How Do Female Gray Treefrogs (*Hyla versicolor*)
Select and Locate Mates?

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**ABSTRACT**.  Female gray treefrogs (*Hyla versicolor*) tend to prefer males with high PN (pulse

number) calls over those with low PN calls.  However, this may be affected by sampling

technique; if females incorporate all stimuli available to them into a single vector that determines

their direction of movement, they may sometimes be "pulled" toward a lower-PN call if there is

a narrow angle between the two different calls.  I tested female choice with 18 and 24 PN calls

separated by 20º, 40º, 60º, 80º, placing the higher PN call further from the female in the first

experiment and keeping the two stimuli equidistant from her in the second.  In Experiment 1,

females preferred speaker B to speaker A at all angles; in Experiment 2, they preferred speaker A

at 40º and 60º but chose randomly at 20º and 80º.  This is not consistent with the hypothesis, and

it appears that females were not distinguishing between the different PN calls.  In order for

females to discriminate between calls, the stimuli may need to be separated by even greater

angles, or calls that differ more in their characteristics may need to be used.  Further studies

could expand upon this one by pursuing these possibilities.

**INTRODUCTION**.  Male gray treefrogs (*Hyla versicolor*) form choruses in the spring and give

advertisement calls to attract females.  While females usually select males with call frequencies

close to the mean, they prefer extreme values of temporal properties, which can lead to strong

directional selection; specifically, female treefrogs are strongly attracted to males with the

highest number of pulses per call (pulse number or PN) (Gerhardt 1994, Gerhardt et al. 1996).

Research on how females actually sample potential mates and choose one has focused on two

main theories: the "best of n" theory, which suggests that females visit a certain number of

potential mates and select the best one, and the "minimum threshold" theory, which suggests that

the female mates with the first male she encounters who meets a certain minimum threshold of

quality (Gibson and Langen 1996, Widemo and Saether 1999). However, Gerhardt et al. (1996) noted that females are less likely to choose a stimulus with higher pulse number when two stimuli were placed at a close angle than when they were placed farther apart, an observation not easily explained by either proposed sampling technique.

I propose an alternate model for the decision-making process of the female treefrog. Townsend and Busemeyer (1995) laid out a dynamic model of decision making called decision field theory, or DFT. According to this theory, females approach potential mates indirectly, changing their preferences as their relative position changes. Rather than choosing a specific male, they incorporate signals from all the males around them into a vector that determines their direction. This would aid them in locating a single male among a dense chorus but would mean that they are not directly "choosing" mates.

This hypothesis predicts that when there is a relatively large angle between the two stimuli, the female will accurately choose the one with the higher pulse number (representing a more desirable male), but that as the angle between them decreases her decision-making process will be altered. If the stimulus with the lower pulse number is closer, she may be "pulled" toward it as she nears it. My experiment is designed to test this prediction, using speakers playing calls with different pulse numbers placed at varying angles from each other, testing the female's choice both when the more desirable speaker is farther away and when they are equally distant from her.

**METHODS**. Females were captured by searching vernal ponds for amplexing pairs during and after the evening chorus. They were stored in a refrigerator for a maximum of three days, at which time they were released if they had not been tested.

The frog was placed on a tarp in the center of a circle with a two meter radius, which was divided into twenty-degree sections. Before carrying out the main trials, I confirmed that the female was exhibiting phonotaxis by playing a single 24 PN stimulus at a distance of one meter from the circle's center. Any frogs that took longer than five minutes to complete this initial test were discarded from the study, and this check for phonotaxis was repeated after the four main trials, controlling for any possible decrease in motivation due to repeated testing.

To test the female, two speakers, one playing a 24 PN stimulus (speaker A) and one playing an 18 PN stimulus (speaker B), were placed around the circle. For Experiment 1, speaker A was on the circle's edge (two meters from the frog) and speaker B was three meters from the frog; for Experiment 2, both were placed on the edge of the circle, equidistant from the frog. Each frog was tested with the speakers separated by 20, 40, 60, and 80 degrees. For each test, I recorded the time it took the female to begin moving (latency), the path she took (recorded via webcam), and the time it took her to reach a speaker. The position of speaker A and the order in which the angles were tested for each frog were selected randomly, as was whether speaker B was placed to the left or right of speaker A for each trial. Between trials the female was given five minutes of quiet to acclimate, and at the beginning of each trial she was not released until 4-6 calls had played, so that she had time to hear each. Playback was timed so that the two calls never overlapped.

