

## Consistency of female choice in the túngara frog: a permissive preference for complex characters

N. M. KIME\*, A. S. RAND†, M. KAPFER‡ & M. J. RYAN\*, †

\*Department of Zoology, University of Texas at Austin

†Smithsonian Tropical Research Institute, Balboa, Panama

‡Institute of Zoology, University of Vienna

(Received 10 February 1997; initial acceptance 20 April 1997;  
final acceptance 17 July 1997; MS. number: A7850)

**Abstract.** Previous phonotaxis experiments in the túngara frog, *Physalaemus pustulosus*, indicated a permissiveness in female preference that allows sexually selected complex call characters to be replaced with various alternative characters. Although they prefer complex to simple calls, females as a group did not discriminate between several alternative complex characters appended to the simple conspecific call. However, these studies did not address the possibility that the apparent permissiveness in female preference occurred because of an averaging of population data. The observed patterns in female preference could result from all females finding a certain set of call variants equally attractive, or from a polymorphism in female call preference. To discriminate between these two alternatives, consistency of mate choice was determined for three pairs of calls that elicited no phonotactic bias in population studies. Individual females did not repeatedly choose one stimulus of a pair over the other, demonstrating that the patterns of permissiveness observed in the population are paralleled by similar patterns within females. A broad preference for complex calls in the *P. pustulosus* species group would permit the evolution of sexually selected call variation through sensory exploitation.

© 1998 The Association for the Study of Animal Behaviour

When females select males based on advertisement signals, a correspondence between the male signal and the receiving properties of the female's sensory system is important for both species recognition and female choice between conspecifics (Andersson 1994). The sensory exploitation hypothesis assumes such correspondence when it suggests that pre-existing properties of the female's sensory system influence the evolution of male signals used in mate attraction (Ryan 1990). If a female's sensory system is biased to respond to a suite of specific signal properties, one would expect a preferred male trait to be one that takes advantage of that bias. This interaction between male trait and female preference, however, does not imply that the two are always tightly matched (Ryan 1990; Shaw 1995). Females may show a broader bias, evidenced by the potential substitution of existing male advertisements with structurally different characters.

Correspondence: N. M. Kime, Department of Zoology, University of Texas at Austin, Austin, TX 78712, U.S.A. (email: nmkime@mail.utexas.edu).

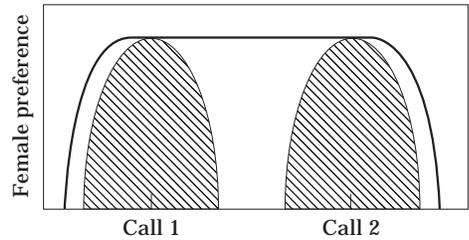
Previous work investigating female preference in the túngara frog, *Physalaemus pustulosus*, demonstrated that sexually selected complex characters of the male call may be replaced with various alternatives that elicit equal phonotactic response from a group of females. The male advertisement call is a frequency-modulated 'whine', which may be followed by one to several 'chucks'. The whine alone is sufficient for species recognition, but females prefer a whine plus added chucks (Rand & Ryan 1981). Although all females prefer the conspecific whine to the calls of hetero-specifics (Ryan & Rand 1993a), their preference for complex calls is more permissive and can accommodate several call adornments (e.g. Ryan & Rand 1990, 1993b, *in press*). If, for example, white noise is substituted in place of the chuck, females choose the whine-white noise variant over the whine alone as often as they do the normal whine-chuck (Rand *et al.* 1992).

Comparisons of the calls and mate preferences of the closely related species within the *P. pustulosus* species group provide evidence for a

permissive female preference for complex calls. *Physalaemus coloradorum* produces whine-like calls but does not produce chucks. When given a choice between a simple conspecific call and a conspecific call to which chucks from *P. pustulosus* have been synthetically added, *P. coloradorum* females prefer the call with chucks (Ryan & Rand 1993a). Although *P. coloradorum* males do not produce chucks, they do make complex calls; whines are often produced in groups of two or more. Female *P. pustulosus* prefer the conspecific whine produced in groups over the single conspecific whine (Ryan & Rand 1993a), and find them as attractive as the whine-chuck (unpublished data). A third species, *P. pustulatus*, adds an amplitude-modulated prefix to the beginning of its whine (Ryan & Rand 1993b); if this adornment is appended to the *P. pustulosus* whine, females find the call as attractive as their own whine-chuck (Ryan & Rand, in press). Thus, the preference for complex calls in the *P. pustulosus* species group is not limited to the complex characters produced by conspecific males but appears to be broad enough to include the complex characters of related species.

