Ambient light alters temporal-updating behaviour during mate choice in a Neotropical frog

Alexander T. Baugh and Michael J. Ryan

Abstract: It is well known that animal decision-making can be influenced by environmental variables, such as the risk of predation. During the breeding season, nocturnal amphibians encounter a range of environmental conditions at breeding aggregations, including variable ambient light conditions. For nocturnal frogs, illumination is expected to minimize conspicuous movement that might increase predator detection. Previous work has shown that female *Physalaemus pustulosus* (Cope, 1864) (= *Engystomops pustulosus* (Cope, 1864)) are sensitive to variation in light levels during mate choice. Here we use an acoustic playback design in which stimuli are adjusted for intensity and complexity during female phonotaxis to show that choosiness is influenced by light level. Frogs were more likely to commit to an initial mate choice despite a dynamic reduction in mate attractiveness under dim light conditions compared with darkness. These results suggest that females are trading off the attractiveness of potential mates with the perceived costs of executing mate choice by committing to an initial decision and thereby reducing assessment time and movement. The dynamic playback design used here provides an approach that could be applied in other systems in which context-dependent decision-making is thought to be important.

Résumé : Il est bien connu que la prise de décisions chez les animaux peut subir l'influence des variables du milieu, comme par exemple, le risque de prédation. Durant la saison de reproduction, les amphibiens nocturnes rencontrent une gamme de conditions environnementales lors de leurs rassemblements de reproduction, en particulier des conditions variables de luminosité. Chez les grenouilles nocturnes, l'illumination devrait réduire les mouvements trop apparents qui pourraient augmenter la détection par les prédateurs. Des travaux antérieurs ont montré que les femelles de *Physalaemus pustulosus* (Cope, 1864) (= *Engystomops pustulosus* (Cope, 1864)) sont sensibles à la variation de l'intensité lumineuse durant leur choix de partenaire. Nous utilisons ici un plan d'expérience comportant une rediffusion acoustique dans laquelle l'intensité et la complexité des stimuli sont ajustées durant le phonotactisme de la femelle de manière à montrer que le choix est influencé par l'intensité lumineuse. En lumière faible, les grenouilles sont plus susceptibles de s'engager envers un premier partenaire choisi, malgré une réduction dynamique de l'attrait du partenaire, qu'en obscurité totale. Ces résultats laissent croire que les femelles font un compromis entre l'attrait des partenaires potentiels et les coûts perçus reliés au choix du partenaire; en s'engageant vis-à-vis leur premier choix, elles réduisent le temps d'évaluation et les déplacements. Le plan de rediffusion dynamique utilisé ici fournit une approche qui pourrait servir dans d'autres systèmes dans lesquels la prise de décisions en fonction du contexte est importante.

[Traduit par la Rédaction]

Introduction

There are few decisions in life more significant than the selection of a mate, particularly if such decision-making is executed under the threat of predation. Previous studies have provided examples of how organisms alter their behaviour when predators are detected or when predation risk is perceived to be high (reviewed in Lima and Dill 1990), including during courtship (Tuttle et al. 1982; Jennions and Backwell 1992) and mate choice (Rand et al. 1997; Dill et al. 1999; Su and Li 2006; Bernal et al. 2007). Mate-choice studies like these have yielded empirical support for the idea that in many species the outcome of the decision process can be dictated by proximate environmental conditions. For example, females may become less receptive under the risk of predation (Dill et al. 1999). Alternatively, receptivity may remain unchanged but preferences may be relaxed when predation risk is perceived to be high, or may favor males that present reduced risk (Rand et al. 1997; Bernal et al. 2007). One of the potential implications of these observations is that the decision-making process itself is plastic, though this is rarely examined directly. In the present study, we test this possibility by asking if perceived predation risk influences the temporal dynamics of mate choice.

The decision-making process during mate choice is considered to have two steps (Valone et al. 1996). First, sensory

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A.T. Baugh.[1,2] The University of Texas at Austin, 1 University Station C0930, Section of Integrative Biology, Austin, TX 78712, USA.
M.J. Ryan. The University of Texas at Austin, 1 University Station C0930, Section of Integrative Biology, Austin, TX 78712, USA; Smithsonian Tropical Research Institute, P.O. Box 0943-03092 Balboa Ancón, Republic of Panamá.

