



Female preferences for temporal order of call components in the túngara frog: a Bayesian analysis

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We employed a Bayesian statistical approach to examine female preferences in the Neotropical frog *Physalaemus pustulosus* for the temporal relationship of the two parts of the conspecific advertisement call. The male advertisement call consists of a 'whine', which is necessary for species recognition, followed immediately by one or more 'chucks', which make the whine more attractive to females. We conducted 42 two-choice experiments with a total of 840 individual tests to compare the attractiveness of a whine with a chuck in a variety of positions relative to the start of the whine against a normal whine or against a normal whine/chuck. Females have a bimodal preference function for chuck position. Chucks placed in a variety of positions after the whine (including the position of a chuck in a normal call) were generally as attractive as a normal whine/chuck. Chucks placed before the whine were generally more attractive than a whine alone, and in some positions as attractive as the normal whine/chuck. Chucks overlapping the end of the whine make the call more attractive than a whine alone, but not as attractive as a normal whine/chuck, while chucks overlapping an initial portion of the whine beginning 50 ms into it are ignored; previous work (Wilczynski et al. 1995, *Animal Behaviour*, 49, 911–929) indicates this region to be critical for species recognition. These results suggest that female *P. pustulosus* have preferences for the temporal relationship of the two parts of the conspecific male advertisement call that far exceed the vocal signals produced by males, and that male calls have evolved calls to exploit one peak of this function.

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The reproductive social behaviour in most species of frogs depends on an acoustic communication system in which the vocal signals of males attract females (Wells 1977; Gerhardt 1988; Rand 1988). Females use the male signals to recognize conspecifics and to reject heterospecifics when choosing a mate. Call variation among conspecific males can support intraspecific preferences in mate choice. Particular spectral features, such as lower dominant frequencies in the call or the characteristics of a frequency modulated sweep (Ryan 1985; Ryan & Wilczynski 1988; Ryan et al. 1992; Wilczynski et al. 1995; Bodner 1996), or temporal characters, such as particular call durations, repetition rates, or amplitude modulation patterns (Gerhardt 1991; Passmore et al. 1992; Sullivan & Hinshaw 1992; Gerhardt & Watson 1995; Jennions et al.

1995) can increase the probability of female approaches to the caller (or, in experimental manipulations, a speaker broadcasting such a call). Examining such variation in call parameters and its effects on female phonotaxis has been an important part of research into the mechanisms and evolution of acoustic communication and mate recognition systems (Gerhardt 1987, 1991; Ryan 1991; Ryan & Keddy-Hector 1992).

We have been engaged in a long-term investigation of acoustic communication and mate choice in the Neotropical frog *Physalaemus pustulosus*, with the aim of understanding the rules governing recognition and attraction. Males of this species produce a two-part advertisement call (Rand & Ryan 1981; Ryan 1985; Rand et al. 1992). The first portion, or 'whine', is a frequency modulated (FM) sweep from 900 to 400 Hz in ca. 300 ms. The second portion, or 'chuck', is a short (ca. 35-ms) signal composed of 14 harmonics of a fundamental frequency near 215 Hz. Nearly all of the acoustic energy in the chuck lies in the upper harmonics above 1500 Hz, and thus the natural chuck, with an average dominant

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frequency of 2500 Hz, is a higher-frequency signal than the whine. Males may produce the whine alone, or a whine followed by up to six chucks.

The whine is both necessary and sufficient for female phonotaxis and mate choice. The first 150 ms of the whine, during which it sweeps through frequencies between ca. 500 and 900 Hz, contains all the information necessary for mate recognition (Rand et al. 1992; Wilczynski et al. 1995). Within this portion of the whine, a signal must progress from higher frequencies to lower, must have a duration longer than 50 ms and must stimulate at least some portion of a higher-frequency region between 560 and 900 Hz, and some portion of a lower-frequency region between 500 and 640 Hz in order to elicit phonotaxis from a female *P. pustulosus*. Such a minimal signal is not as attractive as a full whine. Thus, adding some forms of acoustic energy within the spectrum of the natural whine makes the call more attractive.

The chuck alone will not support female phonotaxis, but when added to the end of a whine it makes the whine more attractive (Rand & Ryan 1981; Ryan & Rand 1990). The more chucks that are added, up to three, the more attractive the call becomes. This portion of the signal is interesting because it represents an exemplary case of an acoustic adornment, a call syllable that is clearly not involved in mate recognition but just as clearly makes a call more attractive to conspecific females. Furthermore, the whine and the chuck largely stimulate different auditory end organs in the anuran inner ear (Ryan et al. 1990). The lower-frequency amphibian papilla, tuned between 100 and 1200 Hz, is stimulated by the whine, while the higher-frequency basilar papilla, with tuning centred at ca. 2100 Hz, is stimulated by the chuck. In *P. pustulosus*, the chuck always follows the whine (Ryan 1985).

In this study, we addressed two questions on the effect of varying the temporal relationship of the whine and chuck on the attractiveness of the call. First, is the natural position of the chuck, immediately following the whine, critical or optimal to enhance signal attraction? Second, would a temporal overlap of the chuck and whine interfere with call recognition, and thus diminish the phonotaxis to the signal, despite the fact that these two signals stimulate different peripheral auditory end organs?

