



Evoked vocal response in male túngara frogs: pre-existing biases in male responses?

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ABSTRACT

Female túngara frogs, *Physalaemus pustulosus*, are preferentially attracted to a whine-chuck advertisement call over a simple whine (Rand & Ryan 1981, *Zeitschrift für Tierpsychologie*, **57**, 209–214). Females also show phonotactic preferences for the whine when a number of other heterospecific or artificial stimuli are added to it, and these calls tend to be as attractive to females as a whine-chuck (Ryan & Rand 1990, *Evolution*, **44**, 305–314). We tested male túngara frogs with the same suite of stimuli using evoked vocal responses as a bioassay to examine sexual differences in responses to signal variation. A whine-chuck elicited greater responses from males than a whine-only. Artificial and heterospecific stimuli that enhanced call attractiveness to females also elicited greater vocal responses from males and, as with females, the effects of these stimuli were similar to that of the whine-chuck. Thus, in both sexes there are pre-existing biases for a suite of stimuli not produced by conspecifics.

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For communication systems to function efficiently there must be some congruence or match between the signal and the receiver. Such patterns of congruence could lead to the impression that the response characteristics of the receiver always map tightly onto appropriate signal variation. We know, however, that this need not be the case. Stimuli that are not present in the conspecific signal repertoire can elicit responses from receivers. Response to such signals is most clearly demonstrated by supernormal stimuli, signals that are exaggerated in form relative to the typical signal and elicit enhanced responses from receivers (Tinbergen 1948). Many sexual communication systems are characterized by responses (female mate attraction) to seemingly exaggerated signals (male sexual displays), and there is considerable interest in how such systems came to be (Darwin 1871; Andersson 1994).

The fact that there can be preferences for supernormal stimuli has important implications for the evolution of communication systems. When communication systems evolve, as in the evolution of more elaborate signals and preference for such signals during sexual selection, there are several possible sequences of evolutionary change in signal and receiver. Signals and receivers can evolve in

concert such that a change in signal form, such as a longer tail, is immediately matched by a change in the preference for that signal form, a preference for the longer tail. Such patterns of a tightly coordinated coevolution of signal and receiver are predicted by two hypotheses for the evolution of female preferences under sexual selection. In both runaway sexual selection and preference for good genes, the signal trait and the preference are genetically correlated such that an evolutionary change in the trait necessarily results in an evolutionary change in the preference (Kirkpatrick & Ryan 1991; Andersson 1994; Ryan 1997). Alternatively, there can be preferences, such as those for supernormal stimuli, that are referred to as 'hidden' or 'pre-existing' because they exist even though the corresponding stimulus that elicits them does not (Basolo 1990a; Endler 1992; Enquist & Arak 1993). Thus in some cases when a male signal form evolves, such as the lengthening of a tail, there already exists a female preference that will favour the newly evolved male trait, as in a response to a supernormal stimulus. The process in which new signals evolve, because they are favoured by such pre-existing or hidden preferences, is referred to as sensory exploitation (Ryan 1990, 1997; Ryan et al. 1990; Shaw 1995). Runaway, good genes and sensory exploitation can all contribute to the evolution of traits and preferences in the same evolutionary lineage, sequentially or simultaneously, often making it difficult to assign primacy to any single cause (Ryan 1997).

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A number of empirical (N. Burley, unpublished data cited in Trivers 1985; Basolo 1990a,b, 1995a,b; Ryan & Rand 1990, 1993a,b; Searcy 1992; Christy 1995; McClintock & Uetz 1996) and artificial neural network studies (Enquist & Arak 1993, 1994; Johnstone 1994; Phelps & Ryan 1998, unpublished data) have revealed pre-existing or hidden biases for signal variants not displayed by conspecifics, or not present in the training regime in neural network studies. These pre-existing preferences are not merely preferences for signals of greater quantity but can be for new forms of signals as well (e.g. the addition of a sword to a fish's caudal fin or a new syllable to a frog's call). In some of these studies pre-existing preferences are thought to have driven the evolution of sexually selected traits in males, that is, male traits evolved by sensory exploitation.

Although the interest in signal-receiver systems in sexual selection has focused on female choice and male traits, many of these communication systems involve a signal, in one or both sexes, that elicits responses from males as well as females (e.g. Jones & Hunter 1993; Morris & Ryan 1996). The female response to these signals is usually manifest in mate attraction, while the male response often involves some escalation or assessment in male-male competition. Although males and females can respond to the same signals, they might respond differently to signal variation. Selection could favour differences in how responses of the sexes change with stimulus variation if the sexes differ in the costs and benefits of making certain kinds of discrimination errors (Wiley 1994). Such sexual differences have been demonstrated, although the role of selection is merely speculative (e.g. Burley 1985; Searcy & Brenowitz 1988; Metz & Weatherhead 1991; Morris & Ryan 1996; M. D. Hauser, P. MacNeilage & M. Ware, unpublished data).