[1]Corresponding author (e-mail: alex.baugh@gmail.com).
[2]Present address: Max Planck Institute for Ornithology: Migration and Immuno-ecology, Schlossallee 2, 78315 Radolfzell, Germany.

information is gathered and used to discriminate between mates. Second, a decision rule is used to select the optimal option. In the dynamic signaling environments common to acoustically advertising lek breeders, females might iterate this two-step process, and in doing so execute decisions through a process of "temporal-updating". We use temporal-updating to mean the adjustment of a behavioural decision during the execution phase following a change, perceived or real, in the available choice options. This usage is distinct from its use in studies of human memory (see Zwaan 1996; Blaisdell et al. 1999).

Temporal-updating, or dynamic reproductive decision-making, might enable animals to make optimal decisions in environments that are in rapid flux. In lek-breeding species, females make mate decisions in the midst of temporally variable social signals. Males gather in breeding aggregations to court females using short duration calls that can vary between repetitions in dynamic features such as complexity (e.g., presence of call embellishments) and amplitude — traits that are known in many systems to influence a signal's attractiveness (Darwin 1871; Ryan and Keddy-Hector 1992; Andersson 1994; Gerhardt and Huber 2002; Greenfield 2002; Ryan and Rand 2003; Searcy and Nowicki 2005). In this context, we ask at what point does a reproductive female, who compares advertising males, make a decision and how does the flexibility of that decision depend on perceived risk of predation?

We tested the hypothesis that enhanced perception of predation risk would lead to reduced flexibility during the mate-choice process. Using dim ambient light to elevate perceived risk and a dynamic playback design, we predicted that female frogs would commit to an initial mate choice despite a dynamic reduction in male attractiveness to a greater degree than females tested under the cover of darkness. This result would suggest that females are trading off "choosiness" against the costs (e.g., time, energy, and conspicuousness) associated with the greater movement incurred when reversing a phonotactic approach. Here we use choosiness to mean the effort an individual is willing to invest in mate assessment (sensu Jennions and Petrie 1997).

The communication system

Túngara frogs, *Physalaemus pustulosus* (Cope, 1864) (= *Engystomops pustulosus* (Cope, 1864)), are small anurans (approximately 30 mm snout-to-vent length) distributed throughout much of Mesoamerica (Weigt et al. 2005). Males advertise vocally to females during the breeding season (May–December) using a species typical call, known as the whine or simple call (Ryan 1985). Males can ornament the whine with one to seven suffixes known as "chucks", thereby producing what is known as the complex call, or whine–chuck. In nature, females use calls to localize an individual male among a chorus and then select a mate by making physical contact, after which the male mounts and clasps the female in a posture known as amplexus. In two-choice phonotaxis tests in the laboratory, the whine–chuck calls are strongly preferred to whine calls (approximately 85% preference; Ryan 1985; Ryan and Rand 2003). Female túngara frogs also exhibit strong preferences for calls of higher amplitude relative to lower amplitude alternatives, which presumably results in attraction towards nearer males and thus reduces travel time (Ryan and Rand 1990). Males are also known, however, to adjust their call amplitude over the course of a call bout (Pauly et al. 2006), and therefore call amplitude has both passive and active dynamic properties.