**RESULTS**. Paired t-tests showed no statistically significant change in latency ($t_{19}=0.346$, $p=0.733$) or time to speaker ($t_{19}=1.170$, $p=0.256$) between the pre-tests and post-tests to confirm phonotaxis (Figure 1), indicating that there was no decrease in motivation as a result of repeated testing.

*Experiment 1.* Ten frogs were tested. Repeated measures analysis found no statistically significant difference between angles in latency (F=0.555, p=0.653) or time to speaker (F=1.333, p=0.301) (Figure 2). Additionally, though the average time to speaker was higher for trials where frogs chose speaker A (the one farther away) than speaker B, ANOVA tests showed that this difference was not significant (F=2.566, p=0.119), nor was there a significant difference between speaker choice for latency (F=1.399, p=0.117). Chi-square tests using percentages showed that females significantly preferred speaker B to speaker A at every angle tested (Figure 3).

*Experiment 2.* Eleven frogs were tested. Again, repeated measures analysis found no statistically significant difference between angles in latency (F=0.979, p=0.417) or time to speaker (F=2.636, p=0.070) (Figure 4). Chi-square tests using percentages showed that females significantly preferred speaker B to speaker A at 40º and 60º, but chose randomly at 20º and 80º (Figure 5).

**DISCUSSION**. In the first experiment, where the more desirable stimulus was placed farther away, females preferred the lower PN stimulus at every angle. They appear have been choosing the nearer stimulus regardless of PN, which would make sense if the calls were not different enough to be distinguished, as choosing the nearest available male would minimize the amount of an energy a female would be putting into searching for a mate. Gerhardt et al. (1996) found that females chose a higher PN call even if it was farther away *if the two calls differed by at least one hundred percent* (he used 12 PN versus 24 PN calls); further experiments confirmed that female frogs are more discriminating when presented with stimuli pairs that differ more in their temporal properties (Murphy and Gerhardt 2000). Since we were using 24 PN and 18 PN calls,

they may not have been different enough to affect female choice. Additionally, Gerhardt was comparing 180º to 36º, while the broadest angle I tested was 80º; this suggests that in addition to the calls being similar, they may have been too close together, even at 80º, for the females to easily distinguish.

In the second experiment, I eliminated distance as a possible factor in the female's choice by placing both speakers two meters from her. In this case, females still preferred speaker B, the lower PN call, at 40 and 60, but choice became random at the extremes of the range of angles tested (20 and 80). Why did they still prefer the lower PN stimulus in some cases even when the two speakers were equally distant? I have no good explanation to offer for this. If, as suggested by Experiment 1, they could not distinguish between the two calls and made their choice based on distance, with the speakers equidistant choice should have been random at *all* angles; if they could distinguish between the calls, I would have expected them to choose A over B. Perhaps the small sample size was a problem and I would have gotten different results had I been able to test more frogs.

It is possible that in the wild females would not need to distinguish between males that are so close together, since male treefrogs are territorial and use their calls as a way of maintaining even spacing between each other; males are only positioned extremely close together when one is calling and the other is a silent satellite male (Fellers 1979). In any case, future improvements to be made on this study are clear: test female choice at variety of wider angles while using the same stimuli as of the same PN as Gerhardt. Perhaps testing at 60º, 100º, 140º, and 180º would yield the necessary resolution.

