (baseline or experimental recording period, a within-subjects variable), and the interaction between treatment and time period on the four dependent variables: call duration, call period, average pulse number and pulse number of the longest call. All call characteristics used in these analyses other than pulse number were temperature-corrected to 20 °C using regressions of male body temperatures on average values of each call characteristic. In order to meet the assumption of multivariate normality required for the MANOVA, I used a reciprocal transformation on both call duration and call period. I assessed whether the data met the assumptions of the MANOVA analysis using the methods of DeCarlo (1997); these assumptions were met following the reciprocal transformation described above.

### Results

Males were significantly more likely to give courtship calls, defined by either criterion, when they were in the clear treatment group (Table 1; Relative criterion  $\chi^2=10.6$ ,  $P<0.001$ ; Absolute criterion  $\chi^2=6.5$ ,  $P=0.011$ ). Very few males gave courtship calls in the opaque treatment, and this proportion was similar to the proportion of males that gave courtship calls under the absolute criterion during the baseline recording period (3 of 40 males gave calls defined as courtship calls in baseline recordings). The pulse number of the longest call given in the experimental period was greater for males in the clear treatment than in the opaque treatment (Table 2; Fig. 2;  $t$  test,  $t_{38}=3.4$ ,  $P<0.001$ ). There was no difference between the

**Table 1** Proportions of males giving courtship calls in each treatment

	Relative criterion	Absolute criterion
Clear treatment	14/21	10/21
Opaque treatment	3/19	2/19

Proportions are shown separately for each of the two criteria used to define a courtship call (see Methods for details)

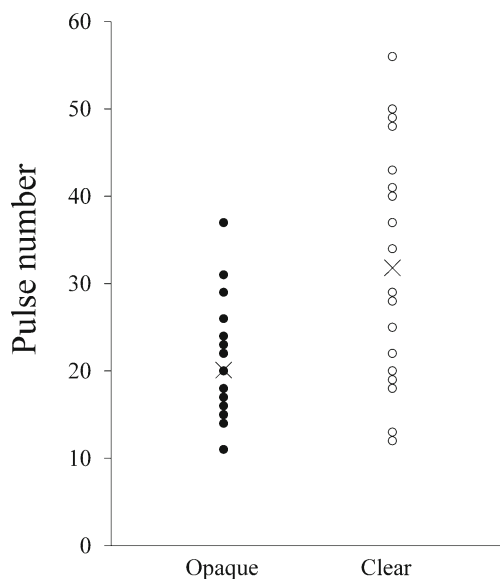
**Table 2** Average values of call characteristics

Time period	Treatment	Call period (s)	Call duration (s)	Average pulse number	Maximum pulse number
Baseline	Opaque	7.06 (0.89)	0.834 (0.046)	15.5 (1.0)	19 (1.3)
	Clear	7.00 (0.58)	0.819 (0.030)	15.8 (0.8)	19.4 (1.2)
Experimental	Opaque	6.33 (0.39)	0.842 (0.043)	15.7 (1.1)	20.6 (1.5)
	Clear	7.18 (0.77)	0.934 (0.053)	17.8 (1.2)	31.8 (2.9)

Each cell represents the average (standard error) of call characteristics measured separately for the baseline and experimental periods for males in the opaque and clear treatments. Call characteristics other than pulse number are reported after temperature-correction to 20 °C (see [Methods](#)). Maximum pulse number refers to the pulse number of the single longest call given during the recording. Although call period and call duration were reciprocal-transformed for statistical analyses (see [Methods](#)), the values presented here are the raw values measured prior to transformation. Opaque treatment,  $N=19$ ; Clear treatment,  $N=21$

treatments in the average pulse number of calls given during the baseline period (Table 2;  $t_{38}=0.2$ ,  $P=0.83$ ).

I found a significant effect of the interaction between treatment and time period on the four calling variables measured in this study ( $F_{4,35}=4.09$ ,  $P=0.008$ ). The main effects of both time period and treatment were also significant (time period,  $F_{4,35}=7.71$ ,  $P<0.001$ ; treatment:  $F_{4,35}=3.11$ ,  $P=0.027$ ). When the call variables were examined individually, there were significant interaction effects between time period and treatment on the maximum pulse number ( $F_{1,38}=15.62$ ,  $P<0.001$ ), average pulse number ( $F_{1,38}=4.69$ ,  $P=0.037$ ) and call duration ( $F_{1,38}=4.50$ ,  $P=0.04$ ), but not on call period ( $F_{1,38}=0.24$ ,  $P=0.63$ ). Call durations and pulse numbers were largest during the experimental period of the clear treatment and were relatively uniform in the other three combinations of time period and treatment (Table 2).



**Fig. 2** Data points represent the pulse number of the longest duration call given during the experimental period by males in the opaque (closed circles) and clear (open circles) treatments. The average long-duration call is indicated by an 'X' for each treatment

## Discussion

Male anurans attend to various aspects of their social environment, although most previous descriptions of this behavior have involved responses to acoustic cues (Wells 1988). This experiment confirms that visual cues elicit changes in calling behavior in male frogs. In particular, males were substantially more likely to give courtship calls when they were able to see an approaching female. As a result, when males could see the female, their average call durations and pulse numbers were higher than in the baseline period or in the opaque treatment in which they were unable to see an approaching female. Although average calling efforts did not differ depending on the experimental treatment, I did not continue recording after females had arrived at the barrier separating her from the male and therefore may not have been able to detect such differences in the context in which they are most likely to be expressed. It is likely that at this close range males increase their overall vocal performance, and indeed an increased calling effort following the production of courtship calls has been found in a previous study (Reichert and Gerhardt 2012). Nonetheless, the courtship calling response to visual cues is a significant behavioral difference between the two treatments and has important implications for an understanding of both anuran sensory ecology and the behaviors associated with the final stages of mate attraction.