It is possible that the sexes harbour differences in pre-existing signal biases that influence the communication system's potential for evolution, especially in cases in which the responses to variation in the same signal could have different fitness consequences for the two sexes. In this study we investigate potential sexual differences in these pre-existing biases.

The System

We have been studying sexual communication in a group of frogs, the túngara frog, *Physalaemus pustulosus*, and its close relatives. The main component of the advertisement call in these species is a whine-like frequency sweep. Túngara frog males can supplement the whine with a suffix, the chuck. Such additions elicit behavioural responses in both sexes: preferential phonotaxis in females, and an increased number of chucks in vocally interacting males. Thus, the chuck is a signal that is part of a communication triad, as it influences the behaviour of both the female and male receivers (Rand & Ryan 1981; Ryan 1985).

Female preference for chucks added to the whine is also displayed by another species, *P. coloradorum*, whose males lack chucks (Ryan & Rand 1993a,b). Phylogenetic reconstruction suggests that the preference for chucks shared

by both *P. pustulosus* and *P. coloradorum* existed prior to the evolution of the chuck. We interpret this shared preference as evidence for sensory exploitation (Ryan et al. 1990; Ryan & Rand 1993a,b; Ryan 1996). The enhanced attractiveness that results from adding a chuck to the whine of *P. pustulosus* can also be elicited by a variety of other stimuli, including a white-noise suffix (Ryan & Rand 1990), the amplitude-modulated prefix of the call of *P. pustulatus* (Ryan & Rand 1993a,b), and the squawk-like suffix of the call of *P. freibergi* (this is a tentative identification of a taxon formerly referred to as *P. petersi*; Cannatella et al. 1998). The prefix of the *P. pustulatus* call is present in all calls produced, and is not added facultatively. The suffix of the *P. freibergi* call, the squawk, might have a similar function to the *P. pustulosus* chuck. *Physalaemus freibergi* males often call without the suffix, and it is our impression from tapes we have analysed that the suffix is more likely to be added during male vocal interactions. There have been no experimental studies, however, of how the squawk mediates male vocal interactions or of its salience as a stimulus in attracting females. Not only can the prefix, squawk, and white noise enhance the attractiveness of the whine, they are equally attractive as a whine-chuck, as is a prefix-whine-chuck (Ryan & Rand, in press). Thus the pre-existing preference for the chuck appears to be a preference much broader than the chuck per se; rather, the chuck appears to be one of a number of stimuli that can elicit this female preference as well as a chuck.

In this study, we determine whether stimuli that enhance female responsiveness to the whine influence the male in an analogous manner. We used evoked male vocalizations as a bioassay to determine whether male túngara frogs would also display enhanced responsiveness to artificial signals that enhance call attractiveness to females.

METHODS

Test Subjects

We collected male túngara frogs in Gamboa, Panama near the laboratory facilities of the Smithsonian Tropical Research Institute. We maintained the males for several days under a natural light:dark cycle and temperature regime. We returned the males to the breeding site when testing was completed. Prior to testing each night, between 1900 and 2400 hours, we placed individual males in plastic bags approximately 4 litres in volume that were filled to about one-quarter depth with water. Males were able to call from the small volume of water that formed in the bottom of the plastic bags. Broadcast and recording of calls through the bags suggested they were almost acoustically transparent, as there was minimal acoustical distortion. The same was true for the burlap walls of the compartments (see below).

We placed individual males, each in a plastic bag, in one of eight neighbouring compartments. Each compartment had two long sides of foam and the top and two short sides were burlap; the bottom was a Formica table top. In 1995, we placed a Mineroff speaker in front of the

burlap barrier at the entrance to the male's compartment, and placed a small lapel microphone (Radio Shack) over the male on top of the burlap (in 1996 each compartment was equipped with a speaker and microphone). We used the lapel microphone and a Marantz PMD 420 tape recorder to record the males' responses during the experiments. We counted the number of whines and chucks produced by the male at a later time; whines and chucks are unambiguous. Once the speaker and microphone were in place, we stimulated the males with a continuous tape of a small chorus.

