

Signal Redundancy and Receiver Permissiveness in Acoustic Mate Recognition by the Túngara Frog, *Physalaemus pustulosus*¹

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SYNOPSIS. The túngara frog has an advertisement call with two structurally and functionally distinct components: the whine is both necessary and sufficient for species recognition, and addition of chucks further enhances call attractiveness. Only the fundamental frequency of the whine contributes to phonotaxis; the upper harmonics play no role. Furthermore, only a small portion of the whine, within the first 0–100 msec, is necessary to elicit phonotaxis; there is some redundancy since either the 0–50 msec or the 50–100 msec portion elicits a response. Most of the remainder of the whine's fundamental further enhances call attractiveness. Only the amphibian papilla in the peripheral auditory system is involved in decoding the whine. In stark contrast, several chuck variants, which stimulate either the amphibian papilla or the basilar papilla, and white noise are as effective in enhancing call attractiveness as is the normal chuck, showing that either peripheral end organ can be involved in the perception of a more attractive call. Thus there is greater receiver specificity for decoding stimuli in interspecific mate choice, and greater receiver permissiveness for decoding stimuli in intraspecific mate choice; it appears that intraspecific mate choice can take advantage of a greater array of neural pathways for call decoding than can interspecific mate choice.

INTRODUCTION

In many species of animals females choose males for the purpose of mating. There are two types of decisions that can be made by females: first, is the signal acceptable; and second, which signal is more attractive. Furthermore, females can exhibit choice at two levels, among species and within their own species. Interspecific mate choice is usually demonstrated if the signal is acceptable (recognized as conspecific), as indicated by a positive response in the absence of competing signals, or if the conspecific signal is preferred over a heterospecific signal. Many species have evolved communication systems that facilitate such choices. Interspecific and intraspecific mate choice have been two important themes in evolutionary biology but often are treated as disparate phe-

nomena. The purpose of this study, however, is to contrast the degree of specificity of acoustic signals and receivers in bringing about interspecific and intraspecific mate choice.

Although females of some species will respond to heterospecific signals in the absence of signals from their own males (Oldham and Gerhardt, 1975; Gerhardt, 1982; Gerhardt and Doherty, 1988; de Winter and Rollenhagen, 1990), females usually prefer conspecific signals. This preference results from the greater congruence between properties of the signal and receiver between conspecifics than between heterospecifics. Thus signal-receiver congruence leads to species recognition, which generates non-random mating (conspecifics with conspecifics) and should exert stabilizing selection on signals.

Variation in signals within a species is much less than variation among species, but females still commonly discriminate among conspecific males, often preferring traits that

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deviate significantly from the population mean (Ryan and Keddy-Hector, 1992). This generates non-random mating among conspecific males, which results in directional sexual selection on signals.

Interspecific and intraspecific mate choice can be based on the same male traits. In these cases, species recognition properties of the signal define a multivariate space within which sexual selection by intraspecific mate choice can act on variation in signal properties. Preferences for signals outside of this communication space might be selected against because of the cost of heterospecific matings (Gerhardt, 1982; Ryan, 1990*b*). Thus species recognition might constrain the degree to which sexual selection acts. However, in a few cases there are mating preferences for heterospecifics due to certain heterospecific traits being more attractive than the comparable conspecific traits (*e.g.*, body size, amount of courtship; Ryan, 1990*b*).

In some mate recognition systems, signals are partitioned into components that influence either interspecific or intraspecific interactions (Emlen, 1972; Rand and Ryan, 1981; Brenowitz, 1982; Littlejohn and Harrison, 1985; Fleischman, 1988). In these cases sexual selection by female choice is decoupled from the constraints of species recognition, and might play a more important role in signal evolution.

Species recognition requires that signals convey information regarding the identity of the species. This constraint should make species recognition signals evolutionarily conservative, and suggests that the receiver should respond preferentially to signals that convey this species-specific information. The parameters for making calls more attractive in intraspecific mate choice can be less restrictive. Several researchers have suggested or demonstrated that there are multiple solutions for increasing signal attractiveness in the context of intraspecific mate choice (reviewed in Ryan, 1990*a*). This argues that there is not just one certain type of information that must be conveyed by the signals (*e.g.*, species identity). There might be a premium on general stimulatory effects which could be achieved by different

means (*e.g.*, increasing stimulus intensity or stimulus repetition rate; Ryan and Keddy-Hector, 1992) because the receiver might be more receptive to a greater range of stimuli that enhance signal attractiveness, relative to the range of stimuli that would elicit species recognition.

Our purpose here is to review recent and ongoing studies of the túngara frog, *Physalaemus pustulosus*, in which we attempt to define those signal properties that are necessary and sufficient to elicit female phonotaxis (and are thus recognized as conspecific), and those that further enhance call attractiveness in an acoustic communication system in which different call components mainly influence either interspecific or intraspecific mate choice decisions.

