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MATING CALL IN THE SPECIATION OF ANURAN AMPHIBIANS*

W. FRANK BLAIR

The University of Texas, Austin, Texas

INTRODUCTION

Analysis of mating call has been used as a tool in the study of anuran speciation only in the past five years. It is somewhat premature to undertake a general synthesis of this work but progress has been made to the point where some generalizations and numerous problems for future study are readily apparent.

The mating call is an especially favorable characteristic of anurans for the investigation of speciational and general evolutionary dynamics in this group. This is true because, with few possible exceptions, the function of the call is limited to the attraction of a mate. The essentially voiceless females are attracted to the calls of the males which generally precede them to the breeding pools. It is to be expected, therefore, that evolution of the call would be influenced by two major factors: (1) the function of attracting a female of the same species; (2) the disadvantage population-wise of attracting a female of another species. It is to be expected that the first function would tend to promote uniformity of call through the species population and that the second would influence differentiation between species.

The foregoing statements about the function of the call are based on observational and circumstantial evidence. Experimental evidence for the specificity of call in attracting the females to the correct species of males has yet to be obtained largely because of the difficulty of setting up an experiment in the brief time in which ripe females are responsive to the males. Under the anuran system of assembling the sexes for reproduction, discrimination rests almost entirely with the female. A sexually excited male tends to clasp indiscriminately any object of appropriate size, sometimes even inanimate ones. Various sex recognition mechanisms have been developed which induce a male to release another male it has clasped (Noble, 1931). In toads (Bufo) a warning vibration serves this purpose (Aronson, 1944; A. P. Blair, 1947). There is no such mechanism to induce a male to release a female of the "wrong" species, and except where there is great disparity in size the determination of whether a mating will be homospecific or heterospecific in a mixed population depends on the discrimination of the female. I have seen female *Bufo valliceps* approach a calling male and hop in front of him. If the male fails to notice her she will

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repeat the performance until the male sees her and clasps. Lowe (1954) observed several instances of a female going to a calling male of her own species in a mixed chorus of two species of spadefoots (Scaphiopus). This same author found no heterospecific pairs among 200 clasped pairs in mixed populations of two species of Scaphiopus and two of Bufo observed on ten nights in New Mexico. Thornton (1955) found eight per cent of heterospecific pairs among 114 in mixed breeding populations of *Bufo woodhousei* and *B. valliceps.* Under the breeding system that pertains in the anura, occasional heterospecific combinations are to be expected as the result of a female passing too near the "wrong" male in responding to the call of a male of her own species. The probability of such mistakes occurring would be related to the concentrations, relative abundance, and dispersion of the pertinent species in the breeding pool.

While focusing our attention on mating call, we are aware that difference in call is only one of several factors that make up the isolation mechanism complex of any pair or group of sympatric species. Ecological factors such as time and place of breeding and mechanical ones such as relative size also may be involved. No one factor in the complex may be completely effective, while the combined effects of all factors may be wholly effective in preventing cross-mating.

The measurements of calls to be discussed here were made by use of a sound spectrograph (Sona-Graph). Use of this instrument provides a visual representation of sounds so that such variables as frequency, time, and modulation patterns may be measured precisely and compared as objectively as any morphological character. The acoustical terminology is made as consistent as possible with that of Chavasse, Busnel, Pasquinelly and Broughton (1954).

INTRASPECIFIC VARIATION

Variation within Populations. Some variations exist between the calls of individuals in a local population, and there are some differences between calls of the same individual. However, these variations fall within relatively narrow limits. Some of the factors responsible for these variations are known. One factor at least is non-genetic. W. F. Blair (1955 a) has shown that frequency increases with temperature in the calls of *Microhyla olivacea* and *M. carolinensis.* Our unpublished data indicate that this is generally true in other anuran calls. The repetition rate in those calls which consist of a series of repeated notes also tends to increase with temperature. Frequency tends to vary inversely with size in the anura. This is shown in Microhyla (W. F. Blair, 1955 a, 1955 b). Another microhylid, *Hypopachus cuneus,* with a structurally similar call is larger than either U. S. species of Microhyla and has a lower frequency than either. Repetition rate also tends to vary inversely with body size. This is true in toads of the United States (W. F. Blair, 1956 a) where the largest, *Bufo marinus,* has the slowest repetition rate and lowest frequency, and the others show increased rate and higher frequency as their size decreases. The dominant frequency ranges from about 640 cps in *B. marinus* to about 5,000 cps in *B. quercicus*, which is the smallest toad. The repetition rate ranges from about 10 notes per second in *B. marinus* to about 120 notes per second in *B. debilis*, which is our smallest "trilling" toad.

The call may vary in relation to the sexual excitement of the individual. Various species of Hyla call from high in the trees in which they live. These tree calls are often given in daylight hours, and they may be heard at long distances from any breeding pool. We are able to compare the tree and breeding-pool calls of one species, *Hyla squirella*, by use of records obtained at Welaka, Putnam County, Florida. The breeding-pool call is about 0.2 seconds in length and consists of a series of closely spaced harmonics. The most distinctive feature of this call is a series of harmonically related emphasized bands which rise in frequency from beginning to end of the call and thus cut across the series of closely spaced harmonics (fig. 1). The tree call, as recorded for an individual about 20 feet high in a palm tree, is noise-like, without harmonic structure, and there is no rise

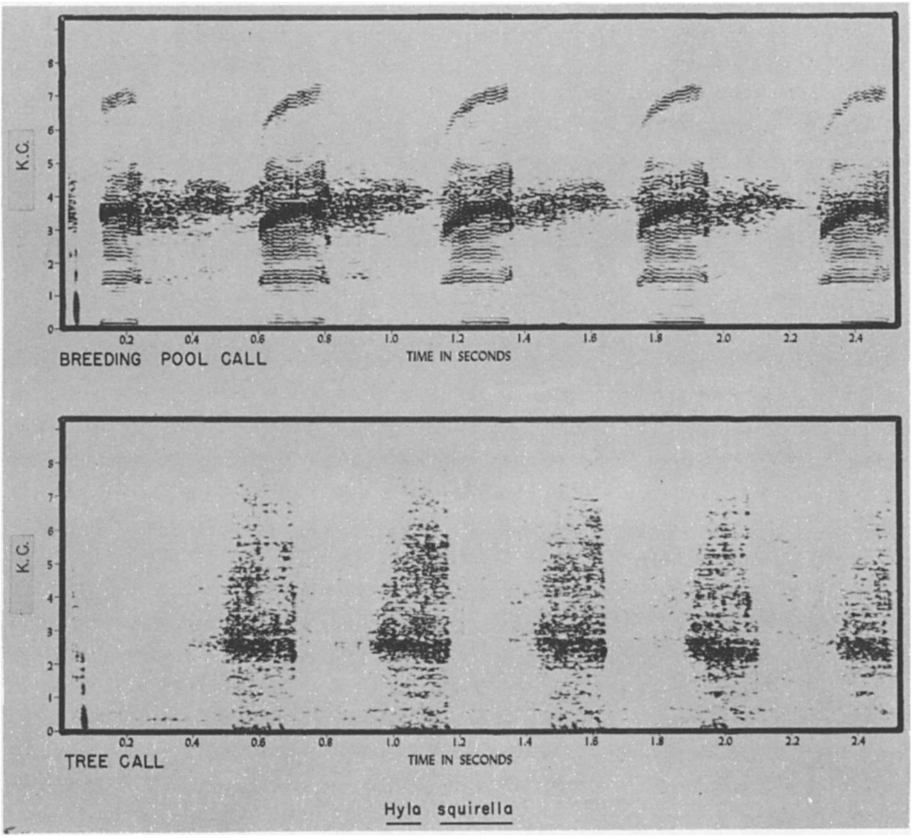

FIGURE 1. Sonagrams of breeding pool calls and tree calls of squirrel treefrog (*Hyla squirella*) recorded at Welaka, Putnam County, Florida. Note harmonic structure and rising frequency in breeding pool call.

in the dominant frequency band from beginning to end of the call (fig. 1). This call is of essentially the same length as the breeding-pool call. In comparison with the breeding-pool call, the tree call sounds flat and monotonous to the human ear. The function of the tree call is unknown.