When a male called in response to the chorus, we began preparations for testing. We tested males singly. If another male began to call, we slightly nudged his bag with a long stick, causing the male to immediately cease calling. We presented the test male with the test series (i.e. 60-s control stimulus, 60-s silence, 60-s experimental stimulus, 60-s silence, 60-s control stimulus; see below). If the male did not vocalize during the first 60 s of stimulus presentation (30 calls), which was the conspecific call, we aborted the test. This allowed us to screen for males that were not responsive to the conspecific call at that time. Most males responded in most experiments. Upon the completion of one test a male was required to resume calling, either spontaneously or in response to the chorus tape, before the next test series was initiated. Each male was tested with all test stimuli or until he no longer responded. Ten males were tested in each experiment, 12 different experiments were conducted, and 26 different males contributed to the data set. The use of males in several experiments does not violate statistical assumptions of data independence. The statistical analysis for each experiment assumes that the data are independent of one another, not that they are independent of other experiments that are analysed separately. Furthermore, we interpret the results from each experiment separately and did not combine data to test for any overall pattern.

We varied the order in which males were tested in experiments to mitigate the influence of any order effects (e.g. whether males habituated across experiments; but see below). Furthermore, we compared the male's responses to the experimental stimulus with his response to the control stimulus during the same experiment, thus further controlling for any effects of decreased calling across experiments. There was no significant difference in the male responsiveness across experiments. In 1995, there was no significant difference in the number of whines (Kruskal–Wallis statistic=3.3, $P=0.65$) or the number of chucks (Kruskal–Wallis statistic=3.2, $P=0.66$) produced in response to the control stimulus in each of the six experiments. In 1996, there also was no significant difference in the number of whines (Kruskal–Wallis statistic=10.1, $P=0.12$) or the number of chucks (Kruskal–Wallis statistic=2.9, $P=0.83$) produced in response to the control stimulus in each of the six experiments

Stimuli

In 1995, we recorded the stimuli from an Amiga 2000 to cassette tapes using the software Future Sound. The stimuli were recorded at a rate of one call per 2 s, thus 30

calls for the 60-s period. Our experience with this communication system suggested 60 s was within the range of natural calling interactions among pairs of males. We scaled the whines in the control and experimental stimuli to the same peak amplitude, while we scaled the peak amplitude of components added to the whine to twice the whine's peak amplitude; this is the average relative amplitude relationship between the whine and chuck in nature (Ryan & Rand 1990). In 1996, we presented the same stimuli with a Gateway notebook computer and the software Signal (Beeman 1996).

Stimuli were broadcast with a Marantz PMD 420 tape recorder or a computer and Mineroff amplifier-speaker. We presented the stimuli such that the amplitude of the whine at the male was 82 dB SPL (re 20 μ Pa) measured by a General Radio (model 1982) sound pressure level meter using flat weighting, and digitally capturing the maximum amplitude. During stimulus presentation, the speaker was approximately 0.5 m from the male.

Prior to beginning the test, we broadcast two or three whines to verify that the broadcast-recording system was operating properly; this was followed by 1 min of silence. The test series consisted of a control stimulus, which was either the synthetic whine or whine-chuck we have used in our female phonotaxis studies (Fig. 1; Ryan & Rand 1993a,b, 1995, in press), and the experimental stimuli, which are detailed below. A test series consisted of: 60-s control stimulus, 60 s of silence, 60-s experimental stimulus, 60 s of silence, 60-s control stimulus.

The following experimental stimuli were used in the experiments (Fig. 1).

Chuck-whine: the standard synthetic whine used in the control with a synthetic chuck appended as a prefix.

Chuck: a chuck only.

Prefix-whine: the prefix from a natural call of *P. pustulatus* preceding the synthetic whine.

Whine-prefix: the synthetic whine followed by the prefix of a *P. pustulatus* call.

Whine-squawk: the synthetic whine followed by the suffix from a natural call of *P. freibergi*.

Whine-noise: the whine followed by white noise in the time and amplitude envelope of the chuck.

Prefix-whine-chuck: the *P. pustulatus* prefix followed by the synthetic *P. pustulosus* whine and chuck.

All of the experimental stimuli, including the standard whine, are the same stimuli used in previous female phonotaxis studies (Ryan & Rand 1990, 1993a,b, 1995, in press).