THE COMMUNICATION SYSTEM

Male *Physalaemus pustulosus* produce a call of varying complexity consisting of a whine that can be produced alone or that can be followed by one to six chucks (Fig. 1; Rand and Ryan, 1981). When a male is calling alone he often emits a simple call, a whine-only, but adds chucks in response to vocalizations of other males. The whine is both necessary and sufficient to elicit phonotaxis from females and to evoke calling from males (Rand and Ryan, 1981), and the direction of the frequency sweep of the whine must be from high to low to elicit species recognition from females and calling from males (Ryan, 1983; Rose *et al.*, 1988). However, females are attracted preferentially to calls with chucks, as is the frog-eating bat, *Trachops cirrhosus*, which uses the call for prey localization (Ryan *et al.*, 1982). The chuck by itself does not elicit a response from male or female frogs (Ryan, 1983).

The call components also differ significantly in structure. A typical whine has a fundamental frequency that sweeps from 900 to 400 Hz in 300 msec. There is substantial energy in the second and fourth harmonics of the whine, and the dominant frequency of the call is about 700 Hz. A typical chuck is only 35 msec in duration, and has a fundamental frequency of 250 Hz with 14 harmonics. More than 90% of the energy is above 1,500 Hz and the average dominant

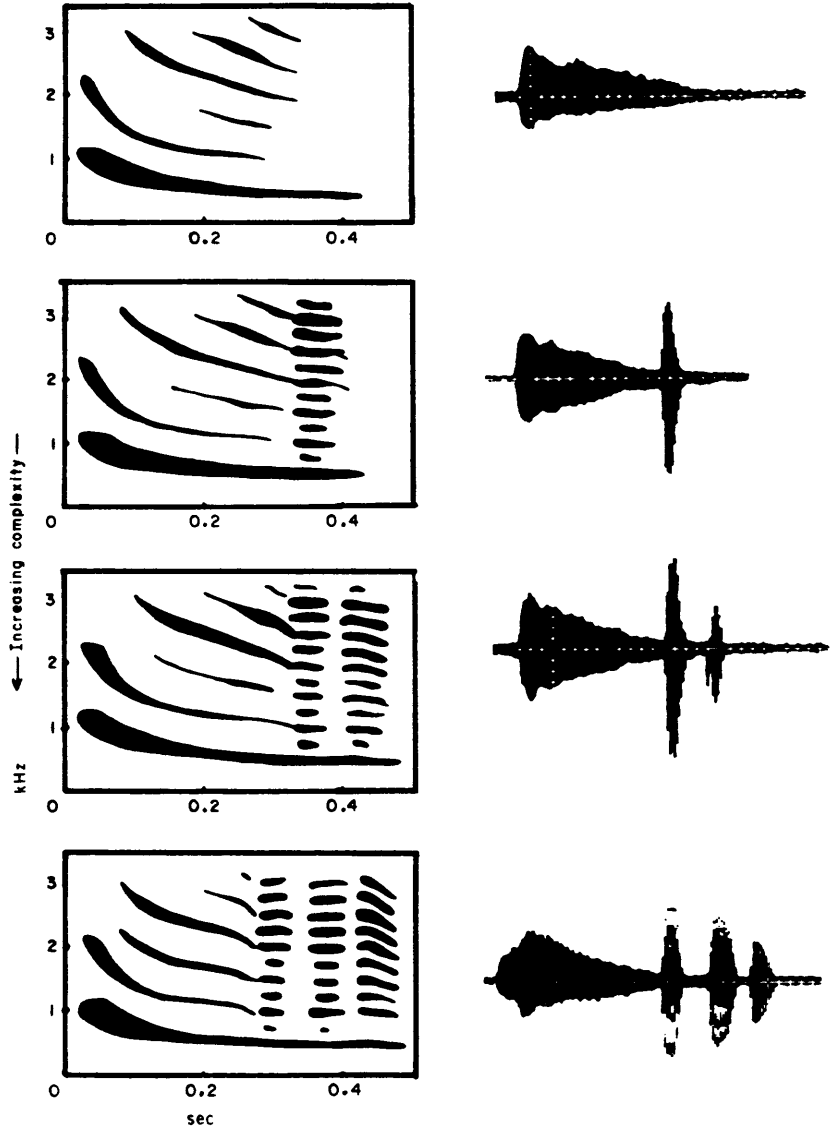


FIG. 1. Sonograms (left) and oscillograms (right) showing the call complexity series of *Physalaemus pustulosus*, as illustrated by calls with 0–3 chucks (top to bottom; from Ryan and Drewes, 1990).

frequency is 2,500 Hz (Ryan, 1985; Ryan and Rand, 1990).

The peripheral auditory system of the túngara frog is approximately tuned to the dominant frequencies of the whine and chuck. Frogs have two auditory peripheral end organs which are most sensitive to frequencies characterizing the advertisement call (Zakon and Wilczynski, 1988). At

threshold intensities the amphibian papilla is most sensitive to lower frequencies (<1,500 Hz) and the basilar papilla is most sensitive to higher frequencies (>1,500 Hz; Zakon and Wilczynski, 1988). In *P. pustulosus*, the amphibian papilla is most sensitive to approximately 500 Hz and the basilar papilla is most sensitive to about 2,100 Hz; thus each end organ tends to be tuned

