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Original Article

Female túngara frogs elicit more complex mating signals from males

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Sexual selection is responsible for the evolution of costly elaborate male traits. When male displays are dynamic, display strategy is sensitive to contextual cues that alter the relative costs and benefits of producing each signal in a male's repertoire. Because females often prefer more elaborate signals, males often respond to female presence by elaborating their display. When added elaboration increases assessment information or reproductive stimulation, females might benefit by extracting the maximum amount of signal elaboration from males. Thus, we expect that females could exaggerate their presence and cause males to produce even costlier and more attractive signals by exhibiting "elicitation" behaviors. We asked whether female túngara frogs elicit increased call complexity from prospective mates. In túngara frogs, adding complexity increases both attractiveness and predation risk. We found that females exhibit a repertoire of movements that function not in mate acquisition, per se, but in display manipulation, by eliciting increased complexity from calling males. The probability that males add complexity to their display increases when females produce these movements. Thus, females actively influence males to produce riskier signals.
Key words: communication, display strategy, elicitation behavior, female choice, proceptive behavior, sexual selection. *[Behav Ecol]*

INTRODUCTION

Female choice can cause the evolution of elaborate male traits through sexual selection in spite of the costs to elaboration imposed by natural selection (Darwin 1871; Kirkpatrick and Ryan 1991; Andersson 1994; Zuk and Kolluru 1998). The distribution of sexually selected male traits is often envisioned as a peak between 2 divergent optima imposed by sexual and natural selection (Maynard Smith 1982). The distinction between static and dynamic male traits complicates this scenario. Males that produce dynamic mate attraction signals can use signals strategically and are sensitive to environmental variables that shift the optimum signal value at any given moment (Lindström et al. 2009). Contextual factors such as predation risk can influence a display strategy to shift toward the natural selection optimum (Magnhagen 1991; Bertram et al. 2004), whereas male competition (Wong and Candolin 2005; Goutte et al. 2010) or female presence (Gautier et al. 2008) can influence a strategy to shift toward the sexual selection optimum. Many males adjust signaling (How et al. 2008) and competitive behavior (Jackson et al. 2006) according to a female's proximity. Producing energetically costly but attractive signals according to female proximity can maximize male fitness (Patricelli and Krakauer 2010). Males can even allocate energetic signaling investment according to female quality (Wong and Svensson 2009).

Displaying males respond not only to female proximity but also to female behavior. Males can increase their fitness by responding to female behaviors that indicate the likelihood of mating. For example, males can reduce energy and time costs if they avoid courting unreceptive females or they can increase the chance of mating by producing the signals that are most attractive to females. Males commonly respond to female proceptive behavior that regulates the progression of courtship (Balsby and Dabelsteen 2002; Crews 2002) and specifically to signals that communicate receptivity (Watkins 1997) or overstimulation (Patricelli et al. 2004). Female behavior can also influence song repertoire development (West and King 1988), and female resistance behavior can incite male competition (Cox and Le Boeuf 1977). Changes in female behavior can also influence male use of mating coercion (Evans et al. 2002).

Given the robust occurrence of male response to female behavior prior to mating, we predict that females should evolve suites of behaviors that function in eliciting from males displays that lie closer to the sexual selection optimum signal value, in spite of the increasing costs of such displays (Figure 1). When increasingly elaborate traits provide more assessment information or reproductive stimulation, females might benefit by extracting the maximum amount of signal elaboration from a potential mate. Such expectations are generally consistent with predictions of theories as disparate as the Handicap Principle (Zahavi 1975; Zahavi and Zahavi 1997), chase-away sexual selection (Holland and Rice 1988; Arnqvist and Rowe 2005), and the influence of sexual stimulation on reproductive physiology (Lehrman 1965; Adkins-Regan 2005). We refer to behaviors that function to elicit from males riskier signals as "elicitation" behaviors. Elicitation behaviors are related to proceptive behaviors that solicit or maintain sexual interactions (Beach 1976), but function specifically to cause a potential sexual partner to increase its sexual display intensity. Female behaviors that specifically manipulate the male trait distribution toward the sexual selection optimum could cause a stronger male response than simple approach or retreat behaviors and would thus demonstrate a female role in mating behavior that has not been previously established.

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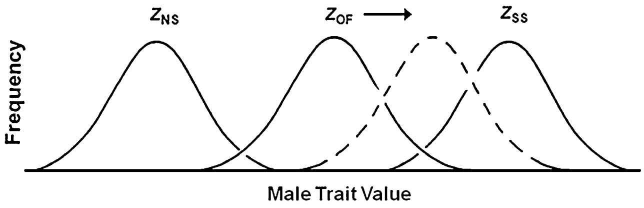

Figure 1
Optimal male trait values. Females could influence male behavior such that he produces signals closer to the sexual selection optimum value. Solid curves show optimal trait values under natural selection (Z_{NS}), sexual selection (Z_{SS}), and actual trait values at the average, as overall fitness (Z_{OF}). Dashed curve shows how actual trait values might shift under the influence of females eliciting signal elaboration.

Although females can share some costs of elaborate male signaling, the costs are sometimes borne primarily by males. In some cases, predators are attracted to elaborate signals due to their enhanced conspicuousness (Endler 1978; Zuk and Kolluru 1998), and although both males and females are sensitive to predation risk during conspicuous courtship (Dill et al. 1999; Bertram et al. 2004; Booksmythe et al. 2008), the risk might be higher for males because they produce conspicuous signals, although this is not always the case and may be less likely in cases of reverse size dimorphism (Pocklington and Dill 1995). Elaborate signals may also be costly due to their energetic investment (Patricelli and Krakauer 2010), and in these cases, females are likely to bear none of the cost of elaborate signals. Thus, if females prefer more elaborate signals, the sexual selection optimum could differ from both the natural selection optimum and the overall fitness optimum signal value, and males might resist producing the sexual selection optimum.

