

# VOCALIZATIONS AND BEHAVIOR OF THE MALES OF THREE SPECIES IN THE *Hyla versicolor* COMPLEX

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**ABSTRACT:** Male *H. versicolor*, *H. chrysoscelis*, and *H. arenicolor* of the *Hyla versicolor* species group of tree frogs have two vocalizations in addition to the mating call; a release call and a territorial call.

The release call, in comparison with the territorial call, appears poorly tuned on a sound spectrogram, is shorter in duration, and is usually given in an irregular series dependent, in part, on the length of time a male is in contact with another male. The territorial call appears well tuned, is longer in duration, and is given in sets of one to four calls in response to calling males nearby or a human imitation of a frog mating call.

The release call appears to function as a mechanism of sex identification. The territorial call appears to function as a spacing mechanism in high density choruses. The spacing produced may aid the females in locating a particular male for mating, rather than functioning as a male-male competitive mating mechanism.

THE vocalizations of anurans and their relations to social interactions between individuals have been summarized by Bogert (1960). Additional behavior patterns, also involving vocalizations, have since been reported for many other species (e.g., Duellman, 1966; Emlen, 1968; Jenssen and Preston, 1968; Pyburn, 1964; Schneider, 1967; Whitford, 1967).

The present report deals with vocalizations in addition to the mating call of three species in the *Hyla versicolor* species group of tree frogs (Blair, 1958b), *H. versicolor* and *H. chrysoscelis* of the eastern United States and *H. arenicolor* of the western United States. The members of the group are morphologically similar, and *H. versicolor* and *H. chrysoscelis* are indistinguishable on morphological characters (Johnson, 1966). The mating calls of the members of this species group also resemble each other more than they do the calls of other North American hylids (Blair, 1958b; Figs. 1A, 2A, 3A).

A call other than the mating call, termed the "turkey root" call, has been known in *H. versicolor* for over 50 years (Overton, 1914). Noble (1954) described "a series of mournful notes" emitted by *H. versicolor* with the vocal sac partially inflated. A series of "yips" emitted by *H. versicolor* when "confused or disturbed" has also been

noted (Bragg, 1943). Individuals giving this call when changing or shifting direction were observed by Harper (1935).

These descriptions probably involve two different vocalizations which are difficult to distinguish by ear, but which can be readily distinguished by both sound spectrographic analysis and the context in which they are emitted. All three species exhibit the same types of differences between the two vocalizations.

All experimental work as well as recording was carried out in the field. The calls were recorded with either a Stancil-Hoffman Mini-tape or Uher 4000 Report-L tape recorder and were analyzed using a Model 6061A Sona-Graph (Kay Electric Co.) and a Type 502A dual-beam oscilloscope (Textronix, Inc.). The effective bandwidth of the narrow analyzing filter of the Sona-Graph was 45 Hz, that of the wide filter was 300 Hz.

## CONTEXT OF THE VOCALIZATIONS

*Type I Call.*—Type I calls are normally emitted by the males of all three species when they come in contact with or are clasped by another male. The Type I call of *H. arenicolor* males may be elicited either by placing another male in contact with it or by grasping the male dorsally. The Type I calls of *H. versicolor* and *H.*

TABLE 1.—Parameters of the Type II call of *H. arenicolor*, *H. versicolor* and *H. chrysozelis*. Frequencies in Hertz, time in seconds, pulse repetition-rate in pulses/sec. Mean in parentheses.