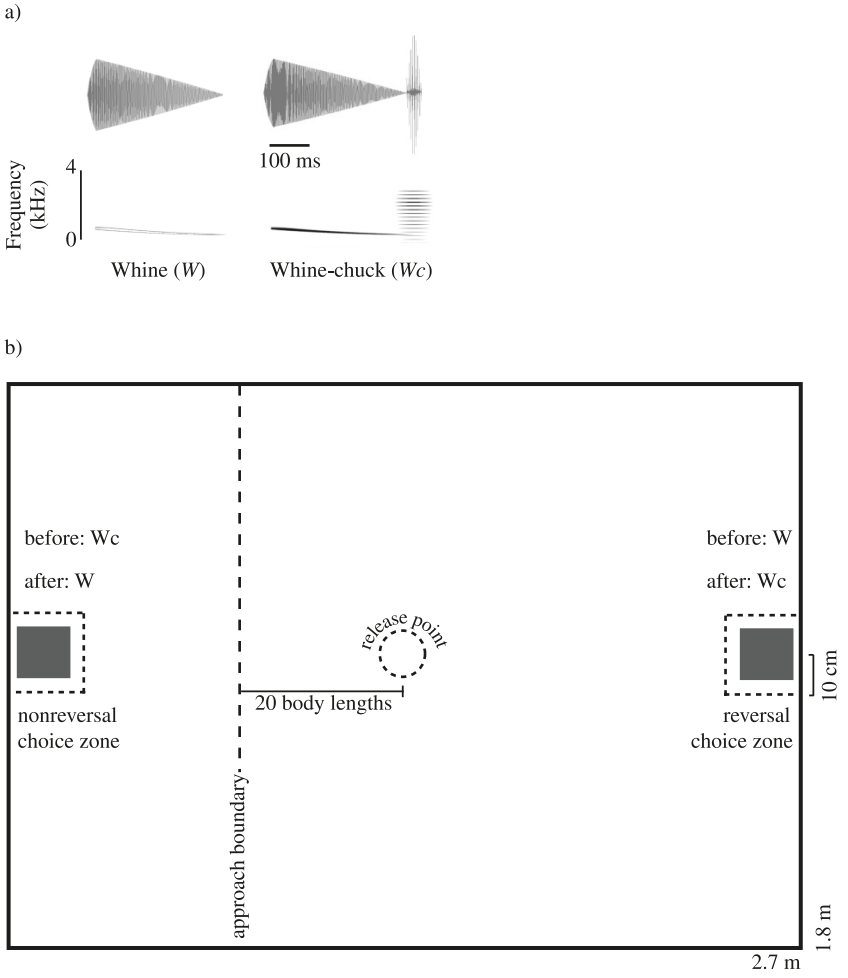
During the breeding season, female túngara frogs encounter a range of environmental conditions at the chorus, including variable ambient light conditions depending on the lunar cycle and cloud cover and they are sensitive to low levels of lights under a wide range of these conditions (Cummings et al. 2008). Túngara frogs breed in a variety of disturbed lowland tropical forest habitats where light spectra are likely to vary widely. Because of this variation, we made no attempt to match the spectrum in our arena to a particular standard (Taylor et al. 2008). These frogs are subjected to a wide variety of predators, most notably including frog-eating bats, but also blood-sucking flies, opossums, other frogs, and snakes (Ryan 1985; Bernal et al. 2006). Calling males are able to visually detect the approach of frog-eating bats (Tuttle et al. 1982). A previous study in túngara frogs showed that females are sensitive to light levels in static mate-choice tests and reported that under dim light females preferentially select a nearer male despite being less attractive (Rand et al. 1997). This study and another using acoustic stimuli of predators to elevate perceived predation risk (Bernal et al. 2007) have shown that the outcome (choice) is influenced by perceived predation risk, but this does not necessarily indicate that the temporal dynamics of the process itself are affected. Our study shows that indeed this is the case.

Materials and methods

Animals

We conducted this experiment during the breeding season between the months of June and September in 2008 at facilities for the Smithsonian Tropical Research Institute in Gamboa, Panamá (9°7′N, 79°41.9′W). We collected frogs as amplectant mated pairs from breeding aggregations between the hours of 1900 and 2200 and performed behavioural testing between the hours of 2000 and 0400. Females that had begun to oviposit were not tested. Each mated pair was held in a small plastic bag under dark and quiet conditions before testing, and separated immediately prior to testing. To prevent resampling, we marked individuals with a unique toe-clip combination and returned them to their original site of collection within 12 h. In marking frogs, we followed the *Guidelines for the Use of Live Amphibians and Reptiles in Field Research*, compiled by the American Society of Ichthyologists and Herpetologists (ASIH), The Herpetologists' League (HL), the Society for the Study of Amphibians and Reptiles (SSAR), and our methods were approved by the Institutional Animal Care and Use Committee at The University of Texas at Austin (permit No. 06041701) and La Autoridad Nacional del Ambiente in Panamá. In total, 20 females were tested twice each (40 trials). These trials were conducted under dim ambient light and are compared with the results from a larger study conducted during 2007 and 2008 in which females (N = 70) were also tested twice each (140 trials) under darkness (Baugh and Ryan 2010). Sequential replicate trials allowed us to determine if testing females

Fig. 1. (*a*) Stimuli used in our study of Túngara frogs, *Physalaemus pustulosus* (currently referred to as *Engystomops pustulosus*). Synthetic whine (W) and whine–chuck (Wc) oscillograms (top) and spectrograms (bottom). (*b*) Phonotaxis chamber showing arena dimensions and position of release point (midpoint of chamber), speakers, choice zones, and approach boundary (75 cm from speaker, approximately 20 body lengths from release point). This figure depicts one of two symmetrical configurations.



multiple times affects behavioural results (see Results). Although subjects were tested over the course of two field seasons, behavioural results were consistent for both treatments and a baseline condition across the data collection periods (see Results).