Male-evoked Vocal Responses

We conducted a total of 12 experiments, and tested 10 males in each test series. We quantified the number of calls and the number of chucks produced during each of the stimulus presentations for each test series. We averaged the numbers of calls and chucks in response to the two control stimulus presentations, one which preceded and one which followed the presentation of the experimental stimulus. Having the experimental stimulus bracketed by two presentations of the control stimulus controlled for temporal variation in male motivation

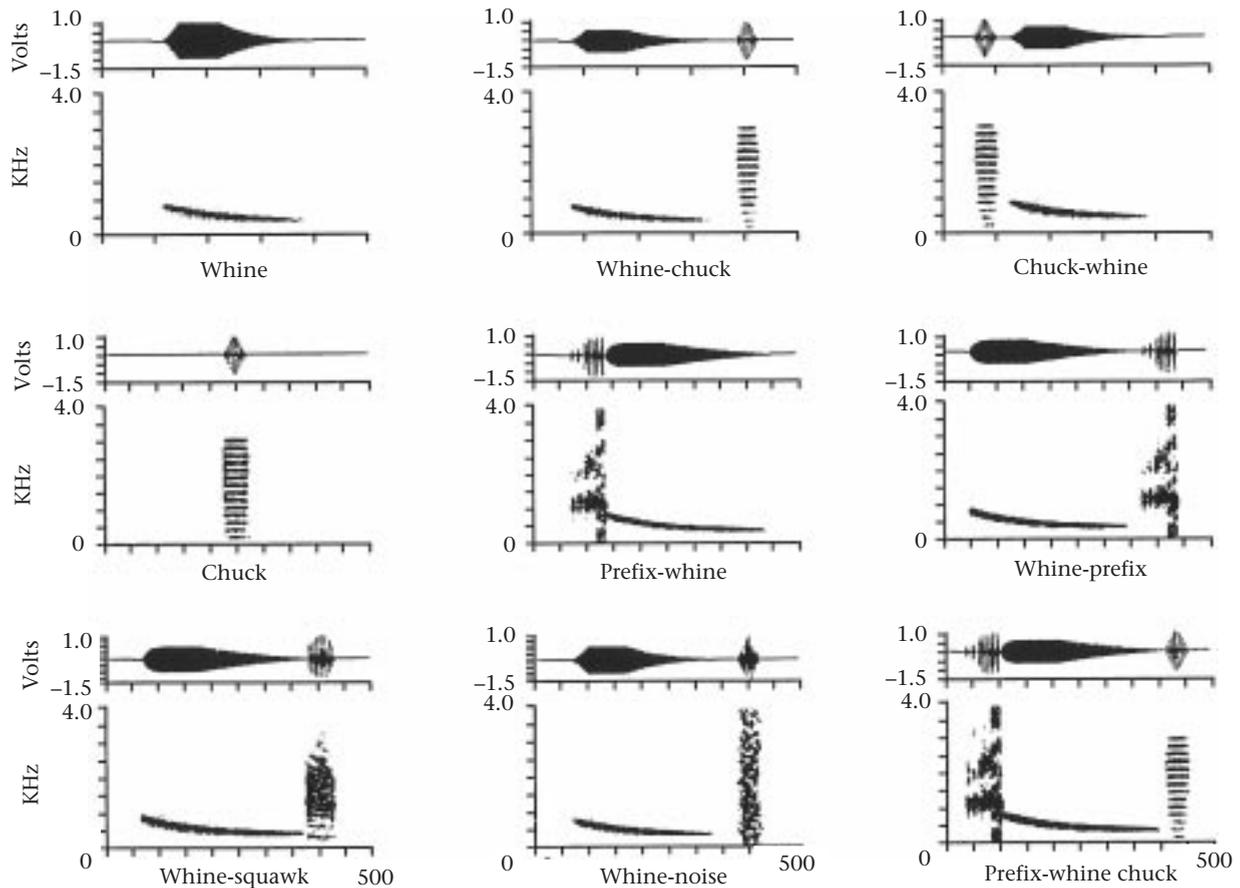


Figure 1. Stimuli used to evoke vocalizations from male túngara frogs. For each stimulus an oscillogram (top) and sonogram (bottom) are shown.

during the test. We compared the (average) numbers of calls and chucks in response to the control stimulus with the responses to the experimental stimulus with a paired *t* test.

RESULTS

The first group of experiments determined how males responded to conspecific chucks. Although some of these experiments had been conducted previously using somewhat different experimental methods (Rand & Ryan 1981; Ryan 1985), we felt it was necessary to repeat them here to validate this experimental method.