In studies of female preference, the precision of preference with respect to existing male traits, and especially the precision of preference within single individuals versus that observed within populations, has not often been investigated (but see Arak 1988; Jennions et al. 1995; Wagner et al. 1995). There are two possible explanations for the observed permissiveness in female preference in *P. pustulosus* (Fig. 1). First, female preference for complex characters may be narrowly defined within individuals but vary among individuals; the evidence for a broader preference seen in previous studies could thus simply be the result of population averaging. Alternatively, individual preference could mirror that of the population, indicating that individual preferences for complex calls are indeed permissive. Experimental differentiation between these two alternative interpretations of previous data is important for the characterization of female preference in the túngara frog.

To discriminate between these two possibilities, one can evaluate the consistency of choice in individual females. Variation in mate choice can be partitioned into two types: within- and among-individual variation. Within-individual variation is environmental, hormonal, or ontogenetic in



**Figure 1.** Two explanations for the observed permissiveness in female preference for complex calls in population studies. First, individual females may have a narrow, polymorphic preference for one of the two distinct male calls depicted here in univariate space (▨). Pooled population data would average the individual preferences, and indicate no preference for either of the two male calls. Alternatively, the preferences of individual females could be permissive (broad curve). In this case, individual females would not prefer one male call over another.

nature. Among-individual variation in mate choice, on the other hand, reflects both genetic and environmental variation causing permanent changes in an individual (Falconer 1989). A polymorphism in female preference is demonstrated when the ratio of within- to among-individual variation is low. Conversely, if high among-individual variation is reflected in similar within-individual variation, one can infer that the variation in responses probably reflects a lack of fixed preference. To date, few studies of female preference have separated within- and among-individual variation (e.g. Gerhardt 1991; Bakker 1993; Möller 1994; Jennions et al. 1995; Wagner et al. 1995). Using repeated two-speaker phonotaxis experiments to evaluate the consistency of female choice, we were able to make this distinction.

Another commonly used measure that quantifies the distinction between within- and among-individual variation is the 'repeatability' of a trait. Repeatability, as defined in population genetics, is an intra-class correlation coefficient that indicates the fraction of total phenotypic variance that is due to permanent (but not necessarily genetic) differences between individuals. Repeatability places an upper limit on heritability; if between-individual variation is reflected in similar within-individual variation, the genetic component of observed variation in female preference must be small (Boake 1989; Falconer 1989). In two-speaker female phonotaxis experiments such as

those commonly used in anuran mate preference studies, however, it is difficult to obtain a numerical repeatability estimate. The responses to stimuli are scored as a dichotomy, and do not easily provide the opportunity to compute repeatability. Therefore, as a similar measure, we evaluate the consistency of female choice over repeated tests.

In this study, we determine the consistency of female choice in the túngara frog. The population shows a substantial range in responses to synthetically induced variation in sexually selected call characters. If this permissiveness is reflected in individual females, we can infer a lack of precise female preference for specific complex characters. This in turn would suggest that the observed female preference for complex over simple calls may be rather broad and would dismiss the possibility of population averaging in the interpretation of previous female choice experiments. Ryan & Rand (1993b, in press) hypothesized that a pre-existing female preference for complex calls has allowed the evolution of several different call adornments among males in the *P. pustulosus* species group. Inconsistency of individual female choice for specific adornments, indicating a permissive preference, is important to the support of this hypothesis.