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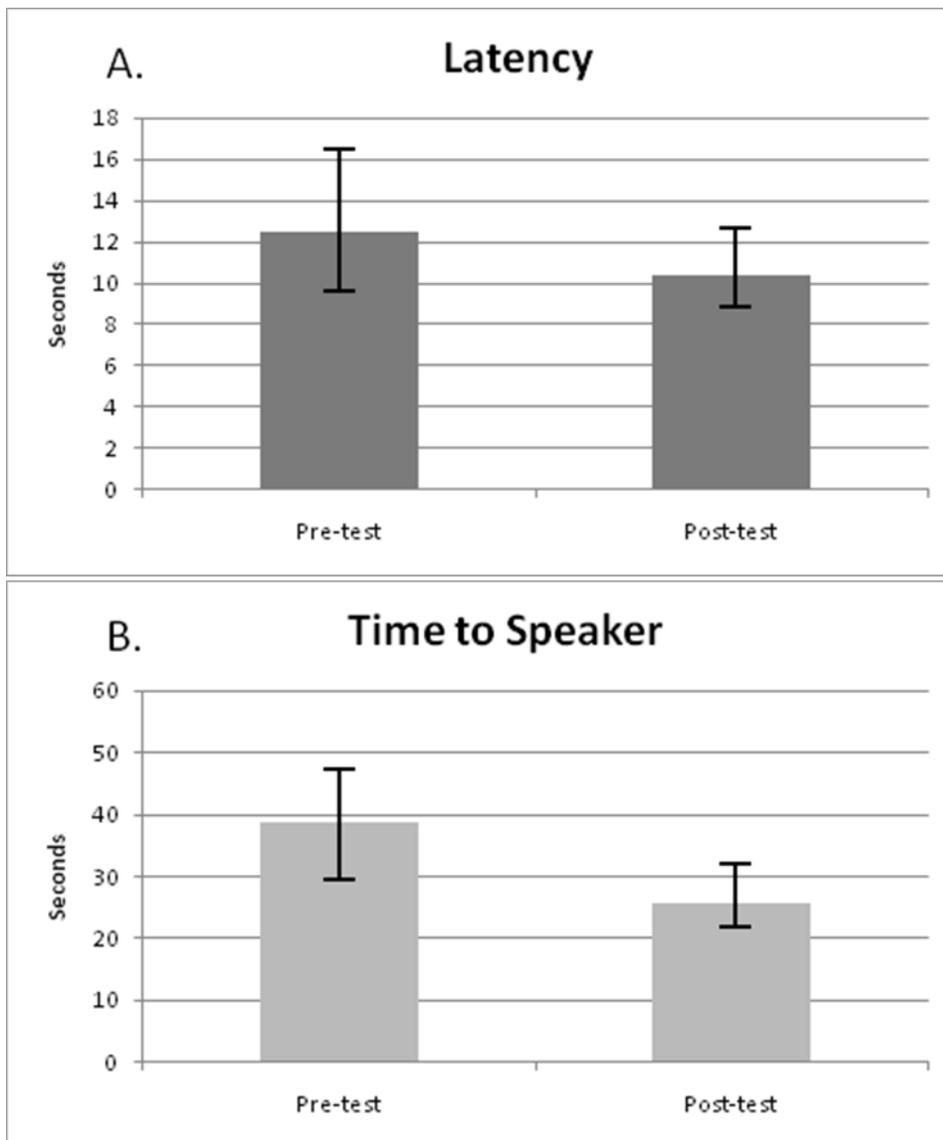
Figure 1: Latency (A) and time to speaker (B) before and after testing. Changes are not statistically significant, indicating there was no decrease in motivation.
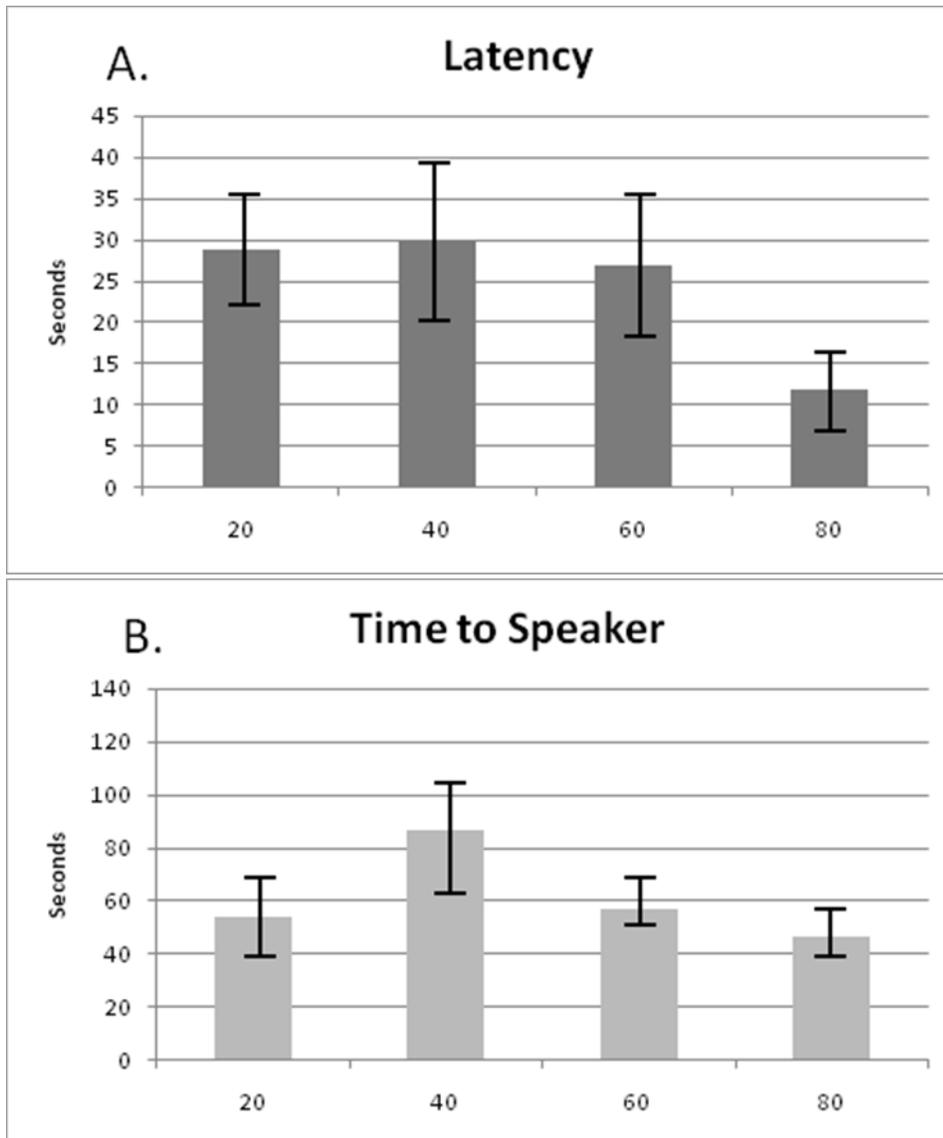
Figure 2: Latency (A) and time to speaker (B) at each angle for experiment 1. No statistically significant variation between angles.