The whine-chuck evoked greater vocal responses from males when compared with a whine-only. Males produced both more whines ($t_9=3.932$, $P=0.003$; Fig. 2a) and more chucks ($t_9=4.88$, $P=0.001$; Fig. 2a) in response to the more complex call. The chuck produced by itself, however, did not elicit significantly more whines ($t_9=0.69$, $P=0.516$; Fig. 2a) and elicited significantly fewer chucks ($t_9=2.33$, $P=0.040$; Fig. 2a) than the control whine. Chuck position relative to the whine was important; the chuck-whine did not significantly increase male responsiveness relative to the whine-only in measures of both whines ($t_9=1.33$, $P=0.217$; Fig. 2a) and chucks ($t_9=1.45$, $P=0.186$; Fig. 2a). The chuck-whine and whine-

chuck, however, were nearly equally effective in evoking calls: whines ($t_9=0.082$, $P=0.936$; Fig. 2b), chucks ($t_9=1.05$, $P=0.322$; Fig. 2b). When the probability levels were adjusted by a Bonferroni procedure to $P=0.012$ to control for experiment-wide error, only one of the previously statistically significant results changed: the chuck-only no longer elicited significantly fewer chucks than the natural call.

The second group of experiments determined whether the additions to the whine that increased call attractiveness to females also evoked more complex calls (i.e. more chucks) from males, if not necessarily more total calls (i.e. more whines). Males produced more whines ($t_9=3.71$, $P=0.005$; Fig. 3) and more chucks ($t_9=3.40$, $P=0.008$; Fig. 3) in response to the whine-noise stimulus than to the control whine. The prefix-whine tended to evoke more chucks ($t_9=2.13$, $P=0.060$; Fig. 3) but not more whines ($t_9=1.66$, $P=0.132$; Fig. 3) than the control. A whine-squawk evoked both more whines ($t_9=2.79$, $P=0.021$; Fig. 3) and chucks ($t_9=3.40$, $P=0.008$; Fig. 3). Bonferroni adjustment of the probability levels in this set of experiments had little effect on the results. The number of whines evoked by the whine-squawk was not statistically significant at the adjusted level of $P=0.016$.

The first two sets of experiments showed that, as with females, a complex call elicited greater responsiveness

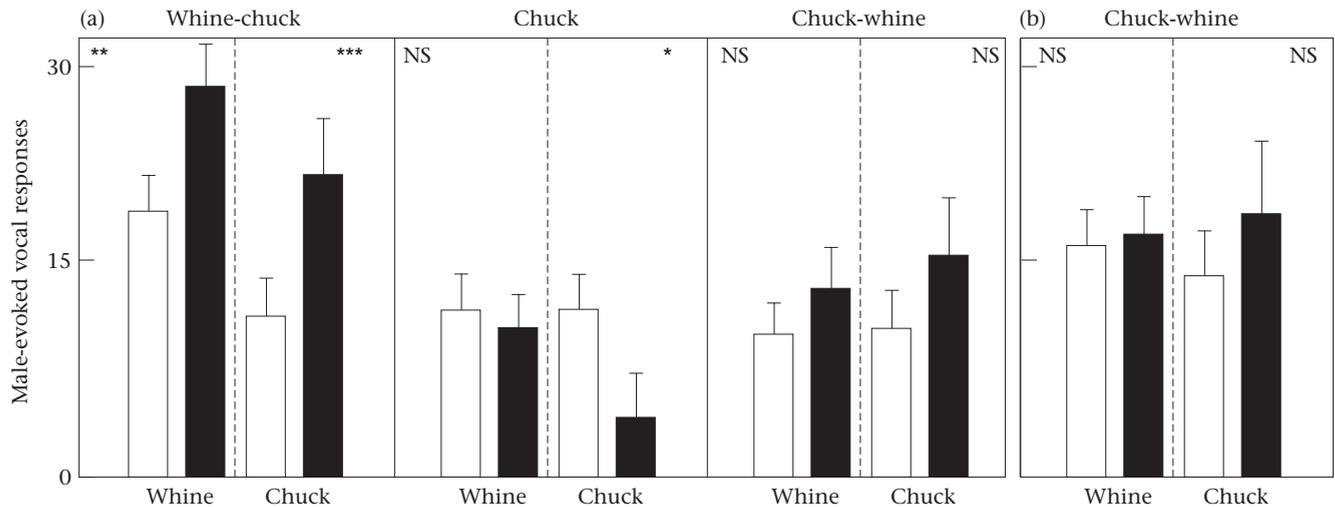


Figure 2. The average (+SE) number of whines and chucks evoked by the control (□) and experimental (■) stimuli. In (a), the control stimulus was the whine, and in (b), the control stimulus was the whine-chuck. The sample size in all experiments was 10. NS, $P>0.10$; * $P<0.05$; ** $P<0.01$; *** $P<0.001$.