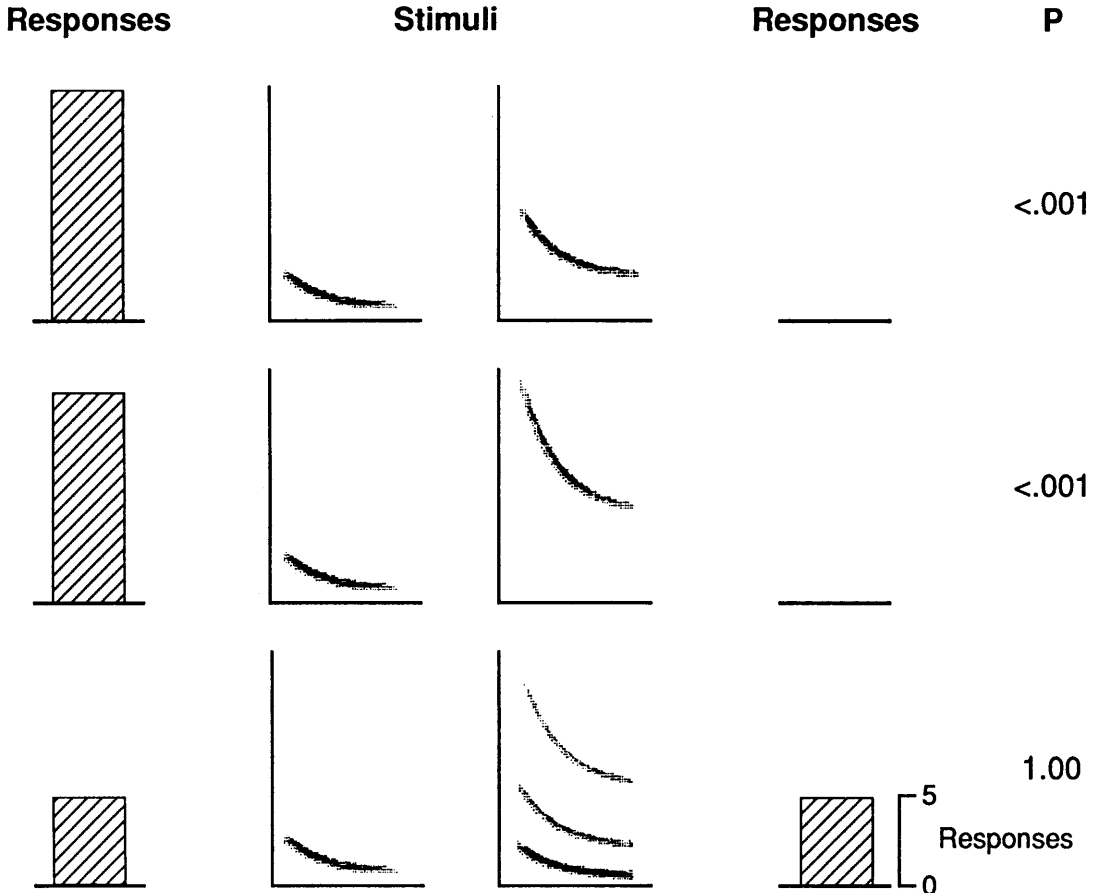


Fig. 2. The number of phonotactic responses of female *Physalaemus pustulosus* when given a choice between variants of the whine containing only the fundamental frequency (left) vs. variants containing only the second harmonic, only the third harmonic, or harmonics 1–3 (right, top to bottom). The null hypothesis of no preference was tested with an exact binomial probability. Details of phonotaxis experiments follow Ryan and Rand (1990).

near the dominant frequency of one of the call components (Ryan *et al.*, 1900).

SALIENT FEATURES OF THE WHINE

We addressed two general questions about features of the whine that might elicit phonotaxis from females: first, what is the most effective stimulus; and second, what is the minimum stimulus needed for eliciting phonotaxis.

The whine has a rich harmonic structure; we determined the influence of these harmonics on female phonotaxis. Only the fundamental frequency influences female phonotaxis; the other harmonics are superfluous. Females preferred a call containing only the first harmonic of the whine to calls containing only the second or only the fourth

harmonic (Fig. 2). Also, there was no preference when females were given a choice between a call with only the first harmonic and a call with the first, second, and fourth harmonics combined; the addition of the upper harmonics does not enhance the attractiveness of the call when the energy in the fundamental frequency of each stimulus is equal (Fig. 2). The efficacy of only the fundamental of the whine in eliciting phonotaxis demonstrates that only the amphibian papilla is used in species recognition since the hair cells in the basilar papilla are all tuned to much higher frequencies; the whine harmonics in the frequency region to which the basilar papilla is sensitive were ignored.