## METHODS

### Experimental Protocol

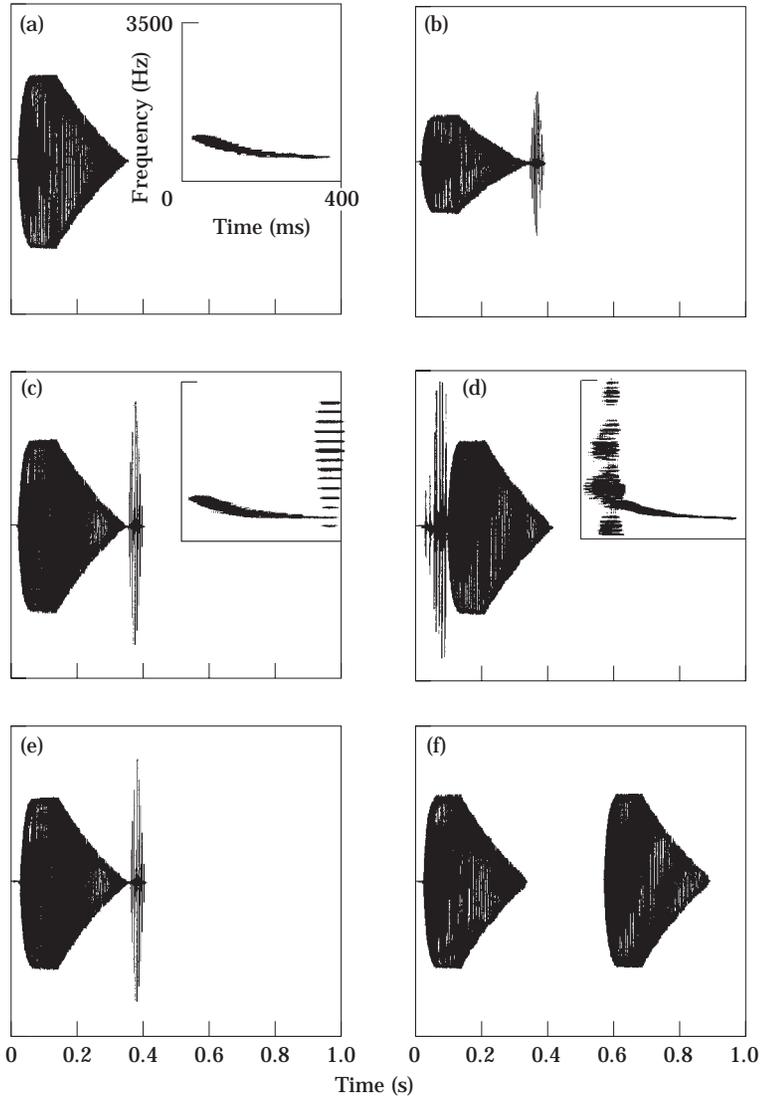
We performed all experiments between 15 May and 15 August 1996 at the Smithsonian Tropical Research Institute facility in Gamboa, Panama. We captured female *P. pustulosus* ( $N=60$ ) in amplexus at 1930–2100 hours, after which we allowed them an acclimation period of at least 1 h. We began female choice experiments at 2200 hours the same evening. We placed a female under a funnel in the centre of the testing chamber, which measured  $3 \times 3$  m and was equipped with foam-padded walls to reduce acoustic reverberation. We then presented two calls to the female from two ADS L2000 speakers placed 3 m apart and equidistant from the female. The stimuli were presented antiphonally, each at a rate of one call per 2 s. Between females, we alternated the speaker from which a particular stimulus was presented to eliminate any side effect. The peak intensity of the whine was 82 dB sound pressure

level (re 20  $\mu$ Pa) at the centre of the chamber where the female was released. After 5 min, we lifted the funnel and allowed the female to choose. If a female remained motionless at the release site for 5 min, stopped moving for 2 consecutive min after leaving the release site, or if she failed to make a choice within 15 min, a no response was scored. If a female approached to within 10 cm of a speaker, a positive response was scored. If a response was scored, the female was immediately tested with a different stimulus pair, for up to 12 tests per female.

Consistency tests, composed of an identical stimulus pair presented twice, were the first and last test presented to a female. The number of other, unrelated phonotaxis experiments between these repeated tests varied from two to 10 ( $\bar{X} \pm SD = 7.2 \pm 3.5$ ,  $N=60$ ), and the time between them varied from 21 to 142 min ( $\bar{X} \pm SD = 62.8 \pm 28.1$  min,  $N=60$ ). When we assigned the dummy variables 0 and 1, respectively, to females that did and did not choose consistently, neither the amount of time between repeated tests nor the number of intervening tests was a good predictor of female consistency (Spearman rank correlation: for time between tests,  $r_s=0.07$ ; for number of tests,  $r_s=0.06$ ,  $N=60$ ). The stimuli presented to individual females during intervening tests also varied from test to test and from female to female. When a female stopped responding, or after she concluded 12 tests, we gave her a unique toe-clip and returned her to the capture site. Females recaptured on subsequent nights were not used for phonotaxis experiments.