We asked whether females perform elicitation behaviors that actively influence males to increase production of costly mating signals, by producing calls closer to the sexual selection optimum. We studied túngara frogs (*Physalaemus pustulosus*), a species with mating signals of established variable costs.

Túngara frog natural history

Male túngara frogs use advertisement calls to attract mates. The advertisement calls can have 2 components: an initial "whine," and a terminal "chuck" (Ryan 1985; Ryan and Rand 2003). Whines can be voiced alone (simple calls) or followed by 1–7 chucks (complex calls). We define signal complexity as the number of chucks affixed to the whine (Ryan and Rand 1981; Ryan 1985; Akre and Ryan 2010a). Females show a robust preference for complex calls over simple calls (Gridi-Papp et al. 2006) and a context-dependent preference for greater complexity (calls with more chucks over calls with fewer chucks, Akre and Ryan 2010b). Males call in choruses, and within a single call bout, one male may produce variable call types, transitioning between both simple and complex calls. When females choose a male, they pair in amplexus and then leave the chorus site for a period of up to a few hours before finding a place to release and fertilize eggs.

Túngara frog males are exposed to predation risk from a number of predators, including frog-eating bats that are common at chorus sites (Ryan et al. 1982). These predators are more likely to attack males producing complex than simple calls (Ryan et al. 1982) and more likely to attack males that produce calls with more chucks than males that produce calls with few chucks (Page RA, unpublished data). Thus, males face a conflict whereby they will improve reproductive success by producing calls with more chucks but increase the probability of mortality with those same calls.

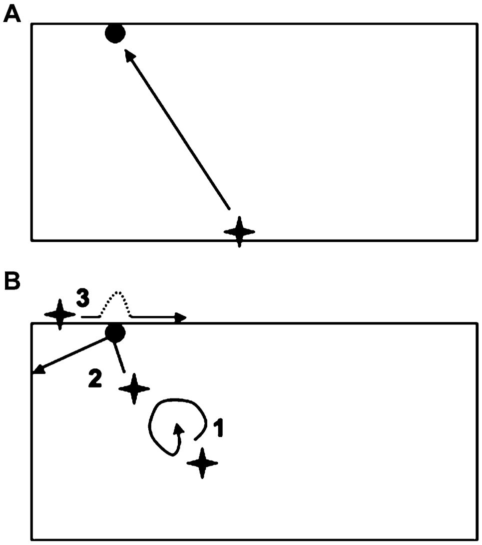

Figure 2
Female locomotive behaviors. Females exhibit a repertoire of locomotive behaviors. Below are drawings of frog movement at the breeding pond, as in Ryan 1985 (female = star, male = circle, and path = arrowed lines). Immediately prior to amplexus, a female approaches a male with directed movements (A). Females sometimes also produce "NAR" movements, such as those shown in (B). These numbered movements represent 1) water circle; 2) body bump; and 3) jump over.

When females choose a mate, they appear to sample several males in a chorus (Ryan 1985) and then move directly toward a male to form amplexus (Figure 2A). Observations of females in small choruses show that in addition to this standard choice behavior, females exhibit a repertoire of ancillary behaviors that do not function to directly approach or retreat from a male but instead seem to capture a male's attention and elicit increased behavioral response from him, specifically, a transition to producing more chucks (Figure 2B). We tested whether these ancillary behaviors elicit increased signal elaboration from males.

METHODS

Data were collected in Gamboa, Panama at the Smithsonian Tropical Research Institute (STRI) between June and September of 2008. We captured single calling males and male–female pairs in amplexus. We tested couples in a 170 × 70 cm cement pond enclosed in a 184 × 92 cm polyvinyl chloride (PVC) and plastic tarp fence in a clearing adjacent to rainforest. We released all frogs after testing at the site of collection, either in pairs or singly, as they were found. We used each frog once, and we followed standard toe-clipping procedures to mark individuals before release. Toe clip procedures followed the Guidelines for *Use of Live Amphibians and Reptiles in Field and Laboratory Research*, compiled by the Herpetological Animal Care and Use Committee of the American Society of Ichthyologists and Herpetologists, available at: http://www.asih.org/files/hacc-final.pdf. All experiments were licensed and approved by STRI, The University of Texas at Austin Institutional Animal Care and Use Committee, and La Autoridad Nacional del Ambiente.

We used a SONY DCR-SR45 Handycam Camcorder with night vision illumination to make video and audio recordings of males responding to female behavior prior to forming amplexus. Other than the night vision camera, no artificial illumination was used during trials, and moonlight, cloud cover, and predator presence varied naturally. We began each trial by releasing a male into the enclosed pond and allowed him to acclimate and begin calling, either naturally or in response to mimic vocalizations. If he did not call within 10 min, we released a second male. We continued to add males until at least one male called consistently. The number of males in the enclosure during a trial varied from 1 to 4 (total trials, $N = 41$; number of calling males: 1) $N = 16$; 2) $N = 18$; 3) $N = 6$; and 4) $N = 1$). When at least one male was calling, we released a female into the enclosure on a patch of land that was obstructed from the males' view by a PVC pipe placed between the female and the water where males called. Once the female was released, we began recording the trial and continued until the female formed amplexus with a male. The female was then reunited with her original male in a plastic container.

