12. Although much intelligible synthetic speech would also be judged unnatural, this may be ascribed to the practice of presenting the speech cues in contexts of minimal variation in the acoustic parameters that are irrelevant to intelligibility, but which affect speech quality nonetheless [Liberman and Cooper, in (*11*)]. A synthesizer that produces a harmonic spectrum, broadband formants, and a fundamental period within the normal range will sound unnatural, and perhaps be unintelligible, despite the acoustic resemblance to natural speech if the synthesis of prosodic variation—of speech rhythm, meter, and melody—is inappropriate [J. Allen, *Proc. IEEE* **64**, 433 (1976)]. The judgment that this kind of synthetic imitation of speech signals is unnatural is, therefore, quite different from the judgment of unnaturalness in the present case.
13. Although the intelligibility of our sinusoidal sentence is predicted by the co-occurrence of tones 1 and 2 but not of tones 1 and 3, the effectiveness of each tone pair will vary as a function of the phonetic composition of the particular utterance. While the resonance associated with the oral cavity is thought to be primary for phonetic perception [G. M. Kuhn, *J. Acoust. Soc. Am.* **65**, 774 (1979)], either the second or third formant may be affiliated with the oral cavity, depending on the phone in question [K. N. Stevens, in *Human Communication: A Unified View*, E. E. David and P. B. Denes, Eds. (McGraw-Hill, New York, 1972)]. Therefore, the critical tone pair will sometimes include tone 2 and sometimes tone 3, depending on the phonetic composition of the utterance.
14. The proposal that listeners "track" formant frequency variations can be entertained as an explanation of our findings only if the meaning of the term formant is extended to mean "any peak in the spectrum." In its present sense, formant refers to a natural resonance of the vocal cavities [L. Hermann, *Arch. Gesamte Physiol.* **58**, 264 (1894)]. Quite literally, then, there are no vocal resonances in our tone complexes (although listeners who succeed in extracting the meaning probably do so because the tones preserve time-varying properties of vocally produced signals). Our preference is to retain the literal meaning of formant and to conclude, therefore, that the difference between voiced speech signals and the tonal signals is that the former contain broadband formant structure and harmonic spectra while the latter contain merely inharmonic peaks with infinitely narrow bandwidths.
15. Our finding is related, in some sense, to early studies of "vowel pitch," in which simple steady-state tones were judged to possess "vocality," or speechlike qualities [W. Kohler, *Z. Psychol.* **58**, 59 (1910); J. D. Modell and G. J. Rich, *Am. J. Psychol.* **26**, 453 (1915); E. B. Titchener, described in E. G. Boring, *Sensation and Perception in the History of Experimental Psychology* (Holt, New York, 1942), p. 374]. More recent studies have shown that listeners may identify brief complex sinusoidal patterns as isolated syllables, and therefore as speech sounds, when they are supplied with restricted response alternatives in judgment tasks with low uncertainty [J. E. Cutting, *Percept. Psychophys.* **16**, 601 (1974); P. J. Bailey, A. Q. Summerfield, M. Dorman, *Haskins Laboratories Status Report on Speech Research, SR-51, 52* (1977), p. 1; C. T. Best, B. Morrongiello, R. Robson, *Percept. Psychophys.*, in press; M. E. Grunke and D. B. Pisoni, in *Proceedings of the Ninth International Congress of Phonetic Sciences* (Institute of Phonetics, Copenhagen, 1979), vol. 2, p. 461]. The present study, however, makes use of neither a closed response set nor a judgment task with low uncertainty to obtain the effect of intelligibility.
16. We recently synthesized "A yellow lion roared," thereby extending the range of tone synthesis to nasal manner as well as the stop consonant, liquid consonant, and vowel phone classes represented here. Similar findings have been obtained with this sentence, indicating that the present results are not due to peculiarities of the sentence used in these tests.
17. We thank C. Marshall, J. Montelongo, and S. Gans for their assistance. We also thank D. Aslin, P. Bailey, A. Liberman, and F. Restle, among many others, for very helpful advice and comments on an earlier version of the manuscript. This research was supported by grants MH 32848 (R.E.R.) and MH 24027 (D.B.P.) from the National Institute of Mental Health and by grant HD-01994 from the National Institute of Child Health and Human Development to Haskins Laboratories.