### Stimuli

Stimuli were synthesized on an Amiga computer (model 2000) at a sample rate of 20 kHz (J. Schwartz, unpublished software). Only the fundamental frequency sweep of the whine was used in synthesizing calls, because the upper harmonics of the whine appear to have no influence on female phonotaxis (Rand et al. 1992; Wilczynski et al. 1995). We used three stimulus pairs for consistency experiments (Fig. 2). The first stimulus pair consisted of a normal intensity whine versus a whine-chuck at half the normal amplitude (0.5-amp whine-chuck). The second pair was a typical whine-chuck versus a *P. pustulosus* whine to which the prefix from *P. pustulatus* had been appended (prefix-whine). The third pair



**Figure 2.** Stimuli used for phonotaxis experiments. Stimulus pairs are side by side. (a) *Physalaemus pustulosus* whine with sonogram (inset). (b) Whine-chuck at half the normal amplitude (0.5-amp whine-chuck). (c) Normal-intensity whine-chuck with sonogram (inset). (d) *Physalaemus pustulosus* whine with *P. pustulatus* prefix (prefix-whine) with sonogram (inset). (e) Normal-intensity whine-chuck. (f) *Physalaemus pustulosus* whine with the grouped structure of *P. coloradorum* (whine-whine).

consisted of a whine-chuck versus a double conspecific whine (whine-whine) similar to that of *P. coloradorum*. For each of the stimulus pairs, 20 females were tested twice as outlined above.

For all three pairs, the test population in previous experiments showed a lack of preference for either stimulus (Ryan & Rand 1990, *in press*, unpublished data). In the first stimulus pair, the

lack of female preference for a whine-chuck presented at half the normal amplitude over a simple whine probably reflects a trade-off between a preference for increased amplitude and a preference for complex calls. The other two stimulus pairs are hypothesized to reflect a permissive bias for complex characters within the *P. pustulosus* species group (Ryan & Rand 1993b, *in press*).

**Table I.** Summary of female choices in two-speaker phonotaxis experiments

	Stimulus pairs		<i>P</i> (two-tailed binomial)
	Call 1	Call 2	
	0.5-amp whine-chuck	Whine	
First test	9	11	0.82
Second test	10	10	1.00
	Prefix-whine	Whine-chuck	
First test	11	9	0.82
Second test	11	9	0.82
	Whine-whine	Whine-chuck	
First test	6	14	0.115
Second test	4	16	0.012

Repeated tests on individual females were separated for statistical analysis (first test, second test) to eliminate any replication effect.

In these tests, both of the alternatives to the chuck represent complex features used by males of closely related species; *P. pustulatus* males adorn their calls with prefixes and *P. colorodorum* males often produce whines in groups of two or more.