Examining these questions bear on the mechanisms by which components of a mate recognition signal are processed and on the evolution of diversity of mate recognition systems. One fundamental question pertaining to both is whether female preferences are more expansive than the normal range of male signals. In previous work we have shown that only a small part of the species-typical whine is necessary and sufficient for mate recognition and that a variety of manipulations of the spectral composition of the whine and chuck can make the key portion of the mate recognition signal of this species more attractive to females (Wilczynski et al. 1995). Here we examine the effect of variation in a very basic feature of the male advertisement signal, the temporal order of its component parts. This feature seems to be invariant within each species of *Physalaemus*, but it can vary among species. If female *P. pustulosus* are shown to be attracted to a variety of temporal relationships between the whine

and chuck, then, in each species, male signals have evolved to exploit only one of many possible female preferences. A second, more mechanistic issue addresses how parts of a signal with different functions (in this case species recognition and individual attractiveness) are processed by females. By artificially varying the temporal relationship of these components, we can ascertain whether the two components are recognized and processed separately, or whether particular temporal relationships can reveal the ability of the two components to interfere with each other.

To investigate these issues, we analysed the data using a Bayesian statistical approach (Gerhardt 1992). Unlike traditional methods of data analysis, Bayesian statistics do not test for statistical significance in the usual sense. Rather, Bayesian analysis reports the likelihood, in the form of a probability statement, that an experimental outcome represents some a priori, quantitatively defined condition. A positive feature of this approach is that it provides more information about the data: it presents the exact probability that an experimental outcome resulted from any one of several competing hypotheses rather than simply reporting that a result is above or below an arbitrary significance value when compared against a single null hypothesis. For a fuller explanation of Bayesian statistics and their differences from traditional parametric statistical hypothesis testing, see Iverson (1984) and Gerhardt (1992).

METHODS

Experimental Design

We conducted two-choice female phonotaxis tests in 1992–1995 as in Ryan & Rand (1990) and Wilczynski et al. (1995) to determine whether the position of the chuck relative to the whine affected female preferences for the call. We collected female *P. pustulosus* in amplexus in and around Gamboa, Republic of Panama, and placed them in an indoor test chamber. The chamber had a cement floor and walls covered with foam to reduce reverberations. Speakers (ADS L200C) were placed at opposite ends of the chamber, 3 m apart. Stimuli for the experiments were synthesized on an Amiga 2000 computer using software developed by J. Schwartz. For each test pair of stimuli, each member of the pair was played through one channel of the computer to one of the speakers in an alternating fashion, with a repetition rate for each stimulus of one call/2 s. The stimulus calls were broadcast at a peak intensity of 82 dB sound pressure level (re: 20 μ Pa) at the centre of the chamber, the site at which females were released. Prior to the experiments, the test stimuli were tape-recorded at this site in the chamber and acoustically analysed and compared against the synthesized signal to test for degradation. The analysis revealed negligible degradation during transmission in the room.

For each experiment, we placed a female in the centre of the chamber, equidistant between the two speakers, under a small inverted funnel. We presented the alternating test stimuli for 2 min while the female remained under the funnel. We then removed the funnel from

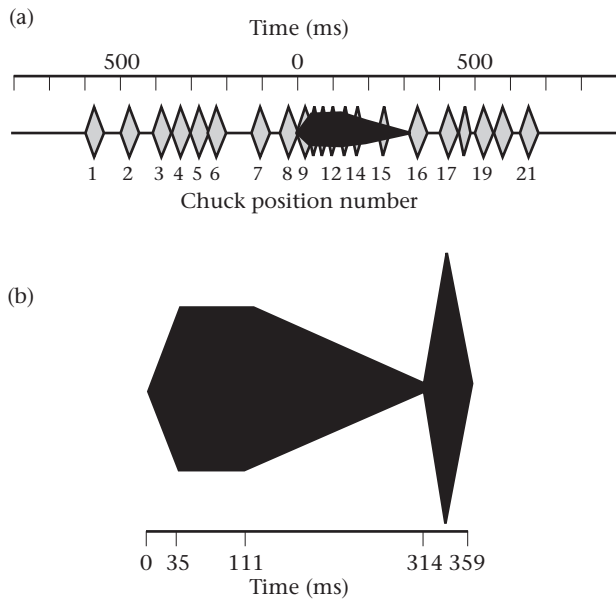


Figure 1. (a) Diagram of chuck placements relative to start of the whine used in the test stimuli. (b) Expanded diagrammatic view of the time course of a normal whine/chuck.

outside the chamber via a string attached to a series of pulleys while stimulus presentation continued. We continued a test trial for 15 min or until the female approached within 10 cm of one of the speakers. Stimulus presentation continued throughout the trial. If a female remained motionless for 5 min after release or at any time during the trial, the trial was terminated and scored as ‘no response’. A trial was also scored as ‘no response’ if the female moved, but did not approach within 10 cm of a speaker by the end of the 15-min trial.

In the first set of experiments, we tested female preferences by pairing a digitized version of a natural whine against the same whine combined with a digitized chuck at a variety of positions relative to the start of the whine. In the second set of experiments, we tested female preferences by pairing a whine plus a chuck in the normal position (immediately following the whine) against the whine with a chuck at a variety of positions relative to the start of the whine. The temporal relations between the whine and various chuck positions are shown in Fig. 1. Setting the beginning of the whine at 0 ms, a chuck normally occurs immediately after the end of the whine, at 314 ms. In each set of experiments, we placed the chuck at different temporal positions before the whine, that is, at times, relative to the start of the whine, of -600 , -500 , -400 , -350 , -300 , -250 , -125 and -35 ms (representing a chuck that ends immediately before the beginning of the whine), during the whine, at 0 (representing an overlap of the beginnings of the whine and the chuck), $+25$, $+50$, $+75$, $+100$, $+125$ and $+225$ ms, or following the whine, at $+314$ (the position of a normal chuck), $+404$, $+439$, $+500$, $+575$ and $+628$ ms (these latter times representing the position of the second through sixth chucks sometimes added by males to the first chuck). We tested 20 females at each of

these 21 chuck positions in each of the two sets of experiments (i.e. against the whine alone and against the whine plus chuck in the normal $+314$ -ms position). Most females were tested with several different stimulus combinations on the night of capture, with tests separated by at least 3 min, but females were tested only once with any specific stimulus pair. The order of tests varied among females.