The range of variation in calls of a single individual was investigated by recording the calls of a marked *Hyla versicolor* on nine different nights over a period of more than three months (table 1). In this time there was a range of 9°C. in ambient air temperatures at which the recordings were made. In this period the repetition rate varied by five notes per second from a low of 25 to a high of 30. The dominant frequency varied only 375 cps from a low of 2250 to a high of 2625. The duration of the call showed the greatest variation, for on the night on which the calls were longest they averaged more than twice as long as on the night on which they were shortest. From table 1 it is seen that the variations in frequency are related to variations in air temperature. The variations in repetition rate also tend to be correlated with air temperature. These observations indicate an increase of roughly 0.44 pulses per second and a frequency rise of roughly 60 cps for each 1°C. rise in temperature. Duration of the call tends to decrease with increased temperature.

TABLE 1

MEASUREMENTS OF THE CALL OF A SINGLE INDIVIDUAL GRAY TREEFROG (*HYLA VERSICOLOR*) AS RECORDED ON 9 DIFFERENT NIGHTS.

Date	Air temperature °C	Mean pulses per second	Mean duration in seconds	Dominant frequency in cps
March 20	18.0	26.0	0.56	2250
April 2	23.0	28.0	0.69	2490
April 25	22.0	26.0	0.59	2500
May 15	24.0	25.5	0.51	2520
May 20	26.0	30.0	0.57	2625
May 21	27.0	30.0	0.30	2675
May 29	22.5	25.0	0.44	2600
July 6	26.0	30.0	0.38	2580
July 9	27.0	30.0	0.35	2600
Range of variation	9.0	5.0	0.39	375

There is individual variation in the calls of anurans in a single breeding population. The calls of 17 *Pseudacris streckeri* were recorded at one pond on a night when the air temperature was 21.5°C. and the water temperature was 18.0°. The dominant frequency varied from a low of 2100 to a high of 2500 cps. The average duration of the call varied from a low of 0.05 second to a high of 0.09 second. However, 11 of the 17 frogs had an average duration of 0.05 and four had 0.06. One had 0.07 and one had 0.09. There was virtually no measurable variation in the length of the call in any individual except the one which averaged 0.09 second. This frog had a range from 0.07 to 0.11 second. The average interval between calls varied from 0.40 to 0.45 second. The variation in interval in calls of a single individual was slight. The difference between longest and shortest interval ranged from 0.02 to 0.14. The number of calls given in a sequence varied from six to 16 among the 17 individuals. Fifteen gave six, seven, or eight calls in a sequence. One gave 10 and another gave 16.

From the preceding discussions it is apparent that the anuran mating call is affected to a considerable extent by environmental factors, particularly temperature. In addition, there is some ontogenetic change in the call, since both frequency and repetition rate are related to body size. Differences other than those attributed to ontogenetic factors, environment or degree of sexual excitement are assumed to have a genetic basis.

Geographical Variation. Minor differences in call exist between local subpopulations, and for a few species there is sufficient evidence to show broader patterns of geographic variations of this character. *Microhyla carolinensis* and *M. olivacea,* which overlap along the forest-grassland boundary in Texas and Oklahoma, show geographical variations in dominant frequency and duration of the call that are such that the greatest differences in calls of the two species occur in their overlap zone (W. F. Blair, 1955 a). The variation in frequency is correlated with variation in body size (W. F. Blair, 1955 b).

TABLE 2

GEOGRAPHIC VARIATION IN THE MATING CALL OF THE CHORUS FROG (*PSEUDACRIS NIGRITA*).

Attributes	Texas	Oklahoma	Florida	Colorado	Minnesota-Wisconsin
Pulses per second	18.8	20.9	28.6	31.2	28.6
Dominant frequency (cps)	2969	3075	3325	2275	3820
Duration in seconds	0.68	0.58	0.39	0.43	0.49
Number of individuals	13	2	3	2	10

Limited data indicate that the call of *Pseudacris nigrita* is different in the northern United States from that of the same species in the South. The calls of 13 individuals from five stations in southeastern Texas have an average repetition rate of 18.8 pulses per second (table 2). The calls of two individuals from northeastern Oklahoma are closely comparable to these, with an average of 20.9 pulses per second. The calls of 10 individuals from northwestern Minnesota and northwestern Wisconsin have a higher repetition rate, with an average of 28.6 pulses per second. Two individuals recorded at an elevation of above 9000 feet in Rocky Mountain National Park, Colorado, have an average repetition rate of 31.2 pulses per second, which is comparable to the rate in the northern populations. When the probable effects of temperature are considered, the differences between the northern, including Rocky Mountain, and Texas-Oklahoma frogs are presumably greater than the raw data indicate. The northern frogs were recorded at temperatures of 18.0 to 19.5°C, while the Texas-Oklahoma frogs were recorded at temperatures ranging from 18.5 to 24.0°C. The temperature effects would thus tend to obscure genetic differences in repetition rate between these geographic segments of the species population. Three individuals recorded on the mainland near Cedar Key, Florida, at an air temperature of 26.5°C., have an average repetition rate of 28.6 pulses per second, which suggests that the peninsular Florida population differs in call from

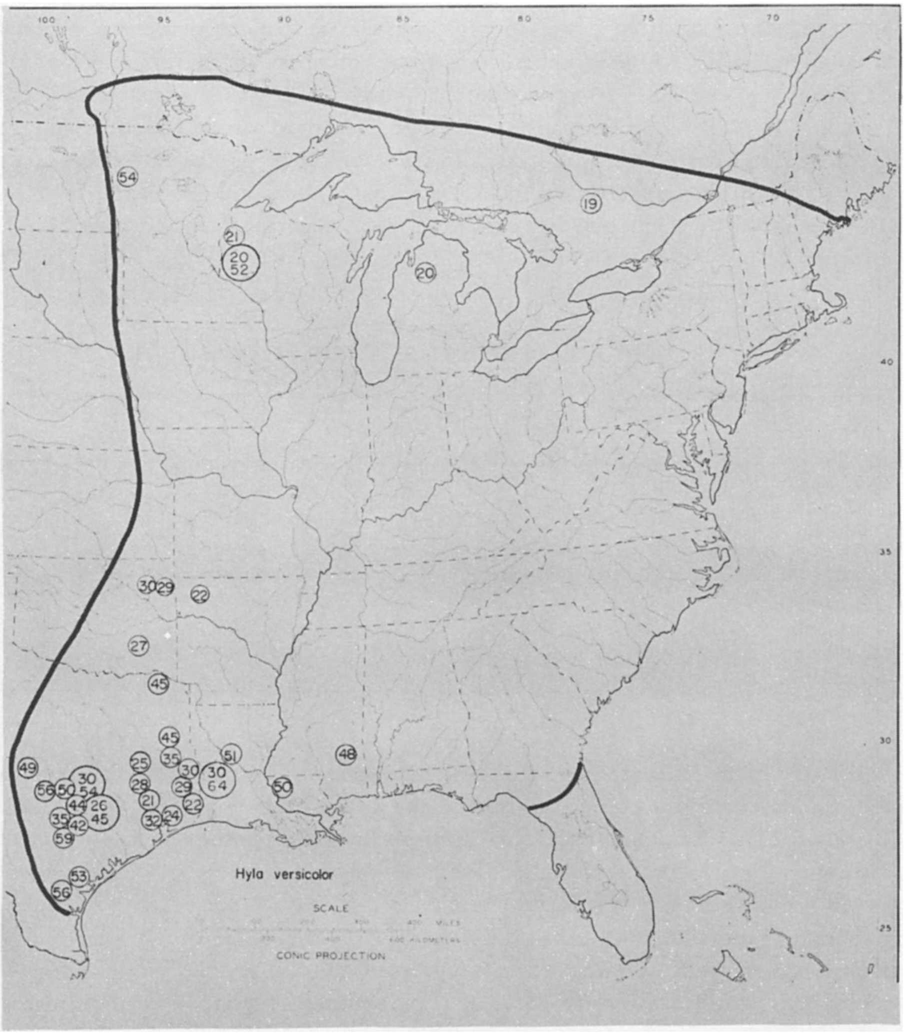

FIGURE 2. Geographic variation in pulse rate in the call of the gray treefrog (*Hyla versicolor*). Figures given are station means for pulses per second. Circles enclosing two values represent stations at which discrete "fast-trilling" and "slow-trilling" types were recorded.

