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THE SENSORY BASIS OF SEXUAL SELECTION FOR COMPLEX CALLS IN THE TÚNGARA FROG, *PHYSALAEMUS PUSTULOSUS* (SEXUAL SELECTION FOR SENSORY EXPLOITATION)

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Abstract.—Male túngara frogs (*Physalaemus pustulosus*) vocalize to attract females, and enhance the attractiveness of their simple, whine-only call by adding chucks to produce complex calls. Complex calls contain more total energy and are of longer duration. By virtue of the greater frequency range of the chuck, complex calls also simultaneously stimulate both the amphibian papilla and the basilar papilla of the frog's inner ear. Female phonotaxis experiments using synthetic stimuli demonstrate that an increase in the call's acoustic energy is not sufficient to account for the enhanced attractiveness of the complex call. However, the stimulation of either or both of the female's sound-sensitive inner-ear organs is sufficient to elicit her preference. We suggest that the female's sensory system generates selection that equally favors at least three evolutionary alternatives for enhancing call attractiveness and that historical constraints imposed by the male's morphology determined which of the alternatives was more likely to evolve. These data are consistent with our hypothesis of sensory exploitation, which states that selection favors those traits that elicit greater stimulation from the female's sensory system and which emphasizes the nonadaptive nature of female preference.

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> "... it is obviously probable that [females] appreciate the beauty of their suitors. It is, however, difficult to obtain direct evidence of their capacity to appreciate beauty"—C. Darwin (1883 p. 413)

Some of the most elaborate morphologies and behaviors in the animal kingdom are male traits that function in the attraction and courtship of females. Darwin (1883) suggested that these traits, often evolved because of female preference motivated by an aesthetic sense. This suggestion was roundly criticized because of its obvious anthropomorphic implications (e.g., Wallace, 1905; Huxley, 1938). We suggest, however, that not only was Darwin not far off the mark, but his notion suggests an important, experimentally verifiable, and usually neglected approach to the evolution of male traits under sexual selection. As "beauty is in the eye of the beholder," the various properties of the female's sensory system determine which traits are "pleasing" to its eyes, ears, or nares, or, more precisely, which traits will be favored by sexual selection due to their superior abilities to attract females. In this study, we attempt to define the sensory basis of sexual selection for complex calls in the túngara frog, *Physalaemus pustulosus.* We are especially concerned with how the female's auditory system determines the possible alternatives for the evolution of more attractive male calls under sexual selection.

A current controversy in sexual selection is how female preferences have evolved in species in which males contribute only sperm (reviewed in Kirkpatrick [1987*a*, 1987*b*]). Much of the debate exists between proponents of two hypotheses: the good-genes hypothesis (e.g., Trivers, 1972; Zahavi, 1975; Hamilton and Zuk, 1982; Borgia, 1987) and Fisher's hypothesis of runaway sexual selection (e.g., Fisher, 1958; O'Donald, 1967; Lande, 1981; Kirkpatrick, 1982). Both hypotheses suggest that the male trait influences the evolution of the female preference, either because the trait is correlated with natural-selection advantages accrued by discriminating females (e.g., good genes) or because the preference and the trait are genetically correlated and the preference evolves as a correlated response to selection on the male trait (runaway sexual selection). We suggest an alternative: sexual selection for sensory exploitation.

Our hypothesis of sexual selection for sensory exploitation states that sexual selection will favor traits that exploit preexisting biases in the female's sensory system (see Ryan, 1990*a*; Ryan et al., 1990). Thus, the sensory system of the female in existence when variation in male courtship arises will greatly influence the evolutionary consequences of such variation. The hypothesis emphasizes that: 1) the female's preference need not be an adaptation to mate with particular males; 2) the female preference exists prior to the evolution of the male trait; 3) the female's sensory system constrains the type of male traits that can be favored by selection; and, 4) the sensory system might thus bias the direction of evolution of male traits. Natural selection, sexual selection, and sensory exploitation need not be mutually exclusive hypotheses for the evolution of female preferences.