Statistical Analysis: Bayesian Probabilities of Individual Preferences

A Bayesian approach to these types of data calculates the relative probabilities that an observed proportion came from any one of several expected proportions defined a priori. Conceptually, it allows one to assign the probability that an empirical result reflects one of several defined theoretical possibilities.

We tested the possibility that the observed proportion of choices for the whine plus chuck at each temporal position would occur if the ‘real’ probability of choosing the test whine/chuck versus the normal whine was either 0.50, 0.75, or 0.90. The 0.50 value is equivalent to the whine and the test whine/chuck being equally attractive, or not distinguishable by females, so that each is selected by females at equal frequencies. The 0.75 value is equivalent to the test whine/chuck being just different enough from the whine alone so that females choose it significantly more often than chance. This proportion is equal to the just-noticeable difference (JND) point, or difference threshold, used in sensory psychophysics to indicate the point at which one signal has become sufficiently different to another signal that a subject can distinguish the two significantly more often than chance in a two-choice discrimination task. Although the statistical benchmark we use comes from measurements of difference thresholds, the task is conceptually equivalent to what Nelson & Marler (1990) termed a ‘just meaningful difference’, that is, it represents the point at which a particular signal in a particular behavioural situation generates a different response than does another signal, rather than representing the absolute ability of the organism to distinguish two stimuli. For that reason, we will refer to this proportion as a JMD rather than an JND point. Based on our results, we cannot claim that the difference threshold we obtain indicates the absolute limit of the organism’s ability to discriminate stimuli, only that it shows the point at which a particular stimulus changes enough to evoke a behavioural change in an organism. The minimum JMD will be constrained to be equal to or greater than the JND, and thus represents a more conservative estimate of how well organisms can perceive stimulus differences. The third value (0.90) is equivalent to the test whine/chuck eliciting the same level of preference against a whine that a whine with a chuck in the normal position (immediately following the whine) elicits when compared against a whine. This value is based on a conservative estimate of the preference obtained from our previous work with this species (Ryan 1985; Rand et al. 1992; Wilczynski et al. 1995), in which such preferences ranged from 18:2 to 20:0 for a whine/chuck over a whine.

In the results of the present study, females chose a whine/chuck over a whine at the 100% level, but using proportions of 1.0 as theoretical estimates in Bayesian calculations reduces other probability terms to 0 and therefore should not be used. We did not test against any proportions less than 0.50 because inspection of the results indicated no cases in which a higher percentage of females preferred the whine alone to a whine plus chuck in any position.

Inspection of the results of matching the test whine/chucks against a whine with a chuck in the normal position indicated that some abnormally placed chucks elicited a higher percentage of female preferences, while in most cases the percentage of females choosing the normal whine/chuck was higher. Therefore, we calculated the Bayesian probabilities using four theoretical proportions: 0.75, 0.50, 0.25, 0.10. The first (0.75) represents the case in which the test whine/chuck was just meaningfully different and preferred more than the normal whine/chuck. The 0.50 proportion represents equal preferences for the normal whine/chuck and the test whine/chuck. The third proportion (0.25) is equivalent to the JMD point at which the two calls are meaningfully different to the female and at which the normal whine/chuck is chosen significantly more often than chance. The last proportion (0.10) represents the percentage at which females would chose the normal whine/chuck if it were paired against a whine alone. This is the situation in which the test whine/chuck is not recognized as different from a whine alone.

Iversen (1984) discusses the calculation of Bayesian probabilities for proportions in detail. The calculation is based on Bayes theorem, which states that the joint probability of two occurrences (P and D) is equal to the probability of the first occurrence times the conditional probability of the second occurrence given the first occurrence, or:

$$\text{prob}(PD) = \text{prob}(P) \times \text{prob}(P | D).$$

Bayes theorem can be used to equate the probability that P is the real value of the population given a sample that yields a value of D ($\text{prob}(P | D)$, termed the 'posterior probability') to the product of the probability that P truly is the real value ($\text{prob}(P)$, termed the 'prior probability', and made as an a priori assumption) and the probability of obtaining a sample value of D given a true proportion equal to P ($\text{prob}(D | P)$). If there are several possible population values, each with its own prior probability, from Bayes theorem it can be shown (Iversen 1984) that the probability of any one population value (P_1) given the data value (D) is

$$\text{prob}(P_1|D) = \frac{\text{prob}(D | P_1) \times \text{prob}(P_1)}{\sum(\text{prob}(D | P_i) \times \text{prob}(P_i))}$$

where $\text{prob}(D | P_i)$ is the probability of the sample value (D) given a particular population value (P_i), and $\text{prob}(P_i)$ is again the 'prior probability', or the probability that P_i is the true proportion.

In our analysis, we took the number of females out of 20 that chose the stimulus with the abnormally placed

chuck as the data value (D). We made no assumptions about differential likelihood of particular 'real' proportions and considered each possibility as having an equal prior probability. For the tests of the artificial whine/chuck against the whine, where we considered three alternative explanations for the proportion obtained at each point ($P_1=0.50$, $P_2=0.75$, $P_3=0.90$), the prior probability for each was therefore $\text{prob}(P_i)=0.33$. For the tests of the artificial whine/chuck against the normal whine/chuck sequence, where we considered four alternative explanations for the proportion obtained at each point ($P_1=0.75$, $P_2=0.50$, $P_3=0.25$, $P_4=0.10$), the prior probability for each was therefore $\text{prob}(P_i)=0.25$. Because the data obtained were simple proportions out of 20, the value of $\text{prob}(D | P)$ in each case was obtained from a table of exact binomial probabilities, which lists the probability of r occurrences in N samples given a true probability of p in the population sampled. Using these values, we were able to calculate the Bayesian probabilities for each of the alternative explanations for the observed preferences for each chuck position in a test whine/chuck relative to a whine alone and relative to a normal whine/chuck.