We also determined the minimum por-

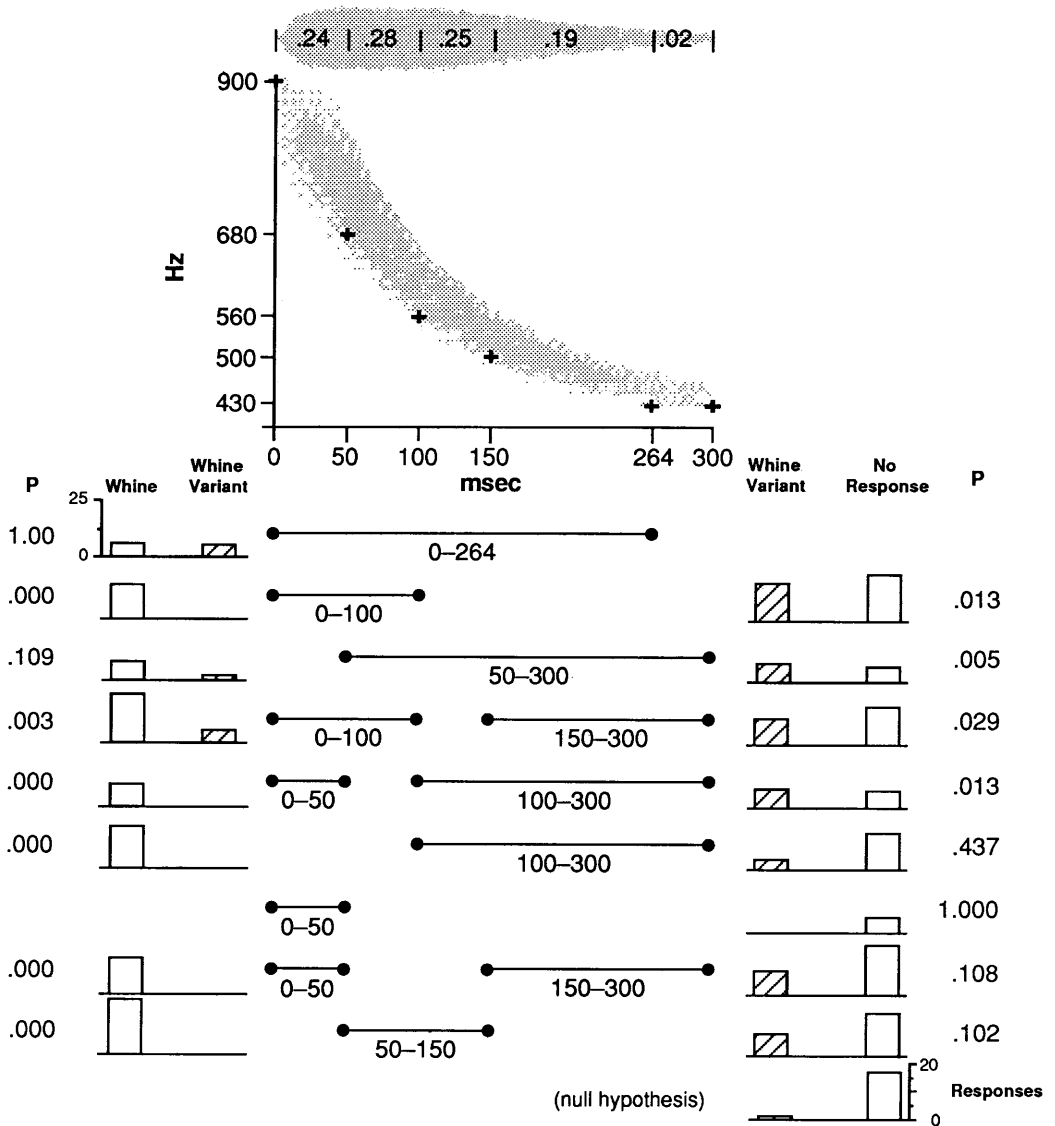


FIG. 3. An oscillogram (top) and sonogram (middle) of a model whine. Hash marks and crosses illustrate portions of the call that were used in various combinations for phonotaxis experiments. The numbers imbedded in the oscillogram indicate the proportion of total acoustic energy in that portion of the call. The horizontal lines in the bottom panel show the portions of the model call that were used for the stimulus. On the left, the number of phonotactic responses exhibited by female *Physalaemus pustulosus* to the stimulus (whine variant) vs. the entire whine are shown. The null hypothesis of no preference was tested with an exact binomial probability. On the right is shown the number of phonotactic responses by females to the stimulus when the alternative stimulus was white noise. A "no response" indicates that females either did not exhibit phonotaxis or approached the speaker broadcasting noise. In experiments in which only white noise was broadcast from one speaker (bottom right, "null hypothesis") 17 females exhibited no responses while 2 approached the silent speaker. Using a Fisher exact test, we tested the hypothesis that female phonotactic preferences between the whine variant and noise did not differ from their response to noise only (17-2, "null hypothesis").

tion of the fundamental of the whine necessary for eliciting phonotaxis. We synthesized portions of the fundamental frequency of the whine (Fig. 3). The onset and the

offset of these whine variants included the following boundaries: 0 msec, 900 Hz; 50 msec, 680 Hz; 100 msec, 560 Hz; 150 msec, 500 Hz; 264 msec, 430 Hz; 300 msec, 430

Hz (Fig. 3). As is shown in the oscillogram in Figure 3, not all portions of the whine had the same amount of call energy.

The full whine is more effective at eliciting female phonotaxis than any other smaller portion of the whine, with two exceptions. The full whine was significantly preferred over all of the following whine variants (Fig. 3): 0–50 msec + 100–300 msec; 0–50 msec + 150–300 msec; 50–150 msec; 0–100 msec; and 100–300 msec. Only when females were given a choice between the full whine and a portion of the whine from 0 to 264 msec or from 50 to 300 msec was there no significant preference for the full whine (although the latter case is almost statistically significant).