the Texas-Oklahoma segment. The Texas-Oklahoma and Florida frogs show little difference in dominant frequency, but their frequency is decidedly lower than that of the Minnesota-Wisconsin frogs (table 2). The lowest frequency is found in the Colorado frogs. The duration of the call is longest in the Texas-Oklahoma frogs, shortest in the Colorado and Florida frogs, and intermediate in the Minnesota-Wisconsin ones. The three groups, Colorado-Minnesota-Wisconsin, Texas-Oklahoma, and Florida, represent three subspecies which have been described on morphological grounds. Much additional work is needed, however, before it will be possible to determine the degree of correlation between geographically varying call characters and geographically varying morphological characters in this widely distributed species.

TABLE 3

MEAN MEASUREMENTS OF THE CALLS OF THE GRAY TREEFROG (*HYLA VERSICOLOR*). STATION SAMPLES POOLED TO FORM A SOUTHERN TRANSECT FROM CENTRAL TEXAS TO EASTERN MISSISSIPPI AND A NORTHERN TRANSECT FROM NORTHWESTERN MINNESOTA TO EASTERN ONTARIO.

	Southern transect			Northern transect	
Atributes	Southwestern fast trillers	Southern slow trillers	Southeastern fast trillers	Northwestern fast trillers	Northern slow trillers
Pulses per second	47.3	26.8	50.8	52.4	20.3
Dominant frequency (cps)	2683	2435	2643	2650	2407
Duration in seconds	0.59	0.60	0.77	0.56	0.60
Number of individuals	28	33	20	6	9

The most complete analysis of geographic variation in call can be made for the gray treefrog, *Hyla versicolor,* although much remains to be done before the complete pattern becomes clear. The evidence consists of a southern transect across a part of the range from central Texas to eastern Mississippi and a northern transect from northwestern Minnesota to eastern Ontario (fig. 2). Repetition rate shows an extremely interesting pattern of distribution. Frogs at the extreme western periphery of the range have a rapidly trilled call. In the south these western frogs have an average repetition rate of 47.3 pulses per second (table 3). Frogs in western Louisiana and in the pine-oak forest of eastern Texas, and in the Ouachita Mountains of eastern Oklahoma and Ozarks of eastern Oklahoma and western Arkansas have a slowly trilled call with an average repetition rate of 26.8 pulses per second. Frogs from western Louisiana east to eastern Mississippi have a rapidly trilled call with an average repetition rate of 50.9 pulses per second. Thus there are eastern and western rapid-trilling populations separated by a slow-trilling population in western Louisiana and eastern Texas. Points of contact between both fast-trilling populations and the intervening slow-trilling segment have been determined. At the known points of contact (fig. 2), slow-trilling and fast-trilling frogs occur in the same breeding aggregation without any evidence of intermediacy of call. The sharp segregation into two call types suggests that a single gene difference might be responsible for the two types. In Texas the contact occurs in the belt of transition from pine-oak forest to grassland. One known point of contact between the western and central populations is about two miles northwest of Columbus, Colorado County, Texas, and another is 6.5 miles southeast of Bastrop, Bastrop County, Texas. In northern Texas, where the forest-grassland boundary swings northeastward, both types were found calling together about 7.7 miles north of Clarksville, Red River County, but only the fast triller could be recorded. Recordings were made of slow-trilling frogs (35 pulses per second) 10 miles southwest of Nacogdoches, Texas, on June 30, 1953. Recordings of fast-trilling frogs (45 pulses per second) were made on May 5, 1956, five miles southwest of Nacogdoches. The difference between these two groups is somewhat minimized by the 7°C. difference in the temperatures at which they were recorded. When the calls are corrected to 22.0°C. by adding or subtracting 0.44 notes per second for each 1.0°C. change in temperature the relationship is 45.8 pulses per second for fast trillers and 32.0 for the slow trillers. No records are available for the western part of the range of the species in Oklahoma to show whether or not there is a fast-trilling population there.

The one known contact between the eastern, fast-trilling population and the slow-trilling one is near Caney, Vernon Parish, Louisiana. Two individuals in a stock collected there by Floyd E. Potter, Jr., later called in a natural situation at Austin. One of these had a repetition rate of 30.0 pulses per second at 27.0°C., and the other had a rate of 64.0 pulses per second at 29.0°C.

The northern transect is similar to the southern one except that no eastern, fast-trilling population is known in the area from which recordings are available. The only known contact between the fast and slow-trilling populations in the north is near Clam Lake, Burnett County, Wisconsin. Only slow-trilling frogs were found in a breeding pool near Clam Lake, but both types were found in a rainpool in a cleared field in an upland situation about two miles away (fig. 2).

There is a wide gap in our knowledge of the distribution of call types in the central United States. The occurrence of the fast type in Minnesota and Wisconsin as well as in Texas suggests that it is distributed along the western periphery of the range of the species. Charles F. Walker has told me of hearing two types of calls in Ohio, which is not unexpected since the forest-grassland border swings far eastward in that latitude.

The fast-trilling populations average about 200 cps higher in their dominant frequency than do the slow trilling ones (table 3). There is little geographic variation in the duration of the call. The longest calls are found in the southeastern, fast-trilling populations.

No one of the several possible hypotheses that might explain the geographical call races of *Hyla versicolor* can be proved on the basis of present evidence. One possible explanation is that *Hyla versicolor* as now recognized actually includes three species of which all meet and overlap the adjacent species without interbreeding. This needs to be tested by breeding experiments and call discrimination experiments, but it seems the most unlikely of several hypotheses. We have been unable to see any morphological differences between individuals of the two call types where they occur together, nor is there any good evidence of ecological separation of the two types in time or place of breeding where they overlap. Another possible explanation would be that the slow-trilling characteristic arose in the center of the range and spread from there. However, it would be difficult to envision any advantage of this call that might favor its spread, and it would seem most likely that a change in call would be at a selective disadvantage and would thus have its spread inhibited. An alternative hypothesis would be that the fast-trilling type arose at the periphery of the range and became established under the conditions of limited gene flow at the periphery. This hypothesis would require that the character arose at least twice, once on the western and once on the eastern side of the range, and it would require numerous origins of the trait at the periphery or a directional dispersal of the character along the periphery.

The most likely hypothesis is that the contacts between the slow-trilling population and the fast-trilling populations to the east and west of it are secondary. These contacts in the South occur in a region in which there is widespread evidence of previous (presumably late Pleistocene) fragmentation of ranges into southeastern and southwestern segments which still remain separate, have evolved into eastern and western species which now overlap in range, or show secondary interbreeding (W. F. Blair, 1951). Pleistocene separation of the ancestral population into southeastern and southwestern fragments which remained undifferentiated in call and concomitant isolation of an intervening population which chanced to undergo differentiation of the call under geographic isolation would be required. Subsequent rejoining of the ranges of the three populations and their northward spread prior to the evolution of effective isolation mechanisms would lead to the situation that exists today. The postulate of a Pleistocene isolate on the western Gulf Coast is not without supporting evidence. A relict toad, *Bufo houstonensis*, is limited to the southeastern Texas coastal area and is disjunct by the distance from there to the Pearl River, Mississippi, from the range of its near relative *Bufo terrestris*. The three populations of gopher frogs, usually referred to as *Rana areolata*, *R. sevosa* and *R. capito*, although Schmidt (1953) has lumped the latter two under a single species name, demonstrate the occurrence of three Pleistocene isolates on the Gulf Coast comparable to what has been hypothesized above as an initial step toward the present situation in *Hyla versicolor*.