### Statistical Analysis

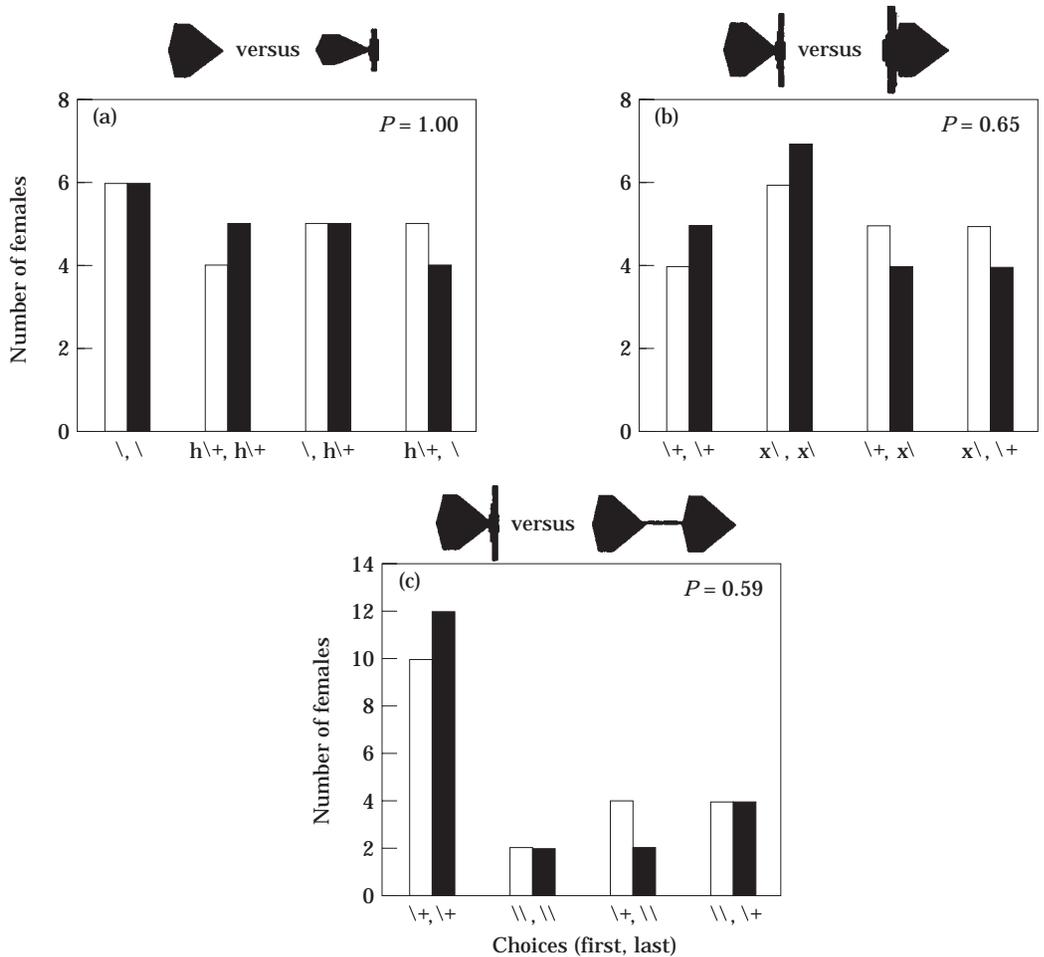
We evaluated overall female preference in stimulus pairs using a two-tailed binomial probability on the pooled data for each pair. We analysed the first and second tests of each female separately to eliminate any replication effect. We tested the null hypothesis that individual females choose randomly (i.e. that each of the four possible choice sequences occurs with equal frequency) using a two-tailed Fisher's exact test. Where overall preferences for stimuli are not equal, Fisher's exact test takes these differences into account.

## RESULTS

In two of the experiments, whine versus 0.5-amp whine-chuck and whine-chuck versus prefix-whine, females as a group chose each of the two stimuli with equal frequency in both the first and second tests conducted on each female (Table I). In the experiment of whine-whine versus whine-chuck, the majority of females chose the whine-

chuck, although this result was statistically significant only in the second test (Table I). In phonotaxis experiments performed in previous years, females as a group chose the two stimuli of all pairs with nearly equal frequency (Ryan & Rand 1990, in press). Chi-square analysis, however, showed that in no case were differences significant between the results of the first and last test and between years (whine versus 0.5-amp whine-chuck,  $\chi^2_2=0.93$ , NS; whine-chuck versus prefix-whine,  $\chi^2_2=1.20$ , NS; whine-chuck versus whine-whine,  $\chi^2_2=2.93$ , NS).

The absolute number of repeated versus non-repeated choices were as follows: whine versus 0.5-amp whine-chuck, 11:9; whine-chuck versus prefix-whine, 12:8; whine-chuck versus whine-whine, 14:6 (Fig. 3). In the tests of whine versus 0.5-amp whine-chuck, and whine-chuck versus prefix-whine, the second choice was clearly independent of the first choice made. In their second test, approximately half of the females chose the same stimulus, and half chose the alternative stimulus. In the test of whine-chuck versus whine-whine, more females appeared to make consistent choices. As stated above, however, overall female preference was skewed towards the whine-chuck. Figure 3 shows the expected values for each of the four possible choice sequences given the null hypothesis of no consistency. These values were calculated from the binomial expansion of the proportion of females choosing each of the two stimuli in their first



