

Sexual Differences in the Behavioral Response of Túngara Frogs, *Physalaemus pustulosus*, to Cues Associated with Increased Predation Risk

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Abstract

Engaging in mating behaviors usually increases exposure to predators for both males and females. Anti-predator strategies during reproduction may have important fitness consequences for prey. Previous studies have shown that individuals of several species adjust their reproductive behavior according to their assessment of predation risk, but few studies have explored potential sexual differences in these strategies. In this study, we investigate whether the acoustic cues associated with predatory attacks or those associated with predators themselves affect the mating behavior of female and male túngara frogs, *Physalaemus pustulosus*. We compared the responses of females approaching a mate and those of calling males when exposed to mating calls associated with sounds representing increased hazard. When presented with mating calls that differed only in whether or not they were followed by a predation-related sound, females preferentially approached the call without predation-related sounds. In contrast to females, calling males showed greater vocal response to calls associated with increased risk than to a call by itself. We found significant differences in the responses of females and males to several sounds associated with increased hazard. Females behaved more cautiously than males, suggesting that the sexes balance the risk of predation and the cost of cautious mating strategies differently.

Introduction

In most species, engaging in mating behaviors entails high risks for both males and females. Advertising has long been recognized as a hazardous activity since Darwin acknowledged the dangers males undertake when displaying to attract females (Darwin 1859). Searching for a mate, however, has only recently been considered a risky behavior (reviewed in Lima & Dill 1990). Females navigating breeding areas in search of a mate are vulnerable to opportunistic predators attracted by signaling males and may be even more susceptible to predation than males themselves (Hedrick & Dill 1993; Pocklington & Dill

1995; Godin & Briggs 1996; Gong & Gibson 1996; Dill et al. 1999). In the case of decorated crickets, for instance, Mediterranean house geckos localize burrows of calling males but cannot reach the cricket inside. Thus, they wait for approaching females also attracted to the calls of the male (Sakaluk & Belwood 1984). In situations like this, selection may act on females to reduce predation-related costs. There is increasing empirical evidence that susceptibility to predation affects female mating behavior in invertebrates, fish, birds and mammals (Gibson & Bachman 1992; Wilson et al. 1994; Gong & Gibson 1996; Johnson & Basolo 2003; Su & Li 2006). While dangers to males have been investigated, and recent

evidence finds dangers to females too, so far there has been almost no attention paid to differences in male and female responses to predation risk (Magurran & Nowak 1991; Su & Li 2006).

Given the differences in mating opportunities of males and females (Trivers 1972), and that anti-predator behaviors result in reduced mating activity, sexual differences in response to predation risk are expected. Females usually have multiple chances to mate and should be under strong selection to reduce their susceptibility to predation in hazardous situations. For males, in contrast, the cost of missing an opportunity to obtain a female is high, and they are expected to incur higher predation risk to attract mates (Lima & Dill 1990; Magnhagen 1991).

In this study we investigate whether the acoustic cues of predatory attacks or the acoustic cues of predators themselves affect the mating behavior of female and male túngara frogs, *Physalaemus pustulosus*. Several predators attack and consume túngara frogs at the breeding ponds, including: frog-eating bats (Tuttle & Ryan 1981), four-eyed opossums (Tuttle et al. 1982), South American bullfrogs (Ryan et al. 1981), and large crabs (Ryan et al. 1981). Female and male túngara frogs use an array of strategies to avoid predation during mating. Females, for instance, are more likely to choose a mate and more likely to choose distant callers in the dark, when predators cannot see them, than under dim light (Rand et al. 1997). Similarly, males cease calling and may dive beneath the water surface in response to the visual threat of an approaching frog-eating bat (Tuttle et al. 1982). Besides visual cues, male túngara frogs use calls of non-conspecific frogs to assess predation risk and to decide when to resume calling after a disturbance (Phelps et al. 2007). Here we ask whether female and male túngara frogs listen to other non-conspecific sounds to avoid predation, specifically the sounds produced by approaching predators or the sounds produced during predatory attacks on nearby frogs. We investigate the responses of females approaching mates and the calling response of males to mating signals in the presence and absence of sounds associated with increased predation risk.

Methods

We collected túngara frogs in the areas surrounding the facilities of the Smithsonian Tropical Research Institute in Gamboa, Panama ($9^{\circ}07.0'N$, $79^{\circ}41.9'W$). All frogs were found at choruses between 19:00 and 22:00 hours, brought to the laboratory where they

were tested, and subsequently returned to the sites where they were found. Prior to returning the frogs, we gave them a unique toe-clip number to prevent them from being retested.