The geographical distribution of the call races of *Hyla versicolor* does not show any general concurrence with the distribution of the three rather nebulously defined morphological subspecies which have been described for this species. The only exception is that the contact between the western, fast-trilling race in the south with the central, slow-calling race occurs at about the eastern boundary of the subspecies *H. versicolor sandersi,* Smith and Brown (1947).

The limited evidence that we now have pertinent to geographic variation in mating call suggests that with adequate geographic sampling this character will prove an extremely valuable tool for revealing past history and evolutionary dynamics of complex, widely distributed species. The main value of this character in this respect lies in the fact that variations in call, with some exceptions, are largely independent of environmental selection. Natural selection could affect call secondarily, however, through its effects on body size, since certain attributes of the call do vary in relation to size. Also, as will be discussed below, call could be influenced by selection under conditions of limited hybridization between populations which had evolved a set of partially effective isolation mechanisms.

INTERSPECIFIC VARIATION

Call analyses are now available for all but a few species of U. S. anurans with the exception of the genus Rana. With minor exceptions which will be discussed below, each species differs distinctly from every other species in at least one, and often more, of the attributes of the call. Nevertheless, groups of species within a genus show basic similarities in call structure, which, along with other evidence, are indicative of evolutionary relationship.

Analysis of call in the genus Scaphiopus (W. F. Blair, 1955 c, 1956 b) supports the morphological evidence and the evidence from breeding tests (A. P. Blair, 1947 b; Wasserman, 1957) that there are two distinct evolutionary lines (subgenera) in the genus. Comparison of the calls in the subgenus Spea leads to the suggestion that there are three U. S. species (W. F. Blair, *op. cit.*). The species *hammondi* and *bombifrons,* which are differentiated in repetition rate, have overlapping ranges and show limited hybridization where they occur together. The species *intermontanus* appears to be an allopatric species most closely related to *bombifrons.*

A preliminary grouping of U. S. toads (Bufo) into species groups (W. F. Blair, 1956 a) is already in need of revision in the light of additional work with call and with breeding tests. On present evidence, three species do not seem closely related to any other U. S. species and will be treated as representing three species groups. These are *B. valliceps, B. marinus,* and *B. quercicus.* One group includes two species, *B. compactilis* and *B. cognatus.* The largest group includes five nominal species, *B. terrestris, B. americanus, B. hemiophrys, B. houstonensis,* and *B. microscaphus.* The ranges of the first two meet, and they are generally treated as conspecific.

The other three are disjunct allopatric populations to the west of the range of these two and apparently represent relicts from a wider, Pleistocene distribution of the group (A. P. Blair, 1955; W. F. Blair, 1957a, 1957b) Another species, *B. punctatus,* appears closely related to this group and presumably speciated prior to the evolution of the allopatric species mentioned above. Another species, *B. woodhousei,* which occurs sympatrically with all of the species of this group except *B. hemiophrys,* has the call markedly differentiated (W. F. Blair, 1956a), but it is genetically so similar that hybrids between it and members with which it has been tested are fertile (A. P. Blair, 1941). Another species, *B. debilis,* has a call that is intermediate in structure between *B. woodhousei* and *B. americanus.* Viable metamorphosed hybrids between *B. debilis* and *B. terrestris* have been produced in my laboratory.

The final species group includes *B. boreas, B. canorus,* and *B. alvarius,* although the evidence for placing the latter species in this group is rather slight at the present time.

Analyses of call in U. S. hylids are now being made along with breeding tests to determine the relationships of the species in this group of frogs. One clear-cut group includes *Hyla cinerea, H. gratiosa,* and *H. andersoni.* Another group includes *H. femoralis* of the southeastern United States and *H. arenicolor* of the Southwest. Another includes *Hyla versicolor* and *H. phaeocrypta* with close affinities to the *femoralis-arenicolor* group.

Detailed studies of call characteristics and variations within and between members of a species group should provide evidence as to how the call differences originated and consequently throw light on the mode of origin of the species. The evidence will be examined as it applies to two currently held theories as to how new species originate. One of these, favored by Muller (1940), Mayr (1943) and others, holds that a new species originates under geographical splitting of a population and continued separation until the two populations have differentiated to the extent that they would behave as separate breeding systems if their ranges again came into contact. Another theory (Dobzhansky, 1940) holds that incipient isolation mechanisms may be reinforced through the action of natural selection under limited hybridization of the two populations.

Allopatric Species. The populations known as *Pseudacris streckeri* and *P. ornata* provide one of a few U. S. anuran examples of a presumably early stage of geographic speciation. The former occurs west of the forest boundary in Texas and Oklahoma except for a relict population in southern Illinois. The latter species occurs throughout Florida and on the coastal plain from North Carolina to southern Mississippi. The few calls of *P. ornata* available for analysis show no detectable difference from the calls of Texas *P. streckeri* other than a 400 cps difference in dominant frequency. Both nominal species breed in winter and both are morphologically rather similar. Mecham (1957) obtained a high percentage of metamorphosis of viable hybrids in crosses between them. One attempted backcross of an apparently mature male to a female *P. streckeri* gave inconclusive evidence of hybrid sterility. These two populations are apparently in an early stage of speciation, and it is doubtful from present evidence that they would behave as separate species if their ranges came to overlap in nature.

Two spadefoots, *Scaphiopus hurteri* and *S. holbrooki*, have a distribution very similar to that of the two Pseudacris. No calls of the latter species are available for comparison, but both nominal species sound very similar as heard by the human ear. Wasserman (1956) found these two to be interfertile populations which are apparently separated by a soil barrier in the Mississippi Valley. The stage of speciation of these two appears to be similar to that of the two Pseudacris, and it seems likely that the same past climatic change was responsible for the fragmentation of ranges in both groups.

The species *Hyla arenicolor*, with a range from Trans-Pecos Texas westward, and *H. femoralis*, with a range from the Mississippi River eastward on the coastal plain, present a different picture. These two species are adapted to life in very different environments. Body size is considerably greater in *H. arenicolor* than in *H. femoralis*. Hybrids between the two have survived through metamorphosis, but they were lost through faulty technique before they could be tested for fertility. The calls of these two species are more differentiated than those of the species pairs discussed above. The calls of both are rather long, ranging from about one to more than three seconds in length. In each species the call consists of a series of notes repeated at an approximately similar rate (15 notes per second in *H. arenicolor*, 12 notes per second in *H. femoralis*). Each note is made up of a series of harmonics of the fundamental, which is about 100 cps in *H. femoralis* and about 175 cps in *H. arenicolor* (fig. 3). The chief difference is in the bands of emphasized harmonics. In *H. femoralis*, there is an emphasized band at about 200 cps and harmonically related bands centering around 2600 and 4800 cps. The third (4800 cps) of these bands is usually the strongest, but the second sometimes exceeds it. In *H. arenicolor*, there is an emphasized band centering around 600 cps and another, usually stronger, band centering around 2400 cps. The call differences between these allopatric species are at least as great as those between the sympatric species *Hyla cinerea* and *H. gratiosa*.