**Figure 3.** Results of phonotaxis experiments for the three stimulus pairs. (a) Whine versus 0.5-amp whine-chuck (\: whine, h\+: 0.5-amp whine-chuck). (b) Whine-chuck versus prefix-whine (\+: whine-chuck, x\: prefix-whine). (c) Whine-chuck versus whine-whine (\+: whine-chuck, \: whine-whine). □: The expected choices for each of the four possible response sequences in repeated female tests, given the null hypothesis of no consistency. The expected number of females choosing in each of the four choice sequences was generated by the binomial expansion of the proportion of females choosing each stimulus in the first test conducted on each female. ■: Female choices. The null hypothesis was assessed by two-tailed Fisher's exact test.

test. Even for the test of whine-chuck versus whine-whine, the observed data did not differ significantly from the expected. When evaluating the repeatability of female choice, Fisher's exact test takes into account asymmetry in absolute preference. As a result, in no case did the females' choices deviate from the null hypothesis: females showed inconsistency of mate choice for the stimulus pairs presented ( $P > 0.59$  in all cases).

## DISCUSSION

For these three pairs of stimuli for which there are no population preferences, female túngara frogs did not make choices consistently. This result indicates that the variation in responses seen in the population is mirrored by equal variation within individual females and is not an emergent property of the population. Thus, individual females are also permissive in their preferences for

complex male calls. The chuck portion of the call may be replaced with alternative call adornments, which in these experiments were a *P. pustulatus* prefix or repetition of the whine. The preference for the whine–chuck also may be eliminated by a substantially louder whine. These large changes do not seem to bias the phonotactic response to the male call.

The lack of evidence for a fixed individual preference with respect to the stimulus pairs tested in these experiments, however, does not indicate that there is no genetic variation in female responses for any other stimuli. Certainly, genetic variation in responses may exist but be on a quantitatively different scale than the stimuli presented. The complex characters of each pair presented in these phonotaxis experiments may have been similar enough to fall within the broad preference of all individual females. Thus, females show a lack of repeatable preference for the call alternatives used in this study. Females may differ, however, in the amount of variation that is allowable. Similarly, females may also differ in the strength of their preference for individual stimuli (Wagner et al. 1995). In the test of whine–chuck versus whine–whine, 12 females consistently chose the whine–chuck (Fig. 3c). It is possible that these females had very strong preferences for the whine–chuck while other females that tested inconsistently had a weaker preference for the same stimulus.

Previous female choice experiments in the túngara frog demonstrated that two alternative explanations for inconsistency of female choice are unlikely to be true for all stimulus pairs. The first alternative is that the complex portion of the call is unimportant in mate evaluation. Female preference for the male chuck has already been established, however, and it has been demonstrated that the chuck is important in sexual selection. Given a choice between a complex and simple call, females strongly prefer a whine–chuck over a whine (Rand & Ryan 1981), and they discriminate between chucks of differing dominant frequencies (Ryan 1985). The chuck is also likely to be important in sexual selection, since studies have shown that the chuck increases the attractiveness but decreases the survivorship of the male. Predators such as the frog-eating bat, *Trachops cirrhosus*, are also attracted to the chuck portion of the call (Ryan et al. 1982); if there were no female preference for the chuck, the maintenance

of this otherwise detrimental male trait would be unlikely.

The second alternative interpretation for low repeatability of female choice is that females were not able to distinguish between the two stimuli presented. A lack of differential response to different stimuli can be attributed to one of two different phenomena (Nelson & Marler 1990). Either the differences between the stimuli are not noticeable to the individual being tested, or the individual perceives the difference between the two stimuli but does not find it important. ‘Just-noticeable differences’ are those which the individual can perceive. ‘Just-meaningful differences’, on the other hand, are differences in signals that warrant a difference in response (Nelson & Marler 1990). For at least one of our tests, it is likely that the differences between the two stimuli fall within the range of just-noticeable differences. Females can discern between a solo whine and a whine–chuck at normal amplitudes (Rand & Ryan 1981); they should therefore be able to discriminate between a normal amplitude whine and a whine–chuck of lower amplitude. That this difference is not meaningful to females probably reflects a trade-off between two important call variables, amplitude and complexity. For the other two stimulus pairs, however, this conclusion is less clear.