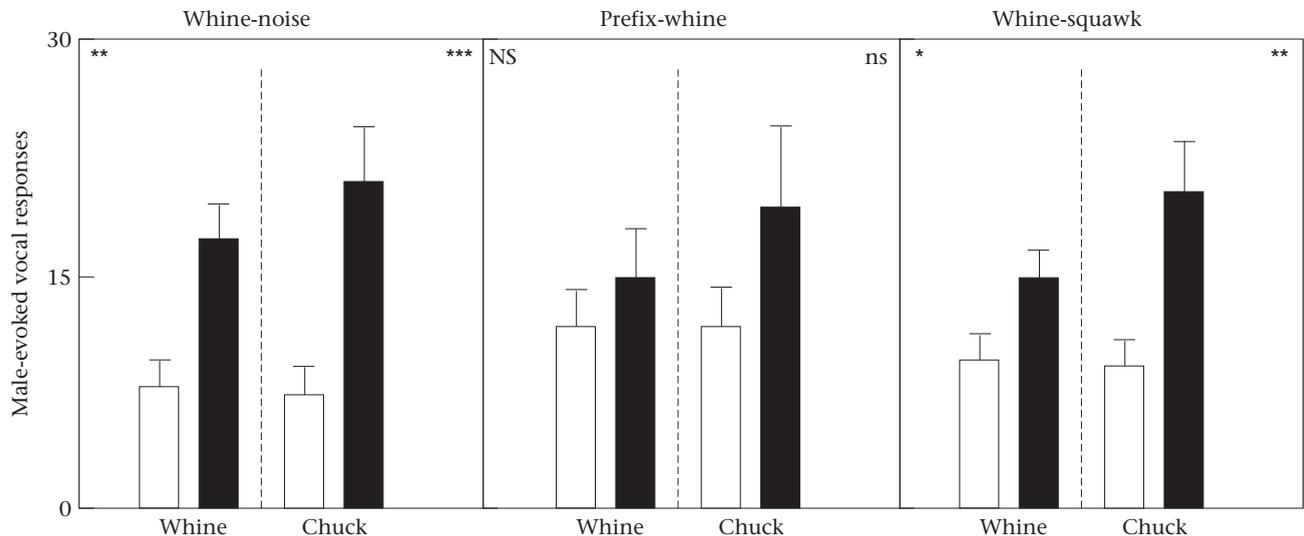


Figure 3. The average (+SE) number of whines and chucks evoked by the control (□) and experimental (■) stimuli. The control stimulus was the whine, and the sample size for each experiment was 10. NS, $P>0.10$; ns, $0.05<P<0.10$; * $P<0.05$; ** $P<0.01$; *** $P<0.001$.

from a male than did a simple call, and this effect could be mimicked by other stimuli that preceded or followed the whine. In the third set of experiments, we asked if the effect of these stimuli was similar to that of the conspecific complex call. We tested the same set of stimuli in the second set of experiments as in this third set, but the control was a whine-chuck instead of a whine. In all cases, the experimental and the control stimuli did not significantly differ in the number of whine and chucks that they evoked. The whine-noise evoked a similar number of calls as did the whine-chuck: evoked whines ($t_9 = -0.382$, $P=0.712$; Fig. 4), evoked chucks ($t_9 = -0.59$, $P=0.572$; Fig. 4). The prefix-whine evoked an almost identical number of whines ($t_9=0.035$, $P=0.737$; Fig. 4) and chucks ($t_9=0.93$, $P=0.376$; Fig. 4) as did the whine-chuck. Switching this prefix to a suffix, the whine-prefix

yielded similar results: there were no significant differences in the number of evoked whines ($t_9=0.22$, $P=0.832$; Fig. 4) or chucks ($t_9=0.39$, $P=0.709$; Fig. 4). The whine-squawk was also as similarly effective as the whine-chuck in eliciting vocalizations: evoked whines ($t_9 = -0.79$, $P=0.451$; Fig. 4), evoked chucks ($t_9=0.82$, $P=0.436$; Fig. 4).

Finally, we asked whether a combination of a prefix and a chuck would act as a supernormal stimulus relative to the whine-chuck. The prefix-whine-chuck did not elicit significantly more whines ($t_9 = -0.28$, $P=0.788$; Fig. 4) than the whine-chuck, but it did show a tendency towards eliciting more chucks ($t_9=2.21$, $P=0.059$). This trend exhibited by evoked chucks, however, was less impressive after the P level for a statistically significant difference was adjusted to 0.01. The Bonferroni