In this study, we utilized data on the neurophysiological properties of the female túngara frog's auditory system to design phonotaxis experiments that elucidated the necessary and sufficient properties for enhancing call attractiveness. These experiments revealed the various call alternatives that would be favored by sexual selection generated by female choice.

Anuran Courtship as a Model for the Sensory Basis of Sexual Selection

Anurans are an especially good model system for integrative studies of neurobiology, behavior, and evolution (e.g., Wilczynski and Ryan, 1988) and are especially tractable for understanding the sensory basis of sexual selection. The advertisement call is used by males to attract females and is fairly stereotyped and is easy to record, analyze, and synthesize. Furthermore, when broadcast from speakers, it will elicit female phonotaxis (Gerhardt, 1988). Auditory processing of advertisement calls has been studied extensively (e.g., Fuzessery, 1988; Walkowiak, 1988; Zakon and Wilczynski, 1988). Of interest here is the fact that significant processing of the signal takes place in the peripheral auditory system. Unlike all other terrestrial vertebrates, amphibians possess two inner-ear organs that are sensitive to airborne vibration: the amphibian papilla and the basilar papilla (Wever, 1985; Lewis and Lombard, 1988). The amphibian papilla is most sensitive to frequencies below 1,200 Hz, while the basilar papilla is most sensitive to higher frequencies, usually above 1,500 Hz. Each papilla can be characterized by those frequencies to which auditory nerve fibers respond at lowest sound intensity. The frequencies with most energy in the advertisement call tend to match the sensitivities of the auditory papillae. In species with calls that have two frequency concentrations of energy, each tends to match one of the papillae, and synthetic calls that simultaneously stimulate both papillae elicit preferential phonotaxis when compared to synthetic calls that stimulate only one of the papillae (Gerhardt, 1974). In other species, the dominant frequency of the call matches the tuning of only one of the papillae (Zakon and Wilczynski, 1988). Thus, the auditory periphery performs the first step in recognition of conspecific calls by functioning as a peripheral filter. Clearly, temporal cues can also be important, and much processing takes place in the central nervous system, but peripheral processing appears to explain a substantial amount of the preference for conspecific calls (e.g., Fuzessery, 1988; Walkowiak, 1988).

Sexual Selection and the Complex Call of Physalaemus pustulosus

The advertisement call of *P. pustulosus* is unusual among anurans in terms of its functional and structural complexity. The call can consist of two separate components, a whine and a chuck (Fig. 1). All calls contain a whine, which can be produced alone (a simple call) or can be followed by 1–6 chucks (a complex call; Rand and Ryan, 1981). The whine is necessary and sufficient for eliciting phonotaxis from females and vocalizations from males (Rand and Ryan, 1981; Ryan, 1983*a*; Rose et al., 1988). Males add chucks to their calls in response to vocalizations of other males, and females exhibit preferential phonotaxis to complex calls. The chuck appears to have evolved under the influence of sexual selection, because it enhances the ability of males to attract females (Rand and Ryan, 1981; Ryan, 1980, 1983*b*, 1985*b*). The sensory basis of this preference and who this preference might generate selection favoring other call variants were investigated in this study.

Although other anurans can have calls with more than one component, it is unusual for the components to differ in structure to the extent exhibited by the complex call of *P. pustulosus*. The whine is about 350