The five allopatric species of the *Bufo americanus* group provide a final series of examples of call differentiation in geographically separate species. The calls of *B. terrestris*, *B. americanus*, and *B. houstonensis* have been described by W. F. Blair (1956 a), those of *B. hemiophrys* and *B. americanus* by W. F. Blair (1957 a), and those of *B. microscaphus* by W. F. Blair (1957 b). Considering *B. terrestris* and *B. americanus* first, both species show geographical variation in call (fig. 4). At the extremes of this variation, *B. terrestris* of northern Florida has an average repetition rate of 74 notes per second and a duration of 4.8 seconds by comparison with a repetition rate of only 30 notes per second and a duration of 10.6 seconds for *B. americanus* in northeastern Oklahoma and northwestern Arkansas. A single individual available from the western extreme of the range of *B. terrestris* has a longer call and slower repetition rate than does the species in Florida. In the northern part of its range, *B. americanus* has a faster repetition rate and shorter call than in Oklahoma and Kansas.

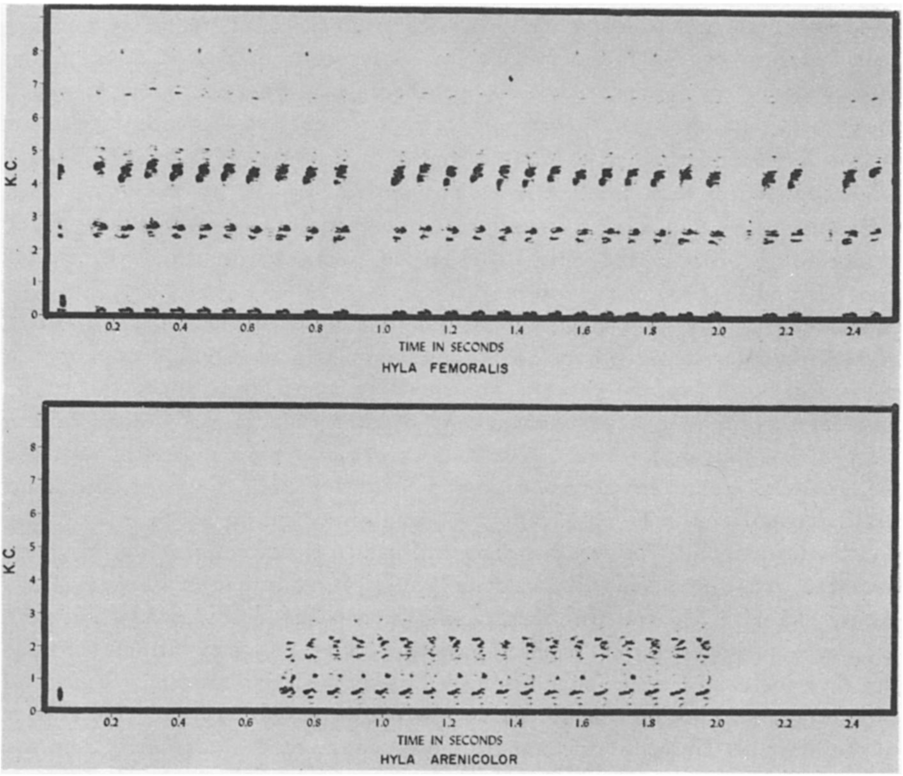

FIGURE 3. Sonagrams of the mating call of *Hyla femoralis* from Perry, Taylor County, Florida, and *H. arenicolor* from Baker Reservoir, Washington County, Utah. Note higher dominant frequency in the former.

In the southern disjunct population, *B. houstonensis*, the call is more similar to that of Oklahoma-Arkansas *B. americanus* than to Mississippi *B. terrestris*, which suggests that this allopatric species represents a relict from a former (possibly late Pleistocene) distribution of *B. americanus* southward west of the Mississippi Embayment.

The call of *B. hemiophrys* is strongly differentiated from the call of *B. americanus* in repetition rate and in duration (fig. 4). The ranges of these species essentially meet or possibly overlap in western Minnesota (W. F. Blair, 1957 a). The greater differentiation in call between *B. hemiophrys* and *B. americanus* than between *B. houstonensis* and *B. americanus* possibly indicates an earlier splitting off of the former than the latter population.

The southwestern relict species, *B. microscaphus,* has a short call comparable in duration to the call of *B. hemiophrys* (fig. 4) but with a repetition rate comparable to that of northern *B. americanus.* The dominant frequency is lowest (averaging 1300 cps) in *B. microscaphus* and next lowest (averaging 1548 cps) in *B. hemiophrys.* This compares with frequencies averaging from 1706 to 2300 cps in the samples available from the three remaining species of the group. The similarities in duration and frequency suggest that *B. microscaphus* is a relict from a Pleistocene extension of the range of *B. hemiophrys* southward. This hypothesis is supported by the presence of a relict population of *B. hemiophrys* in southeastern Wyoming (Stebbins, 1954). The morphological differentiation of *B. microscaphus* from *B. hemiophrys* is greater than that of *B. houstonensis* from *B. americanus.* This differentiation, principally in color pattern, could have proceeded under selection for life in the very different environments in which *B. microscaphus* and *B. hemiophrys* now exist.

Summing up the evolutionary relationships of the allopatric populations of the *B. americanus* group, the oldest speciational event was probably the splitting off of a western short-calling population ancestral to *B. hemiophrys* and *B. microscaphus.* At a later time, a withdrawal of the western population northward left *B. microscaphus* as a series of isolated relicts in tolerable environments in the Southwest. In the East, the long-calling population was split into the populations known as *B. americanus* and *B. terrestris.* The present distribution of the latter is of the kind associated with a presumed Pleistocene glacial-stage refuge in Florida (W. F. Blair, 1951). This splitting was possibly on an east-west basis, with the *B. americanus* population retreating to the Texas coast or farther south at the time the *B. terrestris* population was presumably isolated in Florida and later spreading northward and eastward to its present range. This theory of the distribution would account for the presence of *B. houstonensis* on the Texas coast as a relictual population most closely similar to Oklahoma-Arkansas *B. americanus.* The ranges of the *B. americanus* and *B. terrestris* populations came into contact (fig. 4) in the course of their spread, but the relationships of the two where this has occurred are still in need of clarification.

The splitting off of other groups such as the *boreas-canorus-alvarius* complex, *B. woodhousei, B. debilis,* and *B. punctatus* presumably occurred at a considerably earlier time than the speciational events discussed above.

Summarizing what we know about differentiation in call among allopatric species of anura, there is variation in degree of differentiation. The degree of differentiation is presumably related to the length of time that the isolation has existed. Some allopatric species differ just as much in call as do some sympatric species.

Sympatric Species. The sympatric species pairs available for analysis fall into two groups. In one group the distribution of call characteristics in the respective populations is such and the relations of the two popula-