However, we found that many smaller portions of the whine were sufficient to elicit phonotaxis from females when the alternative stimulus was a burst of white noise with the envelope of the whine. Five whine variants were effective stimuli: 0–264 msec; 0–100 msec; 50–300 msec; 0–100 msec + 150–300 msec; and 0–50 msec + 100–300 msec (Fig. 3). There was no unique 50 msec portion that was necessary to elicit phonotaxis. However, all five effective stimuli did contain at least 50 msec of the first 100 msec (Fig. 3).

The stimulus lacking 0–100 msec did not elicit phonotaxis, while the 0–100 msec stimulus alone was effective. Either the 0–50 msec or the 50–100 msec stimulus elicited phonotaxis if it was combined with the rest of the whine (*i.e.*, 100–300 msec). 0–50 msec alone or when combined with 150–300 msec, and 50–150 msec alone did not elicit phonotaxis (although this might be true of larger sample sizes). Therefore, neither of the first two 50 msec portions alone is sufficient but at least one is necessary to elicit a female response. We realize that in not demonstrating a significant preference between stimuli we might commit a Type II error, especially with some of the smaller sample sizes.

In summary, the fundamental frequency of the whine is both necessary and sufficient for eliciting female phonotaxis. It appears that the upper harmonics of the whine are irrelevant. They are neither necessary nor sufficient to elicit phonotaxis, and their

addition to the fundamental frequency has no statistical effect on the call's attractiveness. Only a small portion of the whine is necessary for eliciting phonotaxis, and that portion is within the 0–100 msec portion of the whine's fundamental. There is some signal redundancy since either the first or the second 50 msec portion is necessary. However, the rest of the fundamental does influence female phonotaxis. With the exception of two portions, the full whine is significantly preferred by females over the other portion tested.

SALIENT FEATURES OF THE CHUCK

By itself the chuck does not contain stimulus features that can elicit female phonotaxis. However, when added to a whine it makes the call more attractive to females. We addressed two questions about features of the chuck that enhance call attractiveness: first, what are the features of the chuck that would enhance the attractiveness of a call without chucks; and second, what features of the chuck would enhance call attractiveness to the greatest extent.

The chuck differs from the whine in its short duration, broader frequency range, and higher dominant frequency. The dominant frequency of the average chuck, 2,500 Hz, is close to the average tuning of the female's basilar papilla, about 2,100 Hz (Ryan *et al.*, 1990). However, the broad frequency range encompasses the spectral sensitivity of both auditory organs of the inner ear. Therefore, we constructed chuck variants that contained only the lower half of the frequency range of the normal chuck (harmonics 1–7, frequency range 215–1,505 Hz) and only the higher half of the frequency range (harmonics 8–14, range 1,720–3,010 Hz; Fig. 4).

We asked whether these stimuli were effective in enhancing the attractiveness of a whine-only by giving females a choice between a whine followed by each of the half-chuck variants and a whine-only. We also determined the attractiveness of the half-chuck variants relative to the full, normal chuck. The full chuck contained the spectral properties of the two half-chucks combined, but in all experiments we equalized the amount of total energy in the chucks being compared. Finally, we determined the