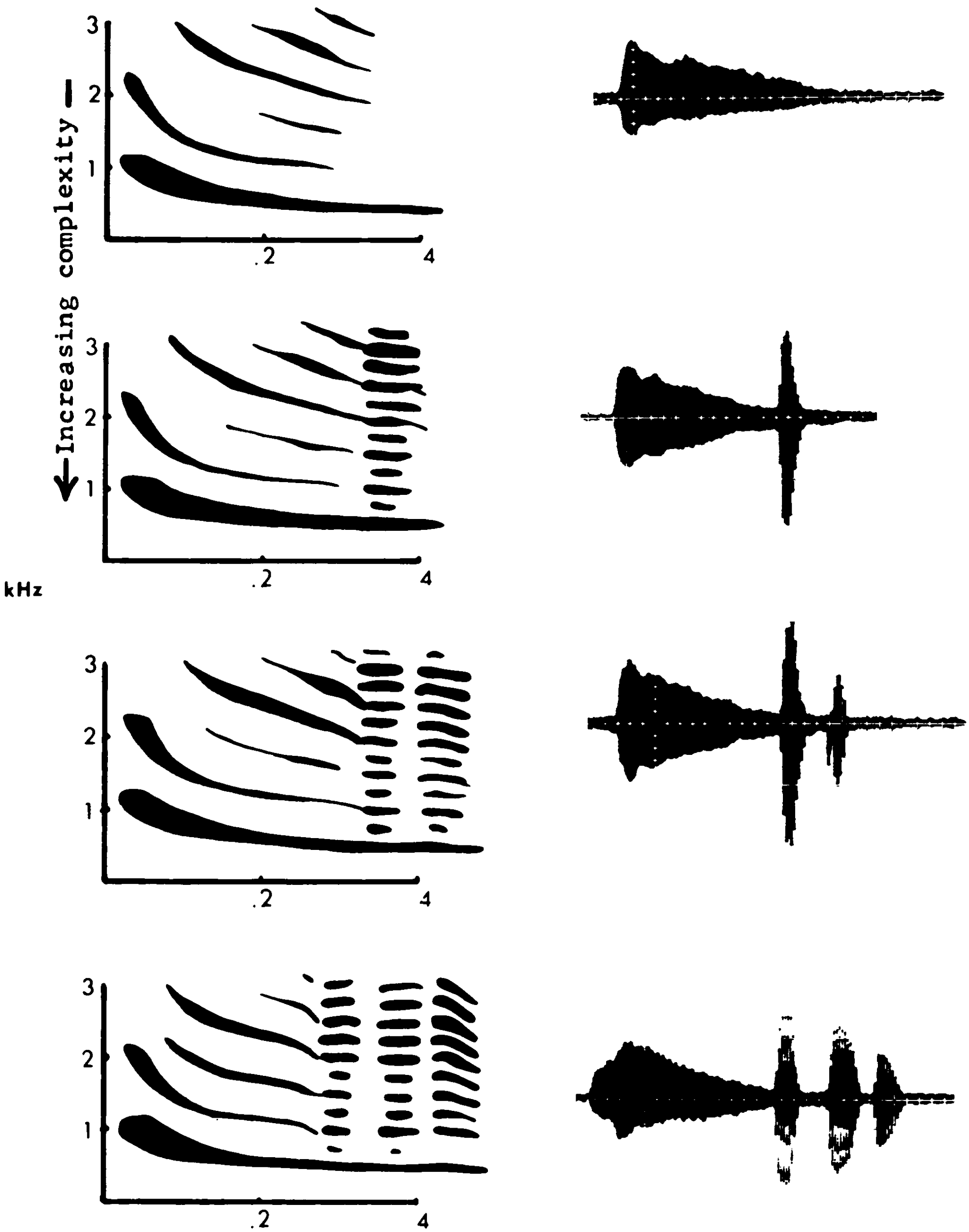

FIG. 1. Sonograms (left) and oscillograms (right) of advertisement calls of the frog *Physalaemus pustulosus* containing a whine and 0–3 chucks (top to bottom).

msec in duration, and during that time, its fundamental frequency decreases from about 900 Hz to 400 Hz (Fig. 1). Although there can be up to three harmonics, most of the energy is present in the fundamental. Rose et al. (1988) showed that the fundamental alone is sufficient for evoking male vocalization. The chuck is much shorter in duration (ca. 40 msec) and has a rich spectrum consisting of 15 harmonics of a fundamental of about 220 Hz. The dominant frequency is usually in the 10th, 11th, or 12th harmonic (ca. 2,400 Hz).

Neurophysiological studies have characterized the tuning properties of the *P. pustulosus* auditory system (Ryan et al., 1990).

