

Mating call characteristics of hybrid toads (*Bufo americanus* × *B. fowleri*) at Long Point, Ontario

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The mating calls of the toads *Bufo americanus*, *B. fowleri*, and their natural hybrids were recorded in May 1981 at Long Point, Ontario, on the northern shore of Lake Erie. The calls of the two species differed substantially in pulse rate and call duration but much less so in terms of dominant frequency. The numbers of pulses per call were not significantly different. Calls of hybrids were intermediate in character. Values for pulse rate, call duration, and dominant frequency agreed with those previously described. The relationship between pulse rate and call duration is hyperbolic as pulse number appears to be relatively constant. The differences in the calls of *B. americanus* and *B. fowleri* appear to be fundamentally due to mechanical properties of the pulse modulating apparatus of the larynx. The characteristics of the calls of the hybrids may be due to intermediate morphology of the laryngeal cartilages that modulate the pulses of a call.

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Les cris d'appel sexuels des crapauds *Bufo americanus*, *B. fowleri* et leurs hybrides naturels ont été enregistrés à Long Point, Ontario, sur la côte nord du lac Érié, en 1981. Les cris d'appel des deux espèces diffèrent considérablement par la durée, mais beaucoup moins par les fréquences dominantes. Le nombre de pulsations par cri n'est pas significativement différent chez les deux espèces. Les cris des hybrides sont intermédiaires. Le nombre de pulsations par cri, la durée et la fréquence dominante ont des valeurs semblables à celles qui ont été décrites antérieurement. La relation entre la fréquence des pulsations et la durée du cri est hyperbolique, car le nombre de pulsations semble relativement constant. Les différences entre les cris des deux espèces semblent dues fondamentalement aux propriétés mécaniques de l'appareil modulateur de fréquences dans le larynx. Il est probable que les caractéristiques des cris des hybrides soient reliés à la morphologie intermédiaire des cartilages du larynx qui modulent les pulsations.

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Introduction

The mating, or advertisement (Wells 1977a), calls of anuran amphibians are important characteristics in species identification enabling mate recognition and social interaction (Bogert 1960; Blair 1968; Wells 1977a, 1977b). Anuran vocalisations often allow positive discrimination between similar or cryptic species (Straughan 1973; Littlejohn 1977). The morphologically indistinguishable treefrogs *Hyla versicolor* and *H. chrysoscelis*, for instance, were first recognized by their distinctive advertisement calls (Blair 1958; Johnson 1966). Except for the frequency modulated calls of *Bufo quercicus*, the mating calls of toads, genus *Bufo*, generally consist of amplitude-modulated series of pulses produced by shunting air through the larynx between the lungs and vocal sac (Martin 1972). The vocal chords produce a carrier, or dominant frequency, which is modulated by the arytenoid cartilages to produce pulses (Martin 1971, 1972; Littlejohn 1977). The distensible vocal sac beneath the chin serves to couple the call to the atmosphere. The repetition rate and modulation of the pulses, the dominant frequency, and the duration of the call are the major variables determin-

ing the differing calls of most toad species. The mating calls of the American toad, *Bufo americanus*, and Fowler's toad, *B. fowleri* (also known as *B. woodhousei fowleri* following Meacham (1962)), differ substantially in duration and pulse rate (Zweifel 1968). These two species are broadly sympatric over much of eastern North America and hybrids between them are documented from many localities (Blair 1941; Volpe 1952; Cory and Manion 1955; Jones 1973). The study of the calls of hybrids may yield valuable information about the genetic and behavioural control of the calls of the hybridizing species (Littlejohn 1977). Zweifel (1968) examined the effects of hybridization on the mating calls of *B. americanus* and *B. fowleri* in New Jersey and Jones (1973) has also presented mating call data concerning these toads.

Hybrid toads have been identified morphologically and genotypically among populations of *B. americanus* and *B. fowleri* on the northern shore of Lake Erie at Long Point, Ontario (D. M. Green 1981, unpublished observations). The present report describes the calls of these hybrids and compares them with the calls of the two parental species.

Materials and methods

The mating calls of 18 male toads were recorded on May 5, 1981, at Long Point, Ontario, using a Uher Report I/C 4000 tape recorder and Uher microphone. The toads were calling from a region of swamp on the northern side of the point between Brant Parkway and Pines Parkway. At least three calls from each individual were recorded. Each toad was captured after its calls had been recorded and its temperature was immediately taken by inserting a thermometer into its throat. Toads were toe clipped for later identification and all are now deposited in the National Museum of Natural Sciences, Ottawa (NMNS Nos. 21963-5).

Audiospectrograms of three calls from each individual were produced with a Kay Elemetrics Corp. Vibralyzer sonagraph using both wide band and narrow band settings. Pulse rates and dominant frequencies were calculated from the audiospectrograms. Durations of calls were determined from the tape recordings by using a stopwatch. The numbers of pulses per call were estimated from duration and pulse rate figures.

