

Predation risk increases permissiveness for heterospecific advertisement calls in túngara frogs, *Physalaemus pustulosus*

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Factors that influence the strength of sexual selection within a population may have important consequences for the evolution and maintenance of reproductive isolation between populations. Here we examine the role of one such factor, predation risk, in influencing female permissiveness for heterospecific advertisement calls. Specifically, we tested the effect of simulated predation risk on mate choice in female túngara frogs, *Physalaemus pustulosus*, using variation in ambient light levels, travel time and the presence of auditory cues of local predators. Simulated predation risk increased female permissiveness for advertisement calls along an artificial gradient of calls intermediate between conspecifics and a congener, *Physalaemus enesefae*. Across the entire gradient, the presence of auditory cues of the predatory frog *Leptodactylus pentadactylus* in association with the conspecific call dramatically increased the likelihood of females choosing the intermediate call. In addition, higher ambient light levels and simulation of increased travel distances both increased the likelihood that females would choose intermediate calls over conspecific calls. These results suggest that, although mate choice may be important in causing reproductive isolation between allopatric populations, spatial or temporal variation in predation risk may strongly influence the expression of mate choice and thus the outcome of secondary contact.

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Sexual selection in allopatry can lead to reproductive isolation if females eventually discriminate against, or no longer recognize, males from other populations (West-Eberhard 1983; Sanderson et al. 1992; Barraclough et al. 1995; Coyne & Orr 1997; Ritchie 2007). In the absence of sexual selection, this isolation can break down and lead to hybridization in sympatry (Seehausen et al. 1997). It stands to reason, then, that any factors in the environment that cause temporally or spatially limited variation in the permissiveness of female preferences can have important implications for the evolution and maintenance of reproductive isolation between populations.

Search costs associated with predation risk have a strong influence on mate evaluation by females (reviewed in Lima & Dill 1990). Predation risk can increase thresholds of mate attractiveness (Demary et al. 2006; Su & Daiqin 2006; Vélez & Brockmann 2006), or even reverse preferences for normally attractive traits (Evans et al. 2004; Schwartz & Hendry 2006, 2007; Dunn &

Whittingham 2007). Predation risk can also reduce evaluation time and mate sampling (Karino et al. 2000; deRiviera et al. 2003; Kim et al. 2007; Bookmythe et al. 2008).

While numerous studies have investigated the role of predation risk in shaping how females respond to variation in conspecific advertisement signals, how predation risk influences permissiveness for heterospecific signals remains unexplored. Despite the historical emphasis on a species recognition function for mate choice, we now know that females are often receptive to a range of signals, even outside the normal distribution of males of their own species (Ryan & Rand 1993; Ryan 1998). Mating with conspecific males is often more of a discrimination preference than purely a species recognition threshold and, when conspecific males are unavailable or the costs of mating with conspecific males are too high, females may accept heterospecific males, especially when hybridization is less costly (Veen et al. 2001; Willis et al. 2004; Wong et al. 2005).

To this end, we examined the effects of simulated predation risk on mate choice in female túngara frogs, *Physalaemus pustulosus*. Túngara frogs in choruses are preyed upon by several species, including smoky jungle frogs, *Leptodactylus pentadactylus* (Ryan et al. 1981). Like many other species of frogs, female túngara frogs choose males based on their acoustic advertisement signals. Females

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Table 1

Average values of seven measurements of the frequency-modulated whine, representing endpoints on the synthetic 'intermediate' transect between the two species

Species	Maximum frequency (Hz)	Final frequency (Hz)	Rise time (ms)	Fall time (ms)	Frequency-sweep shape	Fall shape	Rise shape
<i>Physalaemus pustulosus</i>	884	484	24.02	342.80	0.33	0.50	0.33
<i>Physalaemus enesefae</i>	976	692	301.50	445.70	0.51	0.54	0.55

Modified with permission from Ryan et al. (2003).

express their preference by showing positive phonotaxis to the signals of their preferred mate and show phonotaxis only in a sexual context, providing a robust assay of female choice (Ryan 1985). Female túngara frogs respond defensively to cues of predation risk during mate evaluation, including light levels and search times (Rand et al. 1997) and vocalizations of predators (Bernal et al. 2007). In the absence of signals that elicit positive phonotaxis, females respond to the vocalizations of predatory species by remaining motionless (L. A. Bonachea & M. J. Ryan, unpublished data).