We used JWatcher Video V1.0 to mark the temporal sequence of all female movements and male calls. We could distinguish the vocalizations of each male by differences in their location and call properties, and we designated the focal male to be the male with which the female formed amplexus at the end of the trial.

We asked if females actively influence call production of focal males with their ancillary behaviors. We predicted that if females do use these behaviors to elicit greater call complexity, these movements should be different from the behaviors used to approach or retreat from a male and followed by an immediate increase in number of chucks produced by the male. We also predicted that the number of these movements produced by a female should be 1) negatively correlated with the greatest number of chucks produced prior to female movement because there is less need for eliciting chucks as the number of chucks already produced increases; 2) negatively correlated with chorus size because larger choruses produce more chucks (Bernal et al. 2007); and c) positively correlated with the increase in chuck number that occurs between first female movement and amplexus. These correlations should not occur for mate acquisition movements used to approach or retreat from males. We also predicted that if increasing chuck number is costly, the probability of increasing chucks in response to females should negatively correlate with the number of chucks already produced.

Defining behaviors

We observed all female movements and defined a set of repeatable and recognizable locomotive behaviors. We determined whether or not each behavior clearly moved the female either closer to or farther from the male. If so, we labeled the behavior as approach/retreat (AR), and if not, we labeled the behavior as nonapproach/retreat (NAR). If NAR behaviors elicit greater number of chucks from males, we consider them elicitation behaviors because they do not appear to serve the function of mate acquisition but instead appear to influence male display. If NAR behaviors function to influence male display, they should result in greater escalation of chuck number than is caused by AR behaviors. If AR behaviors result in a lesser escalation of chuck number, they are not considered elicitation behaviors because the primary function is mate acquisition; the escalation of the male's display is an incidental consequence of that movement.

To score female behaviors in the videos, we first familiarized ourselves to recognize the behaviors consistently and then scored all videos with the acoustic track playing to ensure the temporal sequence of events. A person with no knowledge of the study then randomly selected 25% of the trials (10 trials) for blind scoring of female behaviors in the absence of sound to ensure that our scoring was not biased by the males' calls.

Response to female presence

We wanted to determine whether males change the proportion of each call-type produced (0, 1, 2, 3, and 4 chucks) when they become aware of female presence. To do this, we compared call bouts from the current study to call bouts recorded in a previous study where females were not introduced (Bernal et al. 2009). For clarity, we refer to males from the current study as female-present (FP) males and males from the previous study as female-absent (FA) males. To determine how female presence influences male calling, we compared FP and FA males during the portion of the calling bout after FP males could have perceived the first female movement. We calculated the average proportion of the FP bouts that comprised the final portion, where males could perceive a female's presence, to be the final 32% of the bout. Then, we compared FP and FA males during the initial 68% of calling and during the final 32% of calling. We predicted that during the initial 68%, FP and FA males would produce the same proportion of each call type, but that during the final 32%, FP males would produce a greater proportion of calls with multiple chucks.

The total number of calls in a bout varied for each male, thus we analyzed data as the proportion of each call-type produced in a bout. To compare these proportions, we modeled the proportional distribution of call types in a generalized estimating equation (GEE) using the following factors: female presence (absent or present), bout segment (initial and final), and call type (0, 1, 2, 3, or 4 chucks) and then conducted pairwise comparisons with sequential Bonferroni correction.

Response to female movement

We tested whether female movements influence the probability that males decrease, maintain, or increase the number of chucks they produce. We predicted that 1) males would be more likely to increase chuck number when females produced a movement than when females were still and 2) NAR movements would be more likely to increase chuck number than AR movements. To test these predictions, we considered each male's call bout as a series of dyadic call transitions (an initial call and the following call). We tested whether female movement influenced the probability that following calls decreased, maintained, or increased in chuck number relative to the initial call.

We determined the first female movement that males could perceive to be the first movement after crossing the PVC pipe barrier. Túngara frogs have visual sensitivity to movement even on moonless nights (Cummings et al. 2008). Females do not vocalize, so males could use visual or tactile water vibration cues to detect female presence. Our estimate of a male's perception overestimates when he might have first detected her (i.e., he could not see her or detect her surface wave vibrations before crossing the barrier, but he might have detected her later). This would bias our results toward showing no effect of female movement on male calling.

We used the GEE procedure in the generalized linear models function of SPSS 16 to create a linear model of male response probabilities. Our model included the following independent variables: initial chuck number, transition type (decrease, maintain, or increase), and female movement (absent or present and AR or NAR). The dependent variable was the male's response probability. Thus, each individual had several data points in the model, and we used the repeated-subject function to control for individual male differences. We used the Estimated Marginal Means procedure with a sequential Bonferroni correction to generate pairwise comparisons.

Number of female movements

We analyzed correlations between number of female movements and 3 chorus variables. To conduct these correlations, we considered the subset of trials where males produced at least 1 chuck prior to the first female movement. We used this subset of data because males that do not produce chucks might be responding to current increased levels of predation risk. Males reduce chuck production in response both to approaching bats (Ryan et al. 1982) and to "public information" that might indicate predation risk (Phelps et al. 2007). A lack of chucks could cue females to reduce conspicuous behaviors, or females themselves could perceive bat presence or public information about predation risk and reduce conspicuous behaviors accordingly.

We tested whether chorus size negatively correlated with number of female movements. We predicted that females would produce more NAR (but not AR) movements when assessing smaller choruses because larger choruses might decrease the benefits of conspicuous movement. Males in larger choruses produce more chucks (Bernal et al. 2007), so females would have less need to elicit chucks in large choruses.