Acoustic Stimuli

Male túngara frogs produce whine-like mating calls, ranging in fundamental frequency from 1000 to 500 Hz in 300 ms. Based on the mean values of the parameters of the calls in the population, we synthesized an average whine by shaping sine waves using a software developed by J. Schwartz (Pace University at Pleasantville, NY, USA; sample rate 20 kHz and 8 bit). Mean values were calculated based on the calls of 50 males recorded in July 1996 with a Marantz PMD 420 (Mahwah, NJ, USA) recorder and a Sennheiser ME 80 microphone with K3U power module on magnetic cassette tape (Sennheiser Electronic Corporation, Old Lyme, Connecticut, USA). (Additional information on the call parameters used and the synthesis procedure can be found in Ryan and Rand 2003.)

To simulate increased predation risk we used two kinds of experimental stimuli: (i) sounds that indicate the proximity of potential predators, such as the advertisement call of South American bullfrogs, *Leptodactylus pentadactylus*, or the sound produced by the wings of a frog-eating bat in flight (Fig. 1); (ii) sounds that indicate predatory attacks such as the sound of a quick movement in the water, hereafter a 'splash', and the sound of movement in leaf litter, or a 'rustle' (Fig. 2). A splash simulates an attack by a bat or opossum that suddenly tries to catch a frog calling on water, as túngara frogs do in nature. This kind of attack also generates water-borne cues, but for the purpose of this study, we focused only on acoustic cues. A rustle imitates a terrestrial predator such as an opossum walking through leaves approaching the edge of the pond. Given the transient nature of sounds such as a splash and a rustle in the wild, we recorded these stimuli at the breeding ponds imitating events such as the ones described above, a predator attacking a frog calling on water or approaching the edge of the pond. We used a Marantz PMD 420 recorder and a Sennheiser ME 80 microphone to record these sounds. The sound of the approaching bat was recorded by Rachel A. Page. A frog-eating bat, *Trachops cirrhosus*, was held by hand so it would start flapping its wings, and after several flaps the bat was released. The sound produced as the bat flew towards a Sennheiser ME-66 shotgun microphone was

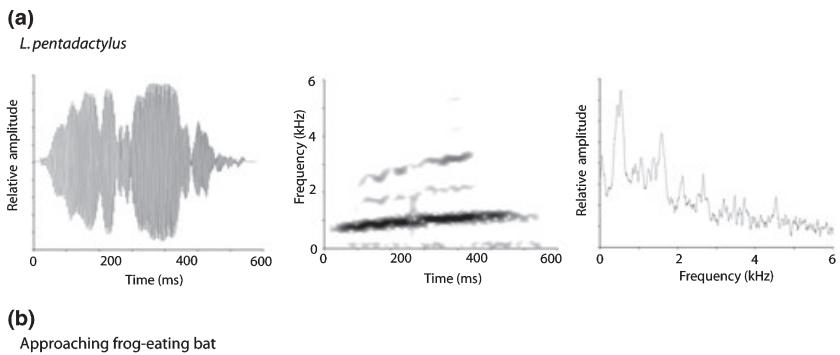


Fig. 1: Oscillogram (left), spectrogram (center) and frequency spectrum (right) of the experimental sounds associated with proximity of potential predators. (a) Mating call of the South American bullfrog, *Leptodactylus pentadactylus*. (b) Sound produced by the wing-beats of an approaching frog-eating bat, *Trachops cirrhosus*.