Stimuli and experimental design

We used two synthetic stimuli in this study and a two-choice playback design (Fig. 1). These signals included a simple whine (W) and a whine with one chuck (Wc). The chuck on Wc is twice the peak amplitude of the whine. Both stimuli were matched for the peak amplitude of the whine before playback and broadcast from small speakers (ADS L210) located at the two poles of an arena. The whines in these signals are identical and consist of only the fundamental frequency; it has been shown previously that the upper harmonics of the whine do not influence mate choice in the laboratory (Ryan and Rand 1990; Rand et al. 1992), and that these synthetic stimuli are as attractive as natural signals (M.J. Ryan, unpublished data). Information on the synthesis procedure can be found in Ryan et al. (2003).

Frogs were tested under infrared light with an ambient visible light in a sound-attenuating chamber (Acoustic Systems, Austin, Texas, USA) measuring 2.7 m long × 1.8 m wide × 1.78 m high (Fig. 1*b*). Before each subject was tested, we calibrated both speakers to 82 dB SPL (re. 20 μPa) at the center of the arena (1.35 m from each speaker) using the W stimulus (GenRad 1982 SPL meter, peak amplitude, flat weighting). Each trial began with the subject placed under a cone at the center of the acoustic chamber (i.e., release point; Fig. 1*b*) for 3 min while the two stimuli were broadcast antiphonally at a rate of one call per 2 s from each of two speakers opposite one another. The cone was then lifted remotely and the phonotactic behaviour was monitored via a ceiling-mounted infrared camera and television monitor outside the chamber. The chamber was divided symmetrically by boundaries (hereafter approach boundaries) at a minimum distance of 75 cm from the speakers (approximately 20 body lengths from release point; broken lines, Fig. 1*b*). These broken lines were visible only to the human observer (outlined by transparencies on the monitor). In each trial, one of the two speakers initially broadcast the preferred Wc stimulus (this "target" speaker

was selected randomly and then alternated between tests and females to minimize any potential side bias; see Results), whereas the opposite speaker broadcast the less preferred W stimulus. When the subject crossed the approach boundary nearest the preferred stimulus (as measured from the face of the speaker), the human observer pressed the spacebar key on the playback computer to initiate a custom program in the acoustic software program Signal®; this program introduced a 500 ms delay to prevent the premature occlusion of a stimulus, and then subtracted the chuck from the approached speaker and simultaneously added a chuck to the unapproached speaker. Also, the amplitude of the distant stimulus (the one that was not initially approached) was amplified by a factor of 2 dB, which equilibrated the mean peak amplitude along the approach boundary (this was empirically determined by averaging the peak amplitude differential at six equally spaced points along the approach boundary transect). In each trial, the same three measurements were recorded as follows: (1) whether or not the subject made a choice, (2) if it involved a reversal or rather a choice for the initially approached speaker (a nonreversal), and (3) the latency to choice (total time lapsed between lifting the cone and choice).

We scored a phonotactic choice when a frog approached one of the two speakers within a radius of 10 cm without simply following the wall. A frog failed to exhibit a phonotactic choice (the trial was disqualified) if it was motionless for the initial 5 min after the cone was raised or during any 2 min interval thereafter, or if the animal failed to make a choice within 15 min after the cone was raised. A prerequisite for these tests was that females must initially approach the preferred stimulus (complex call), which allowed us to examine whether this species-typical preference is dynamically expressed and if it is influenced by ambient light. If a frog failed to do this and instead initially approached and selected the less preferred stimulus (simple call), these responses were recorded but not included in the temporal-updating analysis. In these uncommon instances in which females were responsive but approached the less preferred W stimulus initially (approximately 7% of trials in the present study), we retested these subjects. In all instances these subjects approached the preferred stimulus on a subsequent trial.

The dim light treatment was identical to a previously published experiment (see experiment 3 in Baugh and Ryan 2010) except that we placed a dim ambient source of light (GE-brand night-light model No. 55507; GE, Fairfield, Conneticut, USA) at the center of the chamber ceiling. The night-light was green to the human eye and had spectral and irradiance properties within the range of variation for natural moonlight; there was a broad spectral peak around 510 nm and the arena irradiance was approximately 5.8×10^{-10} W/cm^2 at 100 cm (for additional details, including measurements at natural breeding sites, see Taylor et al. 2008).