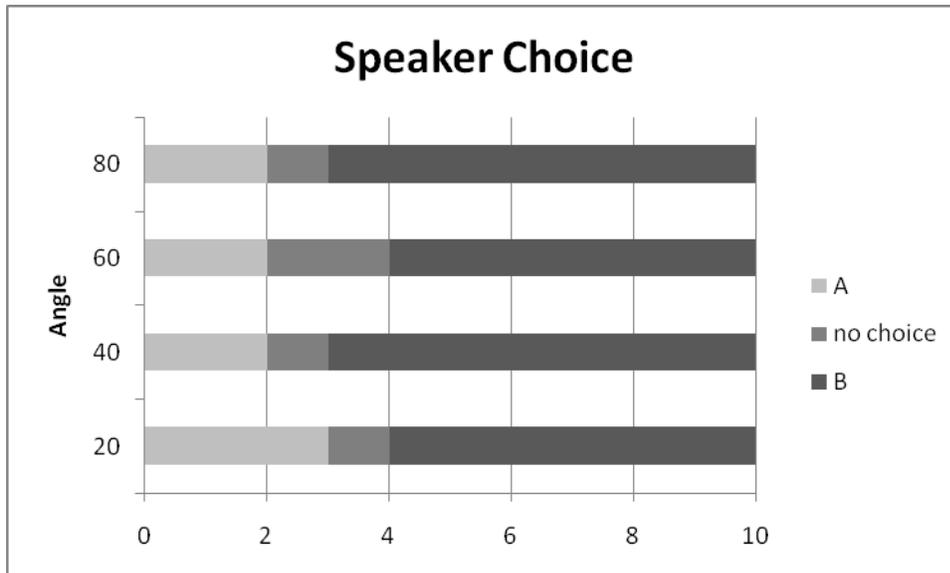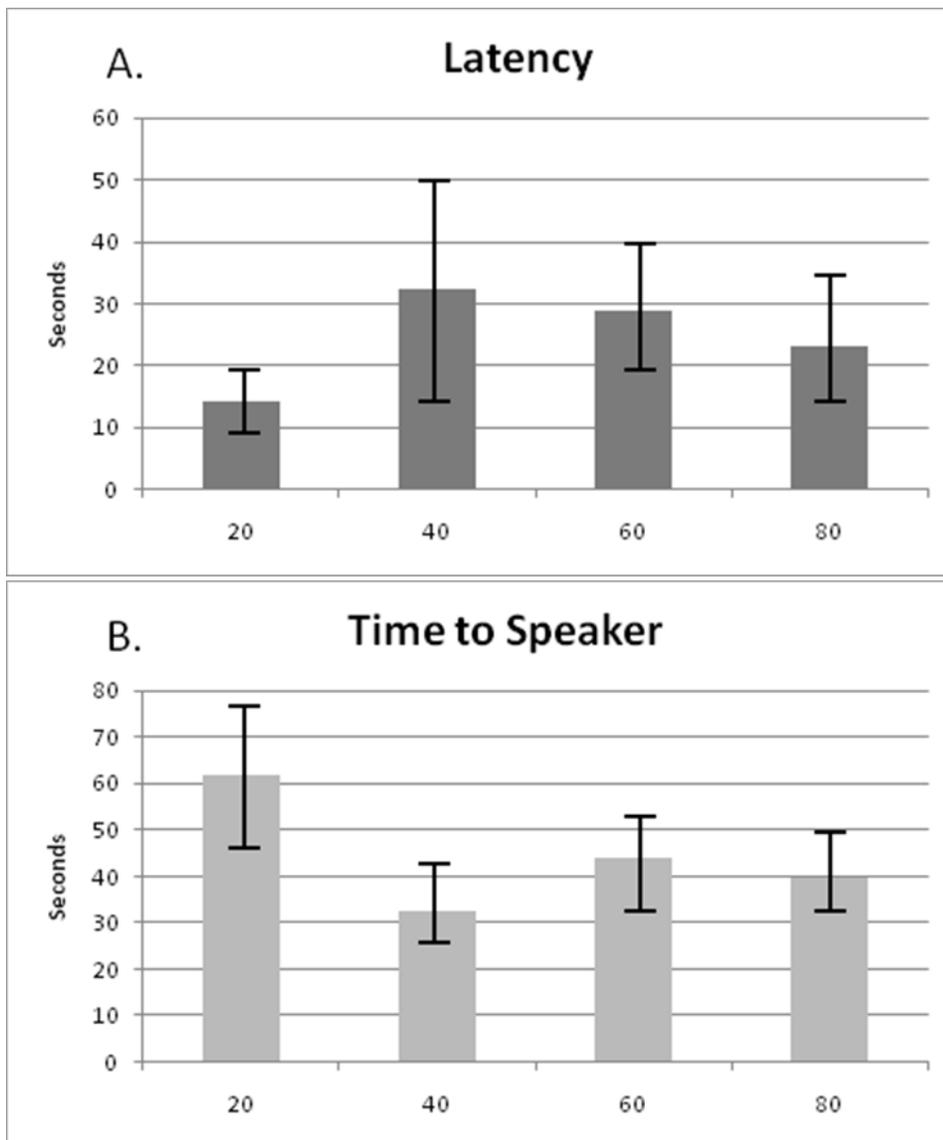
Figure 3. Females preferred speaker B to speaker A at every angle tested. For 20º, $X^2$=11.560, p=0.0007; for 40º, $X^2$=31.360, p<0.0001; for 60º, $X^2$=25.000, p<0.0001; and for 80º, $X^2$=31.360, p<0.0001. "No choice" indicates that the female did not reach a speaker within five minutes.