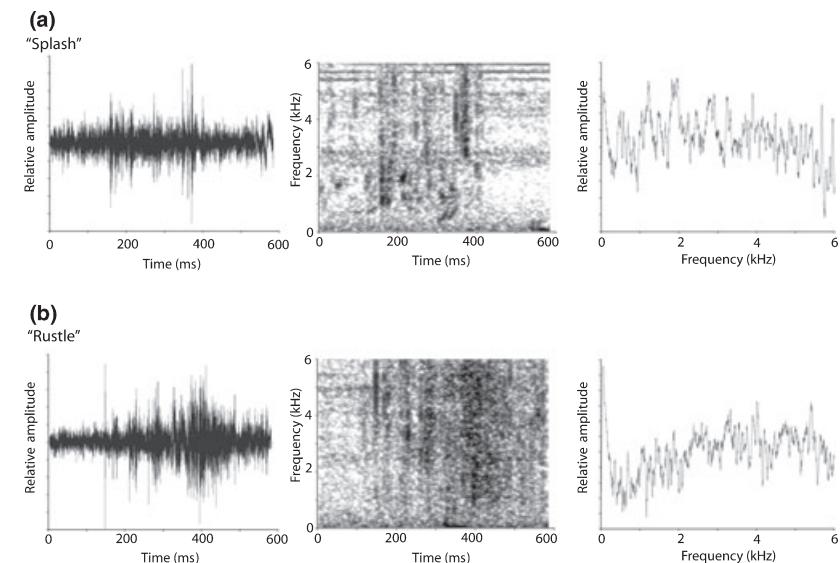


Fig. 2: Oscillogram (left), spectrogram (center) and frequency spectrum (right) of the experimental sounds associated with predatory attacks. (a) 'Splash', sound produced by a quick movement into the water. (b) 'Rustle' sound produced by movement of leaf litter.

recorded using a WM-D6C Sony Tape recorder. A total of five individuals were recorded and the recordings with the least background noise were chosen to be used in the experiments. The advertisement call of *L. pentadactylus* was recorded in the Panama Canal area using a Marantz PMD 420 recorder and a Sennheiser ME 80 microphone, following standard procedures (Heyer 1994).

We appended the sounds that simulated predators or attacks to a synthetic whine. The duration of the splash, the rustle and the sound of the bat in flight was standardized to 600 ms, an appropriate duration to simulate the desired effect and to avoid overlapping with the stimulus broadcast from another speaker.

ker in the tests with females where the stimuli were presented antiphonally from different speakers (see below). The total duration of each stimulus, whine plus threat sound, was 969 ms. The calls with the experimental sounds were broadcast at a rate of one call every 2 s, a typical calling rate for túngara frogs (Ryan 1985). To avoid acoustic masking, we did not broadcast the experimental stimuli at the same time as the whine. Playing the stimuli following the whine is a conservative measurement given that non-conspecific sounds appended to the call can increase call attractiveness to females (Ryan & Rand 1993), and therefore should bias the results in the direction contrary to our prediction.

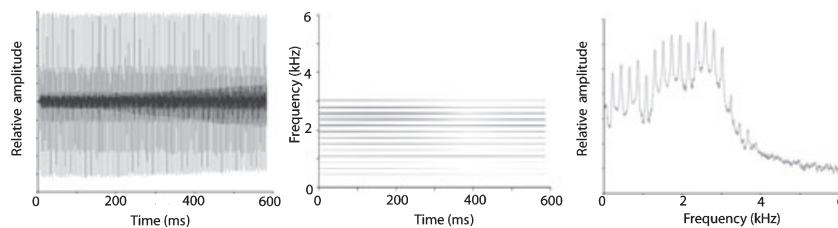


Fig. 3: Oscillogram (left), spectrogram (center) and frequency spectrum (right) of the 'long chuck' used in the experiments as a control stimulus (see text for details).

To explore whether the responses of the frogs were the effect of any relatively long, loud sound appended to the call, we also used a modified natural component of the mating call in addition to the predatory stimuli described above. Male túngara frogs facultatively add burst-like secondary components to the whine, called chucks. These suffixes are shorter than the whine, about 40 ms in duration, and increase both the attractiveness of the call to females and the calling response of males (Rand & Ryan 1981; Ryan 1985). Using the mean parameters of the chuck in the population and the methods described above, we synthesized a call component identical to a natural chuck in all features but duration. We produced a synthetic chuck of equal duration to the experimental stimuli, hereafter 'long chuck' (Fig. 3).

Females – Phonotaxis

In 2002 and 2003, between May and Aug., we performed standard two-speaker phonotaxis tests, offering females a choice between identical mating calls with and without one of the experimental stimuli. Each female was placed under a funnel in the center of a 1.8 m × 2.7 m sound attenuation chamber (Acoustic Systems, Austin, TX, USA). The stimuli were broadcast for 3 min before remotely removing the funnel allowing the female to freely move in the arena. We broadcast the test stimuli antiphonally from speakers in the center of walls opposite one another such that the peak amplitude of the whine of each test call at the center of the arena was 82 dB SPL (20 µPa). A choice was scored when the female approached within 10 cm any of the speakers. No choice was scored if a female stayed at the release point without moving for 5 min, did not move for 2 min, or spent more than 15 min roaming the arena without approaching a speaker. The behavior of the females was observed on a monitor using a wide-lens video system with infrared light source (Fuhrman Diversified, Inc (Houston, TX, USA)). We used two-tailed exact binomial probability tests to evaluate if the responses of females deviated from the 1:1 distribution expected if the experimental stimuli were ignored.