We tested each female twice (identical condition except W and Wc stimuli were alternated to avoid side bias) and used the nonparametric Mann–Whitney *U* test (two-tailed test) to compare the number of reversals with the results from a previous study (females could thus reverse zero, one, or two times within a test condition). To ensure independence, we used a unique pool of females in the present and previous studies. An α criterion of 0.05 was applied. A previous study showed that testing females in two sequential trials does not affect their probability of reversal or latencies (Baugh and Ryan 2010).

Finally, to identify any potential for side bias in the acoustic chamber, we performed trials ($N = 235$) in which both speakers broadcast the identical standard call (W versus W, or Wc versus Wc). We found no evidence of a side bias (selected 122 left sides to 113 right sides; $P = 0.60$).

Results

A post hoc analysis showed reversal behaviour was not influenced by whether subjects required additional testing owing to one or more unsuccessful trials (Baugh and Ryan 2010). Under dim light conditions, we performed 46 trials, which included 40 successful trials ($N = 20$), 3 disqualified trials, and 3 trials in which the females initially approached and selected the W stimulus. In the darkness treatment, we performed 162 trials, which resulted in 140 successful trials ($N = 70$), 12 disqualified trials, and 10 trials in which the females initially approached and selected the W stimulus. Thus, despite testing subjects in both the summers of 2007 and 2008, the trial responsiveness and Wc preferences were consistent across years and treatments. Additional confidence in the present experimental design spanning two field seasons comes from the observation that under baseline static mate-choice conditions (W versus Wc, no stimulus manipulation), females exhibited a normal Wc preference in 2007 (84.5%) and 2008 (86.1%). Additionally, responsiveness (frequency of successful choices) under this baseline condition was high for both 2007 (80.1%) and 2008 (95.6%). Lastly, the latencies to choice in these baseline tests were similar between years (latencies to choice in year 2007 = 168.9 ± 133.1 s (mean ± SD); latencies to choice in year 2008 = 107.3 ± 140.5 s).

We found a significant decrease in the frequency of reversal under dim light conditions (20.0%) compared with darkness (44.3%) (Mann–Whitney *U* test, $U = 483$, $P = 0.005$). The effect of the dim light was specific to reversibility and not preferences generally. In only 7% of trials (both under dim light and darkness) did females approach and choose the whine (and therefore there was no stimulus manipulation), which is within the normal range of preferences under dark conditions (approximately 15%; see Ryan and Rand 2003). In other words, the light source did not affect preferences generally but rather the final choice specifically by reducing the frequency of reversals.

Additionally, under dim light females had shorter latencies compared with darkness for both nonreversal choices (nonreversal choice under dim light = 106.7 ± 98.5 s (mean ± SD); nonreversal choice under dark = 162.2 ± 131.2 s) and reversal choices (reversal choice under dim light = 127.2 ± 77.6 s; reversal choice under dark = 163.8 ± 121.1 s). In other experiments, we have shown that reversals result in protracted latencies owing specifically to the greater amount of time required to reach the choice zone after stimulus manipulation compared with a nonreversal trial (Baugh and Ryan 2010).

Discussion

Although considerable attention has been paid to examining how predation risk influences signalers (frogs: Tuttle et al. 1982; Jennions and Backwell 1992; Phelps et al. 2007; insects: Cocroft 1999; birds and mammals: Klump and Shalter 1984), less research has focused on the influence of predation risk on receiver behaviour. Receivers, however, are also vulnerable to predation and especially receivers that must approach signalers closely to evaluate their signals. Studies that have examined receivers have shown that more choosy females increase exposure time or conspicuousness to predators. This has been shown or suggested in coral reef fish (Reynolds and Côté 1995), guppies (Pocklington and Dill 1995), swordtails (Johnson and Basolo 2003), and bush crickets (Heller 1992), which are vulnerable to motion-detecting predators during mate approach. Results from these field studies have been further supported by experimental studies showing that receivers fail to express mate-choice preferences or have altered preferences during mate evaluation when in the presence of a predator or when predation risk is perceived to be high, owing to reduced cover (Magnhagen 1991; Milinksi and Bakker 1992; Forsgren 1992; Berglund 1993; Hedrick and Dill 1993). These results suggest that females are offsetting their risk of predation by reducing mate assessment.