Figure 4: Latency (A) and time to speaker (B) at each angle for experiment 2. No statistically significant variation between angles.
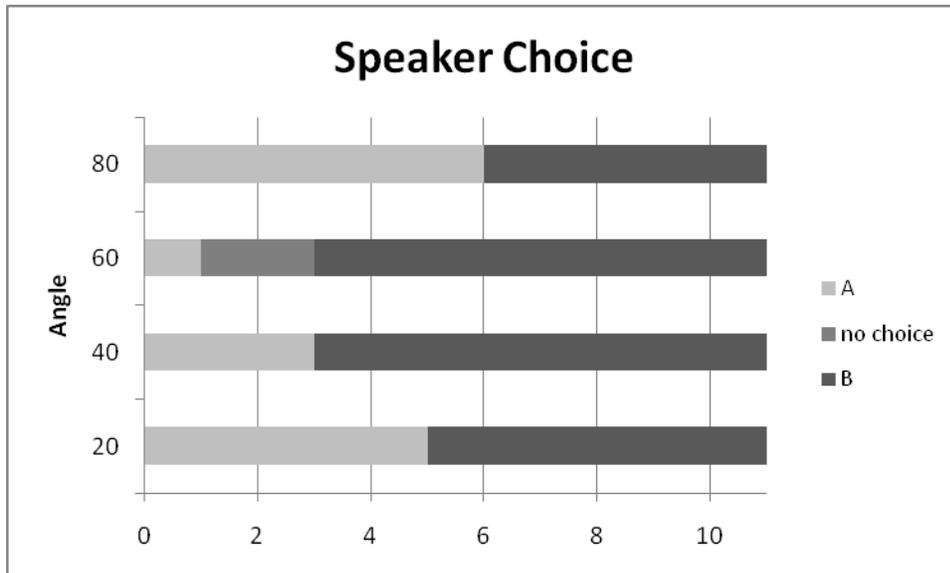
Figure 5.  Females preferred speaker B to speaker A at 40º and 60º but chose randomly at 20º and 80º.  For 20º, $X^2$=1.000, p=0.3137; for 40º, $X^2$=21.150, p<0.0001; for 60º, $X^2$=60.840, p<0.0001; and for 80º, $X^2$=1.000, p=0.3137.  "No choice" indicates that the female did not reach a speaker within five minutes.