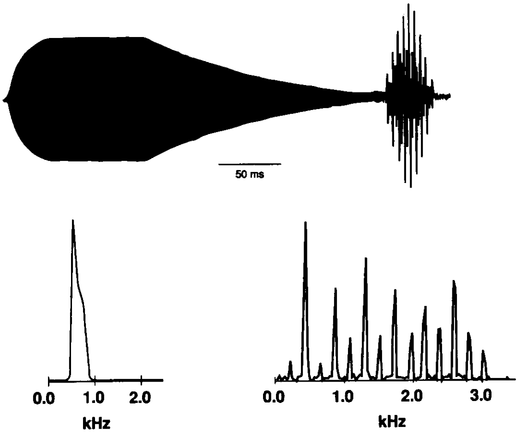

FIG. 2. An oscillogram of a synthetic call (whine + chuck) used in female phonotaxis experiments. Below the oscillogram are the results of the Fourier analyses, which show the distribution of energy across frequencies for the whine (left) and the chuck (right).

Recordings obtained from the torus semicircularis suggest that the most sensitive fibers in the amphibian papilla are tuned to about 500 Hz, while all of the fibers of the basilar papilla are most sensitive to about 2,100 Hz. This is consistent with data from other frogs which show that the amphibian papilla is almost always most sensitive to frequencies below 1,200 Hz and that the basilar papilla is relatively insensitive to sounds less than 1,500 Hz (reviewed in Zakon and Wilczynski [1988]).

That only the fundamental frequency of the whine (ca. 400–900 Hz) is sufficient to elicit vocalizations (Rose et al., 1988) and female phonotaxis (this study) suggests that it is primarily the amphibian papilla that is stimulated. Addition of the chuck changes the call substantially in terms of a number of parameters, including stimulation of both the amphibian papilla and the basilar papilla. The enhanced female preference for complex calls could be due to a change in any or all of these parameters. To determine the sensory basis of female preference, we addressed the hypotheses that females prefer complex calls to simple calls because complex calls: 1) contain more total energy; 2) are longer in duration; 3) add to the energy of the whine that already stimulates the amphibian papilla; 4) recruit basilar papilla stimulation for sensory processing; or 5) simultaneously stimulate both the amphibian papilla and the basilar papilla.

MATERIALS AND METHODS

Female phonotaxis experiments were conducted at the Smithsonian Tropical Research Institute in Gamboa, Republic of Panama, during July and August, 1988. Females were collected at breeding sites between 8:00 P.M. and midnight. Most females were in amplexus at the time of collection. More than 150 females were collected and tested; more than three-fourths of the females responded in more than 200 tests. Some females were tested in more than one experiment (i.e., stimulus pairing). Females were toe-clipped before release to avoid using the same female more than once in the same experiment.

Stimuli were synthesized by digitally adding sine waves and shaping the envelopes of the resulting wave forms using a custom-made sound-synthesis program (provided by J. Schwartz, Brown University), the Future Sound program, and an AMIGA 1000 or 2000 computer. Calls were modeled after a "typical" *P. pustulosus* call. The whine was 310 msec in duration and consisted only of the fundamental frequency which swept from 900 Hz to 430 Hz. The frequency decrease of the sweep was logarithmic. All chucks had a fundamental frequency of 215 Hz and were 45 msec in duration (Fig. 2). The frequency spectrum of the chuck was similar to that of the natural call. Whines and chucks were synthesized separately, and the chucks were digitally added to the end of the whines. The relative amplitudes of the whine and chuck were then adjusted to resemble the natural call; the peak amplitude of the chuck was greater than that of the whine (Fig. 2). Stimulus pairs were recorded antiphonally, each on one of two channels of a Marantz PMD 420 stereo tape recorder. The repetition rate of each stimulus was 0.5 Hz, similar to the natural calling rate of *P. pustulosus*.