Acoustically communicating species offer a unique opportunity to dissect the influence of predation risk on the assessment and selection of mates because playback studies can be conducted in which signals of varying attractiveness can be adjusted dynamically during mate assessment, while all other signaling characteristics are held constant. By applying this approach under the environmental contexts of variable predation risk, one is able to examine specifically the effect of predation risk on receiver choosiness.

Here we used mate selection in túngara frogs as a model for examining the details of acoustically guided behaviour, including temporal aspects of the mate-choice process. We show that during mate approach, females continue to gather information about differences between males, demonstrating that there is an active assessment period during which females use this information to modify their mate choice and this is sensitive to light levels. Based on previous studies (Rand et al. 1997; Bernal et al. 2007), we interpret this result in the context of predation-risk assessment, although alternative explanations might also be relevant. In doing so, we show that not only are mate choices altered by changing the environmental conditions under which mate decisions are made, but that the process of temporal updating during mate choice itself is affected. Females were significantly less likely to update their choices following altered signaler characteristics and had shorter latencies under dimly illuminated conditions. Field observations at breeding ponds indicate that females make faster approaches and choices under moonlit conditions compared with a new moon (L. Bonachea, personal communication). Together these results suggest that females might employ a "fast and frugal" heuristic during the process of mate choice that includes information such as light levels as a proxy for perceived risk (Goldstein and Gigerenzer 2002).

In a previous study we have shown that simple rules may underlie the dynamics of decision-making in naturalistic signaling environments (Baugh and Ryan 2010). These include maintaining commitment to an initial mate preference unless there is a state change in the simple versus complex status of two signaling males. Here we show that the weighting of those options is variable and depends on light level; other factors might also play a role in bounding the probabilistic outcomes of dynamic mate choice. While light levels appear to influence perceived predation risk (Rand et al. 1997; Bernal et al. 2007), there are additional proxies for predation risk that could be used in future studies, including the use of model frog-eating bats (Jennions and Backwell 1992; M.J. Ryan, unpublished data) and acoustic signals that might inform frogs of a predator's presence (Schwartz et al. 2000; Phelps et al. 2007).

Evidence from comparative studies in insects shows that species and populations that occur in areas of high predation risk differ in terms of risk-aversive acoustic communication behaviour compared with those inhabiting areas of low risk (Morris et al. 1994; Heller 1995; Zuk et al. 1998). Given the extensive range and diversity of environments inhabited by túngara frogs, females from populations of variable predation pressure might respond differentially under the conditions used here, thus providing evidence for ecological selection on the receiver side of a predator-exploited communication system. The dynamic playback approach used here, along with proxies for predation risk, could be implemented in studies of mate choice in other anuran species and in acoustically advertising insects and birds in which males compete simultaneously for female attention.

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References

Andersson, M. 1994. Sexual selection. Princeton University Press, Princeton, N.J.

Baugh, A.T., and Ryan, M.J. 2010. Mate choice in response to dynamic presentation of male advertisement signals in túngara frogs. Anim. Behav. **79**(1): 145–152. doi:10.1016/j.anbehav.2009.10.015.

Berglund, A. 1993. Risky sex: male pipefishes mate at random in the presence of a predator. Anim. Behav. **46**(1): 169–175. doi:10.1006/anbe.1993.1172.

Bernal, X.E., Rand, A.S., and Ryan, M.J. 2006. Acoustic preferences and localization performance of blood-sucking flies (*Corethrella* Coquillett) to túngara frog calls. Behav. Ecol. **17**(5): 709–715. doi:10.1093/beheco/arl003.

Bernal, X.E., Rand, A.S., and Ryan, M.J. 2007. Sexual differences in the behavioral response of túngara frogs, *Physalaemus pustulosus*, to cues associated with increased predation risk. Ethology, **113**(8): 755–763. doi:10.1111/j.1439-0310.2007.01374.x.

Blaisdell, A.P., Denniston, J.C., and Miller, R.R. 1999. Posttraining shifts in the overshadowing stimulus–unconditioned stimulus interval alleviates the overshadowing deficit. J. Exp. Psychol. Anim. Behav. Process. **25**(1): 18–27. doi:10.1037/0097-7403.25.1.18. PMID:9987855.