Statistical Analysis: Comparison of Preference Functions

The experimental design produced two preference functions for the two test comparisons, one comparing the whine plus a chuck at various temporal positions relative to a normal whine and one comparing the test whine/chuck combinations to a whine with a normally positioned chuck. The preference functions in each case were expressed as the proportion of choices for each test whine/chuck combination as a function of the temporal position of the chuck.

We compared the two preference functions by making the assumption that the data we obtained for each point on the curves represented some underlying 'real' preference function for the population plus individual variation and other sources of statistical 'noise'. In nonmonotonic curves with multiple peaks and valleys such as the ones we obtained, such 'noise' can render statistical comparisons nonsignificant if it causes a few points on the curves to be abnormally low or high or renders the minima and maxima to be slightly out of phase. To control for this 'noise' in the absence of repeatedly testing new cohorts of 20 animals at each of the comparisons making up the preference function, and thereby to obtain a better idea of the average overall preference function for each test situation, we smoothed each curve using a five-bin rolling average so that the Y value of each point of the preference function equalled the average of the point's value and the values of the two points on either side of it. We then compared equivalent points on the two curves using a Spearman's rank-order correlation.

In a second procedure to compare the curves, we normalized each curve to lie within a range of +1 to -1 around a baseline of 0 on the Y axis and we performed a simple cross-correlation of the curves. This procedure

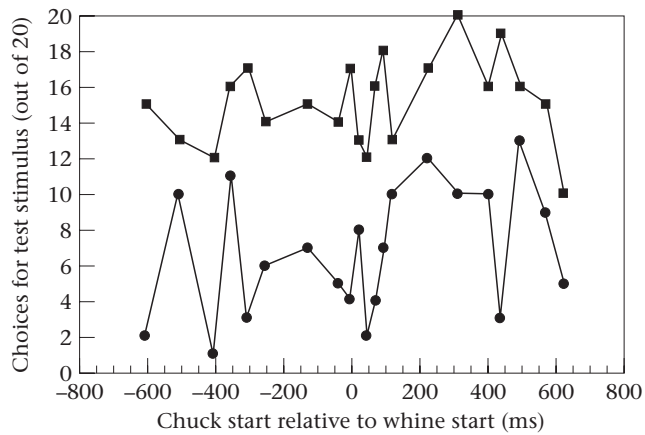


Figure 2. Number of choices (out of 20) made by females for the test stimuli when stimuli were paired against a white (upper line) and against a normal white/chuck (lower line). Test stimuli are defined by the time point at which the chuck begins relative to the beginning of the white with which they were combined.

does not yield a correlation coefficient, but rather simply a secondary function characterized by a peak of a characteristic height related to the similarity of the original functions. We then compared the height of this peak against the outcome of a series of Monte Carlo simulations in which 500 pairs of randomly generated preference functions were similarly normalized, smoothed and cross-correlated with each other. We repeated the 500 pair Monte Carlo runs 10 times. We calculated the average proportion of pairs in each of the Monte Carlo runs in which a cross-correlation peak was equal or greater in size

to the peak found in the cross correlation of the behavioural preference functions. The average proportion for the 10 runs is the probability that a cross-correlation peak of the size we found when comparing the behavioural preference functions would occur by chance. We compared the preference functions in this way to guard against any potential problem associated with applying the probability assumptions underlying normal statistical testing to the comparison of the complex curves representing the behavioural preference functions.

RESULTS

Bayesian Probabilities for Chuck Position Preferences

The proportion of choices for the artificial white/chuck combinations matched against a normal white alone and against a normal white/chuck combination are shown in Fig. 2.

Inspection of the Bayesian probabilities for the choices at each temporal chuck position (Table 1) indicates that a chuck added at nearly any point before, during, or after the white was more likely to be more attractive than a white alone than equally as attractive as a white alone. Exceptions to this were chucks beginning 50 ms into the white, a chuck added 628 ms after the beginning (over 300 ms after the white ended), and a chuck added 400 ms before a white began. In these cases, the white/chuck appeared no different than the white alone. A chuck at +314 ms, which is the position of the normal chuck, resulted in a 20:0 choice for the white/chuck

Table 1. Bayesian probabilities for test stimuli versus white indicating the probability that the stimulus was perceived in one of three possible ways

