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Proximity-dependent Response to Variably Complex Mating Signals in Túngara Frogs (*Physalaemus pustulosus*)

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Abstract

The plasticity of animal behavior allows individuals to maximize fitness in a wide range of contexts. Both production of and preference for mating signals are context-dependent according to internal factors such as hormonal state, and external factors such as predation risk. In many species, male-to-female proximity also defines an important context for mating communication. Males often possess short-distance courtship signals, and females often exhibit distance-related variation in signal response. Such variation in response may occur when a signal's relevance changes with male-to-female distance, but it may also result from perceptual constraints that are unrelated to fitness. Túngara frogs produce variably complex advertisement calls, and sexual selection theory predicts that females should prefer calls of greater complexity. Preference tests, however, have not demonstrated consistent trends for preference between calls of variable complexity. We tested whether proximity to males influences female response to variable signal complexity and found that both preference and memory for signal complexity are proximity-dependent.

Introduction

Behavioral plasticity allows animals to modify decisions and achieve successful outcomes in variable environments. For example, animals produce and respond to mating-related communication signals with great variability according to context (Jennions & Petrie 1997; Lindström et al. 2009). Both external changes in the environment, such as predation risk (Bertram et al. 2004), and internal changes in an individual, such as hormonal state (Lynch et al. 2006), influence receiver response to advertisement signals (Ryan et al. 2007). Proximity to potential mates is a contextual factor that dramatically influences mating-related communication. Males often respond to female proximity by changing the intensity of their display (Brumm & Slater 2006; How et al. 2008; Patricelli & Krakauer 2010), or by producing entirely different signals (Titus 1998; Bourne et al. 2001; How et al. 2007). Females generally prefer closer rather than more distant males (MacLaren 2006; Booksmythe et al. 2008), possibly because of potential costs of spending more time in choosing a mate (Sullivan 1994). Proximity can also influence female response to mating signals by altering patterns of selectivity and discrimination (Doolan & Gerald 1985; Farris et al. 1997; Gerhardt & Schul 1999; Beckers & Schul 2004; Marquez et al. 2008).

We examine the influence of proximity in an attempt to understand female response to signal variation in túngara frogs (*Physalaemus pustulosus*). Túngara frog advertisement calls can have two parts: an initial low-frequency sweep called a 'whine' and a terminal high-frequency burst called a 'chuck' (Ryan 1985; Ryan & Rand 2003a). Whines may be voiced alone (simple calls), or followed by 1–7 chucks (complex calls). Females exhibit a strong preference for whines with chucks over whines without chucks [for one-chuck calls vs. whines: 86% prefer one-chuck calls, N = 3662 (Gridi-Papp et al. 2006)], yet previous studies have not found consistent patterns of preference for more chucks over fewer chucks (Bernal et al. 2009). Frog-eating bats (Ryan et al. 1982) and blood-sucking flies (Bernal et al. 2006) preferentially approach male frogs that make complex calls, and bats preferentially approach males making more chucks over males making fewer chucks (R. A. Page, pers. comm.). Multiple chucks must benefit males in some way such that they continue to produce multiple chucks in spite of the costs associated with these calls. Thus, the lack of consistent female preference for greater complexity has called into question the function of multiple chucks.

Recently, we found that females in low-density choruses elicit greater complexity from males in close-range interactions (K. Akre & M. Ryan, own data), which suggests that multiple chucks may be most relevant to females at close range. In this study, we test whether proximity influences female preference for greater chuck number. Female working memory (Akre & Ryan 2010) and strength of commitment to approach a call (Baugh & Ryan 2010) increase for three-chuck calls relative to one-chuck calls, so chuck number is salient in some contexts. Although these studies demonstrate that females attend to chuck number when choice is delayed or when males change call strategies dynamically, the influence of proximity on female response has not been tested. At close proximity to males, multiple chucks might be more meaningful, or they might stimulate female sensory systems to a greater degree. Both possibilities might contribute to a proximity-dependent female response to calls with multiple chucks.