Túngara frogs are allopatric with all congeners except *Physalaemus enesefae*, which shares a small region of overlap in llanos of Venezuela (Ryan et al. 1996). Female túngara frogs discriminate against the advertisement calls of congener males when given a choice between a conspecific and a heterospecific call (Ryan & Rand 1995, 1999, 2001); however, female túngara frogs show permissive species recognition and will recognize and approach heterospecific advertisement calls when these calls are offered alone (Ryan & Rand 1999, 2001). In this study, we investigated the influences of predation risk on permissiveness to understand how predation may affect the outcome of secondary contact between species.

Using the responses of females to artificial, intermediate calls described by Ryan et al. (2003) as a reference point, we first examined effect of acoustic cues of predation risk on the breadth of signals that female túngara frogs were willing to accept. If females are more willing to accept dramatically different signals (including those of other species) when they are under increased predation risk, then predation risk could have important consequences for sexual selection and reproductive isolation. Next, we used an intermediate heterospecific signal to determine whether other types of cues of predation risk (light level and search time) had similar effects on female permissiveness.

METHODS

General Field Methods

We collected amplexed pairs of túngara frogs from choruses in Gamboa, Panama near facilities of the Smithsonian Tropical Research Institute (9°07.0'N, 79°41.9'W) between August and September of 2009. These frogs were brought back to the laboratory for testing and then released at their original capture sites with their original mates after testing. Prior to release, we gave each female a unique toe clip combination to prevent retesting (see *Ethical Note* below).

Female Phonotaxis

We performed two-choice phonotaxis tests in a 1.8 × 2.7 m sound-attenuating chamber (Acoustic Systems, Austin, TX, U.S.A.), following the procedure of Wilczynski et al. (1995). Females were held in the centre 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 (while the stimuli continued to play) and observed them remotely through a wide-angle video camera and infrared light source (Fuhrman Diversified, Inc., Seabrook, TX, U.S.A.) mounted on the ceiling of the acoustic chamber. Optomotor studies have shown

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. Females were first tested on a simple conspecific discrimination test (simple versus complex call): any female that failed to make a choice in this test was considered unresponsive and did not receive further testing. Only one female of the 21 collected failed to respond.

Permissiveness and Predation Risk along a Conspecific–Heterospecific Gradient

We presented 20 females with a choice between a conspecific call and one of nine treatment calls: a pure conspecific call; a pure heterospecific, *P. enesefae*, call; or one of seven synthetic 'intermediate calls'. These 'intermediate calls', originally synthesized by Ryan et al. (2003), represent a gradient, from 100% conspecific to 100% *P. enesefae*, in seven parameters of the frequency-modulated whine (Table 1). In a parallel set of experiments, we presented females with a choice between each of the nine calls in the gradient and a conspecific call, to which we appended a call of the predatory frog *L. pentadactylus*.

Acoustic Cues and Light

Female túngara frogs were first dark adapted by holding them in a dark cooler for 1 h (Cornell & Hailman 1984; Fan et al. 2001). We

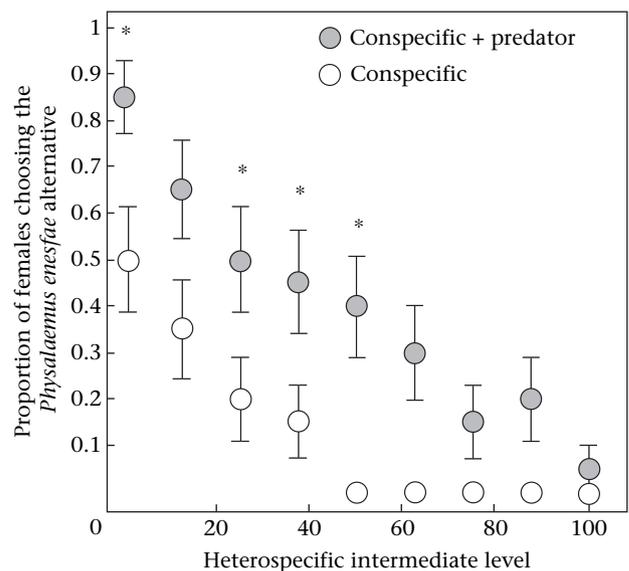


Figure 1. Phonotaxis choices of female túngara frogs. Females were presented with a choice between one of nine synthetic calls along a call gradient from 0, representing the pure conspecific call, to 100, representing the pure heterospecific, *P. enesefae* call (82 dB at chamber centre) and a pure conspecific call (82 dB), to which we appended a call of the predatory frog *Leptodactylus pentadactylus* (86.7 dB). Standard errors were calculated based on binomial theorem with a sample size of 20.

then presented females with a choice between a 0.375 hetero-specific intermediate call and a conspecific call (a synthetic average of the males of Gamboa populations), to which we appended a call of *L. pentadactylus*, following the technique used by Bernal et al. (2007). In the absence of predation risk, females discriminate between the pure conspecific call and the 0.375 heterospecific intermediate call to a degree similar to their discrimination against natural variation in conspecific calls (Ryan et al. 2003). If predation risk indeed does influence discrimination of advertisement calls, then females should be more likely to choose this intermediate call when the conspecific call is associated with cues of predation risk.