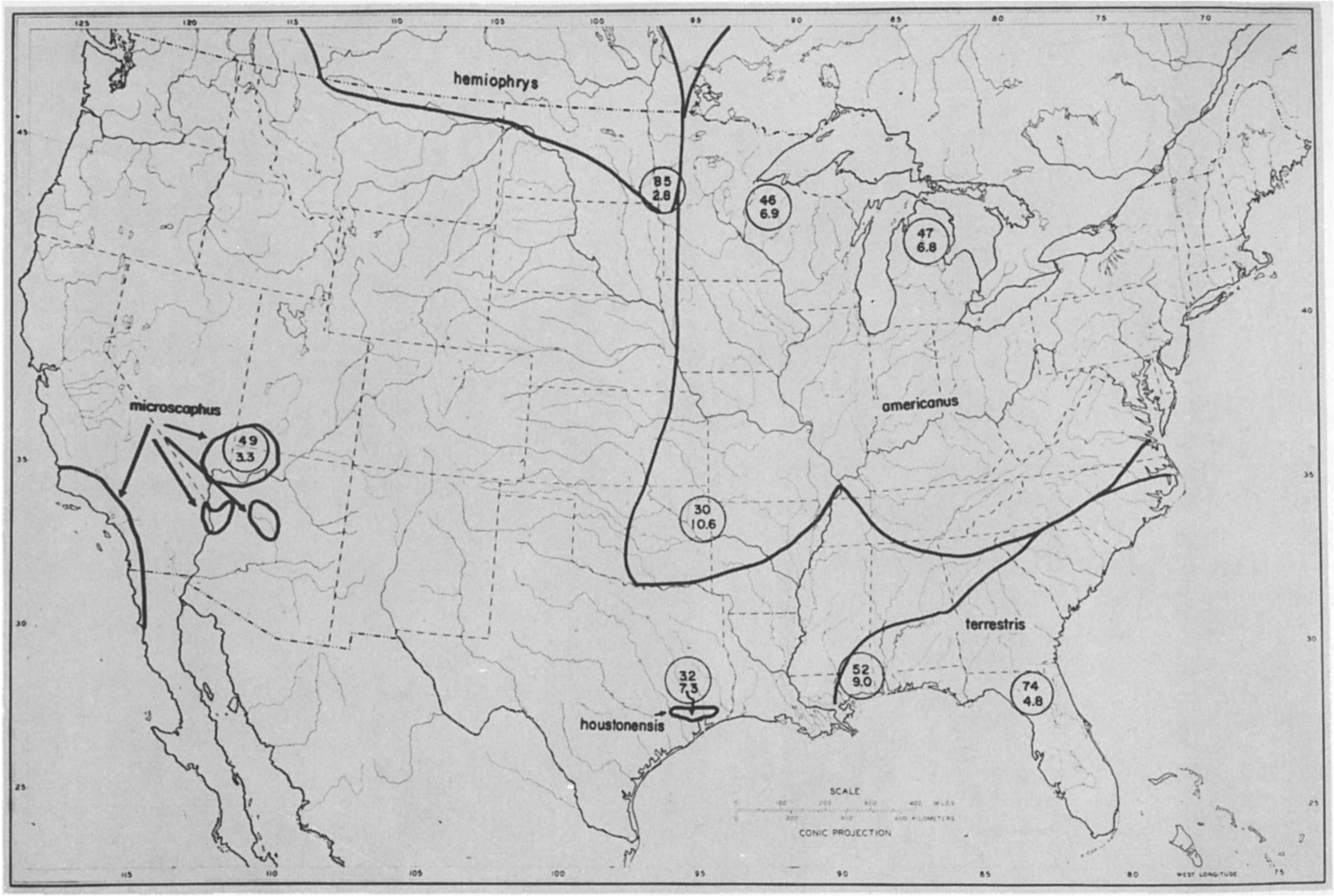

FIGURE 4. Variation in pulse rate and duration of the mating call in the *Bufo americanus* group of toads. Values given are station means. Top value shows pulses per second; bottom shows duration in seconds.

tions in the overlap zone are such as to suggest that reinforcement of partial isolation mechanism complexes has occurred and is occurring. In the other group the situation in respect to call characters is such that it suggests such strong differentiation of call and other isolation mechanisms under geographic isolation that there was no opportunity or necessity for reinforcement after the ranges became sympatric.

The most thoroughly analyzed situation in the first group is that of *Microhyla olivacea* and *M. carolinensis* (W. F. Blair, 1955a). The calls of the two species differ more in frequency and duration in the overlap zone in eastern Texas and Oklahoma than they do to the east and west of this zone. A comparable situation involving *Crinia glauerti* and *C. insignifera* in Australia discovered by A. R. Main has been quoted by Brown and Wilson (1956).

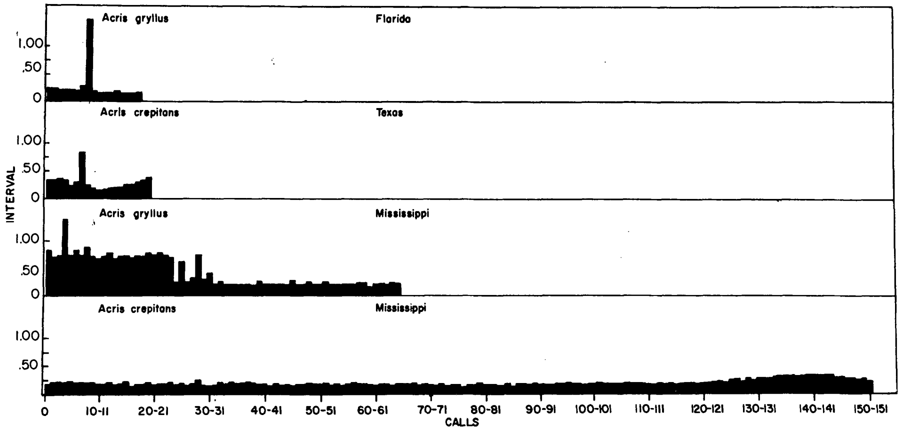

FIGURE 5. Pictorial representation of the intervals between calls in the call sequences of the cricketfrogs, *Acris gryllus* and *A. crepitans*. Intervals expressed in seconds between consecutive calls. Diagrams are for representative individuals. Mississippi individuals are from same breeding pool at Westonia, Hancock County. Note differentiation in respect to interval where the two species occur together.

Another case now under investigation is that of the cricketfrogs, *Acris gryllus* and *A. crepitans*. These two populations have been treated as subspecies in recent taxonomic works (Schmidt, 1953), although various authors (Viosca, 1923; Dunn, 1938; Bushnell, Bushnell and Parker, 1939; Orton, 1947; Neill, 1950, 1954) have pointed out morphological, ecological, cytological or mating call differences as evidence of their behavior as distinct species where they occur together. The range of *A. gryllus* is that of a presumed Pleistocene isolate in Florida, being restricted to Florida and a strip along the coast from the vicinity of Lake Pontchartrain in Louisiana to southeastern Virginia. The range of *A. crepitans* includes most of the eastern United States from western Texas and eastern Colorado eastward except for the northeastern states and most of the range of *A. gryllus*. The two populations have been reported to occur together without interbreeding in western South Carolina, Georgia, Alabama, northern Florida, Mississippi and Louisiana (Neill, 1954). The reports of Neill (1950, 1954) indicate an overlap area in Georgia from about 60 miles north of the Fall Line to northern Oklaloosa County, Florida.

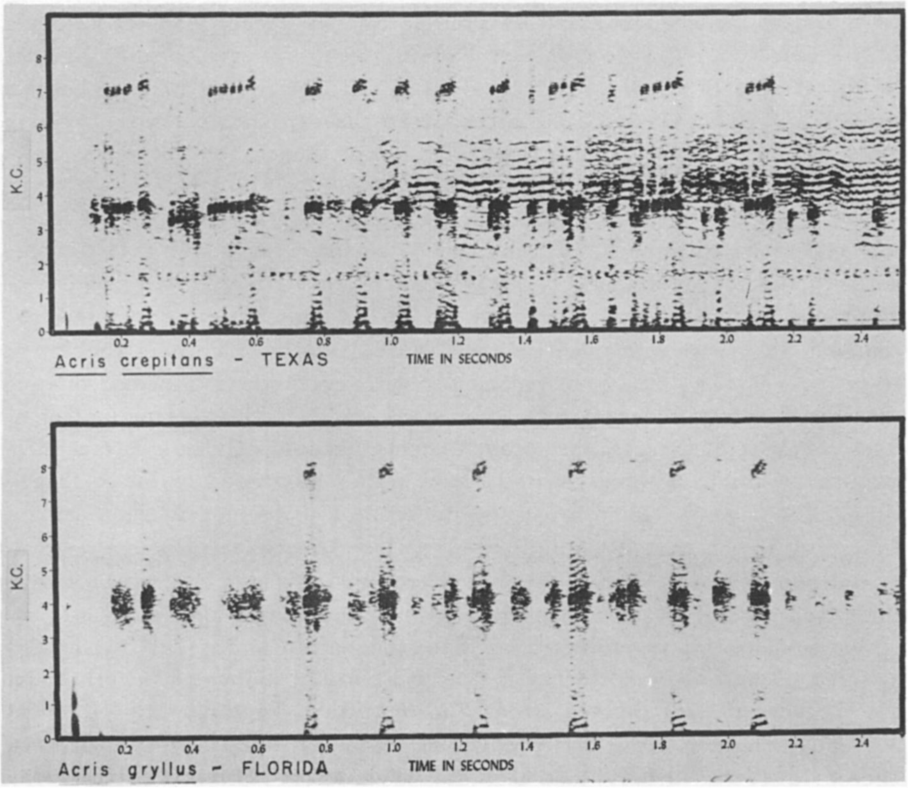

FIGURE 6. **Sonagrams of calls of *Acris crepitans* from Austin, Texas, and *A. gryllus* from Welaka, Florida.** The individual calls of the former are seen against a background of calls of other species. Note pulsed structure of first three calls. Calls of *A. gryllus* seen against background of others of the same species. Note similarity between the two species except for absence of pulsations in calls of *A. gryllus*.