The structure of anuran hearing organs supports the possibility that females require the greater stimulation that occurs at close proximity to males to distinguish number of chucks in a signal. Frogs have two inner ear organs with different frequency ranges to which they are most sensitive: the amphibian papilla (AP) is usually most sensitive to frequencies below 1200 Hz while the basilar papilla (BP) is most sensitive to frequencies above 1500 Hz. The AP has lower thresholds for response than the BP (Capranica 1976; Ryan et al. 1990). The addition of chucks to túngara frog calls adds energy in a higher frequency range to which the BP is most sensitive: about 90% of a chuck's energy is in frequencies greater than 1500 Hz (Ryan et al. 1990). Although females respond specifically to chucks at least as far as 3 m from a male (M. Ryan and S. Rand, unpubl. data), the ability to discriminate between chuck number might require greater BP stimulation. Frequency-dependent discrimination thresholds are reported in other anuran species. For example, green treefrogs discriminate against calls with attenuated high-frequency call components only at high sound levels (Gerhardt 1976), and gray treefrogs discriminate between call rise times more acutely at higher amplitude, especially for high-frequency signals stimulating the BP (Gerhardt & Schul 1999). These studies have been interpreted to indicate that proximity to males should influence which call components are salient to female anurans.

Call amplitude at a receiver's location is commonly used to represent proximity to the sender of a communication signal. Call amplitude changes predictably with proximity; this is the reason that many receivers use ranging, a process by which receivers attend to amplitude as an indication of distance (Naguib & Wiley 2001). Although excess attenuation of calls occurs over distance, the closer a receiver's proximity to signalers, the more predictable the relationship between amplitude and distance. Several studies suggest that anuran response to variable call amplitude has consequences based on the relationship between amplitude and distance. Males respond more aggressively as neighboring males' call amplitude increases (Wells & Schwartz 1984; Owen & Gordon 2005). Call amplitude of neighboring males can also influence nearest neighbor distances in choruses (Brenowitz et al. 1984; Murphy & Floyd 2005). Females can adjust their approach behaviors according to signal amplitude, such that each movement is shorter as amplitude increases (Beckers & Schul 2004). Some females seem to be able to judge a male's call amplitude at the source independent of her distance from the source (Castellano et al. 2004; Murphy 2008), but these studies demonstrate that variability in call amplitude produced by males is not great enough to nullify the general correlation between amplitude and proximity. We have limited data on amplitude variation within túngara frog males, but in an analysis of call bouts from 12 males (Bernal et al. 2009), the amplitude variation within a call bout is such that on average, the standard deviation of the whines' peak amplitude (in absolute amplitude not in dB) is ±10.7% of the mean. As absolute amplitude (i.e. not scaled to dB) varies linearly with distance (a signal that is +6 dB is twice the absolute amplitude and could be perceived as twice as close), then the average change in amplitude within a male's call bout could be interpreted as a difference of ±10% in distance. Although not a trivial effect, the variance will not obscure all the potential distance-related information in the call.

We measured female preference for greater chuck number at three amplitudes representing three male-to-female distances. We also made predictions related to the mechanism that could explain a proximity-dependent response. First, if female discrimination is constrained by sound attenuation over distance, then increasing the energy in the chucks should increase the proportion of females that can discriminate between chuck numbers. Second, if females respond to call complexity at great distances with a non-discrimination task, such as memory, this would demonstrate an ability to perceive the signal at that distance.

Methods

Physalaemus pustulosus were collected in Gamboa, Panama (9°07.0′N, 79°41.9′W) between Sept. and Nov. of 2007 and between June and Sept. of 2008 and 2009. Male–female pairs in amplexus were brought to our Smithsonian Tropical Research Institute laboratory for testing and then released after testing the same night at the site where they were originally collected. While at the laboratory, pairs were stored in dry dark containers to reduce stress and avoid moisture that could stimulate the female to drop her eggs. To avoid using the same female more than once in a given test, we followed standard toe-clipping procedures to mark individuals before release. Toe clip procedures followed the Guidelines for Use of Live Amphibians and Reptiles in Field and Laboratory Research, compiled by the Herpetological Animal Care and Use Committee (HACC) of the American Society of Ichthyologists and Herpetologists (http://www.asih.org/files/hacc-final.pdf).