Results

Calling toads did not seem to be randomly distributed through the breeding area of the swamp. Distinct single species choruses of 10 to 25 toads were separated by about 5 to 10 m. Calling hybrids, however, tended to be located in between choruses of each species or in mixed choruses.

Values for pulse rate, call duration and, to a lesser extent, dominant frequency are closely correlated in toads with body temperature (Zweifel 1968). All recorded individuals had throat temperatures of 16°C, so that it was unnecessary to compensate for temperature effects. Three classes of calls could be subjectively distinguished at Long Point, corresponding to toads morphologically identifiable as *B. americanus*, *B. fowleri*, or hybrids. The distinguishing physical characteristics of these toads are well documented (Wright and Wright 1949; Conant 1975).

The dominant frequencies of the calls of the recorded individuals were between 1500 and 2000 Hz, with a mean of 1770 ± 30 Hz (SE). While the calls of *B. americanus* and *B. fowleri* differed slightly, yet significantly, in dominant frequency, using a *t*-test ($p = 0.05$), their dominant frequencies were not significantly different from those of the hybrids. Dominant frequency correlates negatively with body size (Zweifel 1968). *Bufo fowleri* is smaller, on average, than *B. americanus* and this difference may account for its higher observed dominant frequencies. Body size, as measured by snout-vent length, is not significantly correlated with other parameters of the calls (Zweifel 1968).

The values for pulse rate, call duration and number of pulses per call are listed in Table 1. The advertisement calls of *B. americanus*, *B. fowleri*, and the hybrids were all significantly different from each other in pulse rate and duration ($p = 0.05$). The calls of the hybrids were

intermediate, rather than mosaic (Littlejohn 1977), in these characteristics. The recorded values for pulse rate and call duration (Table 1) for the calls of both species, and their hybrid, are very close to those predicted for a temperature of 16°C by Zweifel (1968).

Despite the significant differences in pulse rate and duration between the calls of *B. americanus*, *B. fowleri*, and hybrids, the number of pulses per call appeared to be quite consistent and did not differ significantly, at $p = 0.05$, between the three groups of toads (Table 1). This is a reflection of the low pulse rate but long duration of the calls of *B. americanus* in comparison with the high pulse rate but short duration of the calls of *B. fowleri*. The mean number of pulses per call was 194.6 ± 8.8 (SE).

A strong negative correlation ($r = -0.849$) was found between pulse rate and call duration. A linear regression with the equation $y = 0.075x + 8.28$ (Fig. 1) was significant using an *F* test. This straight line, though, would predict different values for the number of pulses per call at different points along its length, with a maximum value at the mean point. If the number of pulses per call was constant, though, a nonlinear, hyperbolic curve of the general formula $y = p/x$ would be the actual shape of this relationship. Using the mean values of pulse rate and call duration of the hybrids as the vertex of the hyperbola such that p equals 203.4 (the product of the x and y values of the vertex and thus the

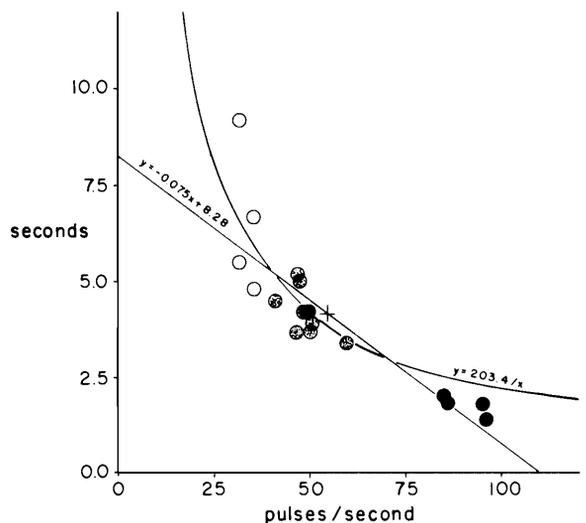


FIG. 1. Pulse rate (pulses per second) versus call duration (seconds) for the calls of toads, *Bufo americanus* (open circles), *B. fowleri* (blackened circles), and their hybrid (stippled circles). Data are from Table 1. Each point represents the mean values from three calls of a single individual. A linear regression line (mean point marked +) and a hyperbolic curve with its vertex at the mean values of pulse rate and call duration of the hybrids are plotted. The hyperbola passes through points of equal pulse number per call.