Species, locality & temperature (°C)	Calls	Mean dominant frequency	Duration	Intercall interval	Pulse repetition-rate
<i>H. arenicolor</i>					
Guadalajara, Mexico (20.8)	3	560	.18-.20 (.19)	.18-.22 (.20)	75-240
(21.0)	6	500	.19-.24 (.21)	.21-.26 (.24)	75-240
Gunlock, Utah (20.0)	4	500	.33-.36 (.34)	— (.59)	60-240
Chiricahua Mts., Arizona (22.0)	3	500	.13-.14 (.13)	.20-.28 (.24)	60-75 <sup>1</sup>
<i>H. versicolor</i>					
Sam Houston Nat. Forest, Montgomery Co., Texas (23.0)	3	2390	.14-.16 (.15)	— (.24)	72-85 <sup>2</sup>
Lexington, Texas (18.5)	6	2100	.14-.24 (.21)	.26-.38 (.31)	50-63 <sup>2</sup>
<i>H. chrysozelis</i>					
8 miles E Bastrop, Texas (19.8)	5	1900	.15-.19 (.16)	.24-.26 (.25)	53-61 <sup>2</sup>
(19.0)	4	1960	.14-.25 (.18)	.22-.26 (.25)	53-64 <sup>2</sup>
(19.0)	4	1880	.14-.20 (.16)	.24-.33 (.30)	64-69 <sup>2</sup>
Elgin, Texas (21.0)	2	2110	— (.16)	— (.23)	69-75 <sup>2</sup>

<sup>1</sup> Amplitude and frequency modulation similar to that seen in *H. versicolor* and *H. chrysozelis*; pulse repetition-rates of 80, 160 and 240 pulses/sec can be seen with the oscilloscope.

<sup>2</sup> Pulse repetition-rates of 80 and 160 pulses/sec may also be present; see text for explanation.

*chrysozelis* males may be readily elicited by placing two males in contact with one another, but we found it difficult to elicit the calls by hand. The Type I calls of all three species may be described phonetically as a series of high-pitched "erps" or "yips." Altig (pers. comm.) indicates that *H. avivoca* has a similar call. Contact is not needed to elicit the call in this species; however, the males must be in close proximity to one another.

**Type II Call.**—A male of any of the three species may be induced to emit the Type II call by producing a high intensity human imitation of a mating call nearby, while the frog is giving its mating call,

Individual male *H. arenicolor* from several populations (Table 1), when confronted with an imitation mating call, stopped giving their own mating calls and emitted a series of Type II calls. During one of these series a male would move about and shift position, first turning in one direction and then another. As the imitation calls were continued, the male would stop moving about, take up a fixed position, and resume giving its mating call. After a second response of this type to an imitation call, it was difficult to elicit the response again by continuing the imitation calls.

Many Type II calls have been heard spontaneously in high density choruses of

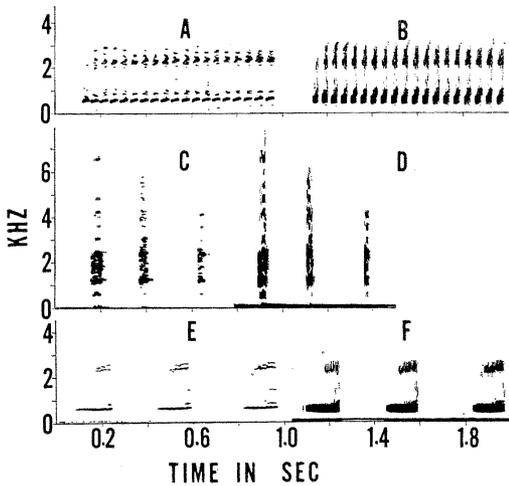


FIG. 1.—Sound spectrograms of the vocalizations of a male *H. arenicolor* from Guadalajara, Jalisco, Mexico, recorded at 21.0 C. A—mating call, narrow band filter; B—mating call, wide band filter; C—Type I calls, narrow band; D—Type I calls, wide band; E—Type II calls, narrow band; and F—Type II calls, wide band.