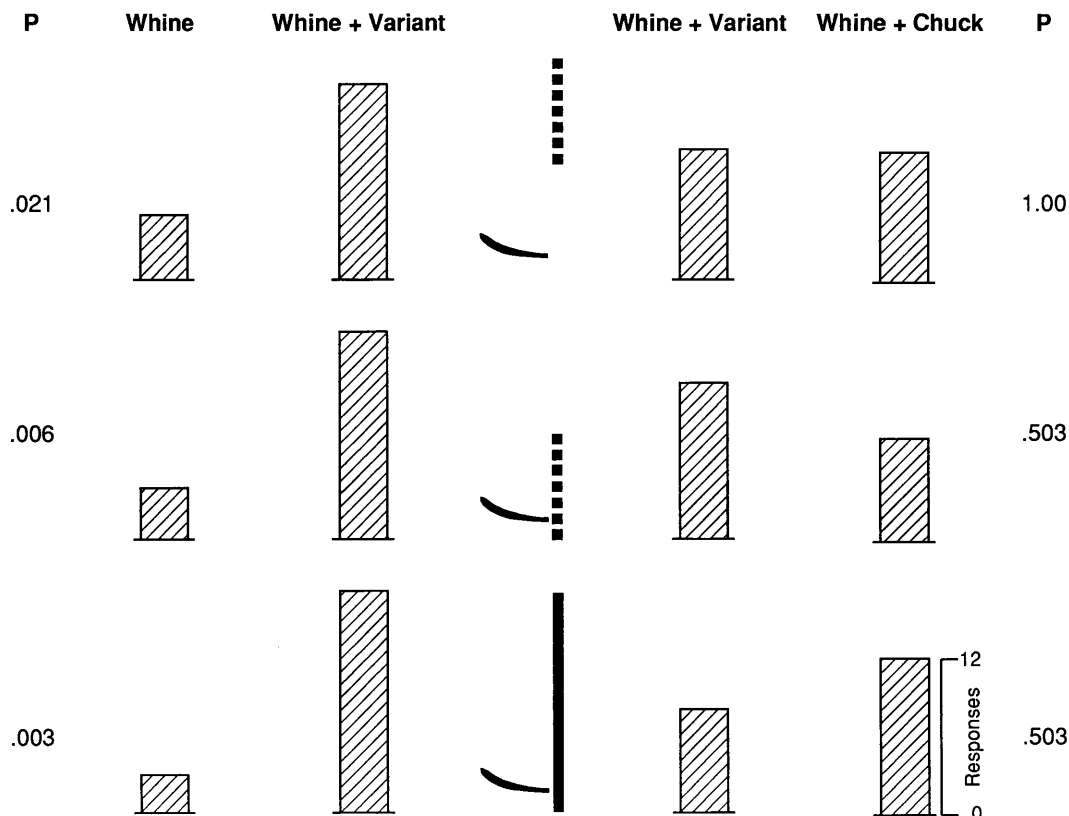


FIG. 4. The number of phonotactic responses of female *Physalaemus pustulosus* in response to stimuli in which a whine followed by a chuck containing only harmonics 1–7, a chuck containing only harmonics 8–14, or followed by a burst of white noise with the same duration as the chuck (middle, top-bottom). Preference for each of these stimuli when paired with either only a whine (left) or whine followed by a normal chuck (right) was determined. The null hypothesis of no preference was tested with an exact binomial probability. See Ryan and Rand (1990) for details.

importance of the harmonic structure per se. We did this by adding to a whine a white-noise burst that was of the same duration and amplitude envelope as the chuck (Fig. 4).

Each of the half-chuck variants, when added to a whine, was more attractive than the whine-only (Fig. 4). Thus these half-chucks would be favored by sexual selection because they increase the attractiveness of the call relative to the simple call. Also, there was no significant difference in female responses to these half-chuck variants and the normal chuck. Finally, we found that the addition of a white-noise burst in the place of the chuck also enhances the attractiveness of the call relative to the simple call, and is no less attractive than the call

with a normal chuck. This also shows that temporal coding of the chuck's periodicity is not likely to play a role in chuck preference.

These results suggest that sexual selection by female choice would favor multiple evolutionary pathways for the evolution of more complex calls. If males could append to their whine the full chuck, either half-chuck variant, or a white-noise burst, they would be equally attractive to females. Because the two half-chuck variants would primarily stimulate different peripheral end organs, this also suggests flexibility in the neural pathways whose stimulation results in calls being perceived as more attractive. Therefore, the female phonotaxis experiments help us understand the forces that favored the

evolution of more complex calls, but not the particular type of complex calls. Two possible explanations for why full chucks instead of half chucks or white noise evolved seem likely: morphological constraints and natural selection. First, it is possible that the male's vocal morphology that was ancestral to the evolution of the chuck was predisposed to produce a full chuck rather than a half-chuck variant or a white-noise burst. An analysis of the vocal morphology of *P. pustulosus* and its close relatives lends credence to this hypothesis (Ryan and Drewes, 1990). Second, although complex calls are favored by sexual selection, there is a natural selection cost incurred due to higher predation risk (Ryan *et al.*, 1982). It is possible that the full chuck would attract fewer predators than the other stimuli tested, but based on our knowledge of hearing in the frog-eating bat, a major predator on the túngara frog (Ryan, 1985), this does not seem likely (Ryan *et al.*, 1983; Bruns *et al.*, 1989).

DISCUSSION

In *P. pustulosus* the whine is both a necessary and sufficient stimulus for species recognition and the presence of the chuck is favored by sexual selection because it further enhances the attractiveness of the call to females. These disparate functions of the call are related to differences in the female's perceptual system that define biologically relevant stimuli.

The whine carries information that identifies the species. This information is not encoded in all parts of the whine. The upper harmonics contain no information relevant to females whatsoever; their presence or absence has no effect on female phonotactic responses. Although the fundamental is necessary, either only the first or only the second 50 msec need be communicated for the females to recognize the call as conspecific. Thus as with other species-specific signals, only a portion, and in this case a relatively small portion, of the signal is necessary to elicit female response. However, most of the other information in the fundamental frequency of the whine, but not in the upper harmonics, is relevant in that it adds to the attractiveness of the whine. Only the beginning (0–50 msec) or only the end (264–300 msec) of the call can be omit-

ted with no effect on call attractiveness. Therefore, we have identified portions of the signal necessary for recognition; there is redundancy since either 0–50 msec or 50–100 msec is necessary. We also have identified those portions of the call that are relevant but neither necessary nor sufficient, and those portions of the call that are superfluous. Thus the whine can not be classified strictly into constituent parts that either are or are not needed to elicit phonotaxis. True, some parts are superfluous and some critical, but others enhance call attractiveness although by themselves could not elicit phonotaxis. In this way comparisons of portions of the whine parallel comparisons of the whine and chuck, and suggests that the partitioning of interspecific and intraspecific mate choice between the two call components is not an absolute dichotomy.