Cocroft, R.B. 1999. Parent–offspring communication in response to predators in a subsocial treehopper (Hemiptera: Membracidae: *Umbonia crassicornis*). Ethology, **105**: 553–568.

Cummings, M.E., Bernal, X.E., Reynaga, R., Rand, A.S., and Ryan, M.J. 2008. Visual sensitivity to a conspicuous male cue varies by reproductive state in *Physalaemus pustulosus* females. J. Exp. Biol. **211**(Pt 8): 1203–1210. doi:10.1242/jeb.012963. PMID:18375844.

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

Dill, L.M., Hedrick, A.V., and Fraser, A. 1999. Male mating strategies under predation risk: do females call the shots? Behav. Ecol. **10**(4): 452–461. doi:10.1093/beheco/10.4.452.

Forsgren, E. 1992. Predation risk affects mate choice in gobiid fish. Am. Nat. **140**(6): 1041–1049. doi:10.1086/285455.

Gerhardt, H.C., and Huber, F. 2002. Acoustic communication in insects and anurans. University of Chicago Press, Chicago.

Goldstein, D.G., and Gigerenzer, G. 2002. Models of ecological rationality: the recognition heuristic. Psychol. Rev. **109**(1): 75–90. doi:10.1037/0033-295X.109.1.75. PMID:11863042.

Greenfield, M.D. 2002. Signalers and receivers: mechanisms and evolution of arthropod communication. Oxford University Press, Oxford.

Hedrick, A.V., and Dill, L.M. 1993. Mate choice by female crickets is influenced by predation risk. Anim. Behav. **46**(1): 193–196. doi:10.1006/anbe.1993.1176.

Heller, K.-G. 1992. Risk shift between males and females in the pair-forming behavior of bush crickets. Naturwissenschaften, **79**(2): 89–91. doi:10.1007/BF01131812.

Heller, K.-G. 1995. Acoustic signalling in palaeotropical bushcrickets (Orthoptera: Tettigonioidea: Pseudophyllidae): does predation pressure by eavesdropping enemies differ in the Palaeo- and Neotropics? J. Zool. (Lond.), **237**(3): 469–485. doi:10.1111/j.1469-7998.1995.tb02775.x.

Jennions, M.D., and Backwell, P.R.Y. 1992. Chorus size influences on the anti-predator response of a Neotropical frog. Anim. Behav. **44**(5): 990–992. doi:10.1016/S0003-3472(05)80596-2.

Jennions, M.D., and Petrie, M. 1997. Variation in mate choice and mating preferences: a review of causes and consequences. Biol. Rev. Camb. Philos. Soc. **72**(2): 283–327. doi:10.1017/S0006323196005014. PMID:9155244.

Johnson, J.B., and Basolo, A.L. 2003. Predator exposure alters female mate choice in the green swordtail. Behav. Ecol. **14**(5): 619–625. doi:10.1093/beheco/arg046.

Klump, G.M., and Shalter, M.D. 1984. Acoustic behaviour of birds and mammals in the predator context. I. Factors affecting the structure of alarm signals. II. The functional significance and evolution of alarm signals. Z. Tierpsychol. **66**: 189–226.

Lima, S.L., and Dill, L.M. 1990. Behavioral decisions made under the risk of predation: a review and prospectus. Can. J. Zool. **68**(4): 619–640. doi:10.1139/z90-092.

Magnhagen, C. 1991. Predation risk as a cost of reproduction. Trends Ecol. Evol. **6**(6): 183–186. doi:10.1016/0169-5347(91)90210-O.

Milinksi, M., and Bakker, T.C.M. 1992. Costs influence sequential mate choice in sticklebacks, *Gasterosteus aculeatus*. Proc. R. Soc. Lond. B Biol. Sci. **2250**: 229–233. doi:10.1098/rspb.1992.0153.

Morris, G.K., Mason, A.C., Wall, P., and Belwood, J.J. 1994. High ultrasonic and tremulation signals in neotropical katydids (Orthoptera: Tettigoniidae). J. Zool. (Lond.), **233**(1): 129–163. doi:10.1111/j.1469-7998.1994.tb05266.x.

Pauly, G.B., Bernal, X.E., Rand, A.S., and Ryan, M.J. 2006. The vocal sac increases call rate in the túngara frog *Physalaemus pustulosus*. Physiol. Biochem. Zool. **79**(4): 708–719. doi:10.1086/504613. PMID:16826497.

