Light Levels Influence Female Choice in Túngara Frogs: Predation Risk Assessment?

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Predictions generated from models of sexual selection are quite sensitive to costs of female choice (Kirkpatrick and Ryan, 1991; Andersson, 1994). One such cost is the risk of predation while a female searches for a mate (Alatalo et al., 1988; Gibson and Bachman, 1991). One might expect a female to search more for a high quality male when predation risks were low and search less when they were high. Hedrick and Dill (1993) showed that female crickets selected the normally less preferred of two calls when it was associated with decreased risk; in this case, the stimulus was broadcast from under cover and thus offered protection from potential predator attack. Lima and Dill (1990) reviewed the effects of risk of predation on behavioral decisions in a variety of situations.

Light levels might influence search costs in frogs. Most frogs use vision in feeding, locomotion, predator avoidance, and acquisition of mates, although they operate at very low light intensities. They are also hunted by visual predators under low light (Ryan, 1985). Environmental light levels could affect predation risks if they influenced either predator or prey detection. Not surprisingly, frog behavior is affected by light levels, and different species are observed to be active at different levels (Jaeger and Hailman, 1981). Buchanan (1993) demonstrated that foraging behavior in *Hyla chrysocelis* was influenced by rapid shifts in illumination. Tuttle and Ryan (1982) showed that *Smilisca sila* males reacted to bat models by decreasing calling and behaved more cautiously at lower light levels, calling from less conspicuous sites and producing fewer multinote calls. They suggested that this was because the frogs could detect the frog-eating bats (*Trachops cirrhosus*) less effectively when the frogs could not see them well. Ryan et al. (1981) found that in dim light male túngara frogs (*Physalaemus pustulosus*) responded to both frog-eating bats and bat models flying overhead by reducing both their calling and their escape response. In total darkness, the frogs did not respond, presumably because they could not see the bats.

Female túngara frogs in search of males are presumably less at risk from acoustically hunting predators that are cuing on calls than are calling males, but moving females probably are at risk from predators that rely on other sensory cues such as visual, high-frequency echo, olfactory, or vibratory cues. Differing light levels are probably associated with different predation risks and therefore may influence how female túngara frogs choose mates. It is not clear, however, whether females should evaluate more light as riskier because it allows predators to detect them better or as less risky because it allows the frogs to see the predators better. Indeed, if differences in illumination cause equal changes in predator detection by prey and prey detection by predators, then changes in illumination would have no net effect on predation risk.

In our studies of the evolution of communication in túngara frogs, *Physalaemus pustulosus* (Rand and Ryan, 1981; Ryan and Rand, 1995; Wilczynski et al., 1995), we have tested female phonotaxis for a variety of male calls. We have used conditions of dim light, the minimum sufficient for an observer. This is more light than the frogs sometimes experience during breeding. Here we report an investigation of female phonotaxis under two levels of light to test the hypothesis that the degree of caution that female túngara frogs exhibit when chosing a mate should be influenced by light intensity.

Materials and methods.—Túngara frogs call and mate at night, often under the forest canopy and sometimes in the rain. Ryan (1985: 166) states, "That it is too dark to see your hand in front of your face is a literal truth in the middle of the jungle on a cloudy, moonless night." Jaeger and Hailman (1981) report that most túngara frog activity occurred at light levels below 0.01 lux, the lowest that the investigators could measure. However, túngara frogs also breed on moonlit nights so that their reproductive behavior occurs under a wide variety of light intensities (Ryan, 1985).

Female túngara frogs select a complex call (whine-chuck) over a simple one (whine) if the whines in both calls are of the same peak amplitude (Rand and Ryan, 1981). Given two simple calls, identical except that one had a peak amplitude twice that of the other, eight of 10 females approached the call with the greater intensity (unpubl. data).

Assuming that detection by visually hunting predators is an important risk to breeding frogs (Ryan et al., 1981), we would expect that female

frogs would use light levels to assess risk of predation and therefore differ in their willingness to approach a mate in the dark and in dim light. We would expect that light level should influence females' preferences for a lower intensity (i.e., more distant), more attractive complex call versus a higher intensity (i.e., nearer), less attractive, simple call. Whatever the effects of light level on phonotaxis, we would expect concordance between these two results. That is, the light intensity under which we saw a higher rate of phonotaxis should be the intensity under which females should be willing to travel further toward a more distant but more attractive call. This prediction makes the as yet untested assumption that call intensity is interpreted as a predictor of distance.

To test the influence of light level on phonotaxis by female túngara frogs, we used a 3 × 3 m, two-stimulus choice test chamber in the Smithsonian Tropical Research Institute Gamboa Laboratory in Panama (Rand et al., 1992). Each female was released in the center of the arena, midway between the two speakers, and stimuli were alternated between speakers in successive tests. We gave a series of 82 gravid females, over 20 nights, choices between a simple whine and a more complex whine-chuck. The peak intensity of the simple whine was 82 dB SPL at the release point, which is the approximate intensity of a real whine measured in the field at 1.5 m. The whine in the whine-chuck was 70 dB SPL at the release site, equivalent to a whine at 6 m. Each female was tested twice, once in dim light and once in the dark. Under dim light conditions, the light level at the frog release point was 0.04–0.05 microeinsteins (Li-Cor Quantum/Photometer LI-189) and < 0.01 microeinsteins under dark conditions (the frog was not visible to the experimenters' dark-adapted eyes without a night-vision goggle). Light levels used in our previous tests of female choice lie between those used in these experiments. Light came from four 25-watt incandescent bulbs mounted in the ceiling of the test chamber so that the floor was illuminated uniformly. The intensity was controlled by a dimmer switch outside the chamber. The calls were broadcast alternately from speakers on opposite sides of the choice test chamber. Female movements were observed through a small window in the wall of the test chamber equidistant from the two speakers. Illumination in the observation room during a test was never brighter than in the test chamber. A female was scored as having made a choice if she approached within 10 cm of one of the speakers (Rand et al., 1992). A female was scored as making no choice if she

remained 5 min without moving from the release point or moved around the test chamber for 15 min without approaching either speaker.