Based on our knowledge of the frequency sensitivities of the two auditory end organs (Ryan *et al.*, 1990), it seems that at least at threshold intensities, in the peripheral auditory system the biologically relevant information in the whine is processed by the amphibian papilla, and the basilar papilla plays no role in the processing of species-specific recognition. Furthermore, the form of stimulation of this end organ is important. Previous research has shown that the sweep must decrease in frequency (Ryan, 1983; Rose *et al.*, 1988), and the call from 0–100 msec, that portion that is necessary for recognition, approximates the most sensitive frequencies of the amphibian papilla. However, once this information is present in the whine, further stimulation of this end organ by other portions of the whine further enhances its attraction to the female.

Since the close relatives of *P. pustulosus* all have whine-like calls with similar dominant frequencies and similar tuning properties of the auditory periphery (unpublished data), this aspect of the communication system appears to be a trait inherited in this lineage.

The response to chuck variants differs drastically from the response to whine variants. Either the lower or the upper half of the chuck both can enhance the attractiveness of the call and make it as attractive as the normal chuck (provided total energy is equal). The dominant frequency of the full

chuck is slightly below the most sensitive frequency of the basilar papilla and contains very little energy in the range to which the amphibian papilla is sensitive. However, the half-chuck variants show that it is not important which end organ in the periphery is stimulated. As long as the total energy is the same, it can be concentrated in the frequency range to which either the amphibian papilla or the basilar papilla is sensitive. Furthermore, the harmonic structure is not important since a white noise chuck, which lacks such a structure, is as attractive as a full chuck. The receptor system is not totally permissive, however. Some stimuli do not enhance the call attractiveness (*e.g.*, only two lower harmonics of the chuck, unpublished data). But in stark contrast to the whine, we see that there are several parts of the chuck and some novel stimuli that are sufficient for enhancing call attractiveness and that no single part of the chuck is necessary. At the neural level this reveals great flexibility in the response of the auditory system to these stimuli.

Our results are consistent with some views of how species recognition and sexual selection will have different effects on the evolution of male traits (Ryan, 1990*b*). A signal involved in species recognition must convey certain information about the genetic compatibility of the soliciting male relative to the solicited female, *i.e.*, that they are conspecific. Dobzhansky (1937) and Paterson (1982) have promoted different views of the evolution of mate recognition systems. Dobzhansky suggests that species recognition is an adaptation that evolved under selection to avoid heterospecific matings, while Paterson argues that it is an epiphenomenon of divergence of taxa evolving in allopatry. Nevertheless, both hypotheses agree on the specificity of the encoded information and predict that such signals usually should be under strong stabilizing selection. The enclosed information needs to be specific because of stringency in the decoding parameters utilized by the receiver. This is what our results show. There are parts of the whine that are required for recognition, and the majority of the fundamental frequency of the whine is needed to produce the stimulus that is maximally attractive to the female.

Sexual selection favors signals that are more attractive to females, and ever since Darwin, researchers have been impressed by the remarkable divergence of signals under sexual selection (*e.g.*, Darwin, 1871; Mayr, 1963; West-Eberhard, 1983), although in general females prefer traits that increase the amount of stimulation of the female (Ryan and Keddy-Hector, 1992). This observation of natural patterns of diversity is consistent with our findings that there are multiple pathways by which male túngara frogs can increase the attractiveness of their calls to females. The sexually selected trait that we observe in nature, the full chuck, is only a single solution to the problem of increasing call attractiveness. When the male's signals are not constrained to communicate information about species identity, they are able to exploit the various means of increasing overall stimulation of the signal to the female. The neural correlate of multiple evolutionary pathways is permissiveness of the receiver, as has been shown in female preferences for chuck variants and white noise. Besides our studies reviewed here, other investigations of crabs (Christy, 1988), fish (Ryan and Wagner, 1987; Basolo, 1990) and birds (Burley, 1985; Searcy, 1992) show that females can prefer male traits that are not expressed by conspecific males.

Good genes hypotheses predict that females prefer mates with genetic constitutions that promote greater survivorship (Pomiankowski, 1988). There also might be more than one way to signal genetic quality, thus the permissiveness of the receiver for signals under sexual selection does not necessarily conflict with a good genes hypothesis, nor does it lend support.

These studies have shown that selection for species recognition and sexual selection can act on different components of the male's advertisement signal and that the parameters used by the receiver to decode the signal, produce a behavioral response, and eventually mate selection, are very different under these two forms of selection. Our results from studies of the túngara frog might contrast with systems in which selection for species recognition and sexual selection both act on the same signal components. Understanding such a contrast in detail might lead

to a better understanding of how interspecific and intraspecific mate choice interact in the evolution of mate recognition systems.