Several call variations were synthesized (Fig. 3). A full chuck (C) contained harmonics 1–15 (215–3,019 Hz). Half-chucks (HC) contained harmonics 1–7 (low half-chuck [LHC]; 215–1,505 Hz; Fig. 3) or harmonics 8–15 (high half-chuck [HHC]; 1,720–3,010 Hz; Fig. 3). Relative amplitude and total energy of the chuck variants were equalized such that they were all within 1

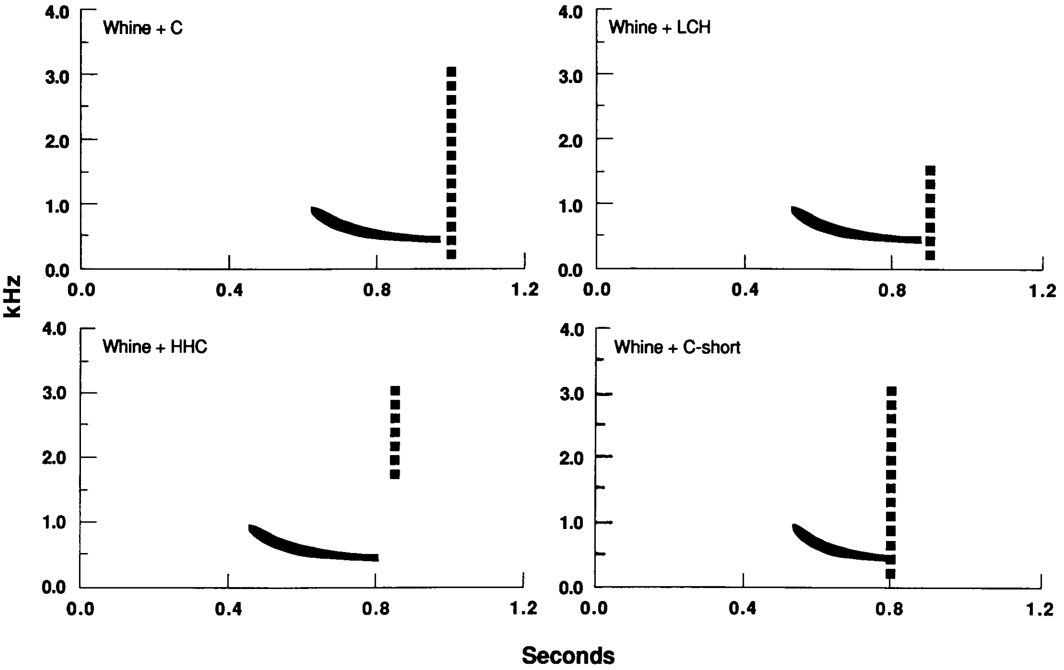

FIG. 3. Sonograms of the four synthetic stimuli used in female phototaxis experiments.

db of one another. As discussed above, the chuck simultaneously stimulates both the amphibian papilla and basilar papilla, the low half-chuck stimulates primarily the amphibian papilla, and the high half-chuck stimulates primarily the basilar papilla. We also synthesized a complex call (whine + C-short; Fig. 3) that was shorter than the whine with a full chuck (whine + C) and the same duration as the whine. The latter call was synthesized by having the chuck overlap the tail of the whine. Data were analyzed by a two-tailed exact binomial probability test, except in the case in which there was an a priori expectation of the directionality of response (Sokal and Rohlf, 1981 p. 166); in this case, a one-tailed test was used. We conducted nine different experiments (stimulus pairings), each consisting of 20 tests (female responses), with the exception of whine + LHC versus whine + HHC. In the latter experiment, there was no significant preference after 20 tests, but the data were such that there was little statistical power; therefore, the sample size was increased. The various stimulus pairs used in each experiment are given below in the Results.

All tests were conducted in an indoor arena that measured 3 m square. An ADS L200C speaker was placed in the center of each of two opposite ends of the arena, and stimuli were broadcast by a Marantz PMD 420 stereo cassette recorder and a Realistic SA 10 stereo amplifier. The peak sound-pressure level (SPL) of each stimulus was equalized at 82 db SPL (re: 20 μPascals) at the center of the arena with a General Radio model 1982 sound-pressure-level meter (flat weighting, peak response), unless otherwise indicated. This approximates the calling intensity of *P. pustulosus* in nature (ca. 90 db SPL at 50 cm). Temperature in the arena was maintained between 24° and 26°C, and testing occurred between 10:00 P.M. and 4:30 A.M.