Our present material consists of recordings in a mixed population in southwestern Mississippi (ghost town of Westonia, Hancock County), a series of recordings of *A. crepitans* from Texas, Oklahoma and Louisiana, and a few recordings of *A. gryllus* from peninsular Florida. The calls of Florida *A. gryllus* and western *A. crepitans* show only slight differences (figs. 5, 6). Where the two species occur together in southwestern Mississippi, however, their calls differ in every measurable characteristic. One way in which the calls differ is in the pattern of time intervals between calls in a call sequence. In the terminology we are using for the calls of these frogs, each individual note is regarded as a call; a series of calls is referred to as a call sequence. In the mixed population, *A. crepitans* has a rapidly repeated series of calls, with very little variation in interval between them (fig. 5). In the call sequence of *A. gryllus* in the mixed population, there is a slow repetition of calls in the initial part of the sequence and a rapid repetition in the closing segment. The individual *A. gryllus* figured had an average interval of 0.65 second separating the calls in the first half of the sequence and an average of 0.22 second separating those in the last half. The *A. crepitans* had an average interval of 0.21 second in the first half of the sequence and one of 0.21 in the last half of the sequence. This difference in call between the two species in the overlap zone was first called to my attention by Percy Viosca, Jr., (oral communication).

The calls of the two species in the mixed population also show a striking qualitative difference. The call of *A. gryllus* is a simple note comparable to that of western *A. crepitans* and Florida *A. gryllus.* That of *A. crepitans* in the mixed population is broken into a series of elements (pulses) in the same manner as the "trilled" calls of various species of *Hyla* (fig. 7). The number of pulses per call increases from two or three in the initial part of the sequence to as many as 10 in the closing part of it. This breaking of the call into pulses occurs occasionally in western *Acris crepitans,* which, however, usually have a call structure similar to that of *A. gryllus* (fig. 6). There also appears to be a difference in the dominant frequency in the mixed population. Ten *A. gryllus* have an average dominant frequency of 3480 cps (range 3400 to 3600). Three *A. crepitans* from the mixed population have an average of 4083 cps (range 4000 to 4200).

Additional work is projected to learn the nature of the call of the two species of Acris in other areas inside and outside the area of overlap, but the present sample indicates strong differentiation. On the basis of present evidence, therefore, the two species of Acris are like the two species of Microhyla (W. F. Blair, 1955 a) in showing strong differentiation of the mating call where their ranges overlap.

The mixed population in southwestern Mississippi was found in a pool formed by the outflow from an artesian well. Aggregations of *A. gryllus* were heard in roadside ditches and other situations in this area, but *A. crepitans* was found only in and near the artesian water, which is a distributional situation previously called to my attention by Percy Viosca, Jr., (oral communication). One of the morphological characters mentioned by Dunn (1938) to separate the two species, the length and degree of webbing of fourth toe on the hind foot, served completely to separate the two species from the mixed population independently of call characters. In other words, all of the individuals having the *A. gryllus* type of call had long, less-webbed toes, and those with the *A. crepitans* call had short, more fully-webbed toes.

The three situations discussed above are readily explainable only by the theory that selection against hybridization in the overlap zone has served to sharpen call differences and thus increase the effectiveness of this isolation mechanism. The only alternative explanation for the increased differences in call in the overlap zone would be that the differences are purely fortuitous, but this explanation seems hardly defensible.

The group of sympatric species in which there is no evidence of reinforcement of call differences includes such pairs as *Bufo compactilis-B. cognatus, Hyla cinerea-H. gratiosa,* and *Hyla versicolor-H. phaeocrypta.*

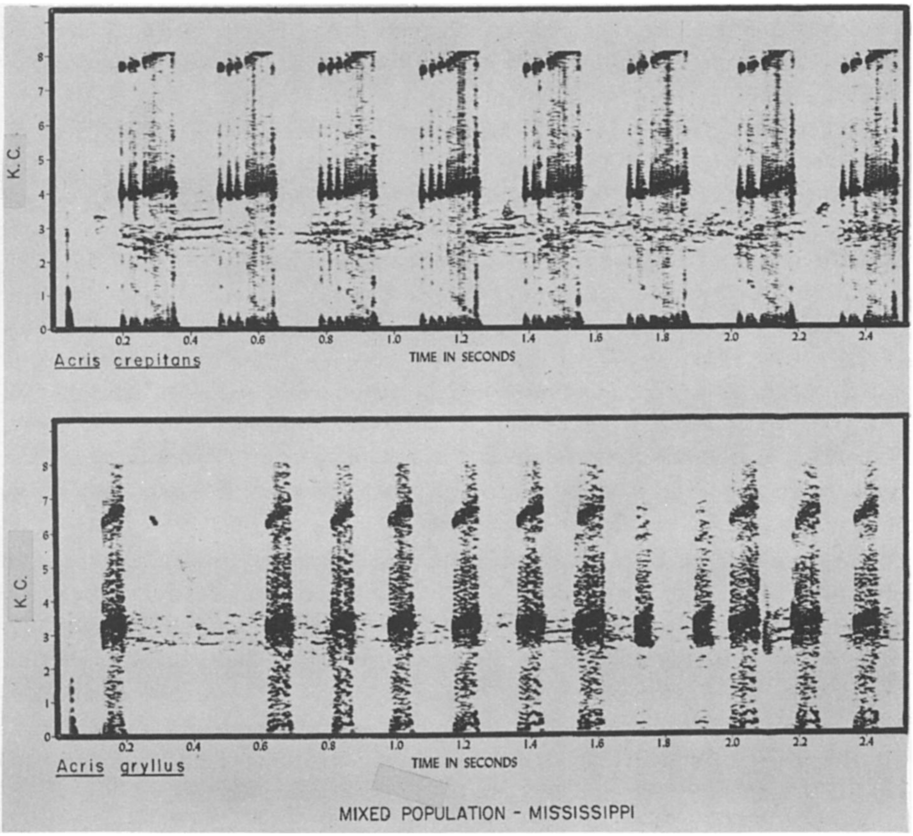

FIGURE 7. Sonagrams of calls of two species of Acris from same breeding pool at Westonia, Hancock County, Mississippi. Note difference between pulsed call of *A. crepitans* and unpulsed of *A. gryllus*. Calls of both seen against faint background of other species.

The ranges of *Bufo cognatus* and *B. compactilis* overlap from southwestern Kansas south through western Oklahoma, western Texas, and eastern New Mexico into Mexico. The calls of these two species are strongly differentiated in duration and to a lesser degree in repetition rate. The call of *B. compactilis* averages about one-half second in duration, and no call has been recorded in excess of 1.7 second. This short call is incessantly repeated. The call of *B. cognatus* is long, averaging about 20 seconds and ranging up to 54 seconds in length. We can find no significant differences between calls of *B. compactilis* from the overlap zone in trans-Pecos Texas and those of the same species in the Austin region, some 250 miles east of the overlap zone. Nor are there any significant differences in call between *B. cognatus* from the overlap zone in the Texas panhandle and individuals from western Minnesota, some 500 miles northeast of the overlap zone.

