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Voice in Salientia. I. Observations on *Hyla versicolor* × *chrysoscelis* Intergrades in Central Oklahoma with a Few Data from Arkansas

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I have been gathering data on toad and frog voices, especially on breeding calls, since about 1940. The earlier phases of this work were all directed toward the possible effect of temperature of water, of air, or of both on the rate of calling. By use of a stop watch at breeding sites, three types of data were secured directly from the animals: (1) the number of calls given by individuals during a given interval of time; (2) the duration of each call; (3) the interval between calls of selected individuals calling without interruption. By noting ranges within these variables and the means at different temperatures, some idea could be secured as to effect of prevailing temperatures on calling rate (Bragg, 1950a).

Later, a portable recorder known as the Sound-Scriber, was utilized. This instrument, while cumbersome to use, had the advantage of making a permanent record on a plastic disc of all sounds made by the animals within its range. Such recordings could then be listened to at any subsequent time and data secured. Furthermore, in case of doubt, the same calls could be heard as many times as desired and checks of accuracy in timing or counting be made by comparison of two or more counts or timing from the same record. Many Sound-Scriber recordings of breeding calls of several species are now avail-

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able and some of these already have been utilized in life history studies (Bragg, 1942, 1944, 1948a).

Still more recently a small, portable tape recorder (the Mohawk Midgetape) has been used in a similar maner. By re-recording the calls heard (from tape to the Sound-Scriber), permanent records of these were made. Extensive tests have shown that results obtained by each of the three methods are comparable and I now use them indiscriminately as circumstances dictate.

Stimulated in part by the work of Blair (e.g., 1955, 1956) but lacking some of the essential equipment used by him, I have recently utilized the method of Frings and Frings (1956) in partial analysis of individual calls. This method involves the making of ferrograms from tape recordings. Finely powdered iron is sprinkled over the recording tape and the excess is blown or snapped off. Since the tape is magnetized where sound has been recorded, the powder held here gives a record of the call in the form of a pattern. This then is removed by transparent adhesive tape (Scotch tape or similar materials) which, now holding the pattern on its adhesive surface, may be stuck down on paper, a filing card, heavy plastic or glass and studied directly or used for lantern slides.

The recorder used runs at a constant tape speed of 1⅞ inches per second (manufacturer's datum). This is equivalent to approximately 47.6 mm. per second. Since each pulse of a call is represented by a thicker or thinner line of iron and the interval between pulses by spaces between these, both are easily translated into fractions of a second; and the number of lines per unit length on the ferrogram is exactly proportional to the number of pulses in a call for this length of record. From such data the number of pulses per second is readily calculated.

So far, such analyses of individual calls have been made only on the Gray Tree Frog, *Hyla versicolor*, recorded at natural breeding places in Oklahoma and Arkansas. This paper presents both types of data for this species only. I expect in later papers to present similar analyses for other species.

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The Calls of Hyla Versicolor

This animal gives at least two and probably three types of call: (1) a "protesting" note; (2) a short, throaty trill; and (3) a very short call which I here call the yip. The first is slightly trilled, at least sometimes, and seems closely related to the second type of call; but it is much shorter and sounds different to the human ear. One hears this to best advantage by immediately confining several calling males in a cloth bag where they characteristically "fuss" at each other for some time. It may be occasionally heard in a breeding congress when one male disturbs another. Its function, therefore, is probably sex recognition, although this is not certain. Because it is rarely heard under natural conditions, it has not been recorded nor analyzed during this study. Its shortness suggests, also, a close relationship to the yip.

The second call, i.e., the trill, is used under two different conditions. It is often given from trees under the influence of humidity and it is also the typical breeding call of the male. Since, in Oklahoma, I have been unable to distinguish any consistent difference in this call when given from trees and from breeding congresses, I consider it as one type of call. My data on it have all been secured from breeding congresses except one recording from trees in which I can discern no difference from calls about a nearby pool secured a few hours later. This call varies greatly as heard. Some individuals have a much higher pitched call than others in the same breeding congress. Despite this, I find a consistent difference among populations. In several congresses heard near Batesville, Arkansas, for example, the calls were hoarser and had a more "throaty" quality than commonly heard in Oklahoma; and they sounded to me exactly like those earlier heard from trees in south central Maine. On the other hand, calls of *Hyla versicolor* heard in two valleys in southeastern Oklahoma and others from a cattle tank near Jacksboro, Texas, were notably hoarser (Bragg, 1948, 1950).