both *H. versicolor* and *H. chrysoscelis*. Similar calls also occur spontaneously in choruses of *H. avivoca* and *H. cinerea* (Altig, pers. comm.). The first Type II calls of *H. chrysoscelis* noted were in a breeding congress 6.5 km SE Elgin, Bastrop Co., Texas. When first approached, this chorus was thought to consist of about 40 individuals. In addition to the constant din of mating calls, notes which we assumed to be Type I calls could be heard on the order of once every 5 sec. Most of these presumed Type I calls were given in a series of two, three or four “weeps.” Closer examination revealed that for every individual giving the mating call there were at least two and frequently three or more silent males in the vicinity of the calling male. (Terrestrial groupings of silent males around a calling male in breeding congresses have been observed in both *Bufo speciosus* and *B. cognatus*, Axtell, 1959; Brown and Pierce, 1967.) In one instance only one male in a group of 3 sitting on a 20-cm segment of a branch was calling. In an-

other instance an oak sapling about 2 m high contained a group of 5 males, in which the greatest distance separating any two was no more than 0.5 m. Again only one male, near the center of the group, was calling. What factor determines which male will call is not known at the present time. The mating call of this male was recorded, and while it was calling, an imitation mating call louder than its mating call was given. During the second of these imitation calls the frog broke off its own mating call and produced a series of three Type II calls. This sequence may be seen in Fig. 3E where the first Type II call overlaps the last part of the imitation call.

In addition to the Elgin locality, spontaneous Type II calls have also been heard in Bastrop State Park, Bastrop Co. (*H. versicolor* and *H. chrysoscelis*) and Sam Houston National Forest (*H. versicolor*) in central and eastern Texas respectively.

The context in which the mating call of anurans is given has been discussed by a number of authors (Blair, 1958a; Bogert, 1960; Brown and Pierce, 1965; Littlejohn, 1958).

#### VOCAL REPERTOIRE OF *H. ARENICOLOR*

The vocal repertoire of an individual from Guadalajara, Jalisco, Mexico, is presented (Figs. 1, 4A, B).

*Type II Call.*—The Type II call has a clear harmonic structure, making it relatively easy to analyze. The dominant frequency is at about 500 Hz for most individuals of this species; however, in the particular individual from Guadalajara, Mexico, the dominant frequency is 560 Hz (Fig. 1E). In this species the dominant frequency is also the fundamental of the tone frequency. The harmonics of the tone frequency ascend as the whole multiples of the fundamental frequency. For example, the second harmonic of the fundamental frequency is about 1120 Hz (Fig. 1E).

Obviously all the harmonics apparent in Fig. 1E are not harmonics of the dominant (tone) frequency. It appears that these

additional harmonic bands are the pulse repetition-rate harmonics discussed by Watkins (1967). These result in spectrographic analysis when the pulse repetition-rate of a tone frequency exceeds the filter band width of the sound spectrograph. The harmonics produced represent the sum and difference of the tone frequency and the pulse repetition-rate (Watkins, 1967). The pulse repetition-rate may be measured on a narrow band spectrogram as the separation between the bands. This pulsing can also be seen with wide band analysis (Fig. 1F), but is more easily measured on narrow band (Fig. 1E). It can be seen from Figs. 1F and 4B that the periodicity changes within the call. At the beginning of the call a periodicity of 240 pulses/sec is present; about half-way through the call a periodicity of 80 pulses/sec appears, and in the last third of the call a periodicity of 160 pulses/sec becomes evident (Figs. 1E, F, 4B). The 80 pulse/sec fundamental of the repetition-rate adds with the 560 Hz tone frequency to give 640 Hz. A second harmonic forms at 560 Hz plus  $2(80)$ , or 720 Hz, etc. Sum frequency harmonics of the 160 and 240 pulses/sec repetition-rates can also be seen. These periodicities may be produced by different parts of the same structure operating at different rates, or they may be produced by three entirely different structures. The former may be more likely, as the periodicities appear to be whole multiples of 80.

The temporal pattern of the Type II calls, as seen in spectrographic analysis, is quite different from that of the Type I calls described in the next section. The mean duration of the Type II calls of the particular individual from Guadalajara, Mexico, is .19 (.18-.20) sec (Fig. 1F). The mean interval between calls is .20 (.18-.22) sec. Measurements of the Type II calls of individuals from several populations are presented in Table 1. In all cases the duration of the Type II calls is long compared to that of the Type I calls to be described below.