We presented females with calls at a peak amplitude of 82 dB SPL (re. 20 μ Pa) for the whine portion at the female's release point. *Leptodactylus pentadactylus* calls 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. The entire experiment was performed under both complete darkness and 0.28 lx light conditions (produced using Current USA Lunar light LEDs and measured using an Extech 403125 light meter). These conditions are slightly brighter than levels we recorded at choruses on full moon nights (mean \pm SE = 0.23 \pm 0.01 lx; L. A. Bonachea & M.

J. Ryan, unpublished data), and optomotor studies have shown that the frogs are able to see at this light level (Cummings et al. 2008).

We performed a repeated measure logistic regression analysis using the general estimating equation (GEE analysis) for binary data with logit link function (SAS online DocTM v.8, page 1452; SAS Institute, Cary, NC, U.S.A.) to assess the effect of stimulus level and light on female choice.

Search Time and Light

We varied perceived travel time of the female to the sound source by varying the call's peak amplitude. Females were given a choice between a 'near' 0.375 heterospecific 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). This final amplitude was near the minimum threshold for eliciting phonotaxis from female túngara frogs (Marsh et al. 2000). To test for an effect of ambient light levels on how females assessed the risk of longer search times, we conducted these experiments both in darkness and at 0.28 lx (near full moon conditions). We also performed a repeated measure logistic