This raises a taxonomic question which I have recently attempted to resolve (Bragg, 1958). According to my present interpretation, the form with the especially hoarse trill is *Hyla versicolor chrysoscelis* Cope; the one with a somewhat higher pitched voice as heard in eastern Arkansas is *H. v. versicolor* LeConte; and the one in central and most of eastern Oklahoma, having the highest pitched voice of the three, is an intergrade between these subspecies, i.e., *H. versicolor* × *chrysoscelis*. The basic difficulty with this interpretation is that such an intergrade would be expected to have a voice of intermediate pitch, not one higher than that of either subspecies. For the purpose of this paper, however, I use the names as outlined above. If the taxonomic question is later resolved differently, it will be easy to determine scientific names from the localities mentioned here.

The third type of call, the yip, seems not to have been recognized before, although I mentioned it briefly in an earlier paper. I have heard it rather rarely and only in congresses of the intergrades. It sounds so different from the typical trill of the breeding call that several companions have thought on first hearing it that another species was admixed with the hylas of breeding congresses, as indeed I myself did when I first heard it. However, I have *seen* an individual of *Hyla versicolor* on at least two occasions change from its typical trill to this call and back again when I could find nothing which might have interfered with the animal. Its function is still obscure.

I have heard literally hundreds of large choruses during the past 20 years in which this call was not heard, some of them covering over an hour's continuous listening. Also, many recordings taken have not picked it up. It is therefore of interest that on August 8, 1958, a large chorus was studied in Cleveland County, Oklahoma, in which many individuals were using this call. The whole pool was surrounded by hylas yipping about as much as trilling. This was at a pool at which *Hyla versicolor* has been heard off and on for about 11 years, yet this is the first record that I have of the yip-call being given here. One might suspect a seasonal factor, the yip used in summer congresses rather than in spring—but this seems doubtful, since I have heard yips from near-by breeding sites in April and May of other years, but with only one or two individuals involved. Because of the rarity of this call, I have recorded it only from this congress and, below, give an analysis of ferrograms of it from one animal.

Temperature and the Breeding Call

Since *Hyla versicolor* calls from the bank rather than from the water, it seems safe to assume that the water temperatures will have little effect on the rate of call (Bellis, 1953). Nevertheless, temperatures of both air and water have always been recorded in my data, as noted below. When 22 congresses were lined up in a table with increasing air temperatures and the rates of calling noted (number of calls started in 10 seconds taken as a unit), the result was not consistent with the assumption of a straight line function for the effect of temperatures on calls. The number of calls per ten seconds varied from one to six with a mean of 3.34+ at temperatures between 16° and 26.5°C. (mean = 20.3+). The model number of calls was essentially the same as the mean (3.3+), thus showing little variation in rate within the temperature range. To show this better, I applied a formula devised by Bellis (1953) which gives the theoretical rates at different temperature levels if the rate increases as a straight line function of temperature. This is: $y = .50 + 151x$, where y = the rate and x = air temperature in °C.

Comparing mean values observed at various temperatures with the computed theoretical values gave as much as 1.83 above the theoretical and as much as 1.04 below it for some individual items and as little as + 0.04 and — 0.92 for others. Individual items at the same air temperatures often failed to conform to each other. For example, 24 calls at 16°C. (water temperature = 21°)

exceeded the theoretical by 1.10 (range = 3–5). Compare this with another congress where 23 calls at 16°C (water = 19°) exceed the theoretical by only 0.06 (range = 2–3). With air and water both 20°C., 47 calls and 25 calls on the same basis gave — 0.08 and + 0.14 respectively (range = 3–4 and 2–5). With air and water both 24°C., 37 calls and 32 calls gave + 0.06 and —1.04 respectively (ranges = 3–6 and 2–4). At the highest temperature (26.5°C.) the theoretical exceeded the observed mean by 1.51 (range = 2–4) with water temperature 1.5°C. lower than air.