We used female phonotaxis in a binary choice test as an assay for call preference and memory. We followed previously successful procedures with some modifications (Ryan 1985; Ryan & Rand 2003a). For each test, we placed a female under a funnel in the center of a sound attenuation chamber measuring 2.7 × 1.8 m, between two speakers (ADS L200C) placed at a distance of either 50 cm or 120 cm on either side of the female, depending on the experiment. Testing was monitored remotely with an IR-illuminated camera (Fuhrman Diversified, Inc., Houston, TX, USA). Each speaker broadcast one call every 2 s, and calls from the two speakers were antiphonal. The funnel was lifted remotely, and once a female was released, we scored her response as a choice for one of the speakers when she approached to at least 10 cm of that speaker within 10 min of being released from the funnel. If she did not reach a speaker within 10 min, if she failed to leave the center of the chamber within 5 min, or if she remained immobile for 2 min at any point in the test after leaving the circle, she was scored as 'no choice.' In addition to speaker choice, we recorded latency to leave the center of the chamber and latency to reach the chosen speaker. We predicted that latency would decrease as call amplitude increased.

Preference Tests

We tested whether female preference for greater complexity differs with call amplitudes that represent three male-to-female proximities: 82 dB SPL (re. 20 μ Pascals), 90 dB SPL, and 94 dB SPL. For these preference tests, one speaker broadcast a whine with one chuck and the other speaker broadcast a whine with three chucks. Calls were broadcast while the female was restrained under the funnel at the center of the arena, and after 3 min, she was released to approach a speaker. The distance from the female to each speaker was 50 cm. A male's call is about 90 dB SPL at 50 cm (Ryan 1985); thus for each amplitude, we can estimate the corresponding natural female–male distance. Speakers broadcast calls such that peak amplitude level of the whine at the center of the chamber was 82 dB SPL, which corresponds with a female-to-male distance of about 1.3 m in nature; 90 dB SPL, which corresponds with the actual distance to the speakers, 50 cm; or 94 dB SPL, which corresponds with a female-to-male distance of about 32 cm.

We first conducted the preference test using synthetic calls that were created to match the average call characteristics of the population (e.g. Ryan & Rand 1995; software developed by J. Schwartz). For the synthetic calls, the chuck/whine amplitude ratio was 2.0 and the chuck duration was 45 ms.

We also conducted the experiment using natural calls to determine whether the amount of energy in the chuck series influenced female choice for three-chuck calls. We used recordings from 20 different males whose calls represent the range of natural variation in this population of túngara frogs (Ryan & Rand 2003b). These natural calls were recorded as whines with 1 chuck and are the same calls used in Bernal et al. (2009). For each natural call, we created a call with three chucks by copying the chuck and appending it to the original one-chuck call twice, with each chuck separated by 4 ms of silence. Natural calls vary along many call parameters, such as the duration of each component, the amplitude rise-time, and the dominant frequency. We tested whether the total energy of the chucks for each natural call correlated with the number of choices for more chucks (range: 0–3 choices). For the natural calls, the chuck/whine ratio ranged from 0.18 to 2.21 V (mean ± SD = 1.07 ± 0.49). The chuck duration for natural calls ranged from 32.9 to 115.5 ms (mean ± SD = 53.7 ± 19.5). This was a repeated-measures study, and treatment order was randomized among females.

Memory Tests

We tested whether female memory for three-chuck calls differs with call amplitude. For these tests, both speakers broadcast whines for 1 min; then for 30 s, one speaker broadcast whines with three chucks, while the other continued broadcasting a whine alone. Following this period, the speakers ceased to broadcast sound for a silent duration of 30 s, after which both speakers again broadcast whines alone, and we released the female to approach a speaker. A previous study showed that when females are tested at 90 dB SPL and speakers are 50 cm away from the center of the chamber, females significantly choose the speaker that originally played chucks (Akre & Ryan 2010). We repeated this memory test at 82 dB SPL with the speakers 120 cm away from the center of the chamber to match the natural distance at which males would produce this call. We also repeated this memory test at 82 dB SPL with the speakers 50 cm away from the center of the chamber to control for the distance difference in the above condition. We compared these results to the previously published data. For these experiments, each female was used for only one choice.

Statistics

To analyze the influence of amplitude on preference for greater complexity, we used the Generalized Estimating Equations (GEE) procedure in SPSS 16® (SPSS Inc., Chicago, IL, USA) to create a binary logistic model of speaker choice predicted by call amplitude with test order. We created separate models for synthetic and natural calls. For the tests using synthetic calls, 107 females completed a series of tests in random order, and our statistical analysis controlled for the fact that most females completed multiple tests, but few completed all conditions, by using the repeated subject function. For the tests using natural calls, each of 20 females, distinct from those females used in the synthetic call tests, completed all three amplitude conditions in a repeated-measures design. Each female was presented with a different natural call for each amplitude condition, and each of 20 natural calls was used once at each of the three amplitudes. Pair-wise comparisons were conducted with the EM means function using a sequential Bonferonni adjustment for multiple comparisons.