Males – Evoked Vocal Response

In 2003, between July and Aug., calling males were captured at their breeding sites and brought to the laboratory where we tested them in evoked vocal response experiments using the same stimuli as used in the phonotaxis experiments with females. Each male was placed inside individual acoustically isolated chambers (30.5 cm × 46 cm × 30.5 cm) following Bosch et al. (2000, 2002). Males were placed with sufficient water to call in plastic bags previously shown to be acoustically transparent by Ryan & Rand (1998). We broadcast the experimental stimuli using a small, wide-frequency-range speaker (Cambridge SoundWorks Inc., (Cambridge, MA, USA) Ensemble IV) and recorded the response of the males with a Radio Shack miniature microphone into a Sony WM-D6 cassette recorder (Tokyo, Japan). The speaker (RadioShack Corporation, Fort Worth, Texas, USA) was positioned in front of the male at about 15 cm, and the microphone was oriented to the calling frog but perpendicular to the speaker to maximize the difference in amplitude between the calls of the focal male and those played back. We presented the stimuli using a JVC XL-PG7 CD-player (Yokohama, Japan) through a Realistic SA-10 amplifier (RadioShack Corporation, Fort Worth, Texas, USA) at 90 dB SPL (20 µPa) at 0.5 m as measured by a GenRad sound pressure level meter (model 1982). This sound pressure level is equivalent to the one used in the experiments with the females (82 dB at 1.25 m). We stimulated the males with a túngara frog chorus recorded on 2 Oct. 1990 in the same population. Once a male was calling, the chorus was turned off and it was tested singly. After a male finished a test, it was required to call again before starting the next test. Males were tested until they responded in all of the experiments or stopped calling.

Two sets of experiments were conducted: (i) males were presented with túngara frog mating calls followed by sounds indicating increased predation risk, as in the female phonotaxis experiments above, and (ii) males were presented with the experimental stimuli without mating calls. In the first set of experiments, half of the males were exposed to synthetic whines for 1 min, silence for 1 min, and

whines with one of the experimental stimuli appended to it for 1 min. The other males in this experiment were exposed to the whine followed by the experimental stimuli for 1 min, silence for 1 min, and the whine by itself for another 1 min. We changed the order of presentation of the stimuli from one male to the next.

In the second set of experiments, we presented each experimental stimulus independently without being appended to a whine. Male túngara frogs are more permissive in their responses to signal variation than females (Bernal et al. in press), and it is possible that a whine followed by any sound will elicit a response. To account for this, and potentially detect more subtle responses of males to sounds that represent increased hazard, we investigated their calling responses to the experimental stimuli alone. For this, we waited until a male was calling spontaneously and then broadcast one of the experimental stimuli without a whine, and only once. We recorded the calling behavior of the males 15 s before and after the presentation of the stimuli.

We digitized the tapes using CoolEdit 2000 (Syntrillium Software Corporation (Adobe, San Jose, CA, USA)), at a sampling rate of 44.1 kHz and 16 bits per sample. Using this software, we also measured the latency to first call following stimulus broadcast (from the beginning of the presentation of the stimuli), number of whines and number of chucks during the presentation of the whine alone and the whine followed by the experimental sounds. We then performed a principal components analysis (PCA) combining those three variables for each treatment, and used the score on the first component as a measure of overall calling response. In this way, we obtained a response score for each male while calling in the presence of the call alone and calling in the presence of the call associated with the experimental stimuli.

In the experiments in which a single experimental stimulus was presented without a whine, we simply counted the number of calls because males rarely added chucks to their calls. Production of whines without chucks is common in males calling while isolated from other calling males (Ryan 1985). We used Wilcoxon signed-rank tests to compare the calling response before and after the presentation of each experimental stimulus.

Comparison between Females and Males

To contrast the responses of the sexes to the experimental stimuli appended to mating calls, we conver-

ted the vocal response of males based on the loadings to the first component of the PCA into a response score that could be compared with the response scores of the females (e.g. choice for whine or for whine with the experimental sound appended). In each trial, the stimulus with the highest calling response was assigned as the one chosen. We compared the number of males and females that responded to each experimental pair of calls using two-tailed Fisher's exact tests.