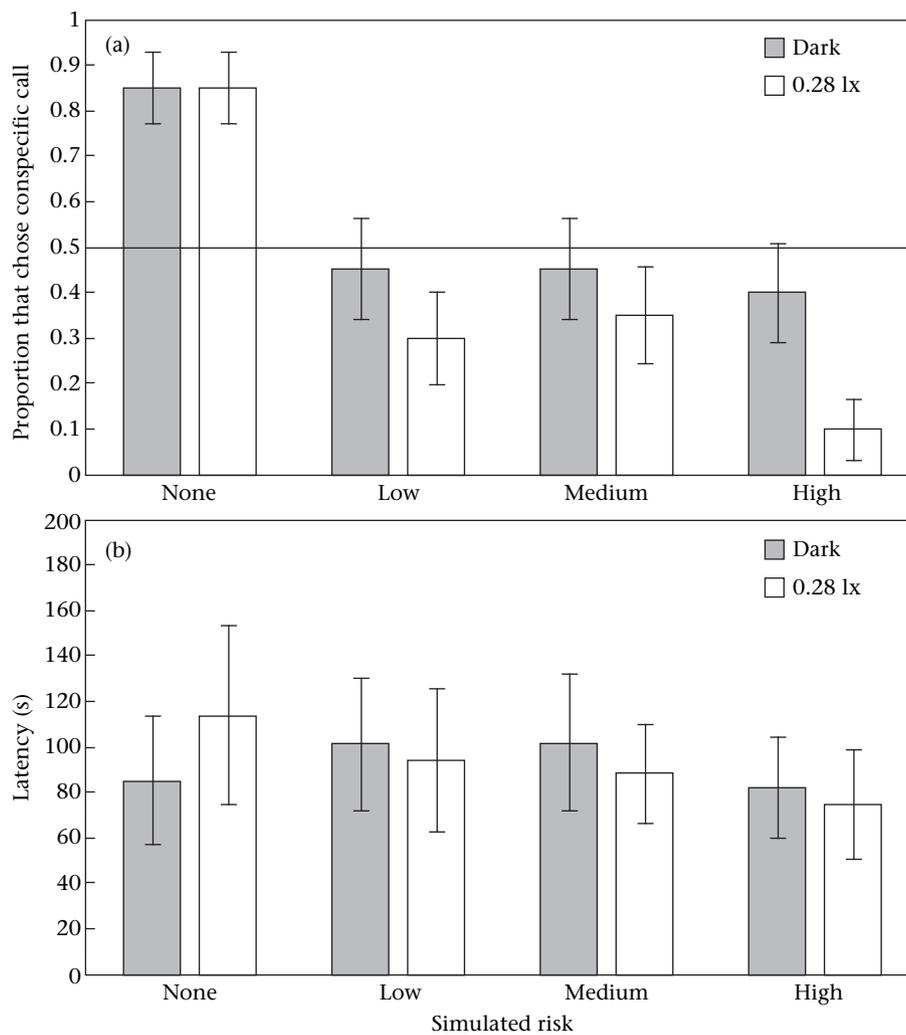


Figure 2. Female túngara frogs' (a) phonotaxis choices and (b) choice latencies under dark and high light (0.28 lx) conditions. Females were presented with a synthetic intermediate call (0.375 *P. enesefae*; 82 dB at chamber centre) and a conspecific call (82 dB), to which we appended a call of the predatory frog *Leptodactylus pentadactylus* at one of three levels (amplitude same as conspecific call: 82 dB; amplitude 2 \times conspecific call: 86.7 dB; amplitude 3 \times conspecific call: 90.2 dB). Standard errors were calculated based on the binomial theorem. $N = 20$ females in each test.

regression analysis using the general estimating equation to assess the effect of simulated distance on female choice.

Ethical Note

Animals were collected, housed and tested in accordance with protocol number 09032701 of the University of Texas Institutional Animal Care and Use Committee (IACUC). Toe clipping was deemed necessary to prevent recapture, and we followed the Guidelines for the Use of Live Amphibians and Reptiles in Field Research compiled by the American Society of Ichthyologists and Herpetologists, Herpetologist's League and the Society for the Study of Amphibians and Reptiles (available at <http://www.asih.org/pubs/herpcoll.html>).

RESULTS

Perceived Risk and Signal Permissiveness

Female túngara frogs were overall more likely to choose the pure conspecific call over the synthetic intermediate calls (Fig. 1). Binary logistic regression analysis indicated that both the proportion of heterospecific call (Wald test: $\chi^2 = 42.971$, $P < 0.001$) and

the presence of the predator stimulus (Wald test: $\chi^2 = 19.559$, $P < 0.001$) significantly affected female choice of calls, with females overall preferring signals closest to the pure conspecific call, but accepting a wider range of signals under simulated predation risk.

Acoustic Cues and Light

Predator stimulus level overall had a significant effect on female choice (Wald test: $\chi^2 = 23.675$, $P < 0.001$; Fig. 2a). Overall, females were less likely to approach the conspecific call with an appended predator stimulus under higher light conditions (Wald test: $\chi^2 = 11.004$, $P = 0.001$), although this trend was driven largely by responses under the high predator stimulus level (interaction term for light by stimulus level: Wald test: $\chi^2 = 12.038$, $P = 0.007$). Neither light levels nor predator stimulus level significantly affected female choice latency (Fig. 2b).

Search Time and Light

Increasing the distance of the conspecific call greatly increased the likelihood that females would choose the intermediate call