We also used the GEE procedure to create linear models with latency as a dependent variable. We created separate models for tests of synthetic and natural calls, modeling latency as both the total time before females made a choice and the time before females left the center of the chamber. In both cases, the independent predictors were call amplitude and test order.

To analyze the influence of amplitude and distance on outcome in the memory tests, we used a separate group of females to test each condition. We tested for memory in each condition using an exact binomial test and compared results between conditions with a Fisher's exact test.

Results

Preference Tests

In the test of synthetic calls, a logistic regression using the generalized estimating equation (GEE) with call choice as the dependent variable and order and call amplitude as the predictors showed that call amplitude was a significant factor in the model (N = 177 choices, 107 females; Wald $\chi^2 = 6.403$; df = 2; p = 0.041; Fig. 1a). A stronger preference for more chucks occurs when call amplitude is higher. Order of signal presentation was not a significant factor (p = 0.102). Pair-wise comparisons with EM means (using the sequential Bonferroni setting) showed choice to be significantly different for call amplitudes of 82 and 94 dB SPL (N = 117 choices, 82 females; p = 0.029). Latency decreased significantly as call amplitude increased, both when measured as the total time before females made a choice (N = 177 choices, 107 females; Wald $\chi^2 = 19.017$; df = 2; $p < 0.001$) and when measured as the time before females left the center of the chamber (N = 177 choices, 107 females; Wald $\chi^2 = 17.911$; df = 2; $p < 0.001$).

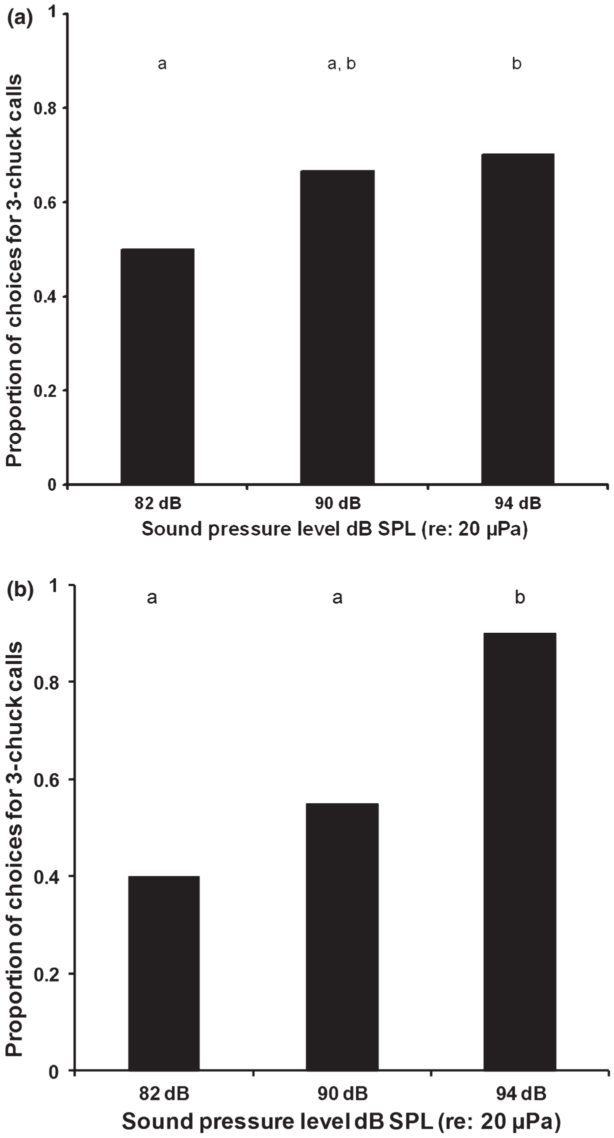

Fig. 1: Female preference for three-chuck calls over one-chuck calls increases with call amplitude in tests of (a) synthetic calls and (b) natural calls. Bars show proportion of females that chose the three-chuck call. Letters mark pair-wise significance, such that proportions labeled with the same letter are not significantly different.