We also tested whether the number of female movements negatively correlated with the highest chuck number produced prior to her first movement. We predicted that if females use movements to elicit chucks, females would produce more NAR movements when fewer chucks were produced prior to movement, but AR movements would not differ.

We also tested whether the number of female movements positively correlated with the increase in chuck number that occurs between the first female movement and amplexus. We predicted that if females use NAR movements to increase chuck number, NAR (but not AR) movements would correlate with chuck number increase.

Complexity of initial call

We tested whether the complexity of the initial call influenced transition response following female movement. Because producing more chucks increases the cost of calling, we predicted a negative correlation between probability of increase and initial chuck number.

RESULTS

Defining behaviors

Females produced 12 recognizable and repeated locomotive behaviors. Five of these behaviors were categorized as AR and 7 as NAR (Table 1; supplementary material). In acoustically blind scoring of female movements in the 10 randomly selected trials, 69 of 73 (94.5%) of movements matched the initial full temporal sequence scoring as AR or NAR behaviors.

Response to female presence

Males produce a greater proportion of more complex calls when females are present. In the initial portion of the bout, prior to female arrival in the FP condition, FA and FP males did not differ significantly in proportion of calls produced with 0, 1, 2, 3, or 4 chucks (Figure 3A). In the final portion of the bout, after female arrival in the FP condition, FP males produced a higher proportion of calls with 3 chucks than FA males did ($P = 0.013$; Figure 3B). All reported P values are 2-tailed. Within the FA group, a higher proportion of calls in the initial bout portions had 0 chucks ($P < 0.0001$), and a higher proportion of calls in the final bout portions had 2 chucks ($P = 0.002$). Within the FP group, a higher proportion of calls in the initial bout portion had 0 chucks ($P < 0.0001$), and a higher proportion of calls in the final bout portion had 2 chucks ($P = 0.004$) and 3 chucks ($P = 0.006$).

Table 1

Locomotive behaviors are classified as AR or NAR behaviors

Classification of female locomotive behaviors

	N_O	% of category	N_F	% increase
AR behaviors				
Water approach	105	55.0	38	23.8
Land approach	38	19.9	21	15.4
Splash entrance	23	12.0	19	13
Water retreat	17	8.9	11	23.5
Land retreat	8	4.2	5	12.5
NAR behaviors				
Body bump	40	36.4	23	35
Slight movement	20	18.2	11	20
Water circle	19	17.3	13	21.1
Frontal Sit	16	14.5	13	68.8
Swim-by	7	6.4	8	28.6
Jump over	4	3.6	4	25
Run-by	4	3.6	4	50

For each behavior, the table lists the total number of observations (N_O), the proportion of all observations within the category, AR or NAR (% of category), the total number of females observed to perform the behavior (N_F), and the proportion of observations in which each behavior was followed by an immediate increase in chuck number (% increase).

Response to female movement

Female movement increases the probability that males will add chucks to their calls. The 3-way interaction of initial chuck number (0–4), transition type (decrease, maintain, or increase), and female movement (present or absent) was significant in the model of male response strategy (GEE; $N = 41$ couples; Wald chi square = 279.9; degrees of freedom [df] = 7; $P < 0.0001$; Figure 4). This means that both female movement and the number of chucks already being produced influence the probability of a male transitioning to produce more, the same amount, or fewer chucks. Pairwise comparisons show that this difference is driven by a differential probability of decreasing and increasing rather than maintaining chuck number. With female movement, males are less likely to decrease chuck number: $P < 0.0001$; males show no change in probability of maintaining chuck number: $P < 0.871$; and males are more likely to increase chuck number: $P < 0.0001$.

Males were most likely to increase chuck number when females produced NAR movements; the interaction of movement type (AR and NAR) and transition type (decrease, maintain, or increase) was significant in the model of male response strategy ($N = 41$ couples; Wald chi square = 9.841; df = 2; $P = 0.007$). Males are more likely to increase chuck number after NAR movements ($P = 0.028$) and are more likely to maintain chuck number after AR movements ($P = 0.028$; Figure 5). Results support the prediction that male response differs between elicitation (NAR) and mate acquisition (AR) behaviors.

Number of female movements

We predicted that the number of males in a chorus would negatively correlate with the number of female movements. We found no correlation ($N = 30$; $r = -0.27$; $P = 0.15$). Results do not support the prediction that elicitation behaviors are density dependent.