Results

The results of all the experiments are summarized in Tables 1–3. Female túngara frogs preferentially approached the mating call that was not associated with a predation attack or an approaching frog-eating bat (Table 1). Whines followed by the call of *L. pentadactylus* or the long chuck, however, were as attractive as a whine by itself.

Males were more responsive to calls associated with increased predation risk than to a single whine. Calls with the experimental stimuli appended to them elicited more calls, more chucks and a shorter latency to response (Table 2). The first principal component from the PCA, used to reduce the variables to a single overall measurement of calling response, explained over 88% of the total variation in all treatments (88.31–89.46%, eigenvalue >1.7). Overall calling response was significantly higher to whines associated with the sound of bat wing-beats, rustle and the long chuck. Males, however, did not significantly increase their calling response when presented with the call of *L. pentadactylus* or the splash. In all the variables measured, however, there were trends to increase calling response to both stimuli: males increased the number of calls and chucks, and also decreased the time to their first response when exposed to the sounds associated with increased danger.

Table 1: Túngara frog female phonotactic responses when presented with identical mating calls (whine) in which one is followed by a sound associated with increased predation risk (ES)

Experimental stimuli (ES)	Whine	Whine + ES	Binomial probability
Rustle	17	3	0.001
Splash	15	5	0.015
Bat wing-beats	18	2	<0.001
<i>L. pentadactylus</i>	13	7	0.074
Long chuck	8	13	0.097

The columns indicate the number of females that approached a whine alone or approached the whine followed by the experimental stimulus.

Table 2: Calling response of male túngara frogs, *Physalaemus pustulosus*, to playbacks of a single mating call (whine) and a call followed by a sound representing increased predation risk (whine + ES)

Experimental stimuli (ES)	Number of calls		Number of chucks		Latency time (s)		Wilcoxon signed-rank tests		
	Whine	Whine + ES	Whine	Whine + ES	Whine	Whine + ES	Z	p	n
Rustle	22.25 (1.90)	29.00 (0.98)	28.15 (4.05)	44.80 (4.93)	4.62 (2.04)	1.32 (0.06)	-2.701	0.007	10
Splash	24.22 (1.68)	25.77 (3.21)	35.44 (3.29)	45.11 (6.25)	2.91 (0.99)	1.31 (0.08)	-1.007	0.314	9
Bat wing-beats	23.80 (1.77)	32.30 (1.30)	32.20 (3.91)	60.10 (5.39)	2.08 (0.36)	1.96 (0.63)	-2.701	0.007	10
<i>L. pentadactylus</i>	22.15 (1.59)	23.80 (2.72)	28.25 (3.70)	40.1 (5.82)	5.21 (2.05)	2.31 (1.03)	-1.784	0.074	10
Long chuck	21.85 (1.99)	32.30 (0.99)	28.00 (2.42)	64.70 (2.90)	6.31 (3.33)	1.74 (0.33)	-2.803	0.005	10

Mean (SEM) is presented. The Wilcoxon signed-rank tests shown are based on principal component analyses for each treatment combining number of calls, number of chucks and latency time.

For details about the procedure see the section Methods in the text.

p-values <0.05 are shown in bold.

Table 3: Calling behavior of male túngara frogs, *Physalaemus pustulosus*, during 15-s intervals before and after the presentation of sounds representing an increased risk of predation alone

Experimental stimuli (ES)	Number of calls		Wilcoxon signed-rank test	
	Before	After	Z	p
Rustle	3.33 (0.64)	1.89 (0.86)	-1.057	0.291
Splash	3.89 (0.65)	2.11 (0.89)	-1.442	0.149
Bat wing-beats	3.56 (0.55)	1.00 (0.60)	-2.264	0.024
<i>L. pentadactylus</i>	3.11 (0.66)	2.00 (1.12)	-1.016	0.310
Long chuck	3.78 (0.62)	2.22 (1.02)	-1.270	0.204

n = 9 individuals in all treatments.

The effect of the experimental stimuli was different when these sounds were presented without the whine. Calling males exposed to sounds associated with increased danger, without the whine, showed a tendency to reduce the number of calls produced (Table 3). Males only significantly reduced their calling behavior, however, in response to the sound of the bat wing-beats.