The order of the tests was reversed for successive females. In the dark, we used a US Army night-vision goggle with a built-in LED infrared illuminator (AN/PVS-7B) to observe the females. We assume that the frogs cannot see in the infrared. There are no data on *P. pustulosus* infrared sensitivity, but Sustare (1976) used electroretinography to show that bullfrogs see no further into the infrared than do humans. The curve of spectral responses of *P. pustulosus* presented by Hailman and Jaeger (1974) shows a rise in the red, but they did not test infrared sensitivity. Probabilities were calculated using Fisher's Exact Test.

Results.—The 82 females tested in both dim light and dark chose 27 times in the dim light and 45 times in the dark (Fig. 1A). Of these 82 females, 32 did not choose in either test, and 22 chose in both. Of the 28 that chose only once, 23 made their one choice in the dark and only five in the dim light. Thus, significantly more females chose in the dark than in the dim light ($P < 0.01$). Females that were tested first in the dark were somewhat more likely to choose (17 of 41) than those tested first in the dim light (27 of 41; $P = 0.046$). Even the females that did not choose either stimulus moved more often in the dark than in the dim light (Fig. 1B). In the dim light, in 37 of the 55 tests scored as "no choice" responses, the females did not move from the release site, whereas in the dark, this was true for only eight of the 37 no choice responses ($P < 0.0001$).

In the dim light, 14 of 27 females chose the louder, simple whine. In the dark, 36 of 45 chose that stimulus (Fig. 1C). Thus, in the dark, many more females chose the apparently closer stimulus over the more attractive but apparently more distant stimulus than they did in the dim light ($P < 0.03$). If one considers females that chose in both dim light and dark, the same pattern is evident but less pronounced, and the proportion choosing simple calls in the dark is not significantly higher than those choosing the simple calls in the dim light (Fig. 1D). But, when one considers the females that chose only once, the pattern is very much stronger. In the dim light the two stimuli are chosen about equally, whereas in the dark, 20 of 23 females chose the simple, louder call ($P < 0.001$, Fig. 1E).

Discussion.—Light levels influence how female túngara frogs respond to male calls. This prob-
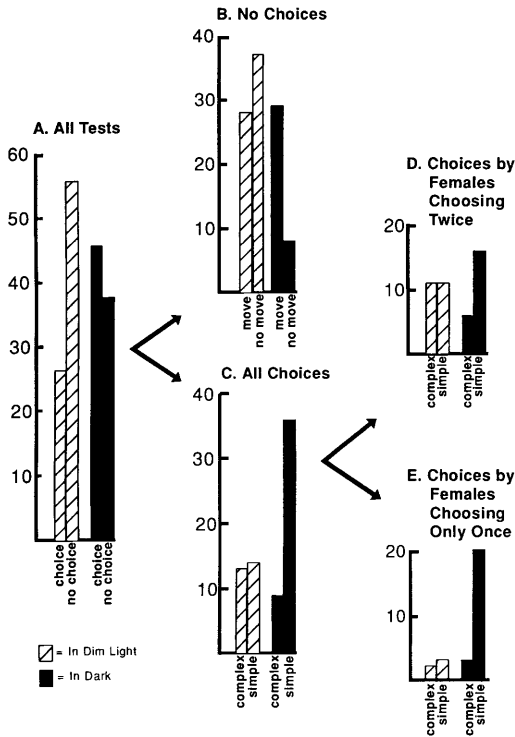
Fig. 1. Phonotaxis by female túngara frogs tested in a two-speaker choice between a quiet complex call (whine) and a louder simple call (whine-chuck), each tested both in dim light and in dark. (A) Results of all 82 females tested under both light regimes (n = 164). (B) Behavior in tests when female did not make a choice (n = 92). (C) Stimuli chosen in all tests where a choice was made (n = 72). (D) Stimuli chosen by females that chose in both tests n = 44. (E) Stimuli chosen by females that chose in only one test (n = 28).

ably results from the influence of light on predation risk. As expected, female behavior was significantly different under the two light intensities in the frequency of movement, frequency of phonotaxis, and stimulus choice. Paradoxically, the light intensity under which the females were more likely to move and choose was not the one in which the less intense, more complex call was preferred. If females were more cautious at higher light levels, one would not have expected them to select the more complex but apparently more distant call under those higher light levels.

A more detailed examination of the data resolves this apparent paradox. It is the females that choose only in the dark that showed a strong preference for the loud, simple call. The females that were so cautious in the experimental set up that they chose only in the dark chose the louder, apparently closer call even though it was the simpler. These choices by females that chose only in the dark is concordant with the greater willingness of females to move and to choose in the dark. Both of these results support the hypothesis that females assess the dark conditions as less risky. Females that chose in the dim light were not more likely to select the apparently closer stimulus.

Conclusions.—Male frogs may be more willing to call under lighter conditions when they can see potential predators, but female túngara frogs seem more willing to choose and more likely to choose more distant calls when predators cannot see them. This finding supports the idea that higher predation risks may reduce the number of calling males a female considers when choosing a mate and so reduce the selective advantage to a male of giving an otherwise more attractive call unless it sounds closer.

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