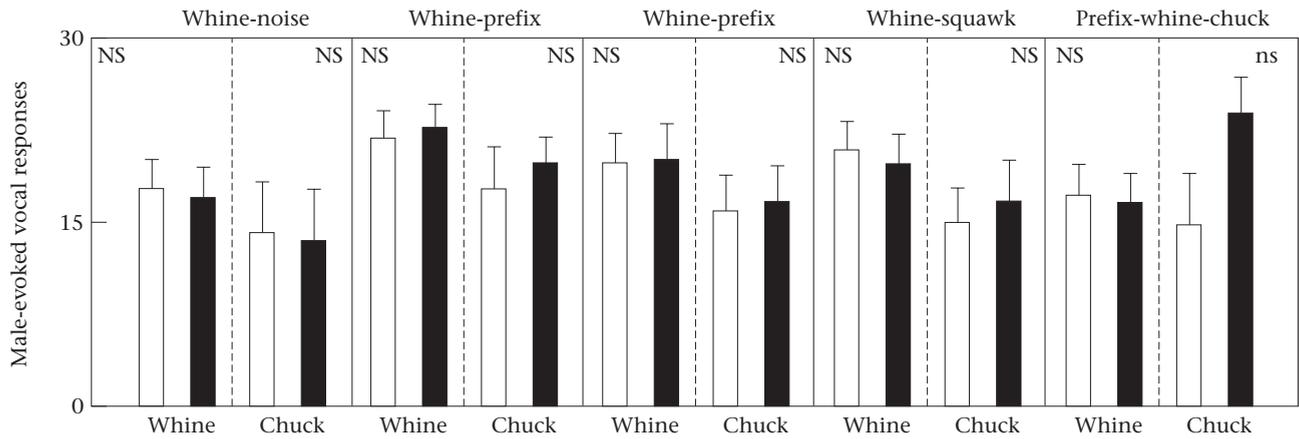


Figure 4. The average (+SE) number of whines and chucks evoked by the control (□) and experimental (■) stimuli. The control stimulus was the whine-chuck, and the sample size for each experiment was 10. NS, $P > 0.10$; ns, $0.05 < P < 0.10$; * $P < 0.05$; ** $P < 0.01$; *** $P < 0.001$.

adjustment made the other statistically nonsignificant results only more so.

DISCUSSION

The male túngara frogs' responses to a variety of stimuli added to the conspecific whine tends to parallel that of females. We discuss the implication of these results for the evolution of sexually selected signals, and compare these results to other studies of sexual differences in other communication systems.

'Pre-existing Preferences' in Male and Female Túngara Frogs and the Evolution of Complex Calls

The male's evoked vocal response to pairs of acoustic stimuli each presented in groups sequentially was similar to the female's phonotactic responses to the same pairs of signals presented alternately. The number of chucks evoked from the male was more sensitive to stimulus variation than was the number of whines. For a given pair of calls, if females had shown a preference in previous studies, the preferred call usually evoked more chucks from males in this study.

First, we review these parallels between the sexes relative to the addition of the naturally occurring conspecific call component, the chuck. A chuck-only does not elicit phonotaxis from females when compared to a whine (Ryan 1985), and in this study it did not evoke greater vocal responsiveness from males. Both this study and previous ones demonstrate that a whine-chuck evokes greater vocal responsiveness from males than does a simple whine (Rand & Ryan 1981), and females prefer a whine-chuck to a whine (Rand & Ryan 1981; Ryan 1985; Ryan & Rand 1990). A previous study showed that neither females nor males respond differentially to a whine-chuck versus chuck-whine (Ryan 1985). The present study is consistent with those. There was a nonsignificant trend for the chuck-whine to evoke more calls ($P = 0.217$) and more chucks ($P = 0.186$) than the whine-only, while unpublished data show a similar nonsignificant trend in

female preferences (14 choices for the chuck-whine versus six choices for the whine, exact binomial probability test, $P = 0.074$).

Male vocal responsiveness and female phonotaxis are also influenced similarly by adding artificial and heterospecific components to the whine. Addition to the whine of a white-noise stimulus that is of the same amplitude envelope as the chuck increases the call's attractiveness to females (Ryan & Rand 1990), and in this study it increased the vocal responsiveness of the male. Increased responsiveness is also apparent in the two heterospecific stimuli tested; addition of the squawk of *P. freibergi* as a suffix, or the amplitude-modulated component of the *P. pustulatus* call as a prefix increased call attractiveness to females in previous studies (Ryan & Rand 1993a,b, in press). These stimuli evoked greater vocal responses from males in this study, although the effect of the prefix was not statistically significant. The male response patterns also show that the alternative stimuli elicit responsiveness similar to that of the whine-chuck, as is it does in females (Ryan & Rand, in press). For both sexes, this was also true if a whine-chuck was contrasted with a prefix-whine-chuck, which resulted from our attempt to construct a supernormal call (this study; Ryan & Rand, in press).

