



Simulated Predation Risk Influences Female Choice in Túngara Frogs, *Physalaemus pustulosus*

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Abstract

While the presence of predators can influence female mate choice, few studies have investigated how females respond to quantitative variation in predation risk. In addition, we know little of how females respond to multiple, independent cues of risk. In this study, we investigated the effects of simulated predation risk on mate choice in túngara frogs, *Physalaemus pustulosus*, using the advertisement calls of predatory frogs, variation in ambient light, and simulated distance. Females showed aversion to conspecific calls associated with the calls of predators, and females were significantly less likely to travel perceived longer distances while the calls of predatory frogs were broadcast. In both the laboratory and field, females chose among potential mates significantly faster under higher light levels. Female responses to acoustic cues of predation risk were significantly influenced by light level, but decisions about travel distances were not. These results demonstrate that female choice is strongly influenced by perceived predation risk and that females can simultaneously evaluate quantitative variation in different cues of predation risk. The changes in search behavior and mate evaluation we demonstrate indicate that predation plays a strong role in limiting signal evolution and possibly reproductive isolation.

Introduction

Choosing and attracting mates is of central importance in the lives of many sexually reproducing organisms. This search for mates often brings individuals into high density, reproductive aggregations which attract large numbers of predators (Cade 1975; Ryan et al. 1981; Zuk & Kolluru 1998). Predation risk imposes strong costs on mate evaluation (reviewed in Lima & Dill 1990), and females often respond accordingly by changing the way they evaluate mates. In some cases, elevated predation risk increases thresholds of mate attractiveness for mating (Demary et al. 2006; Su & Li 2006; Vélez & Brockmann 2006). In other cases, however, the presence of predators can make animals less choosy or even reverse their preferences for normally attrac-

tive mates (Evans et al. 2004; Schwartz & Hendry 2006, 2007; Dunn & Whittingham 2007).

Predation risk also plays a role in determining the amount of time animals will invest in searching for mates. In the presence of predators, fiddler crabs and tailspot wrasses reduced the amount of time spent searching for mates (deRiviera et al. 2003; Karino et al. 2000; Kim et al. 2007). Reduced search time also meant a reduction in the number of potential mates sampled (Karino et al. 2000; deRiviera et al. 2003).

In most cases, the role of predation risk in shaping mate choice is studied by manipulating the presence or absence of risk using a single variable. In this study, we investigate the responses of female túngara frogs, *Physalaemus pustulosus* not just to the presence of risk, but to variation in predation risk using

multiple, independent cues. Like the majority of anuran species, male túngara frogs gather in nightly choruses throughout the breeding season. When reproductively ready, females will enter these choruses and evaluate males, typically three to four times in a breeding season (Ryan 1985). Túngara frogs share choruses with several anuran predators including the smoky jungle frog, *Leptodactylus pentadactylus* (Ryan et al. 1981). In addition, choruses attract other visually orienting predators such as the cat-eyed snake, *Leptodeira septentrionalis*. Encounter rates and detection by these predators likely varies throughout the lunar cycle, as ambient light levels change. Mate choice in túngara frogs is influenced by cues of predation risk. Under dim light, female túngara frogs are less willing to travel long distances to find males (Rand et al. 1997). Although females exhibit a fivefold preference for the conspecific complex call ('whine-chuck') to the simple call ('whine') (Ryan 1985; Gridi-Papp et al. 2006), appending the acoustic cues of predation to the complex call decreases its attractiveness relative to the simple call (Bernal et al. 2007). Not only do túngara frogs respond to the calls of potential predators such as *L. pentadactylus*, they also monitor the calls of frogs that are not a threat to assess predation risk. Phelps et al. (2007) showed that males rely on this public information and begin calling sooner when other harmless frog species begin to call. In this study, we present the results of a series of independent experiments on how females respond to predation risk. We evaluate the responses of females to quantitative variation in cues of predation risk rather than its presence or absence. We also present a variety of cues of predation risk to females, including acoustic cues, light, and simulated distance both independently and simultaneously to better understand how females use information from various sources and modalities while making decisions about potential mates.