The sensory exploitation hypothesis, which asserts that males evolve traits that take advantage of pre-existing biases in the sensory systems of females (Ryan 1990), has been invoked in the evolution of mating signals in the túngara frog. Females of two different species in the *P. pustulosus* species group show a similar preference for the complex characters of either conspecifics or heterospecifics (Ryan & Rand 1993b, in press), pointing to the existence of a preference for complex calls preceding the evolution of the chuck itself. In the species group, a permissive female preference for complex calls would allow specific adornments to the male’s whine to evolve along different paths in different species. Several members of the species group seem to have taken advantage of this flexible bias; in addition to *P. pustulosus*, three other members of the species group produce complex calls. One of the adornments, produced by *P. friebergi* males, is similar to the *P. pustulosus* chuck. The other two adornments, the *P. pustulatus* prefix and the *P. coloradum* whine groups, are unlike the

*P. pustulosus* chuck (Ryan & Rand 1993b, in press).

Previous work (e.g. Rand et al. 1992; Ryan & Rand 1993b, in press) addressed the effects of alternative call adornments on the population as a whole. Based on flexible population responses to variation in complex calls, Rand et al. (1992) suggested that, within certain bounds, the female preference in túngara frogs may simply be for greater auditory stimulation rather than for specific call characters. For this to be the case unequivocally, however, a lack of individual female preference for specific call characters needs to be demonstrated to dispel the possibility of a preference polymorphism within the population. Although females as a group showed no preference for the conspecific adornment over alternative adornments, it is possible that distinct preferences were obscured by the pooling of population data. Each female could have a clearly defined preference for one particular whine adornment which differed from the distinct preference of other females. Gerhardt (1991) addressed this unknown as a major problem in current phonotaxis experiments in anurans and suggested that the repeatability of female choice be assessed to differentiate between- and within-individual variation in preference.

Among- and within-individual variation in female responses both allow for the evolution of different call adornments. The predictions of these two prospects, however, differ enormously. If the observed permissiveness resulted from the averaging of a preference polymorphism within the population, this polymorphism could drive population divergence and speciation, even in sympatry (Turner & Burrows 1995). Consistency data from the current study, however, indicate that the variation is instead within individuals. This in turn lends further experimental support to the hypothesis that females themselves have broad preferences, which subsequently allowed for the evolution of several different call adornments in existing species of the *P. pustulosus* species group, a conclusion concordant with the sensory exploitation hypothesis and phylogenetic data from this species.

A broad preference could promote multiple pathways for acoustic stimuli to elicit increased auditory stimulation once conspecific mate recognition is elicited by the whine. For example, in whine versus 0.5-amp whine-chuck, increased

amplitude counters complexity, although the amplitude must be more than doubled before reversal is observed (Ryan & Rand 1990). In whine-whine versus whine-chuck, repetition of the simple call, and not stimulation of additional auditory neurons or auditory end organs, affords increased stimulation. Female preference thus is not a simple correlation between auditory tuning and male trait but involves complex neural circuits. The responses of the units might be influenced further by complex processes such as neural adaptation, habituation, sensitization and hormonal effects.

Previous population-level data in *P. pustulosus* indicate a permissive female preference, possibly for greater neural stimulation. Given a choice between different call adornments with the potential to elicit equal neural stimulation, females show no preference. The current study adds to this work, demonstrating that the permissive preference seen in the population is a characteristic of the females themselves, and not the result of the averaging of a preference polymorphism in the population. This permissive female preference complements phylogenetic data from the *P. pustulosus* species group, which indicate that the male call has evolved along several possible paths to exploit the sensory biases of females. The nature of the broad female preference, and the complex neurophysiological underpinnings responsible for defining female preferences, should be a subject of future theoretical and empirical research.

## ACKNOWLEDGMENTS

This project was supported by a National Science Foundation grant (IBN 9316185) to M. J. Ryan and A. S. Rand and a Smithsonian Scholarly Studies Award to A. S. Rand and M. J. Ryan. In addition, we thank Carl Gerhardt and two anonymous referees for their helpful comments on an early version of this manuscript.