From this and similar data on a total of 22 congresses, I conclude that the rate of call of *H. versicolor* × *chrysoscelis* as measured by the number of calls started within a unit of time is not materially effected by air temperature between 16° and 26.5°C. Only two individuals (one at 20°C., the other at 24°C.) called at the fastest rate, i.e., 6 calls per 10 seconds. Only one individual at (23.5°C.) called at the slowest, i.e., 1 per 10 seconds.

In one congress, when both water and air temperatures were 19°C., 20 individuals all gave 3 calls per 10 seconds. In another, I sampled the number of calls per unit time at intervals of 15 minutes for over an hour at a pool and always got 3. With both a mean and a mode of just more than 3 for 618 calls in 22 congresses and with ranges narrow, the overall picture is of approximately 3 calls for 10 seconds regardless of temperatures within the limits observed.

Irrespective of the number of calls per unit time, the duration of each call might be affected by temperature differences provided that the intervals between calls were also affected. Timed durations of 1329 individual calls ranged from 0.2 to 2.4 seconds, about a mean of 0.65 — at temperatures between 14°C. and 26.5°C. The longest calls (i.e., the highest mean) were at 16.1°C. where 35 calls had mean duration of 1.41 seconds. But the range was very great (0.3 — 2.2 seconds) indicating much individual variation. But the shortest were at almost the same temperature (16°C.) and the variation less (range 0.2–0.4 second). The mean of 20 calls in this congress was 0.23 second. In another congress the individual durations were greater (mean of 71 = 0.77; range 0.6–1.1). Other data on a total of 21 congresses were similar. Variations in duration of call appear to be great, but unaffected by temperature.

The above data came from calls heard in the various congresses without regard to individuals. It therefore might be that some individuals consistently give longer or shorter calls than their fellows. To test this, eight individuals were selected for study of the duration of their calls. Five of these were from the same congress, and therefore subjected to about the same temperatures (14°C. for both air and water). Ranges and means for these five were respectively as follows: (1) R = 0.7–1.3 and M = 0.94; (2) R = 0.3–1.1 and M = 0.72; (3) R = 0.4–1.0 and M = 0.70; (4) R = 0.4–1.2 and M = 0.75; (5) R = 0.5–1.2 and M = 0.78. The model number in each of these was either 0.7 or 0.8 and the total number of calls timed was 113. The data for the other three individuals were comparable though taken at slightly higher or lower air temperatures. It seems obvious, therefore, that individuals vary considerably in the duration of their calls independent of temperatures.

The interval between calls in 18 congresses showed an overall range of 0.9–8.8 seconds with a mean of 3.35+ seconds using 482 calls at temperatures between 16°C. and 26.5°C.; but variation was about the same in different congresses at the same temperatures as at different temperatures. The longest mean interval was at 17°C. (5.23 seconds), the next longest at 23.5°C. (4.56 seconds). The shortest interval for an individual timed was 0.7 second at 22°C., the longest, 8.8 seconds at 17°C. Other examples could be given, but this seems sufficient to show that the interval between successive calls in *Hyla versicolor* × *chrysoscelis* is not materially affected by temperatures within the limits observed.

I therefore conclude that neither air nor water temperatures materially affect the rate of calling, the duration of calls or the interval between successive calls in natural breeding congresses of *Hyla versicolor* × *chrysoscelis* in central Oklahoma, at least between air temperatures of 14°C. and 26.5°C. and water temperatures of 17°C. and 28°C. Variation is spontaneous in single individuals in all three variables. This substantiates the general impression one gets in listening to a congress. For example, one individual, heard calling consistently at about the same rate, suddenly changed to three calls of noticeably longer duration, then changed back to its original rate. Another did the reverse.