| Number | Chuck position | | Probability | |
|--------|---------------------------------|---------------|-------------------------|----------------------------|
| | Time relative to start of white | Same as white | 1 JND better than white | Same as normal white/chuck |
| 1 | -600 | 0.06 | 0.81 | 0.13 |
| 2 | -500 | 0.39 | 0.60 | 0.01 |
| 3 | -400 | 0.84 | 0.16 | 0.00 |
| 4 | -350 | 0.02 | 0.67 | 0.31 |
| 5 | -300 | 0.00 | 0.41 | 0.59 |
| 6 | -250 | 0.17 | 0.79 | 0.04 |
| 7 | -125 | 0.06 | 0.81 | 0.13 |
| 8 | -35 | 0.17 | 0.79 | 0.04 |
| 9 | 0 | 0.00 | 0.41 | 0.59 |
| 10 | +25 | 0.39 | 0.60 | 0.01 |
| 11 | +50 | 0.84 | 0.16 | 0.00 |
| 12 | +75 | 0.02 | 0.67 | 0.31 |
| 13 | +100 | 0.00 | 0.19 | 0.81 |
| 14 | +125 | 0.39 | 0.60 | 0.01 |
| 15 | +225 | 0.00 | 0.41 | 0.59 |
| 16 | +314 | 0.00 | 0.03 | 0.97 |
| 17 | +400 | 0.02 | 0.67 | 0.31 |
| 18 | +439 | 0.00 | 0.07 | 0.93 |
| 19 | +500 | 0.02 | 0.67 | 0.31 |
| 20 | +575 | 0.06 | 0.81 | 0.13 |
| 21 | +628 | 0.95 | 0.05 | 0.00 |

Bold face indicates the highest probability among the possible choices. See text for further explanation.

Table 2. Bayesian probabilities for test stimuli versus whine/chuck indicating the probability that the stimulus was perceived in one of four possible ways

| Number | Chuck position | | Probability | | |
|--------|---------------------------------|---------------|------------------------------|----------------------------|-------------------------------|
| | Time relative to start of whine | Same as whine | 1 JND worse than whine/chuck | Same as normal whine/chuck | 1 JND better than whine/chuck |
| 1 | -600 | 0.81 | 0.19 | 0.00 | 0.00 |
| 2 | -500 | 0.00 | 0.05 | 0.90 | 0.05 |
| 3 | -400 | 0.93 | 0.07 | 0.00 | 0.00 |
| 4 | -350 | 0.00 | 0.02 | 0.84 | 0.14 |
| 5 | -300 | 0.58 | 0.41 | 0.01 | 0.00 |
| 6 | -250 | 0.04 | 0.79 | 0.17 | 0.00 |
| 7 | -125 | 0.04 | 0.79 | 0.17 | 0.00 |
| 8 | -35 | 0.01 | 0.60 | 0.39 | 0.00 |
| 9 | 0 | 0.31 | 0.67 | 0.02 | 0.00 |
| 10 | +25 | 0.00 | 0.33 | 0.66 | 0.01 |
| 11 | +50 | 0.81 | 0.19 | 0.00 | 0.00 |
| 12 | +75 | 0.31 | 0.67 | 0.02 | 0.00 |
| 13 | +100 | 0.01 | 0.60 | 0.39 | 0.00 |
| 14 | +125 | 0.00 | 0.05 | 0.90 | 0.05 |
| 15 | +225 | 0.00 | 0.00 | 0.66 | 0.34 |
| 16 | +314 | 0.00 | 0.05 | 0.90 | 0.05 |
| 17 | +404 | 0.00 | 0.05 | 0.90 | 0.05 |
| 18 | +439 | 0.58 | 0.41 | 0.01 | 0.00 |
| 19 | +500 | 0.00 | 0.00 | 0.40 | 0.60 |
| 20 | +575 | 0.00 | 0.14 | 0.84 | 0.02 |
| 21 | +628 | 0.13 | 0.81 | 0.06 | 0.00 |

Bold face indicates the highest probability among the possible choices. See text for further explanation.

combination. This is normal for tests pairing a normal whine/chuck against a normal whine, and the Bayesian analysis indicated a greater than 95% probability that this choice is not different from our estimate of such results from earlier work. Chucks positioned at +439 ms, the position where a third chuck would be added when such calls are made, and one placed within the call 100 ms after the beginning of the whine also were most probably similar to choices for a normal whine/chuck. Chucks placed at 300 ms before a whine, at the beginning of the whine, and 225 ms into the whine (overlapping its low-amplitude end portion) all resulted in 17:3 choices for the test whine/chuck combination. Bayesian probabilities indicate that at this level of preference it is slightly more probable that the test combination was acting like a normal whine/chuck than acting like a stimulus that is a JMD better than a whine alone. However, the probabilities for these two cases are too close to argue either case persuasively. Calls with chucks at most positions preceding the whine were more likely one JMD more attractive than the whine alone but not as attractive as a normal whine/chuck. It is significant that in no case did a whine/chuck combination fare worse than a whine alone. That is, no placement of the chuck, including placements that overlapped any portion of the whine, rendered the whine unrecognizable to females, or made the call aversive to them. The whine/chuck combinations we used were all as attractive or more attractive than a whine alone.

The Bayesian probabilities for the test whine/chucks matched against a normal whine/chuck (Table 2) indicate that no abnormal whine/chuck combination was better

at eliciting female preferences than a normal whine/chuck. A possible exception is a chuck placed 500 ms after a whine, but the probability of this stimulus being better than a normal whine/chuck is not strong, and this conclusion is not consistent with the results of tests versus the whine alone. A test whine/chuck with the chuck at +314 ms, its normal position, of course resulted in a preference equal to a normal whine/chuck, because this provides the female with a choice between two equal stimuli. In addition, most whine/chuck combinations with chucks positioned after the normal chuck position (at +400, +500 and +575 ms), overlapping most of the last part of the whine (at +125 and +225 ms), just into the start of the whine (at +25 ms) or well before the beginning of the whine (at -350 and -500 ms) were most likely no worse than a normal whine/chuck in eliciting female choices. Stimuli with chucks placed from 300 ms before the whine to the beginning of the whine or overlapping the middle of the whine and beginning at +75 or +100 ms were most likely a JMD worse than a whine/chuck, but better than a whine alone. Test stimuli with chucks at +50 and -400 ms were no better than if they had been whines alone paired against a normal whine/chuck. This is consistent with the results in the tests matching the whine/chucks against a whine alone, where test stimuli with chucks in these positions were equal in attractiveness to a whine alone. Chucks at -600, -300 and +439 ms also conveyed no advantage when combined with whines in this test. However, these results are not consistent with the comparisons against the whine alone, and therefore the interpretation of results at these positions is problematic.