The female to be tested was placed under a small opaque cone in the center of the arena. She was allowed five minutes to acclimate as the stimuli were broadcast. The cone was lifted by a remote device, and the female was allowed to approach a speaker. A response was recorded if a female approached to within 10 cm of a speaker and ceased movement. If a female approached the speaker along the wall, this approach

TABLE 1. The numbers of responses of female *Physalaemus pustulosus* to pairs of simple and complex synthetic advertisement calls (C = full chuck; LHC = low half-chuck; HHC = high half-chuck; short = shorter in duration; +3 db, +6 db, and +9 db indicate intensity relative to the alternative stimulus; AP = amphibian papilla; BP = basilar papilla). See text for full description of stimuli and hypotheses. All probabilities are derived from two-tailed tests unless there was an a priori prediction of the direction of the response, in which case a one-tailed test was used (noted in parentheses).

Hypothesis	Stimulus (number of responses)		Binomial probability
	Choice 1	Choice 2	
0) Preference for complex calls	whine (1)	whine + C (19)	0.000
1) Total energy	whine + 3db (5)	whine + C (15)	0.042
	whine + 6db (8)	whine + C (12)	0.503
	whine + 9db (18)	whine + C (2)	0.000
2) Duration	whine (8)	whine + C-short (12)	0.503
3) AP or BP stimulation	whine (4)	whine + LHC (16)	0.006 (1-tailed)
	whine (5)	whine + HHC (15)	0.021 (1-tailed)
	whine + LHC (19)	whine + HHC (17)	0.868
4) AP + BP stimulation	whine + C (8)	whine + LHC (12)	0.503
	whine + C (10)	whine + HHC (10)	1.000

was not recorded as a response, since it could also be attributed to escape behavior. Most responses occurred within three minutes.

RESULTS

Females responded readily to at least one of the stimuli in each experiment. In all experiments, there were many cases in which a female approached to within 50 cm of one of the speakers, then crossed to the other side of the arena and paused in front of that speaker at a similar distance before contacting one of the speakers. This behavior is quite similar to the movements of females among males in a chorus (Ryan, 1985*b*), which we interpret as sampling behavior. Whether from a speaker or a male, a call is perceived by the female as being louder as she approaches it. These simple behavioral observations reject the hypothesis that naturally occurring variation in call loudness results in preferential phonotaxis either in the experiments that we report here (but see experiments with "super-intense" stimuli) or in the behavior of females observed under field conditions.

Although Rand and Ryan (1981) and Ryan (1985*b*) demonstrated that females preferred complex calls to simple calls, each of those studies presented females with natural calls having multiple (two or three) chucks versus natural calls with no chucks. Therefore, we initially determined whether females preferred the synthetic complex call with a single chuck to the simple synthetic whine. Females showed an overwhelming preference for the whine + C over the whine (Table 1). We then tested the five hypotheses as to why complex calls are preferred over simple calls.

The first hypothesis suggests that females prefer complex calls because they have more energy than simple calls. Adding a chuck increases total call energy by about 7% (Ryan, 1985*a*). In these experiments, we increased the amplitude of the whine so that it had more energy than the whine + C. The whine was broadcast with a peak amplitude 3 db greater than that of the whine + C; thus, the simple call had a peak sound-pressure level and total energy content 50% greater than that of the complex call. Females showed a statistically significant preference for the whine + C despite its lower peak amplitude and energy content (Table 1). Increased call energy does not account for the enhanced attractiveness of complex calls.

We also gave females a choice between a whine in which the peak amplitude was 6 db greater than that of the whine + C, corresponding to a 100% increase (doubling) of peak amplitude and total energy ("super-intense" simple call). In this experiment, females failed to show a statistically significant preference (Table 1). Finally, we gave females a choice between a whine in which the peak amplitude and total energy were increased by 150% (+9 db) and a whine + C. In this experiment, the preference was reversed; females preferred the more intense simple call to the less intense complex call (Table 1).