*Type I Call.*—A considerable portion of

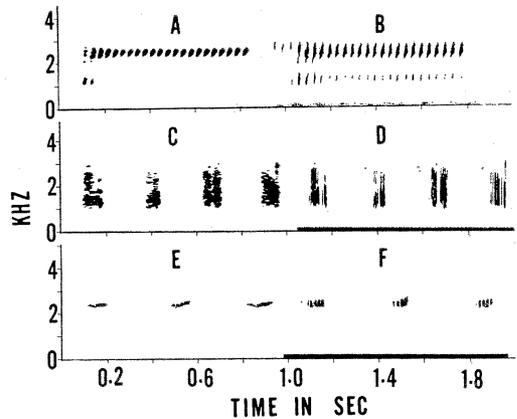


FIG. 2.—Sound spectrograms of the vocalizations of a male *H. versicolor* from eastern Texas, recorded at 23.0 C. A—mating call, narrow band filter; B—mating call, wide band filter; C—Type I calls, narrow band; D—Type I calls, wide band; E—Type II calls, narrow band; and F—Type II calls, wide band.

the energy in the Type I call is concentrated in the second, third, and fourth harmonics of the tone frequency, which has a fundamental frequency near 500 Hz. For the individual from Guadalajara, Mexico, this frequency is about 560 Hz. The higher harmonics of the fundamental of the tone frequency have more energy than those of the Type II call. At comparable intensities, harmonics of the Type II call fundamental frequency are not seen in spectrographic analysis above 3.5 kHz, while harmonics of the fundamental frequency of the Type I call extend almost to 8 kHz (Figs. 1C, E). This 500 Hz oscillator may be amplitude modulated as the Type II call, but the modulation is aperiodic.

The mean duration of the Type I calls is .049 sec and the mean interval between calls is .16 sec (Fig. 1D). Thus the Type I call of *H. arenicolor*, in addition to appearing poorly tuned compared to its Type II call, is also much shorter in duration. The number of Type I calls given by an individual male in a response sequence depends on the length of the time the male is in contact with another male or a human hand, while

Type II calls are given in sets of one to four calls per response sequence.

*Mating Call.*—The mating call of *H. arenicolor* appears to be more like its Type II call than its Type I call in overall structure. The major modification is a grouping of the pulses into pulse-bursts. The frequency composition is similar to that of the Type II calls (Figs. 1A, B).

#### VOCAL REPERTOIRE OF *H. VERSICOLOR*

The vocal repertoire of a male *H. versicolor* from Sam Houston National Forest, Montgomery Co., Texas, is presented (Figs. 2, 4-3, -4).

*Type II Call.*—The dominant frequency of the call of an individual from Sam Houston National Forest is about 2400 Hz (Fig. 2E). In this species the dominant frequency is the second harmonic of the tone frequency. Amplitude and frequency modulation of both the dominant and first harmonic can be seen in wide band analysis (Fig. 2F). The pulse repetition-rate is 50–60 pulses/sec. In addition there may be an oscillator or oscillators giving 80 and 160 pulses/sec repetition-rates as well. These can be seen as small spaces within the harmonic bands on narrow-band analysis (Figs. 2E, 4-4).

The mean duration of the calls of this individual is .15 sec. The mean interval between calls is .24 sec. A summary of the Type II calls of *H. versicolor* males from several populations is presented in Table 1.

*Type I Call.*—The energy contained in the Type I call does not spread into the higher harmonics, as in the Type I call of *H. arenicolor* (Fig. 2C). There is a great deal of energy at frequencies between the harmonics of the fundamental, but little regularity is observed. It appears that some amplitude modulator in the system vibrates in a capricious manner, moving into and then out of periodic vibration. Part of this difference in tuning may be because of a difference in the degree of vocal pouch inflation, since the pouch appears less in-