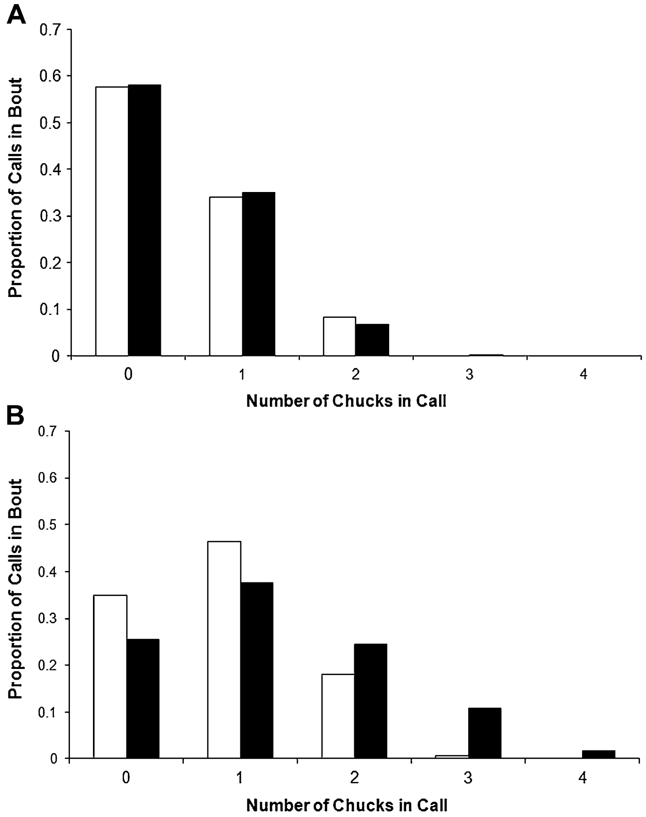

Figure 3
Female presence and male calls. Males produce a higher proportion of calls with more chucks when females are present. Bars show proportion of each call type in a bout when females are not (open bars) or are (dark bars) introduced. (A) Calls do not differ during initial 68% of a bout, prior to female introduction in the females present condition. (B) Calls differ during the final 32% of a bout, after females are introduced in the females present condition.

We predicted that the largest chuck number produced prior to female movement would negatively correlate with the number of NAR but not AR female movements. We found no correlation for NAR movements ($N = 24$; $r = -0.36$; $P = 0.08$) or for AR movements ($N = 24$; $r = -0.07$; $P = 0.76$). The lower sample size results from some females moving immediately, which did not allow a comparison of premovement chuck number. Results do not support the prediction that prior chuck number influences number of NAR movements.

We predicted that the number of NAR but not AR movements would positively correlate with the increase in chucks between the first movement and amplexus. NAR but not AR movements were positively correlated with the increase in chuck number following the first movement ($N = 24$; NAR: $r = 0.54$; $P = 0.006$; AR: $r = 0.31$; $P = 0.14$). Results support the hypothesis that NAR movements elicit an increase in chuck number.

Complexity of initial call

Males were less likely to increase chuck number if they were already producing a higher number of chucks; the interaction of initial chuck number and transition response was significant in the model of transition probabilities (GEE; $N = 41$ couples; Wald chi square = 136.8; df = 7; $P < 0.0001$). Also, initial chuck number and probability of increase are negatively correlated overall ($r = -0.23$; $P = 0.0012$) and for the subset of transitions in response to female movement ($r = -0.31$; $P = 0.0038$). Results support the hypothesis that signal elaboration is increasingly costly to males.

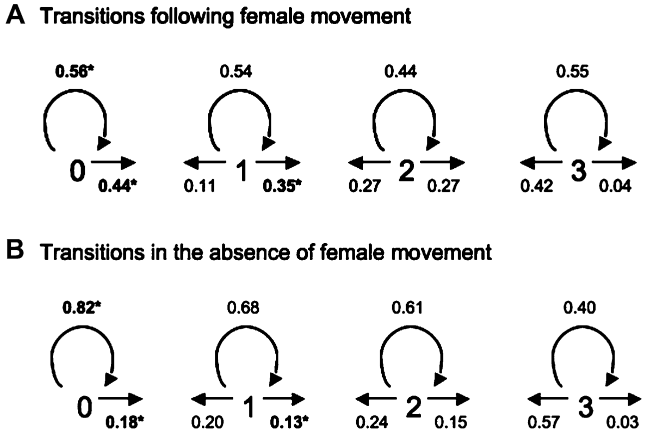

Figure 4
Female movement and call transitions. Males change calling strategy when females move. Arrows show the mean proportion of transitions that decrease (←), maintain (∩), or increase (→) chuck number for initial chuck numbers of 0, 1, 2, and 3 ($N = 41$ males). The first set (A) represents those transitions made following female movement. The second (B) represents all other transitions in a call bout. Overall differences between A and B were significant (GEE; $N = 41$ couples; Wald chi square = 279.9; df = 7; $P < 0.0001$). Boldfaced individual probabilities significantly differ between A and B ($^*P < 0.0045$; GEE EM-Means pairwise comparisons, using the least significant difference setting. All 11 transitions were compared, so the significant P value is derived from 0.05/11).

DISCUSSION

This study demonstrates that túngara frog females possess a repertoire of elicitation behaviors that actively influence the dynamic display of mating signals toward a sexual selection

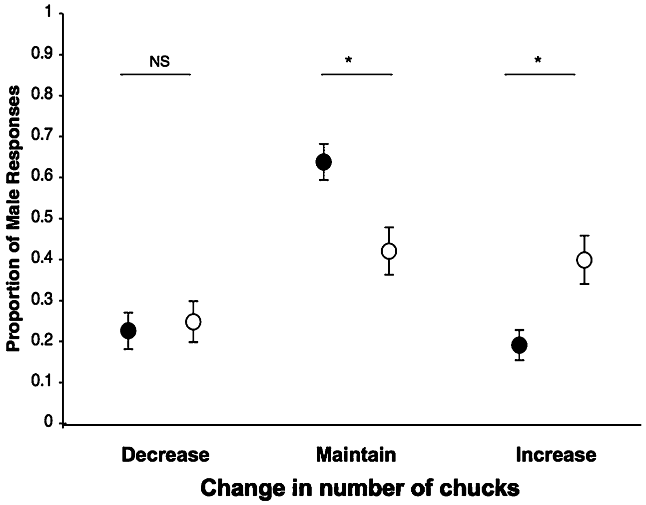

Figure 5
AR versus NAR movements and male response. Circles show mean +/− standard error proportion of responses that decrease, maintain, or increase chuck number when females move. Males ($N = 41$) increase chuck number more often following NAR movements (open circles) and maintain chuck number more often following AR movements (dark circles). $^*P < 0.03$.

optimal value. These elicitation behaviors do not move females directly toward or away from males, instead they appear to function to elicit more elaborate calls from males. Our results show that males are more likely to add chucks to their calls following female movement relative to the rest of a call bout, and they are more likely to add chucks following elicitation behaviors than following acquisition behaviors. Males produce more 3-chuck calls when females are present, thus the increase in chucks cannot be due to an inevitable increase in chucks as bouts progress. Thus, we conclude that females exhibit elicitation behavior to manipulate male display.