Phelps, S.M., Rand, A.S., and Ryan, M.J. 2007. The mixed-species chorus as public information: túngara frogs eavesdrop on a heterospecific. Behav. Ecol. **18**(1): 108–114. doi:10.1093/beheco/arl063.

Pocklington, R., and Dill, L.M. 1995. Predation on females or males: who pays for bright male traits? Anim. Behav. **49**(4): 1122–1124. doi:10.1006/anbe.1995.0141.

Rand, A.S., Ryan, M.J., and Wilczynski, W. 1992. Signal redundancy and receiver permissiveness in acoustic mate recognition by the túngara frog, *Physalaemus pustulosus*. Am. Zool. **32**: 15–17.

Rand, A.S., Bridarolli, M.E., Dries, L., and Ryan, M.J. 1997. Light levels influence female choice in túngara frogs: predation risk assessment? Copeia, 1997(2): 447–450. doi:10.2307/1447770.

Reynolds, J.D., and Côté, I.M. 1995. Direct selection on mate choice: female redlip blennies pay more for better mates. Behav. Ecol. **6**(2): 175–181. doi:10.1093/beheco/6.2.175.

Ryan, M.J. 1985. The túngara frog: a study in sexual selection and communication. University of Chicago Press, Chicago.

Ryan, M.J., and Keddy-Hector, A. 1992. Directional patterns of female mate choice and the role of sensory biases. Am. Nat. **139**(s1): S4–S35. doi:10.1086/285303.

Ryan, M.J., and Rand, A.S. 1990. The sensory basis of sexual selection for complex calls in the túngara frog, *Physalaemus pustulosus* (sexual selection for sensory exploitation). Evolution, **44**(2): 305–314. doi:10.2307/2409409.

Ryan, M.J., and Rand, A.S. 2003. Mate recognition in túngara frogs: a review of some studies of brain, behavior, and evolution. Acta Zool. Sin. **49**: 713–772.

Ryan, M.J., Rand, W., Hurd, P.L., Phelps, S.M., and Rand, A.S. 2003. Generalization in response to mate recognition signals. Am. Nat. **161**(3): 380–394. doi:10.1086/367588. PMID:12699219.

Schwartz, J.J., Bee, M.A., and Tanner, S.D. 2000. A behavioral and neurobiological study of the responses of gray treefrogs, *Hyla versicolor*, to the calls of a predator, *Rana catesbiana*. Herpetologica, **56**: 27–37.

Searcy, W.A., and Nowicki, S. 2005. The evolution of animal communication: reliability and deception in signaling systems. Princeton University Press, Princeton, N.J.

Su, K.F.Y., and Li, D. 2006. Female-biased predation risk and its differential effect on the male and female courtship behaviour of jumping spiders. Anim. Behav. **71**(3): 531–537. doi:10.1016/j.anbehav.2005.04.024.

Taylor, R.C., Klein, B.A., Stein, J., and Ryan, M.J. 2008. Faux frogs: multimodal signaling and the value of robotics in animal behaviour. Anim. Behav. **76**(3): 1089–1097. doi:10.1016/j.anbehav.2008.01.031.

Tuttle, M.D., Taft, L.K., and Ryan, M.J. 1982. Evasive behaviour of a frog in response to bat predation. Anim. Behav. **30**(2): 393–397. doi:10.1016/S0003-3472(82)80050-X.

Valone, T.J., Nordell, S.E., Giraldeau, L.-A., and Templeton, J.J. 1996. The empirical question of thresholds and mechanisms of mate choice. Evol. Ecol. **10**(4): 447–455. doi:10.1007/BF01237729.

Weigt, L.A., Crawford, A.J., Rand, A.S., and Ryan, M.J. 2005. Biogeography of the túngara frog, *Physalaemus pustulosus*: a molecular perspective. Mol. Ecol. **14**(12): 3857–3876. doi:10.1111/j.1365-294X.2005.02707.x. PMID:16202101.

Zuk, M., Rotenberry, J.T., and Simmons, L.W. 1998. Calling songs of field crickets (*Teleogryllus oceanicus*) with and without phonotactic parasitoid infection. Evolution, **52**(1): 166–171. doi:10.2307/2410931.

Zwaan, R.A. 1996. Processing narrative time shifts. J. Exp. Psychol. Learn. Mem. Cogn. **22**(5): 1196–1207. doi:10.1037/0278-7393.22.5.1196.