These results show that in both male and female túngara frogs, a variety of stimuli elicit enhanced responsiveness when added to the conspecific whine. Thus, males display a phenomenon similar to the 'hidden' or 'pre-existing preferences' we have shown in female túngara frogs (e.g. Ryan & Rand 1990, 1993a,b, in press; Ryan et al. 1990). Not only will other stimuli that adorn a whine increase male and female responses relative to an unadorned whine, these adornments are often as effective as the conspecific chuck. We conclude, therefore, that both sexes have a bias towards enhanced response to call complexity that is more general than response towards the whine plus chucks. These response biases might have driven the evolution of the call complexity series in túngara frogs, but these response biases did not favour the chuck per se; it appears that there is nothing superior about the chuck relative to some other stimuli except,

perhaps, that the chuck evolved first. Thus, we suggest that the response biases of the auditory system, including peripheral and central processes, might explain the evolution of complex calls in general, but the details of the male vocal morphology might explain why túngara frogs evolved this specific type of call complexity.

The purpose of this study was not to explicitly define the range of acoustic stimuli that when added to the whine, elicit increased number of calls, and especially increased number of chucks from the male. The addition of all of these stimuli used in these experiments lengthen the signal but do so in quite different ways. Thus the observation that signal length might be a critical factor is not instructive. The question is in what ways can the signal be lengthened to increase male responsiveness. For example, merely 'stretching' the whine is unlikely to influence the male because there is so little energy in the last 50 ms; removing this section from the whine does not influence female phonotaxis (Wilczynski et al. 1995). Furthermore, the addition of chucks that overlap the whine, and thus do not increase signal length, still increase the attractiveness of the call to females (Ryan & Rand 1990). This study is our first attempt to compare the responses of the sexes of túngara frogs to the same signal variation. Future studies will continue to compare male responses to the rather large data set we have already accumulated on female call preferences with an aim toward documenting similarities and differences between the sexes in signals that elicit enhanced behavioural responses, and also to determine to what degree the underlying mechanisms mediating such responses are similar.

Sexual Dimorphism in Response to Sexual Signals

In contrast to this study, others have shown significant differences between the sexes in responses to sexual signals. For example, Narins & Capranica (1976) showed that males and females were differentially responsive to the 'co' and 'qui' notes in the advertisement call of the coqui frog, *Eleutherodactylus coqui*, and Searcy & Brenowitz (1988) demonstrated that male red-winged blackbirds, *Agelaius phoeniceus*, were more responsive to environmentally degraded songs than were their female counterparts. M. D. Hauser, P. MacNeilage & M. Ware (unpublished data) also showed differences in the responsiveness of the sexes. Male rhesus macaques produce copulation calls. Hauser et al. used a habituation-dishabituation paradigm to test for just meaningful differences among calls. Females had a longer time to habituation and were more likely to dishabituate in response to presentation of a call of another individual.

There is evidence of sexual differences in pre-existing biases for artificial traits. In male red-winged blackbirds, which have red epaulets, the addition of red leg bands elicits heightened aggressive responses from other males (Metz & Weatherhead 1991), but there is no evidence that females attend to the naturally occurring red signal (e.g. Smith 1972), and thus might be expected to ignore red leg bands as well. Burley (1985) noted sexual differences in preference for leg-band colours in zebra finches,

Taeniopygia guttata. In a more recent study, Morris & Ryan (1996) showed sexual differences in response to signals absent in conspecifics in the swordtail fish *Xiphophorus nigrensis*. Males in this species lack the vertical bars that are present in their sister species, *X. multilineatus*. Nevertheless, female *X. nigrensis* are more attracted to males with bars added, as are female *X. multilineatus*, while male *X. nigrensis*, unlike males of the sister species, do not respond to the presence of bars in male-male aggressive encounters. The bioassays in these last two studies were similar to ours: aggressive responses in males and mating responses in females.

The motivating interest in sexual selection is understanding sexual dimorphism. Most studies have addressed sexual dimorphisms in signal traits, asking why males are more elaborate and extreme in these traits than are females. Studies of female mating preferences and the perceptual mechanisms underlying these preferences have increased our understanding of how female preferences can result in the evolution of these sexual dimorphisms in morphology (Andersson 1994; Ryan 1994, 1997). We suggest that another fruitful avenue of investigation is understanding potential sexual differences in perception that results from the action of sexual selection (cf. Jacobs 1996). To what extent do males and females perceive their social environments in the same way and, when they exist, how do perceptual differences between the sexes influence sexual selection?

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