The elicitation (NAR) behaviors we describe probably vary with male chorus size. Túngara frog elicitation behaviors should be more common in low-density choruses because larger high-density choruses produce more chucks (Bernal et al. 2007), thus the benefits of eliciting more chucks are reduced in large choruses. In this study, females tended to produce fewer movements when more males were in the chorus, but the relationship was not significant. The range of chorus sizes tested (1–4 males), however, samples only a small range of chorus sizes that occur naturally. The influence of chorus size on female movement would be better established with a wider range of chorus sizes.

During the period between a female's first movement and amplexus, males show a greater increase in chuck production when females produce more NAR, but not AR, movements. This supports our finding that NAR movements influence male production of chucks. However, the number of NAR movements during this period does not correlate to the number of chucks initially produced by males. The borderline P value for this relationship suggests that further examination controlling for female and environmental variation could be informative.

Males are less likely to add chucks when they are already producing a higher number of chucks. This pattern might occur because the benefit of more chucks diminishes as more chucks are added (Bernal et al. 2009) or because adding more chucks is risky due to increasing costs incurred from predation (Page RA, unpublished data). Energetic costs are probably not significant because adding chucks does not increase oxygen consumption (Bucher et al. 1982). The risk of adding chucks could explain why males' optimum signal differs from the sexual selection optimum preferred by females.

We do not know why females elicit signal elaboration from males. The immediate result is an increase in chuck number produced by the male, and a greater number of chucks could function to influence the female's or male's reproductive physiology, assist in mate assessment, or both. These possibilities suggest 3 different evolutionary frameworks.

Chase-away selection is a hypothesis that explains the evolution of elaborate male traits, but it is also grounded in female sensory and reproductive physiology (Holland and Rice 1988; Arnqvist and Rowe 2005). This hypothesis predicts that when mating is costly, females should evolve stimulus response thresholds that males must surpass for mating to occur. The catch is that females with few potential mates and a limited window of time for reproduction risk reproductive failure. Female elicitation behaviors could be favored by selection to rescue females from reproductive failure in instances in which ovulation is imminent, but potential mates are not exceeding her threshold of reproductive stimulation.

The Handicap Principle (Zahavi 1975; Zahavi and Zahavi 1997) asserts that females assess heritable variation in males by attending to costly displays; Zahavi and Zahavi (1997) point to the túngara frog and its complex calls as a classic example. It follows from this premise that females should evolve elicitation behaviors to test the degree to which males are willing to engage in costly behavior. A similar phenomenon can occur in the context of dominance signaling, for example, in Harris sparrows, badge size signals fighting ability, which can be tested by challengers in dominance interactions (Rohwer 1975). In the case of túngara frogs, adding chucks could force males into competition with neighboring males (Goutte et al. 2010), and females might judge the interactions that occur between males, as occurs in several bird species (Otter and Ratcliffe 2005).

Elicitation behaviors also fit within the framework of sexual stimulation influencing reproductive physiology (Lehrman 1965; Adkins-Regan 2005). Producing more chucks might acoustically stimulate hormone production in females, which could influence her reproductive physiology or her motivational state in ways that increase the probability of successful mating. Behaviors that facilitate reproduction in conspecific individuals of the opposite sex occur across diverse taxa (Crews 1998). A variety of male courtship behaviors facilitate ovarian development and consequently reproductive state (Wingfield 2006), and acoustic signals specifically have been shown to influence female reproductive physiology in birds (Lehrman 1965; Cheng 2008). Social acoustic stimuli are known to trigger hormonal response in anurans (Wilczynski et al. 2005); the time course of these effects is usually thought to be on the orders of hours, but few studies have examined effects at a smaller time scale.

A more circuitous advantage to elicitation behaviors might be in their effect on male sexual performance. Males might experience a process similar to behavioral efference, by which aggressive displays contribute to a feedback loop of increasing aggression in the signaler (Bond 1989). This scenario could apply to reproductive displays as well, if a male that produces more chucks self-stimulates the release of hormones that influence his own reproductive behavior. This could result in increased reproductive success for a male and for his mate. Male mice release some hormones in an immediate response to perceiving a receptive female (Bronson and Desjardins 1982). Adkins-Regan (2005) suggests that an immediate hormonal response to females such as this may contribute to changes in a male's attractiveness, mating stamina, or sperm mobilization.

Documenting the existence of elicitation behaviors does not allow us to discriminate among hypotheses about their function, but it does provide evidence of a previously unappreciated female behavior. These results indicate that despite a long history of recognition for the power of female mate choice in driving sexual selection (Trivers 1972), there is still an underappreciation of the ways that females can actively influence male behavior (Gowaty 1997; Clutton-Brock 2007).