4 August 1980; revised 23 December 1980

Mate Selection and Behavioral Thermoregulation in Fowler's Toads

Abstract. *Male Fowler's toads produce mating calls that are affected by the body size and temperature of the caller. Females are able to discriminate between variations in these calls and select the largest available males. By thermoregulation, males are able to alter their calls to make them more attractive to females.*

In courtship, avian and mammalian males commonly advertise their status vocally, visually, or chemically to potential mates. Many males of the order Anura also vocally communicate their species, sex, and reproductive status to receptive females (*1*). Unlike birds and mammals, amphibians are ectothermic, which is often considered a primitive condition in vertebrates. The lack of physiological thermoregulation, however, confers on toads an ability more typical of humans: vocal deception during courtship.

Mate selection has been shown to occur in a number of toad species (*2, 3*). All studies demonstrate that the size of the male is important. While each observes that there are many more males than females at the breeding site, most argue that female choice is responsible for nonrandom matings. All suggest that females exercise their preferences by discriminating among the calls of conspecific males.

If females select males by size, we would expect some aspect of a male's call to be associated with his size. The calls of Fowler's toads *(Bufo woodhousei fowleri)* appear to be related to the size of the caller (*4*). Larger males tend to produce calls that are longer in duration and lower in frequency and pulse rate than the calls of smaller males. Some of these trends occur in other anuran species (*5*).

Although, until recently, little attention has been given to the size-sound correlates of anuran vocalizations, considerable interest has been shown in the effects of temperature on anuran mating calls (*4, 6*). In general, as temperature increases, male calls are shorter in duration and higher in frequency and pulse rate. In other words, the effects of temperature are the opposite of the effects of size. Herein lies the problem for the selecting female. How can she discriminate between a large warm male and a small cold male?

Because of the confounding effects of size and temperature on mating calls, the abilities of females to discriminate between males may be affected if females preferentially selects the calls of males of a certain size class and if the males are not distributed around the pond randomly with respect to body size and temperature. To assess the roles of discrimination and behavioral thermoregulation in mate selection, we studied a small population of Fowler's toads in Durham, North Carolina.

To determine whether matings were random, we collected pairs in amplexus and unmated, calling males on nights of heavy breeding activity. The length (snout to ischium) of all individuals was measured with vernier calipers. From these measurements it is clear that Fowler's toads are sexually dimorphic with respect to body size. Females (67.9 ± 6.6 mm) were significantly larger than males (60.5 ± 3.9 mm) [Student's t (56) = 5.240, $P < .001$]. There is little or no assortative mating based on size in this species. When females have the maximum opportunity to select preferred males, the sizes of the females are not significantly correlated with those of their mates (*7*). Matings, however, are not random. Mated males are significantly larger than unmated males (57.6 ± 3.3 mm) [(Student's t (43) = 2.90, $P < .005$]. Females clearly select the larger males, as has also been shown for *Bufo quercicus* (*3*).

To determine whether females discriminate between conspecific males solely on the basis of their calls, we stripped the amplexed females of their mates, refrigerated the females overnight, and exposed them to two mating calls the following evening. The test calls corresponded to those of large males of different sizes (*8*) and were played at equal volume over loudspeakers 4.5 m apart at the ends of a screened T-maze. After 5 minutes' exposure to the calls, the females, housed in modified Bartlet squirrel traps, were released one at a time from the base of the T by lifting the trap door. The orientation and position

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of the females were recorded immediately before and 5 minutes after their release. She was assumed to have responded to the calls if she was found within 0.5 m of either loudspeaker. Of the 22 females tested, 12 faced the call of the larger male before release, while only three faced the call of the smaller male. Given the opportunity to approach either call source, all responding females (N = 14) selected the call of the larger male. Thus, not only are females able to discriminate between males solely on the basis of their calls, they also prefer calls that are associated with larger body size.

The great discrepancy between the number of males and females during nights of breeding activity suggests that male competition is also an important component of the breeding system. Several mechanisms that tend to reduce male competition, at least at the time when females select their mates, have been documented. Such mechanisms include territoriality (*9, 10*), acoustic spacing (*11*), and the exclusion of some males from the breeding population (*12*). In certain cases, these mechanisms do not allow females to select from among the winners of male competition. In *Rana catesbeiana* bullfrogs, for example, small males, which are least likely to be selected, attempt to intercept females (*10*). Interception of incoming females is a strategy that is effectively employed by *Hyla cinerea* males (*13*). In fact, *Bufo bufo* males appear to actively search the pond for females (*14*).

Although a male may increase his chances of gaining a mate by actively searching for and intercepting females, which enter the pond area silently, mating calls are still the most important factor contributing to his success (*15*). Breeding commonly occurs at night, often during heavy rains. It follows that acoustic communication is likely to be far more important than visual or olfactory communication. Consequently, it is likely that the temperature of the calling site is important, due to the effects of temperature on mating calls.