In some congresses the rate of calling is quite rhythmic, all individuals calling at essentially the same rate. In others, variations are so great as to be obvious to the ear without measurement.

All of the above data are from intergrading populations in central Oklahoma. A few have also been secured for *Hyla v. versicolor*. On the evening of May 20, 1949, at 8:15 o'clock in Adair County, Oklahoma, 12 individuals in a large congress taken to be of this subspecies were calling at a mean rate of 3.0 calls per 10 seconds with no range at all. Air temperature was 25°C., water, 24°C. At 10:00 o'clock just after a light shower accompanied by a drop in temperature, another congress about 10 miles distant from the site of the first was found. Air temperature here was 15°C. and water, 18°C. Only six individuals could be timed, but every one called much more slowly (mean = 1.79 calls per 10 seconds, range 1–2). The rate of calling was sufficiently different in these two congresses as to be readily discernible by ear. There was also a marked difference in duration of call. In the first congress, the calls varied more and averaged longer (mean of 15 = 1.39 seconds, mode = 0.9, ranges 0.8–1.5) as opposed to mean = 0.87, mode = 1.0, range 0.7–1.0 second. Mean interval between calls varied also (2.82 seconds at the higher as compared to 6.10 seconds at the lower temperature).

These data, while few, seem to point to a marked effect of temperature on calling, a result not to be expected from the findings on the intergrades. Further data seem needed, but only a few have yet been secured. A single individual in northeastern Oklahoma, calling with air temperature 25°C. (water = 24°) averaged 6.17 calls per 10 seconds, but another in eastern Arkansas averaged 2.39 at 20°C. (both air and water). In the Arkansas congress two individuals had close to the same duration (means = 0.854 and 0.878 second on the basis of 17 and 18 calls, respectively). But in another congress on the following evening in the same region at a different pool, 21 calls taken at random ranged from 0.3 to 1.0 second with a mean duration of 0.65 second. Temperatures were different (29° and 24° for air and water respectively).

From such variations, supplemented by general observations, I am inclined to think that individuals vary independent of temperatures within wide limits and that rates of calling depend more upon the number of individuals calling in any one place than upon the temperatures of either water or air.

Analysis of Individual Calls

A single call of each of five *Hyla v. versicolor* was compared with those of three intergrades on the basis of ferrograms. The ferrogram of the breeding call of *H. versicolor* appears as a series of approximately evenly spaced parallel lines, standing vertically. The width of each line corresponds exactly to the duration of each element or pulse in the call and the width of the spaces between the lines to the interval between these elements. Measuring lines and spaces in mm., therefore, gives values corresponding to duration in seconds; and the number of lines in a given distance along the ferrogram gives the number of elements for this distance. Such measurements and counts were made directly by means of a Bausch and Lomb measuring magnifier and translated to duration mathematically.

The duration of pulses (elements) in the three intergrades was just more than 0.01 second (mean = 0.0104 ⅓ second) and the variation in pulses was negligible (R = 0.0103–0.0105 second). The intervals between elements were approximately twice as much (M = 0.022 ⅔, R = 0.0173–0.0252 second). The number of pulses per second varied between 28 and 40, with a mean of 33 (when expressed to the nearest whole number). These values were secured at air temperatures between 20° and 24°C.

Four of the individuals of *H. v. versicolor* were calling in a single congress in eastern Arkansas where air and water temperatures were each 18°C. Pulses of their calls varied as means, between 0.0097 and 0.0122 second. The fifth specimen, from a different congress in the same region at slightly higher temperatures (23° and 22°C., air and water respectively), had pulses of 0.0042 seconds; the mean for all five was 0.00981 ⅓ (just less than for the intergrades). Intervals were comparable (M = 0.01865 second) but more variable. For example, the individual with the shortest call element (0.0099 second) had the longest interval (0.0204 second) but the overall mean was also just less than for the intergrades (0.01865 second). Those at 18°C. varied between 23 and 45 pulses per second. The one at 23°C. had 42 (as expressed to nearest whole number).