In summary, nearly all artificially placed chucks increased the attractiveness of their whines compared with a whine alone, and several placements before or after the normal chuck position made the test stimulus as attractive as a normal whine/chuck. Considering both sets of preference tests leads to the general impression that test stimuli with chucks placed before the whine resulted in a call that was more attractive than a whine alone, but less attractive than a normal whine/chuck, while test stimuli with chucks in a variety of positions after a whine were as attractive as a normal whine/chuck. For those test stimuli in which chucks and whines overlapped in time, stimuli in which the chuck overlapped only the very beginning of the whine or overlapped its middle and end portions were at least more attractive than a whine alone, and possibly as attractive as a normal whine/chuck, while stimuli in which the chuck overlapped the whine starting 25 ms into it were no more attractive than a whine without a chuck.

Comparison of Preference Curves

Running averages that compute means over several consecutive data points provide a smoothed curve representing a simplified view of the general shape of some underlying function. Such curves decrease the height or depth of peaks and troughs where there is considerable variability in the data or where there are several anomalous data points (as in our data for chucks placed before the whine) or where the data change rapidly (as in our data for chucks overlapping the beginning of the whine), while accentuating peaks where values are consistently high over several points (as in our data for chucks placed after the whine). For those reasons, conclusions based on the relative heights of peaks and troughs within curves are problematic. Nevertheless, the smoothed curves do represent the general trends in the raw data presented above. In each case, the smoothed curve indicates an area of elevated preference for chucks starting before the beginning of the whine, where stimuli are more attractive than a whine alone, but not as attractive as a normal whine/chuck, a shallow trough in preference for chucks overlapping the beginning of the whine, where stimuli are not more attractive than a whine alone, and another, higher, preference peak for chucks placed after the whine, where most stimuli are as attractive as a normal whine/chuck until attractiveness begins to fade for chucks placed 500–600 ms after the beginning (and therefore 200–300 ms after the termination) of the whine (Fig. 3). A Spearman rank correlation of the equivalent points in the two functions was significant ($r_s=0.75$, $N=21$, $P<0.0001$), suggesting that the shapes of the preference functions obtained under the different choice conditions did not differ significantly.

A simple cross-correlation between the two smoothed, normalized preference functions resulted in a strong peak, suggesting again that the preference function shapes were similar (Fig. 3). The proportion of 500 randomly generated curves in each of 10 Monte Carlo simulations that resulted in cross-correlation peaks of this size or greater ranged from 0.12 to 0.09. The average

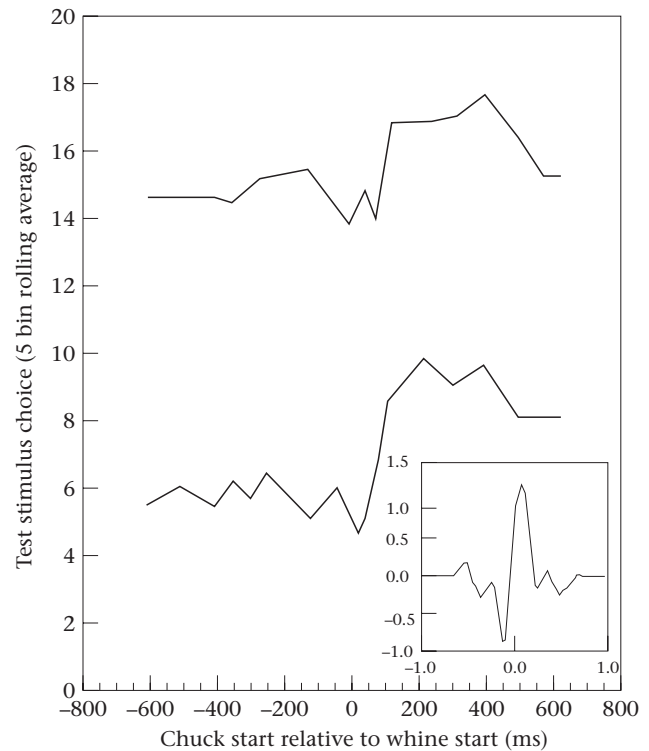


Figure 3. Smoothed preference curves for the test stimuli paired against a whine (upper line) and against a normal whine/chuck (lower line). Curves were prepared from the data plotted in Fig. 2 using a rolling average in which each data point is averaged with the four points around it. Insert shows cross-correlation peak obtained by a simple cross-correlation of the two smoothed curves after normalizing them to the same baseline. The Y axis does not represent a correlation coefficient; rather it denotes the height of the peak in arbitrary units. The X axis denotes the position of the peak within an arbitrary space defined by the length of the two original curves.

\pm SD probability over all 10 Monte Carlo runs was 0.099 ± 0.015 . This suggests that there is less than a 10% probability that the similarity between the experimentally derived preference functions could have arisen by chance.