Methods

We collected pairs of túngara frogs in amplexus from choruses in Gamboa, Panama near facilities of the Smithsonian Tropical Research Institute (9°07.0'N, 79°41.9'W) between August and October of 2008. These frogs were then brought back to laboratory, tested, and released back at their original capture sites with their original mates. Prior to release, we gave each female a unique toe-clip combination to prevent retesting. In any test involving light levels, we first dark adapted females by holding them in a

dark cooler for 1 h (Cornell & Hailman 1984; Fan et al. 2001).

We performed two-choice phonotaxis tests in a 1.8 × 2.7 m sound attenuating chamber (Acoustic Systems, Austin, TX, USA). Females were held in the center of the chamber under a plastic funnel for 3 min, while test stimuli were broadcast antiphonally from speakers on either short side of the chamber. We then released the females and observed them remotely through a wide-angle video camera and infrared light source (Fuhrman Diversified, Inc., Seabrook, TX, USA) mounted on the ceiling of the acoustic chamber. Optomotor studies showed that the females are not sensitive to the IR light being emitted by this source. Females were scored as having made a choice when they entered a 10-cm zone around either speaker. A female failed to make a choice if she did not leave the start zone after 5 min, stayed stationary for longer than 2 min, or failed to enter the choice zones after 15 min.

Acoustic cues of predators and harmless heterospecifics

To test how females respond to variation in predation risk, we presented female túngara frogs a choice between a simple call and a complex call, to which we appended a natural call of either a *Leptodactylus labialis* (a harmless sympatric species) or *L. pentadactylus* (a large predator of túngara frogs). The technique of appending calls follows that of Bernal et al. (2007).

The peak amplitude of the whine of each call was 82 dB SPL (re. 20 μ Pascals) at the female's release point. The calls of the two *Leptodactylus* species were presented at one of three amplitudes: the same peak amplitude as the whine (82 dB SPL); approximately twice the peak amplitude of the whine, 86.7 dB; or approximately three times the peak amplitude of the whine, 90.2 dB.

We used a repeated-measure logistic regression analysis using the general estimating equation (GEE analysis) for binary data with logit link function (SAS online DocTM, ver. 8, p 1452; SAS Institute, Cary, NC, USA) to assess the effect of stimulus level and species identity, as well as their interaction, on what females chose ($n = 20$). We used full-factorial general linear models with Type III sum of squares to assess the effects of stimulus level and species identity, as well as their interaction on choice latency, or how long it took females to make a choice from when they were released ($n = 20$).

Acoustic cues of predators and light levels

As light levels change throughout the lunar cycle, the likelihood that a moving female will be detected by predators also changes. Under higher light conditions, females may respond more strongly to the presence of acoustic cues of predators. To address this question, we repeated the *L. pentadactylus* series under total darkness in the human visible spectrum and at 0.28 lux light conditions (produced using Current USA Lunar light LEDs and measured using a Extech 403125 Light meter). These conditions are slightly brighter than levels we recorded at choruses on full moon nights ($0.23 \text{ lux} \pm 0.01 \text{ SE}$), and optomotor studies show that the frogs are able to see at this light level (Cummings et al. 2008).

We used a repeated-measure logistic regression analysis using the general estimating equation (GEE analysis) for binary data with logit link function to assess the effect of light levels, stimulus level, and their interaction on what females chose ($n = 20$). We used full-factorial general linear models with Type III sum of squares to assess the effects of light levels, stimulus level, and their interaction on choice latency or how long it took females to make a choice from when they were released ($n = 20$).