## REFERENCES

- Arak, A. 1988. Female mate selection in the natterjack toad: active choice or passive attraction? *Behav. Ecol. Sociobiol.*, **22**, 317–327.
- Andersson, M. 1994. *Sexual Selection*. Princeton, New Jersey: Princeton University Press.

- Bakker, T. C. M. 1993. Positive genetic correlation between female preference and preferred male ornament in sticklebacks. *Nature, Lond.*, **363**, 255–257.
- Boake, C. R. B. 1989. Repeatability: its role in evolutionary studies of mating behavior. *Evol. Ecol.*, **3**, 173–182.
- Falconer, D. S. 1989. *Introduction to Quantitative Genetics*. New York: Longman.
- Gerhardt, H. C. 1991. Female mate choice in treefrogs: static and dynamic acoustic criteria. *Anim. Behav.*, **42**, 615–635.
- Jennions, M. D., Backwell, P. R. Y. & Passmore, N. I. 1995. Repeatability of mate choice: the effect of size in the African painted reed frog, *Hyperolius marmoratus*. *Anim. Behav.*, **49**, 181–186.
- Möller, A. P. 1994. Repeatability of female choice in a monogamous swallow. *Anim. Behav.*, **47**, 643–648.
- Nelson, D. A. & Marler, P. 1990. The perception of birdsong and an ecological concept of signal space. In: *Comparative Perception* (Ed. by W. C. Stebbins & M. A. Berkley), pp. 443–478. New York: John Wiley.
- Rand, A. S. & Ryan, M. J. 1981. The adaptive significance of a complex vocal repertoire in a neotropical frog. *Z. Tierpsychol.*, **57**, 209–214.
- Rand, A. S., Ryan, M. J. & Wilczynski, W. 1992. Signal redundancy and receiver permissiveness in acoustic mate recognition by the túngara frog, *Physalaemus pustulosus*. *Amer. Zool.*, **32**, 81–90.
- Ryan, M. J. 1985. *The Túngara Frog: a Study in Sexual Selection and Communication*. Chicago: The University of Chicago Press.
- Ryan, M. J. 1990. Sexual selection, sensory systems and sensory exploitation. *Oxf. Surv. evol. Biol.*, **7**, 157–194.
- Ryan, M. J. & Rand, A. S. 1990. The sensory basis of sexual selection for complex calls in the túngara frog, *Physalaemus pustulosus* (sexual selection for sensory exploitation). *Evolution*, **44**, 305–314.
- Ryan, M. J. & Rand, A. S. 1993a. Phylogenetic patterns of behavioral mate recognition systems in the *Physalaemus pustulosus* species group (Anura: Leptodactylidae): the role of ancestral and derived characters and sensory exploitation. In: *Evolutionary Patterns and Processes* (Ed. by D. R. Lees & D. Edwards), pp. 251–267. London: Academic Press.
- Ryan, M. J. & Rand, A. S. 1993b. Sexual selection and signal evolution: the ghost of biases past. *Phil. Trans. R. Soc. Ser. B*, **340**, 187–195.
- Ryan, M. J. & Rand, A. S. In press. Phylogenetic inference and insights into the evolution of communication in túngara frogs. In: *Neural Bases of Communication* (Ed. by M. Konishi & M. Hauser). Cambridge: MIT Press.
- Ryan, M. J., Tuttle, M. D. & Rand, A. S. 1982. Sexual advertisement and bat predation in a neo-tropical frog. *Am. Nat.*, **119**, 136–139.
- Shaw, K. 1995. Phylogenetic tests of the sensory exploitation model of sexual selection. *Trends Ecol. Evol.*, **10**, 117–120.
- Turner, G. F. & Burrows, M. T. 1995. A model of sympatric speciation by sexual selection. *Proc. R. Soc. Lond. Ser. B*, **260**, 287–292.
- Wagner, W. E. Jr, Murray, A.-M. & Cade, W. H. 1995. Phenotypic variation in the mating preferences of female field crickets, *Gryllus integer*. *Anim. Behav.*, **49**, 1269–1281.
- Wilczynski, W., Rand, A. S. & Ryan, M. J. 1995. The processing of spectral cues by the call analysis system of the túngara frog, *Physalaemus pustulosus*. *Anim. Behav.*, **49**, 911–929.