In the test of natural calls using the GEE analysis, call amplitude was a significant predictor of speaker choice (N = 60 choices, 20 females; Wald χ^2 = 13.301; df = 2; $p < 0.001$; Fig. 1b). Order of signal presentation was not a significant factor ($p = 0.675$). Pair-wise comparisons showed choice to be significantly different for call amplitudes of 82 and 94 dB SPL (N = 40 choices, 20 females; $p < 0.0001$) as well as 90 and 94 dB SPL (N = 40 choices, 20 females; $p = 0.01$). Full-test latency was not predicted by call amplitude (N = 60 choices, 20 females; Wald χ^2 = 0.148; df = 2; $p < 0.929$) nor was latency to leave the center of the chamber (N = 60 choices, 20 females; Wald χ^2 = 5.187; df = 2; $p < 0.075$).

The strength of preference for greater complexity did not differ between synthetic and natural calls (two-tailed Fisher's exact test; 82 dB: N = 80 choices and females, $p = 0.606$; 90 dB: N = 80 choices and females, $p = 0.424$; 94 dB: N = 77 choices and females, $p = 0.130$).

The total energy in the natural chuck did not have a significant correlation with number of choices for greater chuck number (N = 60 choices, 20 females; $r^2 = 0.11$, $p = 0.403$).

Memory Tests

Females did not exhibit memory for the speaker that originally played chucks in the 82 dB SPL condition at the natural distance of 120 cm (exact binomial two-tailed: N = 41 choices and females; $p = 0.3488$) or at 50 cm (N = 45 choices and females; $p = 0.7660$; Fig. 2), and the responses at these two distances were not significantly different from one another (N = 86 choices and females; $p = 0.669$). The response to calls at 90 dB (N = 40 choices and females; previously reported in Akre & Ryan 2010) was significantly different than both 82 dB SPL

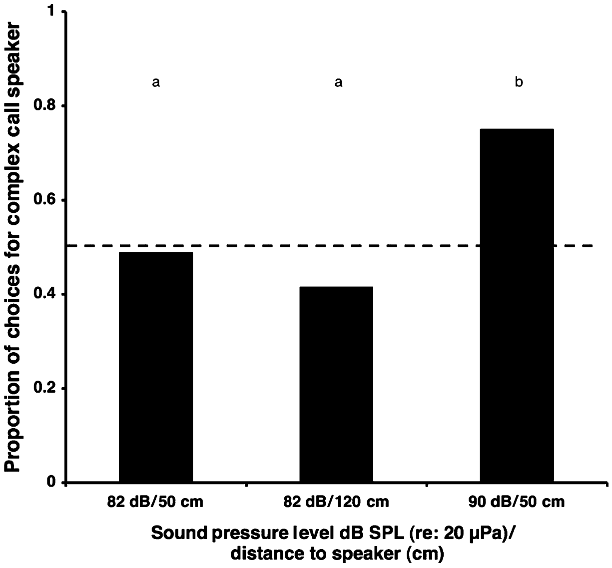

Fig. 2: Memory for three-chuck calls occurs only for high amplitude calls. Bars show proportion of choices for the speaker that originally played three-chuck calls. Dashed line shows null hypothesis of 50%. Letters mark pair-wise significance, such that proportions labeled with the same letter are not significantly different.

conditions (Fisher's exact two-tailed: at 120 cm, N = 81 choices and females, p = 0.004; at 50 cm, N = 85 choices and females, p = 0.015).

Discussion

Call amplitude, which co-varies with proximity, influences both female preference and memory for call complexity. In preference tests between calls with one and three chucks, preference strength for three-chuck calls increased with call amplitude for both synthetic and natural calls. Thus, chuck number influences mate choice at close proximity, and female preference for greater complexity could explain why males produce multiple-chuck calls in spite of the increased predation risk associated with those signals.

We do not know the mechanism for amplitude-dependent difference in female response to chuck number. The pattern we find here, that is, more discrimination and memory at higher amplitudes, could result from the lower thresholds of the BP relative to the AP (Ryan et al. 1990). Alternatively, the critical difference could occur in the brain, beyond the sensory end organ, during neural processing of stimuli. In this case, females could perceive differences in chuck number at lower amplitudes and longer distances from the sender but have no reason to respond differently. The amount of energy in the chuck series did not correlate with number of choices for three-chucks, but several points suggest that the more parsimonious interpretation of our data is that females do not discriminate chuck number at lower amplitudes because they cannot. (1) Amplitude influences both preference and memory, which are two cognitive processes; (2) our data match previous findings that frequency influences anuran amplitude threshold for discriminating temporal call features (Gerhardt 1976; Gerhardt & Schul 1999); (3) once females do discriminate between chuck numbers at close range (higher amplitudes), the response follows Weber's law (K. Akre, H. Farris, A. Lea, R. Page & M. Ryan, own data), suggesting that discrimination is physiologically constrained even at high amplitudes.