Simulated distance and light

As sound attenuates predictably with distance, under ideal conditions – 6 dB with each doubling of distance – we varied estimated travel time of the female to the sound source by varying the call's peak amplitude. When played at equal amplitudes, female túngara frogs strongly prefer 'complex' calls to 'simple' calls. Females were given a choice between a 'near' simple call at 82 dB SPL at the female's release point, which should have a perceived distance of 1.5 m, and 'far' complex calls, given at: 76 dB SPL (3 m); 70 dB SPL (6 m); and 64 dB SPL (12 m). The final amplitude is near the threshold for eliciting phonotaxis from female túngara frogs (Marsh et al. 2000). These experiments were conducted in the dark and at 0.28 lux.

We used a repeated-measure logistic regression analysis using the general estimating equation (GEE analysis) for binary data with logit link function to assess the effect of light levels, simulated distance, and their interaction on what females chose ($n = 20$). We used full-factorial general linear models with Type III sum of squares to assess the effects of light levels, simulated distance, and their interaction on choice latency or how long it took females to

make a choice from when they were released ($n = 20$).

Other predators and public information

To test how females responded to a suite of potential predators, we used phonotaxis to determine a female's preference between a 'near' simple call (82 dB SPL) and a 'far' complex call (76 dB SPL), while broadcasting calls of other local species from a third speaker located at the center of the back wall, in contrast to the previous phonotaxis experiments. We recorded the advertisement calls of *Bufo marinus*, *Hyla microcephala*, *Leptodactylus insularum*, *Leptodactylus labialis*, and *Leptodactylus pentadactylus* from túngara frog collection sites using a Marantz PMD 660 digital recorder (Marantz America, Inc., Mahwah, NJ, USA) and Sennheiser ME 67 microphone (Sennheiser Electronic Corporation, Old Lyme, CT, USA). In addition, we synthesized an artificial call bout by repeating the 'mew' call of the túngara frog (Ryan 1985) at a rate of one call per two-seconds. The 'mew' is used in territorial interactions between males and does not elicit female phonotaxis.

We compared the choices of females hearing calls of predators (*B. marinus*, *L. insularum*, and *L. pentadactylus*) and harmless species (*H. microcephala* and *P. pustulosus* 'mew') to females hearing only the conspecific advertisement calls. We also tested the responses of females to the calls of *Leptodactylus labialis*. Male túngara frogs use the calls of *L. labialis* to assess predation risk (Phelps et al. 2007), but whether or not females also used this public information was not known. Each test was analyzed using a Fisher's exact test to test against and expected even split ($n = 20$).

Light levels in natural choruses

Females encounter variation in risk of attack by visual predators across a lunar cycle because of changes in ambient light levels. To see how female responses to light in the laboratory matched up with the behavior of frogs in natural choruses, we marked off a section of a pond in Gamboa, Panama measuring 1.8 m by 2.7 m, the same size as the floor of the phonotaxis arena. Males were allowed to choose calling sites on their own. The number of males in the demarcated area was variable, but did not vary significantly across the lunar cycle ($3.5 \pm 0.03 \text{ SE}$).

On 26 nights over the course of a single lunar cycle, we measured light levels at the chorus and

collected females in amplexus from adjacent areas. We released them, one at a time, from a release point in the center of the demarcated area. We then followed females as they moved through the area using an infrared video camera (Sony DCR-HC52 MiniDV Handycam, Sony Corporation, Minato, Tokyo, Japan). As in the laboratory, we did not consider data from any female that failed to leave the release point within 5 min, stayed stationary for more than 2 min outside the release point, or failed to make a choice within 15 min. Again, we scored a choice when a female approached within 10 cm of a male. In every trial, this was followed by amplexus. In addition, we also did not consider data from any female that left the demarcated area. As in other studies observing movements of females throughout choruses (Ryan 1985), females were often observed to approach a calling male at a distance of 10–20 cm and pause. We made note of the number of males a female approached at this distance and the length of time females took to make a choice, or the choice latency. In several cases, females paused at the release site before beginning to move. This time was subtracted from choice latency to obtain a new value for the amount of time spent moving in the chorus. Both total latency and time spent moving were analyzed against ambient light level using a general linear model with Type III sum of squares.