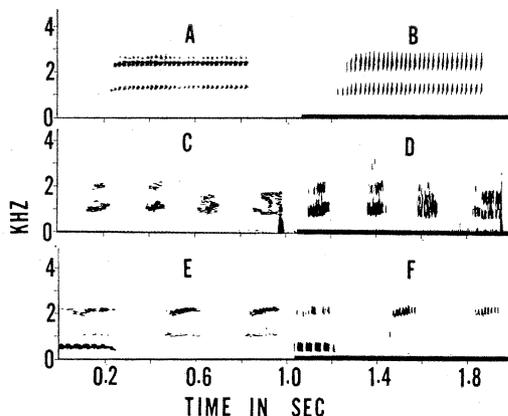


FIG. 3.—Sound spectrograms of the vocalizations of a male *H. chrysoscelis* from central Texas, recorded at 19.0 C. A—mating call, narrow band filter; B—mating call, wide band filter; C—Type I calls, narrow band; D—Type I calls, wide band; E—Type II calls, narrow band; and F—Type II calls, wide band.

flated during the Type I call than during the Type II call.

In temporal pattern the mean duration of the Type I calls is .083 sec. The mean interval between calls is .18 sec, but it is highly irregular (Fig. 2D). As in *H. arenicolor* the Type I calls are considerably shorter and less tuned than the Type II calls.

*Mating Call.*—The mating call of *H. versicolor* has a spectral energy distribution comparable to its Type II call but differs greatly from it in the patterns of amplitude and frequency modulation (Figs. 2A, B).

#### VOCAL REPERTOIRE OF *H. CHRYSOSCELIS*

The vocal repertoire of a male *H. chrysoscelis* from Elgin, Bastrop Co., Texas, is presented (Figs. 3, 4-5, -6).

*Type II Call.*—The Type II call of *H. chrysoscelis* cannot be distinguished from that of *H. versicolor*, either by ear or by spectrographic analysis. The frequency composition of the calls of the individual from Elgin happens to differ slightly from that of the *H. versicolor* previously described, but examination of Table 1 reveals

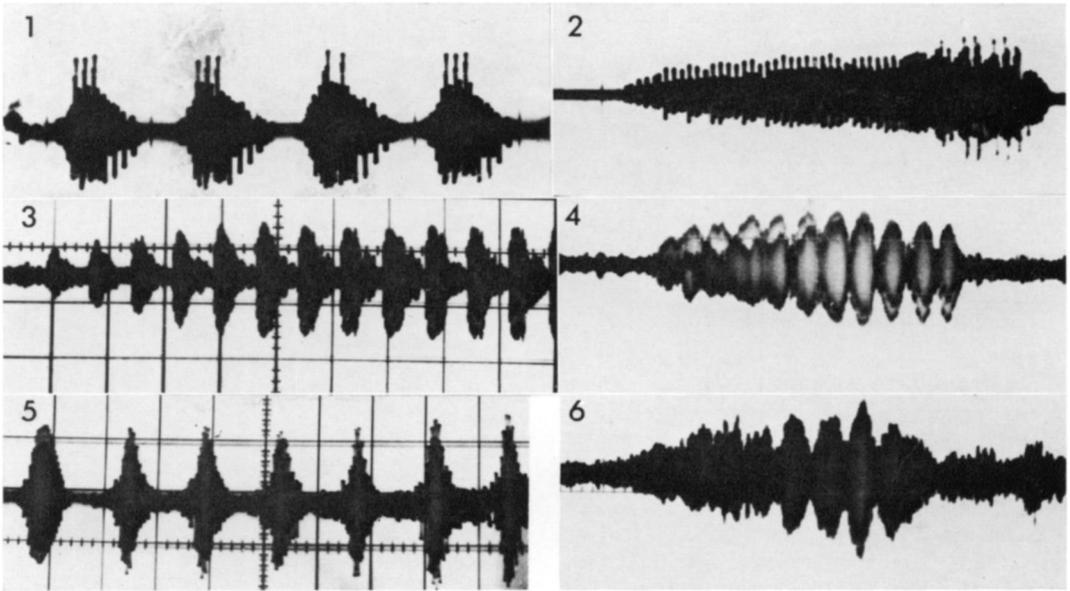


FIG. 4.—Photographs of oscilloscope tracings of the mating calls and Type II calls of the three species. (1, 2) Mating call and Type II call respectively of the *H. arenicolor* in Fig. 1, (3, 4) mating call and Type II call of the *H. chrysozelis* in Fig. 3, (5, 6) the mating call and Type II call of the *H. versicolor* in Fig. 2. (1) was taken at a sweep speed of 20 msec/cm; all others were taken at 25 msec/cm.