Many recent studies emphasize that animals are responsive to cues in multiple sensory modalities (Hebets and Papaj 2005). These data add to a growing number of studies that demonstrate that vision plays a role in the behavioral interactions of nocturnal anurans (Hödl and Amézquita 2001; Amézquita and Hödl 2004; Taylor et al. 2007), a group that is better known for its acoustic communication system. Most previous experimental studies of nocturnal vision in anurans focused on female attraction to visual cues or signals produced by males (e.g., Taylor et al. 2008; Gomez et al. 2009; Taylor et al. 2011). I found that males were highly responsive to visual cues associated with an approaching female and altered their calling behavior in a way that is likely to be even more attractive to the female.



Similarly, Akre and Ryan (2011) found that male túngara frogs increased the production of costly ‘chuck’ notes in response to what were likely visual cues associated with female movements during phonotaxis. Thus, there is now evidence that both sexes not only are attentive to and evaluate properties of acoustic signals, but also that they are responsive to visual cues. These findings open the door for future studies of interactions between the two modalities. In particular, based on the results of this study, it will be interesting to determine the timing relationship between female movements and male courtship calling, the threshold, in terms of amount of movement or distance to the signaler, at which female cues elicit courtship calling behavior, and the effects of such variables as ambient light levels and the density of competitors on the likelihood that female cues elicit courtship calling.

Female mate preferences are often tested in playback tests that measure a female’s response to the broadcast of synthetic signals (Gerhardt and Huber 2002). These tests are assumed to measure a proxy for female mate choice because similar female behavior in a natural chorus normally results in her mating with the calling male towards whom she moves (Gerhardt 1982). I do not question the utility of phonotaxis tests, but my data underscore the additional complications that occur in natural interactions that are less easily simulated by simpler laboratory procedures. Specifically, I found that males are highly responsive to their surroundings and are especially attentive to visual cues in a way that an approaching female is likely to elicit an abrupt change in male calling behavior including the production of courtship calls and an overall increased vocal performance (see also Reichert and Gerhardt 2012). The effects such behavior might have on mating preferences measured in standard laboratory phonotaxis tests are unknown, but potentially of great importance to the interpretation of female preference functions. Specifically, preference functions are often based on the time a female takes to approach a target signal (e.g., Bush et al. 2002). My data suggest that in a natural context, females approaching a signaling male would elicit courtship calls. These courtship calls, being especially attractive to females (Klump and Gerhardt 1987), may alter the speed with which a female approaches the signaling male. These effects may be particularly pronounced for males with advertisement calls that are generally less attractive to females. Previous studies of female preference functions indicate that females’ preferences are asymmetrically biased against less attractive calls (Gerhardt et al. 2000; Schwartz et al. 2002); in other words, a highly unattractive male may benefit to a greater extent from a given amount of change in a call characteristic in the direction of the female preference than would a male whose calls were initially more attractive. Because of this, courtship calling may be especially beneficial to males with

relatively unattractive advertisement calls. If males can detect females by visual cues, their courtship call production may therefore tend to equalize female approach times in the natural context, suggesting that preference functions measured in the laboratory may over-exaggerate female preferences as they are expressed in nature. This in turn could be a partial explanation for the common observation that strong female preferences measured in the laboratory often are not detected in field studies (Dyson et al. 1992; Sullivan and Hinshaw 1992; Friedl 2006).

Finally, these data provide additional evidence that males modulate their vocal performance in response to cues in the social environment. Frogs are known to be highly sensitive to cues indicating increased competition and respond by adjusting properties of their own vocalizations (e.g., Lopez et al. 1988; Bosch and Marquez 2001; Schwartz et al. 2002; Reichert 2011b). While these responses to competition often increase the attractiveness of males’ calls to females (e.g., Wells and Schwartz 1984; Wells and Taigen 1986; Baugh and Ryan 2010; Baugh and Ryan 2011; Reichert 2011a), less attention has been given to the causes and consequences of males’ vocal responses to females themselves (Morris and Yoon 1989; Byrne 2008; Akre and Ryan 2011). The high effort courtship calls given by males are likely to be energetically costly and to limit future calling opportunities (Wells and Taigen 1986; Runkle et al. 1994), yet are extremely effective in attracting females (Klump and Gerhardt 1987). I found that males are most likely to perform such behaviors when visual cues indicating a nearby female are available. In the noisy chorus environment, males can only attract females from a limited distance; thus, a strategy of monitoring the environment for female cues and only producing the highest performance calls when females are present should balance the costs of high performance calls while maximizing the likelihood of attracting a mate.

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**Ethical standards** The Missouri Department of Conservation gave permission to collect frogs. The University of Missouri Animal Care and Use Committee approved the experimental procedures (protocol number 6546).

**Conflict of interest** The author declares that he has no conflict of interest.

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