Call amplitude influenced not only discrimination and memory but also both latency to leave the starting position and latency to make a choice in the tests of synthetic calls. This was true even though the distance from the females' starting position to the speaker was the same for each condition. One interpretation of this result is that females are generally more responsive to males that produce high amplitude calls. Responsiveness increases with call amplitude in other anurans (Beckers & Schul 2004). Females prefer to approach a speaker that is louder at the source when it is paired with a closer speaker that is quieter at the source, but equally loud at the female's starting point (M. Ryan & A. Lea, pers. comm.). Amplitude-dependent latency, however, was only apparent in the tests that used synthetic calls. In the tests of natural calls, variation in multiple call properties (such as duration and dominant frequency) extinguished the influence of amplitude on latency, which suggests that call amplitude at the source is weighed along with multiple call variables in mate choice decisions.

Other studies of anuran response to mating calls have found similar patterns of increased discrimination between call features at high amplitude (Gerhardt 1976; Gerhardt & Schul 1999). The influence of amplitude on discrimination, however, depends on what type of call feature is being discriminated. For example, amplitude has an opposite influence on discrimination acuity for differences in amplitude itself. At high sound levels, the ability to discriminate between two different amplitudes decreases in insects and anurans, although birds and mammals show the opposite trend (Wyttenbach & Farris 2004). Discriminating between chuck numbers may depend on female processing of duration, total energy, or BP-specific call energy.

Proximity-dependent receiver response might occur commonly in a variety of communication systems. To better describe these proximity-related communication dynamics, a signal's active space can be described as a set of stratified layers. Active space is the area over which a signal influences a receiver's response (Morton 1975; Marten & Marler 1977; Marten et al. 1977; Wiley & Richards 1978). If a signal elicits a repertoire of different responses according to proximity, then the distance over which each response occurs can be envisioned as a series of stratified layers spreading from the sender's location (Fig. 3). For example, in túngara frogs, the female behavioral threshold for approaching multiple-chuck calls is around 61 dB SPL, which corresponds to a distance of about 12 m (R. Taylor, M. Ryan, & K. Akre, own data). The threshold for discriminating multiple-chuck calls from whines is around 72 dB SPL, which corresponds to a distance of about 3 m (M. Ryan & A. Rand, own data). The threshold for both remembering three-chuck calls and discriminating three-chuck and one-chuck calls is around 90 dB SPL, which corresponds to 50 cm. So the first stratum of active space for three-chuck calls is 50 cm in

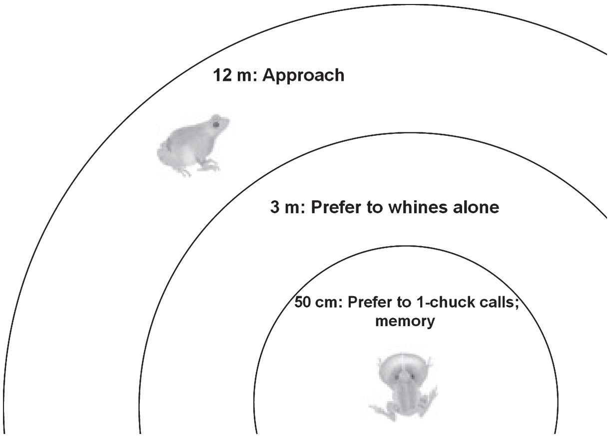

Fig. 3: This stratified active space depicts the area over which a male's three-chuck call stimulates each response in the female's response repertoire. Distances are not shown to scale.

diameter, the next is a diameter of 3 m, and the third stratum about 12 m in diameter. A complete measurement of active space for each receiver response to a signal could improve our understanding of how the environment influences signal evolution.

In summary, we show that signal amplitude, and therefore male-to-female proximity, influences female túngara frog response to mating signals. Female preference for more to fewer chucks at close proximity explains why males produce calls with multiple chucks in spite of the increased predation risk associated with those calls. In general, we emphasize that there is no single signal preference, as preference can vary within a number of contexts including the distance of receiver to the signal course.

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