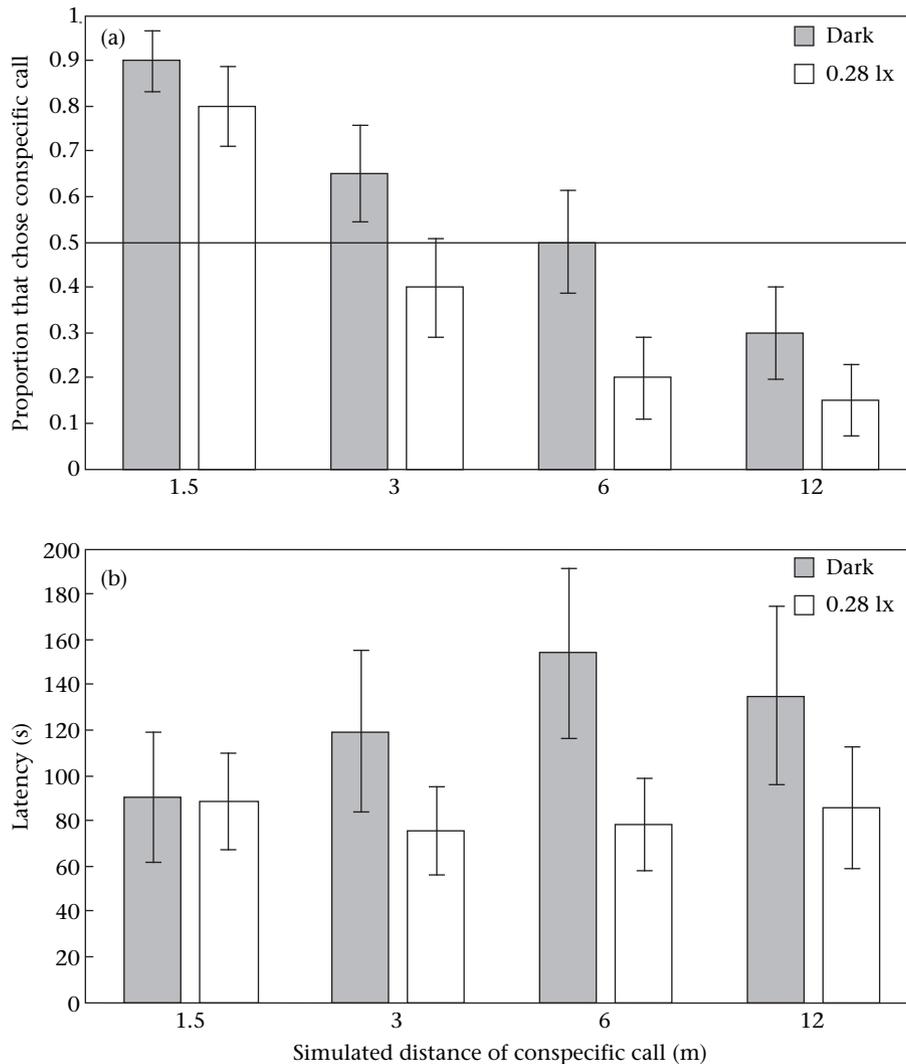


Figure 3. Female túngara frogs' (a) phonotaxis choices and (b) choice latencies under dark and high light (0.28 lx) conditions. Females were given a choice between a 'near' intermediate call (0.375 *P. enesefae*; simulated at 1.5 m, 82 dB at centre) and a 'far' conspecific call simulated at 3 m (76 dB), 6 m (70 dB) or 12 m (64 dB). Standard errors were calculated based on the binomial theorem. $N = 20$ in each test.

(Wald test: $\chi^2 = 24.852$, $P < 0.001$; Fig. 3a). Light level had an overall significant effect on which call females chose (Wald test: $\chi^2 = 9.078$, $P = 0.003$), showing more dramatic responses to simulated distance, but this was largely driven by responses at a simulated distance of 6 m and, thus, is not generalizable (interaction term for light by distance: Wald test: $\chi^2 = 9.346$, $P = 0.025$). While the simulated distance of the conspecific call did not affect females' latency to make choices, females chose significantly faster under high light conditions (general linear model: distance: $P = 0.281$; light: $P < 0.001$; distance \times light: $P = 0.109$; Fig. 3b).

DISCUSSION

Simulated predation risk, whether in the form of increased search times, improved detection by visual predators or proximity of predators, caused an increase in permissiveness in mate choices made by female túngara frogs. Females, given a choice between a pure conspecific call and a call intermediate between *P. pustulosus* and *P. enesefae*, never chose calls that were greater than 0.375 heterospecific in the absence of predator cues; however, when we associated the conspecific call with predator cues, at least a small portion of females chose all the intermediate calls including the pure heterospecific call. The addition of cues of predation risk in association with conspecific calls greatly increased the likelihood that females would choose the 0.375 heterospecific intermediate call. This demonstrates that cues of predation risk can profoundly influence permissiveness of female mate choice. This result also strengthens the conclusion of Ryan et al. (2003) that female mate choice in túngara frogs is permissive and generalized (Shepard 1987), rather than categorical (Ehret 1987), although there is categorical perception along certain vectors of call variation (call complexity; Baugh et al. 2008).

We found that simulating longer travel times to reach the conspecific call caused females to choose the intermediate call more often. While not universal, our findings suggest that light conditions can exaggerate the way females respond to other cues of predation risk. In the case of our manipulations of perceived travel times, females made choices significantly faster under higher light conditions. A reduction in search times in response to predation risk has been demonstrated in other systems as well (Karino et al. 2000; deRiviera et al. 2003; Kim et al. 2007; Booksmythe et al. 2008). While the effect of reduced search time is somewhat unclear in the context of these two-choice tests in the laboratory, reduced search times in the more complex arena of natural choruses may mean that females sample fewer calls from each potential mate and/or sample fewer mates. Both could cause an overall decrease in the strength of sexual selection acting on male signals.

These results strengthen the hypothesis that predation risk is a factor limiting the expression of female choice. In addition, our results demonstrate that the permissiveness of female mate choices can be dramatically increased under higher levels of perceived predation risk. Because predation risk can vary over time within populations, notably as light levels change with lunar phases and detection by visually hunting predators improves, the overall strength of selection acting on male advertisement signals may be inconsistent and wax and wane over time. In addition, spatial variation in the abundance and variety of predators feeding on different populations can cause variation in the strength of female preferences over a geographical area. If predation regimes remain constant over time, these differences in the strength of sexual selection can affect mechanisms of premating isolation, leading to or preventing the evolution of reproductive isolation between populations.

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