Females approaching a mate and calling males significantly differed in their responses to all stimuli with the exception of the whine followed by the call of *L. pentadactylus* (rustle: p < 0.001, splash: p = 0.014, bat wing-beats: p < 0.001, *L. pentadactylus*: p = 0.122, long chuck: p = 0.032). In all cases, a higher proportion of males than females responded to the mating calls associated with increased danger, and to the long chuck.

Discussion

Our results showed differences between reproductively active female and male túngara frogs in their response to sounds associated with increased predation risk.

While several studies have shown that some prey species respond to acoustic cues signaling the presence of a predator (Hendrie et al. 1998; Jones et al. 2002; Baxter et al. 2006; Phelps et al. 2007), to our knowledge this is the first study to reveal sexual differences in these responses.

Females avoided mating calls associated with sounds that indicate a predation attack but did not evade those coupled with the call of a common predator, *L. pentadactylus*. This behavior suggests that females perceived no threat when hearing calls of *L. pentadactylus*. Calling *L. pentadactylus* probably does represent a serious hazard even though they are also engaged in attracting mates. They are a voracious predator of túngara frogs (Ryan et al. 1981) and, as in other frog-eating frogs, males probably feed while calling (Schwartz et al. 2000). We are confident that females do not mistakenly recognize the call of *L. pentadactylus* for a túngara frog call; the two calls differ in the direction of their frequency sweeps and túngara frogs are sensitive to this call parameter (Rose et al. 1988). It is possible that female *P. pustulosus* from the population we sampled have had little experience with this predator. Where we collected females for this study, *L. pentadactylus* are not as abundant as in other areas such as the site studied by Ryan et al. (1981). In other species, response to predators varies with predator density (e.g. guppies, Godin & Briggs 1996; damselflies, McPeek 1990; salamanders, Storfer & Sih 1998), and this relationship could be tested in túngara frogs.

Most of the sounds we used in our study affected female phonotaxis. This effect could be due to the experimental sounds acoustically interfering with the mating call. The fact that the long chuck did not alter the responses of females suggests that this is not the case. If long, loud sounds following the

whine interfere with the call, the long chuck should elicit the same effect as the other experimental stimuli we presented. It seems more likely that the decrease in attractiveness is due to the association of the whine with our experimental sounds. In our tests using risk-related sounds, female túngara frogs were presented with two identical whines, which should therefore offer equal benefits. This balance was likely disrupted when a potential cost was associated with one of the calls.

Studies examining the influence of risk on reproductive activity have generally concluded that predators reduce mating behavior of their prey (Tuttle & Ryan 1982; Sih et al. 1990; Dill et al. 1999; Johnson & Basolo 2003; but see Schwartz et al. 2000). Male *P. pustulosus* reduce their calling activity when exposed to visual cues imitating an approaching frog-eating bat (Tuttle et al. 1982). We expected similar responses to acoustic cues associated with high predation risk, in particular, to the sound of an approaching bat. In our study, however, male túngara frogs behaved contrary to our predictions, as they increased calling in response to those mating calls followed by sounds that represent increased risk of predation. Our results suggest that male túngara frogs do not perceive the sounds we presented as indicators of increased hazard as they did not cease calling. Whether or not these stimuli were associated with a whine, they did not result in decreased calling with one exception, the wing-beats of bats. When presented by themselves, they did result in decreased calling, but not when they followed a whine. Túngara frog males may be using the calls of other males to further assess the level of predation risk and modulate their response to sounds that otherwise would be perceived as a threat. In accordance with this idea, male túngara frogs that cease calling following the release of a bat model or a disturbance, resume calling faster when hearing conspecific calls than in silence (Jennions & Backwell 1992; Phelps et al. 2007).

It is clear from our results that reproductively active male and female *P. pustulosus* differ in their predator avoidance strategies when using acoustic cues as proxies for increased predation risk. Females behaved more cautiously than males, suggesting that the sexes balance the risk of predation and the cost of cautious mating strategies differently. In our experiments, because females were presented with a two-choice paradigm, there was no cost to females of losing mating opportunities when avoiding sounds indicating increased hazard. For males, in contrast, reducing or ceasing their calling response has a

direct negative impact in their ability to attract females. This situation reflects the scenario for both sexes in nature. In túngara frogs, the operational sex ratio is strongly male biased and thus females have multiple opportunities to mate, while males have fewer chances of attracting a mate (Ryan 1985). Females actively choose a mate from a pool of calling males while males vocally compete with neighboring males to attract a mate. Intense intrasexual competition to obtain a mate, combined with high predation risk, probably led males to tune their response to predators in a finer way than females.