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REFERENCES

- Basolo, A. 1990. Female preference predates the evolution of the sword in swordtails. *Science* 250:808-810.
- Brenowitz, E. A. 1982. Long range communication of species identity by song in the red-winged blackbird. *Behav. Ecol. Sociobiol.* 10:29-38.
- Bruns, V., H. Burda, and M. J. Ryan. 1989. Ear morphology of the frog-eating bat (*Trachops cirrhosus*, Family Phyllostomidae): Apparent specializations for low-frequency hearing. *J. Morphol.* 199:103-118.
- Burley, N. 1985. The organization of behavior and the evolution of sexually selected traits. *Ornithol. Monogr.* 37:22-44.
- Christy, J. H. 1988. Pillar function in the fiddler crab *Uca beebei* (II): Competitive courtship signalling. *Ethology* 78:113-128.
- Darwin, C. 1871. *The descent of man and selection in relation to sex.* (reprint of original) Random House, New York.
- de Winter, A. J. and T. Rollenhagen. 1990. The importance of male and female acoustic behaviour for reproductive isolation in *Ribautodelphax* planthoppers (Homoptera: Delphacidae). *Biol. J. Linn. Soc.* 40:191-206.
- Dobzhansky, T. 1937. *Genetics and the origin of species.* Columbia University Press, New York.
- Emlen, S. T. 1972. An experimental analysis of the parameters of bird song eliciting species recognition. *Behaviour* 41:130-171.
- Fleischman, L. J. 1988. Sensory influences of physical design on a visual display. *Anim. Behav.* 36:1420-1424.
- Gerhardt, H. C. 1982. Sound pattern recognition in some North American treefrogs (Anura: Hylidae): Implications for mate choice. *Amer. Zool.* 22:581-595.
- Gerhardt, H. C. and J. A. Doherty. 1988. Acoustic communication in the gray treefrog, *Hyla versicolor*: Evolutionary and neurobiological implications. *J. Comp. Physiol.* 162:261-278.
- Littlejohn, M. J. and P. A. Harrison. 1985. The functional significance of the diphasic advertisement call of *Geocrinia victoriana* (Anura: Leptodactylidae). *Behav. Ecol. Sociobiol.* 16: 363-373.
- Mayr, E. 1963. *Animal species and evolution.* Belknap Press, Cambridge, Massachusetts.
- Oldham, R. S. and H. C. Gerhardt. 1975. Behavioral isolating mechanisms of the tree frogs *Hyla cinerea* and *Hyla gratiosa*. *Copeia* 1975:223-231.
- Paterson, H. E. H. 1982. Perspectives on speciation by reinforcement. *So. African J. Sci.* 78:53-57.
- Pomiankowski, A. N. 1988. The evolution of female mate preferences for male genetic quality. *Oxford Surv. Evol. Biol.* 5:136-184.
- Rand, A. S. and M. J. Ryan. 1981. The adaptive significance of a complex vocal repertoire in a neotropical frog. *Z. Tierpsychol.* 57:209-214.
- Rose, G., R. Zellick, and A. S. Rand. 1988. Auditory processing of temporal information in a neotropical frog is independent of signal intensity. *Ethology* 77:330-336.
- Ryan, M. J. 1983. Sexual selection and communication in a neotropical frog, *Physalaemus pustulosus*. *Evolution* 37:261-272.
- Ryan, M. J. 1985. *The tungara frog, a study in sexual selection and communication.* University of Chicago Press, Chicago.
- Ryan, M. J. 1990a. Sexual selection, sensory systems, and sensory exploitation. *Oxford Surv. Evol. Biol.* 7:157-195.
- Ryan, M. J. 1990b. Signals, species and sexual selection. *Amer. Sci.* 78:46-52.
- Ryan, M. J. and R. Drewes. 1990. Vocal morphology of the *Physalaemus pustulosus* species group (Family Leptodactylidae): Morphological response to sexual selection for complex calls. *Biol. J. Linn. Soc.* 40:37-52.
- Ryan, M. J., J. H. Fox, W. Wilczynski, and A. S. Rand. 1990. Sexual selection for sensory exploitation in the frog *Physalaemus pustulosus*. *Nature* 343:66-67.
- Ryan, M. J. and A. Keddy-Hector. 1992. Directional patterns of female mate choice and the role of sensory biases. *Am. Nat.* (In press.)
- Ryan, M. J. and A. S. Rand. 1990. The sensory basis of sexual selection for complex calls in the tungara frog, *Physalaemus pustulosus* (sexual selection for sensory exploitation). *Evolution* 44:305-314.
- Ryan, M. J., M. D. Tuttle, and R. M. R. Barclay. 1983. Behavioral responses of the frog-eating bat, *Trachops cirrhosus*, to sonic frequencies. *J. Comp. Physiol.* 150:413-418.
- Ryan, M. J., M. D. Tuttle, and A. S. Rand. 1982. Sexual advertisement and bat predation in a Neotropical frog. *Am. Nat.* 119:136-139.
- Ryan, M. J. and W. Wagner. 1987. Asymmetries in mating preferences between species: Female swordtails prefer heterospecific mates. *Science* 236: 595-597.
- Searcy, W. A. 1992. Song repertoire and mate choice in birds. *Amer. Zool.* 32:71-80.
- West-Eberhard, M. J. 1983. Sexual selection, social competition and speciation. *Quart. Rev. Biol.* 58: 155-183.
- Zakon, H. and W. Wilczynski. 1988. The physiology of the VIIIth nerve. In B. Fritzsche, M. Ryan, W. Wilczynski, T. Hetherington, and W. Walkowiak (eds.), *The evolution of the amphibian auditory system*, pp. 125-155. John Wiley and Sons, New York.