Results

Acoustic cues of predators and harmless heterospecifics

Female túngara frogs were overall significantly more likely to choose the complex call over the simple call, regardless of the level of the predator, *L. pentadactylus*, call appended to it (GEE analysis intercept -2.1972 , $n = 20$ females, $p = 0.009$). Females were significantly more likely to choose the complex call when *L. labialis* calls were appended to it than when *L. pentadactylus* calls were appended (Wald $\chi^2 = 9.411$, $n = 20$, $p = 0.002$). Stimulus level overall had a significant effect on female choice (Wald $\chi^2 = 11.720$, $n = 20$, $p = 0.008$; Fig. 1a), though this is solely driven by responses to *L. pentadactylus* calls, as indicated by a significant interaction term between stimulus level and stimulus identity (Wald $\chi^2 = 11.261$, $n = 20$, $p = 0.010$). Female túngara frogs also took significantly longer to make choices in tests with *L. pentadactylus* calls than they did in tests with *L. labialis* calls (General Linear Model: $n = 20$, stimulus $p = 0.015$; Fig. 1b).

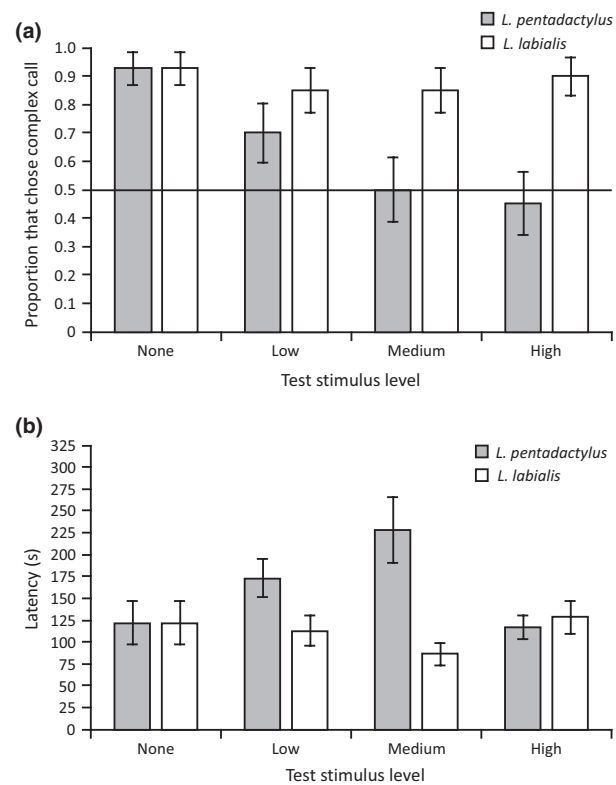


Fig. 1: Phonotaxis choices (a) and choice latencies (b) of female túngara frogs. Females were presented with a simple call (82 dB in center) and a complex call (82 dB) to which we appended a natural call of either *Leptodactylus labialis* (a harmless sympatric species) or *L. pentadactylus* (a large predator of túngara frogs) at one of three levels (same amplitude as white: 82 dB, 2× white: 86.7 dB, 3× white: 90.2 dB). Error bars represent standard errors (a) and 95% confidence intervals (b), respectively. Standard errors were calculated based on the binomial theorem. Although appending the calls of a harmless species had no effect on female choice, females were significantly less likely to choose the conspecific call associated with predator cues. Overall, females took longer to make choices at intermediate levels of simulated predation risk, choosing quickly again once the simulated distance of the predator approached that of the conspecific male stimulus. The addition of cues of a harmless heterospecific had no effect on how long females took to make a choice.

Acoustic cues of predators and light levels

There was no significant effect of light level on female preference at any amplitude of *L. pentadactylus* call. Females, however, chose significantly faster under higher light levels (General Linear Model, $n = 20$: light $p < 0.001$, stimulus level $p = 0.072$, stimulus \times light $p = 0.008$; Fig. 2).