Females might also be more sensitive to the sounds indicating potential threats than males because of the vulnerability of moving towards a potential mate, and the possibility of adjusting their behavior without incurring higher costs. A female, for instance, can alter its path and choose another male that is not as close to the perceived threat. Calling males, however, must call to attract a mate. Alternative mating strategies have not been described in túngara frogs despite the extensive work done on this species. This lack of alternative behaviors for males may also underlie their willingness to engage in risky behaviors.

Few studies have investigated the use of acoustic signals in anurans to detect predators or other dangers in spite of the relevance of this sensory modality in this group (Schwartz et al. 2000; Grafe et al. 2002). This study is the first demonstration that *P. pustulosus* females use acoustic cues associated with predators and predation attacks to modulate their mating behavior, and the first study to demonstrate different responses in males versus females in response to acoustic cues signaling predation risk.

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compiled by the American Society of Ichthyologists and Herpetologists (ASIH), the Herpetologists' League (HL), and the Society for the Study of Amphibians and Reptiles (SSAR), available at <http://www.asih.org/pubs/herpcoll.html>.

Literature Cited

- Baxter, D. M., Psyllakis, J. M., Gillingham, M. P. & O'Brien, E. L. 2006: Behavioural response of bats to perceived predation risk while foraging. *Ethology* **112**, 977—983.
- Bernal, X. E., Rand, A. S. & Ryan, M. J. (in press): Sexual differences in responses to non-conspecific advertisement calls: receiver permissiveness in male and female túngara frogs. *Anim. Behav.* in press.
- Bosch, J., Rand, A. S. & Ryan, M. J. 2000: Acoustic competition in *Physalaemus pustulosus*, a differential response to calls of relative frequency. *Ethology* **106**, 865—871.
- Bosch, J., Rand, A. S. & Ryan, M. J. 2002: Response to variation in chuck frequency by male and female túngara frogs. *Herpetologica* **58**, 95—103.
- Darwin, C. 1859: On the Origin of Species. Murray, London.
- Dill, L. M., Hedrick, A. V. & Fraser, A. 1999: Male mating strategies under predation risk: do females call the shots? *Behav. Ecol.* **10**, 452—461.
- Gibson, R. M. & Bachman, G. C. 1992: The cost of female choice in a lekking bird. *Behav. Ecol.* **3**, 300—309.
- Godin, J-G. J. & Briggs, S. E. 1996: Female mate choice under predation risk in the guppy. *Anim. Behav.* **51**, 117—130.
- Gong, A. & Gibson, R. M. 1996: Reversal of a female preference after visual exposure to a predator in the guppy, *Poecilia reticulata*. *Anim. Behav.* **52**, 1007—1015.
- Grafe, T. U., Dobler, S. & Linsenmair, K. E. 2002: Frogs flee from the sound of fire. *Proc. R. Soc. Lond. B Biol. Sci.* **269**, 999—1003.
- Hedrick, A. V. & Dill, L. M. 1993: Mate choice by female crickets is influenced by predation risk. *Anim. Behav.* **46**, 193—196.
- Hendrie, C. A., Weiss, S. M. & Eilam, D. 1998: Behavioural response of wild rodents to the call of an owl: a comparative study. *J. Zool. (Lond.)* **245**, 439—446.
- Heyer, W. R. 1994: Recording frog calls. In: Measuring and Monitoring Biological DIversity. Standard Methods for Amphibians (Heyer, W. R., Donnelly, M. A., McDiarmid, R. W., Hayek, L-A. C. & Foster, M. S., eds). Smithsonian Institution Press, Washington, DC, pp. 285—287.
- Jennions, M. D. & Backwell, P. R. Y. 1992: Chorus size influences on the anti-predator response of a Neotropical frog. *Anim. Behav.* **44**, 990—992.
- Johnson, J. B. & Basolo, A. L. 2003: Predator exposure alters female mate choice in the green swordtail. *Behav. Ecol.* **14**, 619—625.
- Jones, G., Barabas, A., Elliot, W. & Parsons, S. 2002: Female greater wax moths reduce sexual display behavior in relation to the potential risk of predation by echolocating bats. *Behav. Ecol.* **13**, 375—380.
- Lima, S. L. & Dill, L. M. 1990: Behavioral decisions made under the risk of predation: a review and prospectus. *Can. J. Zool.* **68**, 619—640.
- Magnhagen, C. 1991: Predation risk as a cost of reproduction. *Trends Ecol. Evol.* **6**, 183—186.
- Magurran, A. E. & Nowak, M. A. 1991: Another battle of the sexes: The consequences of sexual asymmetry in mating costs and predation risk in the guppy, *Poecilia reticulata*. *Proc. Roy. Soc., Biol. Sci.* **246**, 31—38.
- McPeek, M. A. 1990: Behavioral differences between *Enallagma* species (Odonata) influencing differential vulnerability to predators. *Ecology* **7**, 1714—1726.
- Phelps, S. M., Rand, A. S. & Ryan, M. J. 2007: The mixed-species chorus as public information: Túngara frogs eavesdrop on a heterospecific. *Behav. Ecol.* **18**, 108—114.
- Pocklington, R. & Dill, L. M. 1995: Predation on females or males: who pays for bright male traits? *Anim. Behav.* **49**, 1122—1124.
- Rand, A. S. & Ryan, M. J. 1981: The adaptive significance of a complex vocal repertoire in a neotropical frog. *Z. Tierpsychol.* **57**, 209—214.
- Rand, A. S., Bridarolli, M. E., Dries, L. & Ryan, M. J. 1997: Light levels influence female choice in túngara frogs: predation risk assessment? *Copeia* **1997**, 447—450.
- Rose, G. J., Zelick, R. & Rand, A. S. 1988: Auditory processing of temporal information in a neotropical frog is independent of signal intensity. *Ethology* **77**, 330—336.
- Ryan, M. J. 1985: The Túngara Frog: A Study in Sexual Selection and Communication. Univ. of Chicago Press, Chicago, IL.
- Ryan, M. J. & Rand, A. S. 1993: Species recognition and sexual selection as a unitary problem in animal communication. *Evolution* **47**, 647—657.
- Ryan, M. J. & Rand, A. S. 1998: Evoked vocal responses in male túngara frogs: Preexisting biases in male responses? *Anim. Behav.* **56**, 1509—1516.
- Ryan, M. J. & Rand, A. S. 2003: Mate recognition in túngara frogs: A review of some studies of brain, behaviour and evolution. *Acta Zoologica Sinica* **49**, 713—726.
- Ryan, M. J., Tuttle, M. D. & Taft, L. K. 1981: The costs and benefits of frog chorusing behavior. *Behav. Ecol. Sociobiol.* **8**, 273—278.