DISCUSSION

In several species, females have been shown to find attractive male signals with adornments that do not exist in nature (Burley 1985; Ryan & Wagner 1987; Basolo 1990; Ryan & Keddy-Hector 1992; Ryan & Rand 1993a, b; McClintock & Uetz 1996; Jones & Hunter 1998) or with characteristics that exceed those normally produced by males (Morris & Fullard 1978; Pollack & Hoy 1981; Sullivan 1983; Klump & Gerhardt 1987; Ryan & Rand 1990; Ryan & Keddy-Hector 1992). These reports suggest that the stimulus space defining female preferences may far exceed the signals produced by their conspecific males. In previous work, we have shown that the normal spectral characteristics of the male chuck do not uniquely define the preference of the female. Placing a noise burst, a single frequency within the tuning of the basilar papilla,

a chuck without its lower harmonics, or a chuck with only accentuated lower harmonics after a whine makes the whine more attractive to females (Ryan & Rand 1990; Wilczynski et al. 1995). The present results show that the same is true with regard to the placement of the chuck in time relative to the whine. Many positions other than the normal position immediately after the whine make the call more attractive, and some alternative positions that males never produce are as attractive as the normal placement. In both the spectral and temporal domains, male *P. pustulosus* have adopted only one of several possible stimuli that would be attractive to conspecific females. In fact, any number of signals added before or after make the species-specific whine more attractive to female *P. pustulosus* than the whine alone (Ryan & Rand 1990, 1993a, b, in press). Like females, male *P. pustulosus* also show enhanced behavioural responses to natural or artificial signals added to the conspecific whine (Ryan & Rand 1999). Not every sound will enhance the whine, but those that do include not only noise bursts and conspecific chucks, but the acoustic prefixes and suffixes found in other species in this genus and some artificial sounds like whistles in the appropriate frequency range. Given the large array of possible attractive signals, why any particular form or placement of acoustic adornment occurs in any species is unknown. One reason might be constraints on the vocal production system imposed by phylogeny and morphology. Several phenotypes of chuck form and chuck timing might be similarly favoured by selection, but the ancestral condition of the male larynx might make some phenotypes more likely to occur than others. Unfortunately, we know too little about the mechanisms by which anuran larynges produce complex calls like those of *P. pustulosus* to assess this possibility in more detail.

We took the unusual approach of using Bayesian statistics to analyse our results instead of the usual parametric or nonparametric hypothesis testing statistics generally used in studies of animal behaviour. Unlike classical statistical testing, this Bayesian approach does not assign a particular significance level by which to accept or reject any of the hypotheses raised. The probabilities are left to speak for themselves, and therefore each observer of the data is left to decide how to interpret their significance. This introduces some subjectivity into the analysis of experimental results, but note that in classical statistical testing, the decision to accept a particular significance level, for example, 0.01 versus 0.05, as indicating a difference between groups is also a subjective one, as is the interpretation of *P* values such as 0.04 or 0.06. Any potential problem introduced by this subjectivity is offset by the advantage of the Bayesian analysis in allowing us to avoid making simple dichotomous choices when we have no real basis for deciding what the correct comparison should be. It allows us simply to report the probabilities that our data are consistent with any of several hypothetical possibilities. In our study, we examined whether the test stimuli were equivalent to a whine alone, equivalent to a normal whine/chuck, or different from either. This last possibility was represented by the JMD (Nelson & Marler 1990) points; that is, the points at

which the test stimulus was just noticeably different (more or less attractive) than the whine, but not as attractive as a normal whine/chuck. By examining all these possibilities, we can obtain a better picture of the way signal attractiveness changes over the range of stimulus conditions we used.

The analysis reveals some important features of the call recognition and preference system of this species. No placement of a chuck, even one that overlaps the whine, degrades the whine to such an extent that it is unrecognizable to females. At worst, placement of a chuck in an abnormal position renders the combination equivalent to a whine alone. Males may realize no gain in attractiveness when putting a chuck in some of the positions we tested, but in no case would they make their call worse than no chuck at all. This suggests that the fundamental species recognition function of the whine is largely independent of, and not masked by, either the sequential or simultaneous reception of the second call syllable produced in this species. While a chuck does not appear to interfere with the fundamental species recognition function of the whine, the converse does not appear to be true. Chucks that overlap an initial portion of the whine lose the ability to make the whine more attractive. This portion corresponds to a critical area of the whine both necessary and sufficient to stimulate female phonotaxis (Wilczynski et al. 1995). Thus, at the moment when this critical portion of the whine is perceived, the chuck seems to be ignored.

We currently have no data that can determine the mechanism by which this differential interference is achieved. Although the nonlinear peripheral auditory phenomenon of two-tone suppression has been demonstrated in anuran amphibians (Capranica & Moffat 1980; Wilczynski & Capranica 1984) and shown to be important in bullfrog communication (Capranica 1965; Capranica & Moffat 1980), it is unlikely that this mechanism explains our results. Two-tone suppression in amphibians universally results in higher frequencies suppressing responses to lower frequencies, and is restricted to frequency interactions within the amphibian papilla. It is possible that a simple masking phenomenon is responsible for the lack of chuck efficacy when it overlaps the initial portion of the whine. The initial portion is the highest amplitude part of the whine and, by sweeping through frequencies from about 500 to 960 Hz, is the part closest to the tuning of the basilar papilla (ca. 2100 Hz; Ryan et al. 1990), which detects the chuck. Critical ratios and critical band characteristics, which provide an estimate of the width of frequency filters, in different parts of the amphibian auditory system (Ehret & Capranica 1980a, b; Megela & Capranica 1982; Narins 1982; Freedman et al. 1988; Simmons 1988), as well as direct measurements of the bandwidth of amphibian and basilar papilla fibres (Ronken 1991) have shown that critical bands for amphibian papilla fibres in the range of 500–700 Hz are relatively narrow. In contrast, critical bands for the basilar papilla fibres are relatively wide, and at 30 or 40 dB above threshold their bandwidth might encompass frequencies contained in the initial part of the whine. Therefore in principle it is possible that

simultaneous energy in the basilar papilla range (the chuck) and the upper amphibian papilla range (the initial part of the whine) could result in interference of the basilar papilla detection of the chuck by the initial part of the whine, but not interference of the amphibian papilla detection of the initial whine by the higher frequencies of the chuck. However, it is difficult to see how the whine frequencies, which are well away from the centre frequency of basilar papilla fibres, could so effectively mask the chuck without being very much higher in amplitude than the chuck.