Search time and light level

Given a choice between a simple call simulated at a distance of 1.5 m and a complex call simulated at

distances of 3, 6, and 12 m, females overall showed no preference (GEE analysis intercept 1.099, $p = 0.778$). Females were overall less likely to choose the farther complex call than the closer simple call (Wald $\chi^2 = 20.941$, $p < 0.001$; Fig 3a). Light level had an overall significant effect on which call females chose (Wald $\chi^2 = 6.047$, $p = 0.014$), but this is largely driven by responses at a simulated distance of 3 m and is thus not generalizable (interaction term for light by distance Wald $\chi^2 = 9.901$, $p = 0.019$). While the simulated distance of the complex call had no effect on how long females took to make choices, females, again, chose significantly faster under high light conditions (General Linear Model: distance $p = 0.763$, light < 0.001 , distance \times light = 0.484; Fig. 3b).

Other predators and public information

Given a choice between a 'near' simple call and a 'far' complex call, females were significantly less likely to choose the complex call when we also played call bouts of the three predatory frogs: *L. pentadactylus* ($p < 0.001$), *B. marinus* ($p = 0.027$), and *L. insularum* ($p = 0.011$). While playing call bouts of *H. microcephala* and synthetic *P. pustulosus* 'mew' repetitions had no effect on what females chose, females listening to *L. labialis* calls were significantly more likely to choose the 'far' complex call ($p = 0.032$). These results are summarized in Table 1.

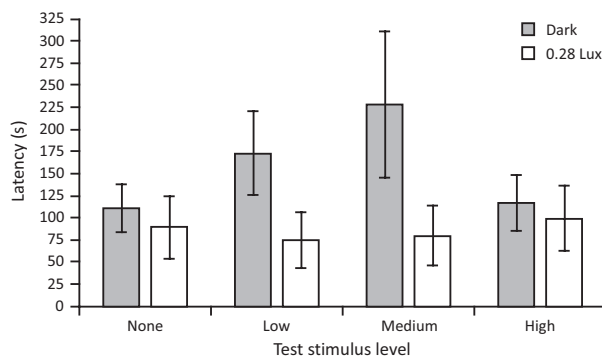


Fig. 2: Choice latencies for female Túngara frogs under dark and high light (0.28 lux) conditions. Females were presented with a simple call (82 dB in center) and a complex call (82 dB) to which we appended a natural call *Leptodactylus pentadactylus* (a large predator of túngara frogs) at one of three levels (same amplitude as whine: 82 dB, 2x whine: 86.7 dB, 3x whine: 90.2 dB). Females overall chose significantly faster under higher light conditions. Error bars represent 95% confidence intervals.

Light levels in natural choruses

Light levels were highest on full moon nights ($0.23 \text{ lux} \pm 0.01 \text{ SE}$) and too low to measure on new moon nights (Fig. 4). Females chose significantly faster on full moon nights (General Linear Model $p = 0.031$), but did not approach fewer males (Fig. 4).

Discussion

Female túngara frogs actively use information about predation risk when making mate choice decisions, both in terms of what they choose and how long they spend evaluating males. The placement of a risk cue (predator advertisement calls or distance) in association with a normally preferred stimulus was