- Sakaluk, S. K. & Belwood, J. J. 1984: Gecko phonotaxis to cricket calling song: A case of satellite predation. *Anim. Behav.* **32**, 659—662.
- Schwartz, J. J., Bee, M. A. & Tanner, S. D. 2000: A behavioral and neurobiological study of the responses of gray treefrogs, *Hyla versicolor*, to the calls of a predator, *Rana catesbeiana*. *Herpetologica* **56**, 27—37.
- Sih, A., Krupa, J. & Travers, S. 1990: An experimental study on the effects of predation risk and feeding regime on the mating behavior of the water strider. *Am. Nat.* **135**, 284—290.
- Storfer, A. & Sih, A. 1998: Gene flow and ineffective antipredator behavior in a stream-breeding salamander. *Evolution* **52**, 558—565.
- Su, K. F. Y. & Li, D. 2006: Female-biased predation risk and its differential effect on the male courtship behavior of jumping spiders. *Anim. Behav.* **71**, 531—537.
- Trivers, R. L. 1972: Parental investment and sexual selection. In: *Sexual Selection and the Descent of Man* (Campbell, B. ed). Aldine-Atherton, Chicago, IL, pp. 136—179.
- Tuttle, M. D. & Ryan, M. J. 1981: Bat predation and the evolution of frog vocalizations in the Neotropics. *Science* **214**, 677—678.
- Tuttle, M. D. & Ryan, M. J. 1982: The role of synchronized calling, ambient light, and ambient noise in anti-bat behavior of a treefrog. *Behav. Ecol. Sociobiol.* **154**, 171—174.
- Tuttle, M. D., Taft, L. K. & Ryan, M. J. 1982: Acoustic location of calling frogs by *Philander* opossums. *Biotropica* **13**, 233—234.
- Wilson, D. S., Clark, A. B., Coleman, K. & Dearstyne, T. 1994: Shyness and boldness in humans and other animals. *Trends Ecol. Evol.* **9**, 442—446.