These experiments demonstrate that the enhanced attraction of the complex call is not due simply to its rather slight (<10%) increase in the total energy content of the call. However, preference for the complex call is not completely intensity-independent and can be overriden and even reversed, if the energy in the simple call is increased drastically. Even in these experiments, females often sampled both stimuli from relatively close distances, as described above.

The second hypothesis is that the enhanced attraction of the complex call is due to its slightly longer duration. Females did not discriminate between whine + C and whine + C-short (Table 1). Interpretation of this experiment is ambiguous, because the shortening of the whine might disrupt other species-specific information (besides call duration) contained in this call. Other studies are in progress to investigate in detail the parameters of the whine that are necessary and sufficient for species identification.

The third hypothesis suggests that the additional stimulation of the amphibian papilla by the lower-frequency energy of the chuck is sufficient to explain the enhanced attractiveness of the complex call to females. This hypothesis predicts that the whine + LHC should be preferred by females over the whine. Our initial experiments demonstrating preference for complex calls over simple calls predicts the direction of the preference in this experiment; thus, these data were analyzed by a one-tailed test. Significantly more females preferred the whine + LHC to the whine (Table 1). The result of this experiment suggests that energy in the chuck stimulating the amphibian papilla is sufficient to elicit preferential female phonotaxis when compared to the whine. It does not prove that this portion of the chuck is necessary.

The fourth hypothesis states that the energy in the chuck stimulating primarily the basilar papilla is responsible for the enhanced attractiveness of complex calls. We tested this hypothesis in an experiment analogous to that described above, but we presented females with a choice between a whine + HHC and a whine. For the same reasons as in the above experiment, data were analyzed by a one-tailed test. In this comparison, females showed a statistically significant preference for the whine + HHC relative to the whine (Table 1). Thus, the whine + HHC and its stimulation of the basilar papilla is a sufficient component for eliciting preferential phonotaxis from females, although not a necessary component.

Although both the whine + LHC and the whine + HHC are more attractive than the whine, they need not be equally attractive alternatives to the female. However, when given a choice between these two call alternatives, females did not exhibit significant discrimination (Table 1).

The fifth hypothesis suggests that the enhanced attractiveness of the complex call relative to the simple call is due to the simultaneous stimulation of both the amphibian papilla and basilar papilla by the chuck. Experiments three and four showed that, relative to the whine, costimulation of the two papillae is not necessary to elicit preferential phonotaxis from females. However, simultaneous stimulation of both the amphibian papilla and basilar papilla may be a more attractive alternative than stimulation of either papilla alone, as has been shown in some other frogs (e.g., Gerhardt, 1974). Our results do not support this hypothesis; females did not exhibit preferential phonotaxis when a whine + C was compared either to a whine + LHC or a whine + HHC (Table 1). These results suggest that a chuck with only the low-frequency energy, only the high-frequency energy, or the full-frequency spectrum are all similarly attractive to females.

DISCUSSION

This study reconfirms experiments by Rand and Ryan (1981) and Ryan (1985*b*) demonstrating that female *P. pustulosus* prefer complex calls to simple calls. This study also demonstrates that it is not merely the increased call energy provided by the chuck that enhances its attractiveness. Even if call energy is increased by 50%, a simple call would still not be as attractive as a call with a chuck. The "super-intense" simple call would be as attractive as the complex call only if a male could increase the energy in the call by 100%, and would be more attractive only if total energy were increased by 150%. Such a feat would entail more than doubling the power generated by the lungs. Certainly, morphological and physiological considerations constrain achievement of such an option (Ryan, 1985*b*).