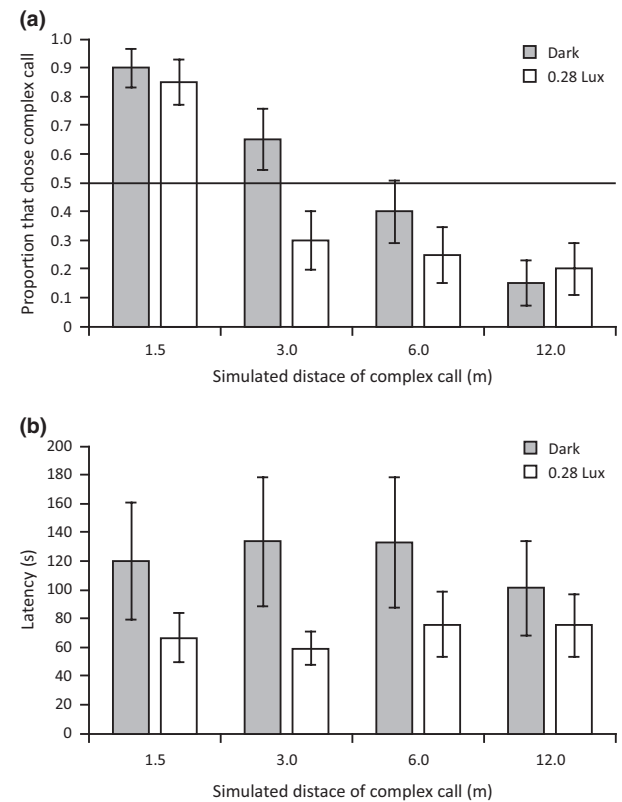


Fig. 3: Phonotaxis choices (a) and choice latencies (b) of female túngara frogs under dark and high light (0.28 lux) conditions. We presented females with a choice between a 'near' simple call (simulated at 1.5m, 82 dB at center) and a 'far' complex call simulated at 3 m (76 dB), 6 m (70 dB), or 12 m (64 dB). Error bars represent standard errors (a) and 95% confidence intervals (b), respectively. Standard errors were calculated based on binomial theorem. At a simulated distance of 3 m, females were less likely to travel to the distant complex call under simulated full moon conditions.

Table 1: Phonotaxis responses of female túngara frogs given a choice between a conspecific simple 'whine' call simulated at a distance of 1.5m and complex 'whine-chuck' call simulated at a distance of 3m

| Experimental stimulus | Effect | Dominant frequency (kHz) | Binomial probability |
|----------------------------|--------|--------------------------|----------------------|
| <i>L. pentadactylus</i> | – | 0.5 | <0.001 |
| <i>B. marinus</i> | – | 0.6 | 0.027 |
| <i>L. insularum</i> | – | 0.8 | 0.011 |
| <i>P. pustulosus</i> 'mew' | None | 1.22 | 0.5 |
| <i>L. labialis</i> | + | 1.9 | 0.032 |
| <i>H. microcephala</i> | None | 2,9, 6 | 0.363 |

A third speaker at the center of the back wall of the chamber played either silence or one of six experimental stimuli: call bouts of *Bufo marinus*, *Hyla microcephala*, *Leptodactylus insularum*, *Leptodactylus labialis*, *Leptodactylus pentadactylus*, or synthetic bouts of the 'mew' call of *Physalaemus pustulosus*. A negative effect (–) was scored if females were less likely to travel to the distant complex call while hearing a given stimulus and a positive effect (+) was scored if they were overall more likely to choose the more distant complex call. Binomial probabilities with a $p < 0.05$ are indicated in bold.

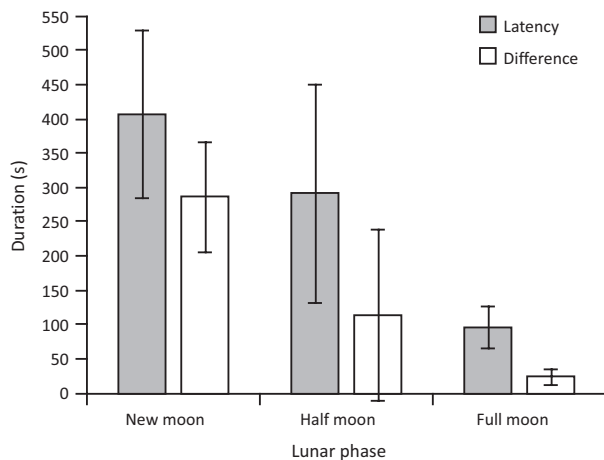


Fig. 4: Choice behavior of female túngara frogs in natural choruses. We released females into chorus site in Gamboa, Panama and followed them using an IR video camera on 26 nights across a single lunar cycle. Choice latency (total time from release to amplexus) is given as well as the difference between choice latency and latency to first movement. This 'difference' represents only time spent moving throughout the chorus and removes individual variation in response to capture. As with the laboratory choice tests, female chose significantly faster under brighter, full moon conditions. Error bars represent 95% confidence intervals.