Behaviors that influence males to produce signals closer to a sexual selection optimum may be widespread in anurans and other taxa. Several anuran studies report elaborate courtship interactions (Kluge 1981; Bourne et al. 2001; Ovaska and Rand 2001; Owen and Tucker 2006), some including females vocalization (Tobias et al. 1998), that might include elicitation behaviors. Active female influence toward a sexual selection optimum is also likely in other taxa where males invest more energy into signaling (Patricelli and Krakauer 2010) when females are present. We expect that these female behaviors are common because when females prefer costly signals, the sexual selection optimum signal value will always differ from the overall fitness optimum for a male. This perspective should influence models of escalating behaviors in dynamic interactions that predict low occurrence of escalation (Payne and Pagel 1996) because the potential costs and benefits of escalation in male–female courtship interactions differ from the costs and benefits in competitive or aggressive interactions.

In summary, female túngara frogs possess a repertoire of elicitation behaviors that effectively influence males to increase the number of chucks in their calls, thereby pushing their signaling strategy toward the sexual selection optimum and increasing the costliness of mate advertisement.

SUPPLEMENTARY MATERIAL

Supplementary material can be found at http://www.beheco.oxfordjournals.org/.

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REFERENCES

Adkins-Regan E. 2005. Hormones and animal social behavior. Princeton (NJ): Princeton University Press.

Akre KL, Ryan MJ. 2010a. Complexity increases working memory for mating signals. Curr Biol. 20:502–505.

Akre KL, Ryan MJ. 2010b. Proximity-dependent response to variably complex mating signals in túngara frogs (*Physalaemus pustulosus*). Ethology. 116:1138–1145.

Andersson M. 1994. Sexual selection. Princeton (NJ): Princeton University Press.

Arnqvist G, Rowe L. 2005. Sexual conflict. Princeton (NJ): Princeton University Press.

Balsby TJS, Dabelsteen T. 2002. Female behaviour affects male courtship in whitethroats, *Sylvia communis*: an interactive experiment using visual and acoustic cues. Anim Behav. 63:251–257.

Beach FA. 1976. Sexual attractivity, proceptivity, and receptivity in female mammals. Horm Behav. 7:105–138.

Bernal XE, Akre KL, Baugh AT, Rand AS, Ryan MJ. 2009. Female and male behavioral response to advertisement calls of graded complexity in túngara frogs, *Physalaemus pustulosus*. Behav Ecol Sociobiol. 63:1269–1279.

Bernal XE, Page RA, Rand AS, Ryan MJ. 2007. Cues for eavesdroppers: do frog calls indicate prey density and quality? Am Nat. 169:412–415.

Bertram SM, Orozco SX, Bellani R. 2004. Temporal shifts in conspicuousness: mate attraction displays of the Texas field cricket, *Gryllus texensis*. Ethology. 110:963–975.

Bond AB. 1989. Toward a resolution of the paradox of aggressive displays: II. Behavioral efference and the communication of intentions. Ethology. 81:235–249.

Booksmythe I, Detto T, Backwell PRY. 2008. Female fiddler crabs settle for less: the travel costs of mate choice. Anim Behav. 76:1775–1781.

Bourne GR, Collins AC, Holder AM, McCarthy CL. 2001. Vocal communication and reproductive behavior of the frog *Colostethus beebei* in Guyana. J Herpetol. 35:272–281.

Bronson FA, Desjardins C. 1982. Endocrine responses to sexual arousal in male mice. Endocrinology. 111:1286–1291.

Bucher TL, Ryan MJ, Bartholomew GW. 1982. Oxygen consumption during resting, calling and nest building in the frog *Physalaemus pustulosus*. Physiol Zool. 55:10–22.

Cheng M. 2008. The role of vocal self-stimulation in female responses to males: implications for state-reading. Horm Behav. 53:1–10.

Clutton-Brock T. 2007. Sexual selection in males and females. Science. 318:1882–1885.

Cox CR, Le Boeuf BJ. 1977. Female incitation of male competition: a mechanism in sexual selection. Am Nat. 111:317–335.

Crews D. 1998. The evolutionary antecedents to love. Psychoneuroendocrinology. 23:751–764.

Crews D. 2002. Diversity and evolution of hormone-behavior relations in reproductive behavior. In: Becker JB, Breedlove SM, Crews D, McCarthy CL, editors. Behavioral endocrinology. Cambridge (MA): Bradford Books, MIT Press. p. 223–287.

Cummings ME, Bernal XE, Reynaga R, Rand AS, Ryan MJ. 2008. Visual sensitivity to a conspicuous male cue varies by reproductive state in *Physalaemus pustulosus* females. J Exp Biol. 211:1203–1210.

Darwin C. 1871. The descent of man and selection in relation to sex. London: Murray.

Dill LM, Hedrick AV, Fraser A. 1999. Male mating strategies under predation risk: do females call the shots? Behav Ecol. 10:452–461.

Endler JA. 1978. A predator's view of animal color patterns. Evol Biol. 11:319–364.

Evans JP, Kelley JL, Ramnarine IW, Pilastro A. 2002. Female behavior mediates male courtship under predation risk in the guppy (*Poecilia reticulata*). Behav Ecol Sociobiol. 52:496–502.

Gautier P, Barroca M, Bertrand S, Eraud C, Gaillard M, Hamman M, Motreuil S, Sorci G, Faivre B. 2008. The presence of females modulates the expression of a carotenoid-based sexual signal. Behav Ecol Sociobiol. 62:1159–1166.

Goutte S, Kime NM, Argo TF, Ryan MJ. 2010. Calling strategies of male túngara frogs in response to dynamic playback. Behaviour. 147:65–83.

Gowaty PA. 1997. Sexual dialectics, sexual selection, and variation in reproductive behavior. In: Gowaty PA, editor. Feminism and evolutionary biology: boundaries, intersections, and frontiers. New York: Chapman & Hall. p. 351–384.