If we now compare the data for the two groups, eliminating minor fractions, the intergrades had 33 pulses per second in the call with each element representing 0.01+ second and the interval between these, 0.027 second. Comparable values for *H. v. versicolor* (Arkansas) are 38, 0.01 and 0.02— second. From these figures it seems evident that individual variation rather than temperatures accounts for the difference in the calls.

As earlier mentioned, I have succeeded in recording the yip call only from one congress of intergrades in central Oklahoma and have made ferrograms of this call from only one individual. Air and water temperatures were both 24°C. Twenty-six of these yips varied in duration between 0.0378+ and 0.2206— second with a mean of just above 0.1 second. The intervals between successive yips varied greatly. Sometimes a single yip was uttered between two trills. At other times yipping continued intermittently for 10 to 20 seconds. One individual recorded yipped at about the usual rate for an estimated 30 seconds then suddenly speeded up greatly, giving a series of very short yips rapidly repeated. This was heard and noted at the breeding site as well as later in the recording.

Some of the ferrograms suggested that the yip is made up of a series of very short pulses with short intervals between them, which would explain why it often sounds slightly trilled as heard in nature. However, not all yips sound this way and some of the ferrograms seemed to show no break in the sound, since they were not made up of lines and spaces. To be certain of this they were studied under a binocular microscope. In one ferrogram, a portion of the call showed lines and spaces, whereas the remainder was completely undifferentiated. This suggests that this particular call was rapidly trilled for a small fraction of a second, the remainder being made of a one sound-element. In the trilled fraction of this call, I measured a few of the lines and the spaces between them (all that could be seen clearly enough under a microscope). Translated into time, the durations of the individual elements were 0.0021+ second, and the intervals between them about five times as long, 0.151+ second.

So far as these few data show, therefore, this peculiar call is given at different times by the same individual in three different ways: (1) trilled, (2) partly trilled, and (3) (with some doubt) wholly trilled, the last point judged from yips heard in nature, but not used for ferrograms.

Discussion

It has long been known that voice variation occurs in *Hyla versicolor* but no satisfactory interpretation of this seems to have appeared. Independent of individual variation, populations are also known to vary, sometimes even those of closely adjacent regions. Since a slower sound differs in pitch from a higher one, and since temperature sometimes, at least, affects rate in the breeding calls of other species (Bragg, 1940, 1943, 1948; Bellis 1953, 1957) it was a reasonable assumption that temperatures may be the deciding factor in some of the differences that various workers had noticed in breeding calls of *Hyla versicolor*. The results of this paper show clearly that this is not the case. This confirms the conclusions of Bragg (1950) and of Bellis (1953) for intergrades in central Oklahoma; and the limited data secured for true *H. v. versicolor* in Arkansas tends to substantiate it for this form. This negative result has a bearing upon the taxonomic question as to differentiation of *Hyla v. versicolor* from *H. v. chrysoscelis* (Bragg, 1950a) on the basis of calls because if the hoarser call in *H. v. chrysoscelis* is not based on size (Bragg, 1958) nor upon temperatures, it is now a reasonable assumption that it is based upon some structural difference involved in voice production in the two subspecies. Such morphological difference has not even been looked for, so far as I know. To search for it seems, therefore, a logical next step.

Summary

Data are presented which seem to show that the rate and duration of, and intervals between, calls of *Hyla versicolor* × *chrysoscelis* are not materially affected by prevailing temperatures, within the limits of 16°–26.5°C. All these usually vary individually irrespective of temperature and of each other.

Occasionally one finds a chorus in which all animals are calling at the same rate, usually 3 per 10 seconds. From this and other general observations it seems clear that one calling male influences another in a typical breeding congress. Limited data tend to show the subspecies, *H. v. versicolor* to be similar.

Study of ferrograms of breeding calls shows each to be made up of a series of pulses of short duration, thus accounting for the trilled effect as heard.

A peculiar yip call, the function of which is not clear, is described for the first time (heard only in intergrades). Ferrograms show this to be untrilled or partly trilled at a very fast rate. From hearing it under field conditions it is believed sometimes to be wholly trilled.

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