that these call parameters overlap when additional individuals of both species are considered. The dominant frequency is about 2100 Hz, and the first harmonic is about 1000 Hz (Fig. 3E). As in *H. versicolor*, there is amplitude and frequency modulation of the tone frequency. The pulse repetition-rate is 70–75 pulses/sec (Fig. 3F). Again it appears that there is an oscillator or oscillators producing pulse repetition-rates of 80 and 160 pulses/sec (Figs. 3E, 4–6).

The mean duration of the calls is .16 sec, with an interval between calls of .20 sec (Fig. 3F). A summary of the Type II calls of *H. chrysozelis* from two populations is presented in Table 1.

*Type I Call.*—The Type I call of *H. chrysozelis* is similar to that of *H. versicolor*. The energy in the call is not distributed in the higher harmonics of the tone frequency to any great extent (Fig. 3C). There is, however, a great deal of energy

at frequencies between the harmonics of the tone frequency. Previous suggestions regarding the causal basis for the call structure in *H. versicolor* apply to this species as well.

The mean duration of the Type I calls is .10 sec, with a mean (although highly irregular) interval between calls of .20 sec (Fig. 3D). As in *H. arenicolor* and *H. versicolor*, the Type I calls of *H. chrysozelis* are considerably shorter and less tuned than its Type II calls.

*Mating Call.*—As in previous species the mating call of *H. chrysozelis* is more similar to its Type II call than to its Type I call, the major modification again consisting of a grouping of the pulses into pulse bursts (Figs. 3A, B). The pulse burst rate of *H. chrysozelis* is about 1.7 times that of *H. versicolor* at the same temperature (Ralin, 1968) and is the only known way of distinguishing between the two species at the present time (Johnson, 1966). The

pulse burst rate of *H. arenicolor* is about .85 that of *H. versicolor* at the same temperature (Pierce, 1968).

#### DISCUSSION

In recent years information has accumulated concerning vocal communication, call structure, and behavior in anuran amphibians. The most complete study to date on the structure of anuran calls and the behavior associated with the different types of calls has been that of Capranica (1968) on *Rana catesbeiana*. This study primarily involved animals kept in the laboratory under simulated natural conditions, and it is not known whether these behaviors and vocalizations occur in wild populations, since the most complete field study of some of these behaviors (Emlen, 1968) did not include spectrographic analyses of the vocalizations. Most reports of anuran vocalizations and behavior have consisted of field observations of the behavior and phonetic descriptions of the associated vocalizations (Duellman, 1966; Whitford, 1967).

Contextually, there are adequate data to justify terming the Type I vocalization a "release" call in the sense of Bogert (1960). The adaptive value of the release call, and its role in anuran breeding congregations, seems fairly clear. It apparently serves as a mechanism of sex identification, allowing the males to save the time and energy involved in gamete production and amplexus for a successful mating.

Territorial behavior, with or without associated aggressive and warning behaviors, has at the present time been reported for less than a dozen anuran species. This behavior may be divided into two broad functional categories: (1) male-male interactions during the breeding period involving the chance or ability to mate with a female (Martof, 1953; Jenssen and Preston, 1968; Duellman, 1966; Lutz, 1960; Pyburn, 1964); and (2) interactions involving any combination of the sexes, including immature as well as sexually mature animals, which are more or less directly related

to obtaining food and shelter rather than mates (Sexton, 1960; Test, 1954). The behaviors described here obviously fall into the first category above.