sufficient to reverse female preferences in several tests. Ambient information about potential risk (light levels) on its own did not affect what females chose, but strongly influenced how long females spent eval-

uating males, both in the laboratory and in the field. Public information in the sense of *L. labialis* calls is known to influence male call latencies after a simulated predation event (Phelps et al. 2007) and appears to be interpreted similarly by females in their phonotaxis decisions.

From information theory, we understand that the amount of information needed to distinguish between two options increases as the similarity of those two options increases (see discussion in Phelps et al. 2006). This means that we would expect to see the highest latencies when either we present females with identical options or the attractiveness of one option is offset enough by predation risk to make the two options equivalent. We must also recognize that predation risk itself may impose a cost on evaluation time. If females suffer increased vulnerability to predators during mate searching, we might then expect to see that females spend less time evaluating as predation risk increases. This trade-off may explain the pattern seen in Fig. 1b, where females initially took longer to make choices as simulated predation risk increased, but then chose quickly again once the simulated proximity of the predator was near the distance of the conspecific advertisement call.

Light levels significantly influenced female choice behavior in a number of ways, most notably by changing the amount of time females took to make choices. In both the laboratory and the field, females chose significantly faster under high light conditions (Figs 3b and 4, respectively). This result has been demonstrated previously for túngara frogs (Baugh & Ryan 2010; Bonachea & Ryan 2011) and likely represents a strategy for reducing the window of vulnerability to visual predators (Bonachea & Ryan 2011). An important consequence of this reduction in search time is the potential reduction in the number of mates sampled, as in Karino et al. 2000, which would indicate that females sample less of the variation in male traits under this type of predation risk.

While female túngara frogs actively assess predation risk, it has been suggested that females could also gain information about predation risk by relying on male calls, the idea being that if males are calling, they must not have detected predators. Phelps et al. (2007) also showed that males attend to heterospecific calls in assessing predation risk. Our results suggest that females do the same. Females were more likely to choose the farther, but more attractive complex call while hearing the calls of *Leptodactylus labialis*. This suggests that females, as do males, use the

advertisement calls of this species to make decisions about predation risk.

Our results demonstrate that female túngara frogs are able to respond not only to the presence or absence of predation risk, but to finer scale variation in risk. It is important to point out that studies using a presence/absence design may result in false negatives if the manipulated level of predation risk is too low. While Bernal et al. (2007) also appended the calls of *L. pentadactylus* to the complex call, they used a level of the predator stimulus corresponding to our 'low' stimulus level. At higher amplitudes, females show a considerably stronger, significant response. Our study is the first to demonstrate that females are able to simultaneously use independent cues of risk (as in our trials where light and travel distance were manipulated simultaneously). For túngara frogs, this finding suggests that mate evaluation and sampling, and thus the strength of sexual selection, varies not only spatially with respect to the locations of predators, but also temporally across a lunar cycle.

While the role of survival costs and predation risk acting directly on male traits has certainly been well recognized as influencing signal communication, it is now clear that these same factors also place a check on the elaboration of male traits by acting indirectly on female preferences or cause selection for the elaboration of traits that do not increase detection by predators (Cummings et al. 2003). When females encounter high rates of predation, we can predict weaker expression of preferences and dramatic changes in sampling behavior, weakening selection for further elaboration. In addition, we can predict that when encounter rates with predators vary between populations, predation risk may place a limit on the speed of the evolution of communication systems in some populations more than others, potentially leading to reproductive isolation over time.

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