By adding a chuck to the call, males stimulate both the amphibian papilla and basilar papilla of the female and elicit preferential female phonotaxis. However, our experiments show that there are at least two other stimuli that result in calls as attractive as a full chuck; calls with either only the low-frequency energy or only the high-frequency energy would also have been favored by sexual selection if each variant had the same energy content. The female sensory system, therefore, would generate equally strong sexual selection favoring the three alternative modifications of the male's call: calls with full chucks, calls with low half-chucks, and calls with high half-chucks.

There are several possible explanations as to why males evolved a full chuck rather than either of the half-chucks. Random genetic variation is one possibility. Also, other factors besides female choice, such as predation (Ryan et al., 1982), might generate differential selection on call variants. Another, perhaps more likely, possibility is a morphological and phylogenetic constraint. Drewry et al. (1982) showed that the production of the chuck is due to a fibrous mass in the larynx that vibrates independently of the vocal cords. The fibrous mass is present but is much smaller in closely related species that do not produce chucks (Ryan and Drewes, 1990). A change in the size of the fibrous mass might necessarily result in a chuck with the full frequency spectrum. Although each of the half-chucks could evolve with further changes in the larynx, pharynx, and vocal sac that would filter either half of the full frequency spectrum, this would require additional evolutionary changes, and there would be no sexual selection favoring such changes. Thus, the full chuck might have been the most parsimonious solution for evolving a more attractive call. Therefore, we suggest that the female's sensory system defined the possible evolutionary alternatives for more attractive male traits and that morphological and phylogenetic constraints on the male determined which of those alternatives was achieved.

Our hypothesis of sexual selection for sensory exploitation suggests that preexisting sensory biases determine which male traits will be favored by sexual selection (see Ryan, 1990*a*; Ryan et al., 1990). Consistent with this hypothesis, our study shows that the preference exhibited by female *P. pustulosus* could be exploited by alternative traits. However, without historical data, we can not determine whether this sensory bias preexisted the evolution of the chuck. These historical data are currently being sought.

Sexual selection for sensory exploitation has historical antecedents in ethology (e.g., Barlow, 1977 p. 121), but it is not analogous to selection for novelty (West Eberhard, 1979; Burley, 1985). For one, the sensory mechanisms are probably quite different (e.g., habituation; cf. Hinde, 1970). Selection for novelty might be best considered as a subset of selection for sensory exploitation. Sensory exploitation is quite similar to the concepts of "latent aesthetic preferences" and "sensory drive" discussed by Burley (1985) and Endler and McLellan (1988), respectively (see also West Eberhard [1979], Lorenz [1981], Borgia [1987], and Kirkpatrick [1987*a*, 1987*b*]).

This study has investigated how a simple whine is made more attractive by adding a chuck. The female's sensory system could also be disposed to favor other call variants, perhaps not evolutionarily accessible to the male because of morphological constraints. Future studies will attempt to identify other types of sufficient and super-normal stimuli defined by the female's sensory system and to determine how the male's morphology might constrain or promote the evolution of these alternatives.

Our approach to understanding the evolutionary dynamics of male traits and female preferences under sexual selection differs from those models that emphasize the coevolution of male traits and female preferences. Natural selection and runaway sexual selection theories implicate the trait in the evolution of the preference (e.g., Andersson, 1987). We suggest that sensory biases underlying preferences might exist prior to a trait for a variety of reasons (see also Burley [1985] and Borgia [1987]). Sensory exploitation also implies that the sensory system can bias the direction of evolution (Ryan, 1990*b*), a factor that has been included in some genetic models of sexual selection (Lande, 1981; Kirkpatrick, 1982). A potential bias in the direction of the evolution of male traits is not trivial, since we have the (only poorly documented) suspicion that often it is the more complex calls (Rand and Ryan, 1981), faster call rates (Gerhardt, 1988), more intense calls (Gerhardt, 1988), larger song repertoires (Searcy and Andersson, 1986), brighter colors (Hamilton and Zuk, 1982), longer tails (Andersson, 1982), and more decorated bowers (Borgia et al., 1985), that are favored by female choice (Ryan, 1990*a*). An understanding of the underlying sensory biases in each of these systems could lead to major insights regarding the direction in which male advertisement traits evolve under sexual selection.

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