To our knowledge, the earliest suggestion of territoriality in anuran breeding congregations was a study reporting that *Rana clamitans* males retained the same positions relative to one another in breeding choruses, even after movement to another breeding site (Martof, 1953). Later Brode (1959) reported that *R. clamitans* males living along creeks defended their territories from other males but allowed females to pass through the territories unmolested. Recently, Jenssen and Preston (1968) elicited a "growling" response from a male of this species by playing a mating call 2-3 m from it. The male also advanced toward the speaker. Behaviors and vocalizations associated with competition for mates have been documented for representatives of other families as well. Males of *Dendrobates galindoi* and *Prostherapis panamansis* giving the mating call exhibit territorial behavior involving both an apparent warning call and actual aggression (Duellman, 1966). Male *Scaphiopus hammondi* emit a vocalization other than the mating call and attack other males intruding into their calling territories (Whitford, 1967). Fighting between males of the nest-building species *Hyla faber*, in some cases possibly resulting in death, has been observed by Lutz (1960). There is no indication of a territorial or warning call in this species (B. Lutz, pers. comm.). The most direct competition reported between males for females occurs in the hyliid, *Phyllomedusa callidryas* (Pyburn, 1964). In this species a male will approach an amplexed pair and attempt to dislodge the male and take its place. When an intruder approached within 8 cm of a pair, both males raised the posterior portions of their bodies and uttered barely audible "clucks." These clucks were also occasionally heard from unattached males.

The adaptive value and function of the

Type II call in the *H. versicolor* complex is far from clear. From the information now available on the territorial behavior of breeding males of other species, there appears to be no general correlation between either the presence of physical aggression or its severity and the possession of a warning or territorial call. One possibility is that the Type II call in these three species simply serves as an extension of the release call, enabling sex identification at a distance. This would save the time and energy involved in even clasping another male; however, this does not preclude other functions as well. In addition, this does not account for the groups found in high density choruses of *H. versicolor* and *H. chrysoscelis*, where these calls occur spontaneously. The Type II call in these species may function as a territorial call, but perhaps more in spacing out the calling males than in male-male competition for matings. There is some circumstantial evidence for this point of view. The literature indicates that females of the genus *Hyla* select a specific male to approach and frequently initiate amplexus by contacting the male (*H. chrysoscelis*, Littlejohn, 1958; *H. cinerea*, Blair, 1958a; *H. arenicolor*, Brown and Pierce, 1965). In the high density choruses we found it extremely difficult to localize and isolate a particular male for recording purposes. Ripe females moving into the breeding congress might have the same difficulty. There are several lines of evidence to support this view: (1) when Littlejohn et al. (1960) tested the ability of *H. versicolor* and *H. chrysoscelis* females to discriminate for their own call in preference to the other, they noted that the females did not orient toward the conspecific call until the calls were out of phase; and (2) it has been demonstrated that relative intensity plays a major role in the orientation of the female (Gerhardt, 1968), e.g., increasing the relative intensity of a hybrid *H. cinerea* × *H. gratiosa* mating call to 5 db above that of a pure *H. cinerea* call was sufficient to reverse a *H. cinerea* female's natural pref-

erence for the pure call in a choice situation. If there were no spacing and all the males present in a chorus were calling, females might be confronted with approach-approach conflicts which would be difficult to resolve. Although it might seem more probable that selection would modify the approach behavior of the females, we feel that in this case selection did modify the behavior of the males. If one male or a group of males possessed the territorial call and if females were better able to localize males in this group over males in another group, then selection for the call would result.

We have found no evidence of combat between males of these species either in our own observations or in the literature, and although the males continue to emit mating calls, it is difficult to elicit territorial calls after the first or second response sequence. Thus it is possible that the territorial call functions to space out the calling males in a manner enabling the females to localize and approach a specific male. Since it appears that a female on its way to a calling male would have an equal chance of accidentally contacting one of the non-calling males of these groups, the silent males may not be at a disadvantage, and may have the same chance for a mating as the calling male.

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