An alternative to a masking explanation would be to evoke a higher-order process like attention (Kahneman & Triesman 1984). Such an explanation would postulate that the perceptual systems in these vertebrates have a limited capacity to process streams of information (as proposed for humans: e.g. Triesman 1969; Wickens 1984; Lavie 1995), and that the capacity is not allocated equally among perceptual categories. Once the critical portion of the whine is detected, attention is focused on its processing to the detriment of other signals. Therefore, when the critical initial portion of the whine and chuck overlap, attention is selectively focused on the whine, and the chuck is ignored, eliminating its capacity to enhance the attractiveness of the call. When the two components do not overlap, as when the chuck is either at the beginning or at the end of the whine, attentional competition is not a factor and both call components can be assessed by the frog's call analysis system. Distinguishing between masking and selective attention is impossible given the data we currently have for this system. Manipulations of the relative amplitudes of the whine and chuck, as well as tests of the perception of other stimuli during the critical portion of the whine, would be valuable for exploring the mechanism of this phenomenon.

Females also seemed to disregard chucks placed well before or long after a whine, at least in the tests parring such stimuli against a normal whine. At the repetition rate we used of one call/2 s, calls from alternate speakers followed each other with about a 1-s delay. We did not test females with chucks placed so far in time from whines that they were closer in time to the stimulus coming from the alternate speaker. At the longest displacements, however, chucks approached the midway point between the times the alternate stimuli appeared from the two speakers, and therefore we cannot discount the possibility that at these points females are becoming confused about which whine serves as the reference for the displaced chuck. The fact that the results were inconsistent for some of the extreme chuck placements (e.g. -300 and -600 ms) in the tests versus a whine compared to those versus a whine/chuck may have been caused by varying degrees of such confusion among females. The ability of chucks displaced well beyond the times tested here might also enhance the attractiveness of whines if such confusion were eliminated.

Viewing the results across all chuck positions in graphic form (Fig. 2) reveals substantial variation among adjacent points at some points in the preference function. One possible reason for this variation is that there are differences among females in the strength of their preferences

or their tolerance for unusually extreme signals. As different groups of females were tested at each chuck position, this could induce more, unpredictable measurement error at some points more than others. Another possible reason is that there may be inconsistency within females in the expression of their preferences, which we would not be able to correct because we tested each female only once at a chuck position. Although the extent of variation among females has not been examined systematically, Kime et al. (1998) did show that female *P. pustulosus* do not show 100% consistency in their responses in a similar set of behavioural tests in which they were tested repeatedly, but rather respond in a probabilistic manner. The large number of tests we performed precluded our obtaining multiple replicates for each chuck position with different cohorts of females to compensate for these potential sources of statistical variation, and therefore we used an averaging technique instead. The similarity in preference functions we obtained after this for both the comparisons of test stimuli against a normal whine and against a normal whine/chuck indicate a bimodal preference function inherent to the call analysis system of this species which dictates how acoustic adornments must be placed for them to be effective. The function indicates that chucks placed either after or before the whine serve to make the call most attractive. The test situation may change the baseline of the preference function, but not its shape. It is not surprising that a chuck placed in or immediately around its usual position would enhance a call, but it is surprising that the position immediately before the beginning of the whine is also attractive. This part of the preference function is not exploited by *P. pustulosus* males, but it is interesting to note that one *Physalaemus* species, *P. pustulatus*, produces an additional call component before, rather than after, the whine (Ryan & Rand 1993a, b). Female *P. pustulosus* prefer a conspecific whine to which the *pustulatus* prefix has been appended when it is matched against their conspecific whine (Ryan & Rand 1993a, b). In addition, there is no significant difference in attraction to the *pustulatus* prefix+whine versus the whine+*pustulosus* chuck (Ryan & Rand, in press). It may be that placement in one position has no advantage over the other, but, once a position is adopted, vocal mechanics or features of the vocal control system limit the ability to switch to the alternate position.

No *Physalaemus* species places an additional component overlapping the whine. At least part of the reason may be that the vocal system constrains the ability to produce overlapping sounds. Even if this were not the case, the preference function indicates that overlapping additional call components with the whine would either produce no benefit (if it overlaps the critical whine portion) or would provide a suboptimal benefit relative to a placement after the whine. This presumes that a similar preference function occurs in other species in this genus; it would be very interesting to examine whether this is true. It would also be important to examine whether bimodal preference functions for acoustic adornments are present in species that produce no additional call components. We have demonstrated previously that female

P. coloradorum, a species that produces only a whine, find a whine with a *P. pustulosus* chuck appended to it more attractive than their own whine alone (Ryan et al. 1990; Ryan & Rand 1993a). Whether they would find chucks in other positions attractive remains to be investigated.

Data from this species complex suggest that female preference functions exceed the limited vocal repertoire of their conspecific males (Ryan & Rand 1993a; Kime et al. 1998). Furthermore, those acoustic adornments that do exist naturally among the species of this genus fit the predictions of the preference function we describe here for *P. pustulosus* females. It may be that within each *Physalaemus* species, males evolve calls that exploit one small part of a standard array of potential female preferences. Comparing the variation in both calls and preference functions across species, and examining the covariation of calls and preference functions within species, would provide further insights into the nature of sexual selection and the evolution of communications systems.

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