To assess whether males were randomly distributed about the pond, all captured males on a given night were measured and classified as to whether they were calling from the pond bank or from the water at the pond's edge. The water temperature was 20°C and the air temperature 22°C. Air, land, and water temperatures are good indicators of body temperature (*16*). The results (Fig. 1) show that the males in the water were significantly larger than the males on the bank [Student's t (30) = 2.26, $P < .05$].

Table 1. Relation between size of male Fowler's toad and temperature of water or land where caught.

Size	Number of males			Total
	Cold	Warm	Hot	
Small	2	4	1	7
Medium	10	10	8	28
Large	5	2	1	8
Total	17	16	10	43

The above findings are confirmed by data that were collected throughout the breeding season as part of another aspect of the study. Captured males were classified as small (52 to 56 mm), medium (57 to 61 mm), or large (62 to 67 mm). The temperature of the site where each male was caught was classified as cold (14.5° to 16.4°C), warm (16.5° to 18.4°C), or hot (18.5° to 20.4°C). The number and size of males found in each temperature class are shown in Table 1. Large males were most commonly found in cold microhabitats [G (4) = 20.52, $P < .005$].

Gerhardt (*17*) showed that female gray tree frogs (*Hyla versicolor*) prefer males whose calls indicate a body temperature similar to that of the selecting females. Their preference may enable them to discriminate between conspecific males and males of their sibling species *Hyla chrysoscelis*. But, no calling site selection based on temperature has been shown for gray tree frogs.

Fowler's toads represent, to my knowledge, the first documented case of behavioral thermoregulation in mate selection by amphibians. By calling from cold microhabitats, large males are able to alter their calls to make themselves sound larger than they really are and thereby increase their attractiveness to females.

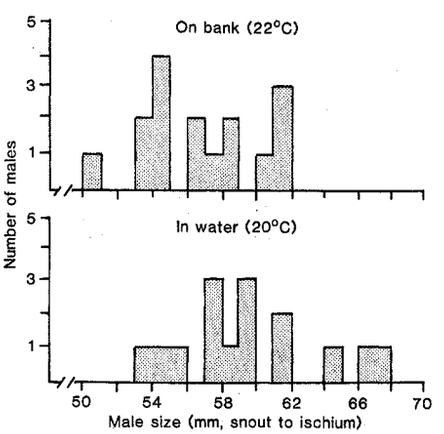

Fig. 1. Size distributions of male Fowler's toads calling from the pond bank or from the water. Temperature was estimated to the nearest 0.5°C from measurements obtained with a dry-bulb field thermometer with 1°C graduations.

There is, however, a cost to large males in selecting colder calling sites in the water at the pond's edge. By occupying these sites, large males effectively displace smaller males onto the warmer pond bank. On the bank, smaller males may be even less attractive to females due to the effect of the warmer temperature on their calls, but they have first access to females entering the pond from the outlying fields and woods.

LINCOLN FAIRCHILD*
Department of Zoology,
Duke University,
Durham, North Carolina 27708

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7. The maximum opportunity for a female to select a preferred male occurs when the ratio of available males to selecting females is greatest. This occurs early in the evening on nights when many females enter the pond or on nights when very few females enter the pond. The correlation between the sizes of mated pairs is not significant in either case.
8. The two test calls that were used came from one call produced by a large male (65.4 mm) and recorded in the field. Two duplicate continuous tape loops were made of this call. One of these loops was played at normal speed. The other was played slightly slower, resulting in a call that was of slightly lower frequency, longer duration, and lower pulse rate than the other call. The slowed call corresponded to that of a larger male (about 69 mm). Since males in the population ranged from 52 to 69 mm in length, both these calls represent those of large males, one slightly larger. The larger male call was 1.8 seconds in duration, 1.8 kHz, and 104 pulses per second. The smaller male call was 1.0 second in duration, 2.1 kHz, and 130 pulses per second. These calls were played on separate channels, randomly determined, of a stereo amplifier.
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18. I thank J. F. Downhower for critically reading the manuscript; P. H. Klopfer, H. M. Wilbur, S. Vogel, and R. P. Erickson for their helpful comments on the manuscript; and P. J. Morin and E. A. Fairchild for their assistance in the field. Partially supported by a research-in-aid award from Sigma Xi and by a grant from the Graduate School of Duke University.
* Present address: Department of Zoology, Ohio State University, Columbus 43210.

22 September 1980; revised 18 March 1981