Gridi-Papp M, Rand AS, Ryan MJ. 2006. Animal communication: complex call production in the tungara frog. Nature. 441:38.

Holland B, Rice WR. 1988. Perspective: chase-away sexual selection: antagonistic seduction versus resistance. Evolution. 52:1–7.

How MJ, Hemmi JM, Zeil J, Peters R. 2008. Claw waving display changes with receiver distance in fiddler crabs, *Uca perplexa*. Anim Behav. 75:1015–1022.

Jackson RR, Walker MW, Pollard SD, Cross FR. 2006. Influence of seeing a female on the male-male interactions of a jumping spider, *Hypoblemum albovittatum*. J Ethol. 24:231–238.

Kirkpatrick M, Ryan MJ. 1991. The paradox of the lek and the evolution of mating preferences. Nature. 350:33–38.

Kluge AG. 1981. The life history, social organization, and parental behavior of *Hyla rosenbergi Boulenger*, a nest-building Gladiator Frog. Misc Pubs Mus Zool Univ Mich. 160:1–170.

Lehrman DS. 1965. Interaction between internal and external environments in the regulation of the reproductive cycle of the ring dove. In: Beach FA, editor. Sex and behavior. New York: Wiley. p. 344–380.

Lindström J, Pike TW, Blount JD, Metcalfe NB. 2009. Optimization of resource allocation can explain the temporal dynamics and honesty of sexual signals. Am Nat. 174:515–525.

Magnhagen C. 1991. Predation risk as a cost of reproduction. Trends Ecol Evol. 6:183–186.

Maynard Smith J. 1982. Evolution and the theory of games. Cambridge: Cambridge University Press.

Otter KA, Ratcliffe L. 2005. Enlightened decisions: female assessment and communication networks. In: McGregor PK, editor. Animal communication networks. Cambridge: Cambridge University Press. p. 133–151.

Ovaska K, Rand AS. 2001. Courtship and reproductive behavior of the frog *Eleutherodactylus diastema* (Anura: Leptodactylidae) in Gamboa, Panama. J Herpetol. 35:44–50.

Owen PC, Tucker JK. 2006. Courtship calls and behavior in two species of chorus frogs, genus *Pseudacris* (Anura: Hylidae). Copeia. 2006: 137–144.

Patricelli GL, Krakauer AH. 2010. Tactical allocation of effort among multiple signals in sage grouse: an experiment with a robotic female. Behav Ecol. 21:97–106.

Patricelli GL, Uy JAC, Borgia G. 2004. Female signals enhance the efficiency of mate assessment in satin bowerbirds (*Ptilonorhynchus violaceus*). Behav Ecol. 15:297–304.

Payne RJH, Pagel M. 1996. When is false modesty a false economy? An optimality model of escalating signals. Proc R Soc B Biol Sci. 263: 1545–1550.

Phelps SM, Rand AS, Ryan MJ. 2007. The mixed-species chorus as public information: túngara frogs eavesdrop on a heterospecific. Behav Ecol. 18:108–114.

Pocklington R, Dill LM. 1995. Predation on females or males: who pays for bright male traits? Anim Behav. 49:1122–1124.

Rohwer S. 1975. The social significance of avian winter plumage variability. Evolution. 29:593–610.

Ryan MJ. 1985. The túngara frog, a study in sexual selection and communication. Chicago (IL): University of Chicago Press.

Ryan MJ, Rand AS. 1981. The adaptive significance of a complex vocal repertoire in a neotropical frog. Z Tierpsychol. 57:209–214.

Ryan MJ, Rand AS. 2003. Sexual selection in female perceptual space: how female túngara frogs perceive and respond to complex population variation in acoustic mating signals. Evolution. 57:2608–2618.

Ryan MJ, Tuttle MD, Rand AS. 1982. Bat predation and sexual advertisement in a neotropical anuran. Am Nat. 119:136–139.

Tobias ML, Viswanathan SS, Kelley DB. 1998. Rapping, a female receptive call, initiates male-female duets in the South African clawed frog. Proc Natl Acad Sci USA. 95:1870–1875.

Trivers RL. 1972. Parental investment and sexual selection. In: Campbell BG, editor. Sexual selection and the descent of man, the Darwinian pivot. New Brunswick (NJ): Transaction Publishers. p. 136–179.

Watkins GG. 1997. Inter-sexual signalling and the functions of female coloration in the tropidurid lizard *Microlophus occipitalis*. Anim Behav. 53:843–852.

West MJ, King AP. 1988. Female visual displays affect the development of male song in the cowbird. Nature. 334:244–246.

Wilczynski W, Lynch KS, O'Bryant EL. 2005. Current research in amphibians: studies integrating endocrinology, behavior, and neurobiology. Horm Behav. 48:440–450.

Wingfield JC. 2006. Communicative behaviors, hormone-behavior interactions, and reproduction in vertebrates. In: Neill JD, editor. Knobil and Neill's physiology of reproduction. Elsevier Academic Press. p. 1995–2040.

Wong BBM, Candolin U. 2005. How is female mate choice affected by male competition? Biol Rev. 80:559–571.

Wong BBM, Svensson PA. 2009. Strategic male signalling effort in a desert-dwelling fish. Behav Ecol Sociobiol. 63:543–549.

Zahavi A. 1975. Mate selection—a selection for a handicap. J Theor Biol. 53:205–214.

Zahavi A, Zahavi A. 1997. The handicap principle, a missing piece of Darwin's puzzle. Oxford: Oxford University Press.

Zuk M, Kolluru GR. 1998. Exploitation of sexual signals by predators and parasitoids. Q Rev Biol. 73:415–438.