TABLE 1. Characteristics of the mating calls of toads at Long Point, Ontario, May 5, 1981. All specimens had body temperatures of 16°C. Data are averages of values from three calls from each toad. Standard errors are in parentheses. All figures are rounded to one decimal place

	Pulses/s	Call duration (s)	Pulses/call
<i>B. fowleri</i> , NMNS No. 21965(1-4)			
	85.7	1.8	154.3
	96.0	1.4	134.4
	84.8	2.0	169.6
	94.9	1.8	170.8
Means	90.4 (3.0)	1.8 (0.1)	157.3 (8.5)
<i>B. fowleri</i> × <i>americanus</i> , NMNS No. 21963(1-10)			
	50.1	3.8	187.9
	47.5	4.5	213.8
	50.7	3.9	197.7
	46.9	5.2	243.9
	48.5	4.2	203.7
	49.1	4.2	206.0
	41.1	4.5	185.0
	59.6	3.4	202.6
	46.4	3.7	171.7
	48.8	4.2	205.0
Means	48.9 (1.5)	4.2 (0.2)	203.4 (5.4)
<i>B. americanus</i> , NMNS No. 21964(1-4)			
	35.2	4.8	169.0
	35.2	6.7	235.8
	31.5	5.5	173.3
	31.2	9.2	287.0
Means	33.3 (1.1)	6.5 (1.0)	216.3 (28.1)

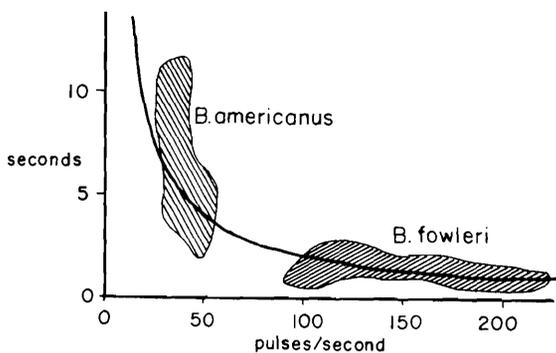


FIG. 2. Pulse rate (pulses per second) versus call duration (seconds) for the calls of toads, adapted from Jones (1973, Fig. 4, p. 441). Shaded areas bound regions occupied by individual points in the original illustration. The same hyperbola illustrated in Fig. 1 has been plotted.

average number of pulses per call of the hybrids), a hyperbolic curve has also been plotted on Fig. 1, with good agreement. Similar data and figures for pulse rate and call duration given by Zweifel (1968) and by Jones

(1973) also indicate a hyperbolic distribution. The same hyperbolic curve plotted in Fig. 1 is well applied to Jones' (1973) data (Fig. 2). Although Jones (1973) has been criticised for failure to consider the effects of temperature on the calls of toads (Loftus-Hills 1975), changes in temperature would in no way affect the shape of the curve but merely the position of points along it. All studies have found the calls of *B. americanus* to vary considerably in duration but very little in terms of pulse rate while the opposite is true for the calls of *B. fowleri*. The calls of hybrids occupy the region of the curve in between the calls of the two species.

Discussion

The acoustical data document the presence of mature male hybrids between *Bufo americanus* and *B. fowleri* at Long Point, Ontario. Allozyme data (D. M. Green 1981, unpublished data) indicate that presumed hybrid individuals at Long Point are probably of the F1 generation. The intermediacy of the call characteristics of the recorded hybrids supports this conclusion.

Pulse rate and call duration seem to be sufficient to allow discrimination between the calls of *B. americanus* and *B. fowleri* (Fig. 1). Dominant frequency has been shown to vary inversely with body size (Bogert 1960; Zweifel 1968; Martin 1972) and has been invoked as an important carrier of information for females (Licht 1976; Wilbur et al. 1978). Unlike dominant frequency, which is controlled by passive elements of the voice box, pulse rate and call duration are actively controlled by nervous impulse (Martin 1972) and appear to carry mate recognition information largely independent of body size (Zweifel 1968). A fourth parameter, pulse number per call, has not previously been widely considered. Both species of toads emit about the same number of pulses in a call despite significant but reciprocal differences in pulse rate and duration. The calls are structurally very similar, either compressed or drawn out, as the case may be (Zweifel 1968). This suggests that the number of pulses per call is under the same control in both species and provides a reason for the observed interdependence of pulse rate and call duration.

As call duration appears to be functionally dependant upon pulse rate, the underlying difference between the calls of these two species of toads may be one of simple mechanics of the pulse-modulating arytenoid cartilages of the larynx. The vibration of these cartilages governs pulse rate (Martin 1972) and, although they are activated by nervous impulse, it is their mechanical properties such as thickness and resonance frequency that determine their vibration rate. Increased DNA per cell and larger cell volumes in the tetraploid treefrog *Hyla versicolor* result in calls of lower pulse rate and longer duration than calls of its diploid sibling species, *H. chrysoscelis* (Ralin 1977). The reduced pulse rates in the calls of *H. versicolor* and of other polyploid frogs relative to the calls of their diploid counterparts (Bogart and Wasserman 1972) cannot be attributed to allelic genetical differences but to the mechanical properties of larger cells in the larynx and, by extension, thicker pulse modulating cartilages (Ralin 1977). Polyploidy and gross differences in genome size, of course, are not the only means by which vibrational differences in the arytenoid cartilages may be effected. It appears that the necessary attributes governing the differences in the calls of *B. americanus* and *B. fowleri* are not programmed behavioural differences but simply morphological differences of the pulse modulation apparatus. The characteristics of the calls of the hybrids may be explained by an intermediate morphology of this apparatus.

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