There is no indication of reinforcement of call differences between *Hyla cinerea* and *H. gratiosa* where they occur together. Both species have typical coastal plain distributions suggestive of Pleistocene speciation in Florida, and their initial separation could have occurred on different glacial-stage islands in what is now peninsular Florida. The species *H. gratiosa* extends westward to southeastern Louisiana. The species *H. cinerea* extends westward to south-central Texas and northward in the Mississippi Embayment to southern Illinois. The latter species occurs throughout the range of *H. gratiosa* and extends beyond it on the west, in the Mississippi Embayment, on the northeast, and in southern Florida.

The calls of *Hyla cinerea* and *H. gratiosa* are structurally very similar and differ chiefly in the distribution of energy in the frequency spectrum (W. F. Blair, 1957c). The calls of these species differ from those of other U. S. treefrogs except *H. andersoni* in that a large number of harmonics of the fundamental are more or less equally emphasized. The fundamental (about 450 cps) in *H. gratiosa* is noticeably stronger, however, than the other harmonics. In *H. cinerea,* the eleventh and twelfth are usually somewhat emphasized in relation to the others. The result of this distribution of energy is to give the call of *H. cinerea* a higher pitch than that of *H. gratiosa.* Five calls of *H. cinerea* from four stations in central and eastern Texas have an average dominant frequency of 2860 cps (2700 to 3000) by comparison with a frequency of 2973 (2850 to 3150) in 11 individuals from southwestern Mississippi and 3470 cps (3200 to 3850) in five individuals from northern Florida. The slightly lower average frequency in the Texas frogs cannot be considered significant in view of the small size and overlap of the samples. The calls of the Texas frogs are shorter (0.11 second) than those of the Mississippi (0.17 second) and Florida (0.16 second) frogs. However, the length of the call in the Mississippi and Florida frogs is more like the length of the call of three *H. gratiosa* (0.16 second) from eastern Mississippi than is the call of the Texas frogs from outside of the overlap zone.

The range of *Hyla phaeocrypta* (= *avivoca*), which extends on the Gulf coastal plain from South Carolina to the Mississippi River in Louisiana, falls entirely in the range of *H. versicolor.* The two species are morphologically quite similar, although *H. versicolor* is somewhat larger than *H. phaeocrypta.* As in *Bufo compactilis* and *B. cognatus,* the calls of these two species of treefrogs are strongly differentiated. The calls of 10 *H. phaeocrypta* recorded in Perry County, Mississippi, average 1.99 seconds in length and have an average repetition rate of only 9.7 notes per second.

The call race of *H. versicolor* from the same region (table 3) has an average call length of only 0.77 second and a repetition rate of 50.8 notes per second. In addition, *H. phaeocrypta* has evolved a complex modulation pattern (W. F. Blair, 1957c) that is quite different from the simple pattern of *H. versicolor.* While the call race of *H. versicolor* that occurs sympatrically with *H. phaeocrypta* has a faster repetition rate than the race that occurs to the west of it, there are two reasons to doubt that the accelerated repetition results from hybridization-induced reinforcement. First, the contact between these call races of *H. versicolor* (fig. 2) occurs about 100 miles west of the western boundary of *H. phaeocrypta.* To rationalize this discrepancy would require a formerly wider distribution of *H. phaeocrypta* westward or a spread of the fast trilling character beyond the zone of sympatry. Secondly, the duration of the call of *H. versicolor* is longer, and therefore more like that of *H. phaeocrypta,* in the zone of sympatry than in any other area (table 3).

The available analyses of mating call in allopatric and sympatric species pairs of anurans strongly imply that differentiation of mating call to the extent that the differences serve as an important isolation mechanism has occurred under geographic isolation. They also imply equally strongly that in some instances reinforcement of call difference as an isolation mechanism does occur when previously isolated populations come into contact before developing a completely effective set of isolation mechanisms. To summarize, allopatric species pairs show every degree of differentiation in call from essentially none (*Pseudacris streckeri* and *P. ornata*) to strong differentiation (*Hyla femoralis* and *H. arenicolor*). In some species, as in *Hyla versicolor,* the presence of call races suggests that geographic separation has been followed by secondary contact and interbreeding prior to the evolution of an isolation mechanism complex. Some sympatric species show strong differentiation in mating call both inside and outside of the area of contact. These are presumed to have differentiated the call under geographic separation. The only alternative would be the unlikely possibility that differences reinforced in the area of contact had subsequently spread throughout the ranges of the respective species. Other sympatric species show accentuation of differences in the zone of sympatry as an apparent result of natural selection.

LOSS OF CALL

In spite of its functions of aggregating populations for reproduction and of species identification, the call is vestigial or has been lost in some anurans. In the United States, all of the instances of call loss or reduction are found in the far west, where the number of species is relatively few for any genus and the identification function may be relatively unimportant. The large desert toad, *Bufo alvarius,* of the Southwest has a vestigial call and vestigial vocal pouches (Blair and Pettus, 1954). The large size of this toad apparently precludes cross-mating with any sympatric species of toads. Another species of the same presumed species group, *B. boreas*, apparently lacks a mating call, or at most has a very weak one. A "release note" is used by males of both species, and various reports of a weak mating call in *B. boreas* may refer to this note. In the *Rana boylei* group of the extreme western United States and Mexico, only one (*R. boylei*) of the six species possesses a vocal pouch (Zweifel, 1955). All of these allopatric species are disjunctly distributed except *R. boylei* and *R. muscosa*, which show slight overlap. *R. boylei*, the species which has retained the voice shares practically all of its range with another species, *R. aurora* (Zweifel, *op. cit.*). The four Mexican species, *R. tarahumarae, R. moorei, R. pueblae,* and *R. pustulosa,* all occur in the range of *R. pipiens.* Another voiceless western anuran, *Ascaphus truei,* is a primitive type with no other representative of its suborder outside of New Zealand.

Inger (1954) has described a remarkable instance of geographic variation in the presence or absence of vocal pouches in *Rhacophorus leucomystax* of the Philippines and adjacent areas. Vocal pouches are present in some areas and absent in others. Three of 37 males from northeastern Borneo had vocal pouches.

NATURAL HYBRIDIZATION

All of the well authenticated reports of natural hybrids between species of U. S. toads that have been published involve crosses between *Bufo woodhousei* and members of the *B. americanus* group (A. P. Blair, 1941, 1942, 1955; Volpe, 1952; Cory and Manion, 1955; Stebbins, 1951; W. F. Blair, 1956a) or *B. valliceps* (Thornton, 1955; Volpe, 1956). As originally held by A. P. Blair (1941) and generally concurred in by the other workers, the disturbance of ecological isolation mechanisms through man's interference with the environment is probably responsible for this hybridization. The untrilled call with broad side-band structure of *B. woodhousei* is very different from the trilled call of *B. valliceps* and the trilled, finely tuned call of the members of the *B. americanus* group. It is evident in these instances of hybridization that call difference alone is not sufficient to prevent some sympatric hybridization when other isolation mechanisms are weakened or eliminated. Sympatric hybrids between *Scaphiopus couchi* and *S. hurteri* (Wasserman, 1957) are also attributed to man's disturbance of the landscape. Hybrids are also known between *Scaphiopus hammondi* and *S. bombifrons* (W. F. Blair, 1955c), but the degree of hybridization is unknown.

There is limited information about the calls of species hybrids. The call of a laboratory-produced, field-raised hybrid between *Bufo terrestris* and *B. houstonensis* is intermediate in repetition rate between the calls of the parental species. The former species has a shorter call with a faster repetition rate than the latter one (W. F. Blair, 1956a). The hybrid had an average duration of 8.0 seconds and a repetition rate of 39.0 pulses per second at an air temperature of 23.0°C. Two *B. terrestris*, similarly laboratory produced and field raised, and recorded at the same temperature, had average durations of 5.7 and 5.8 seconds and repetition rates of 52.0 and 53.3 pulses per second. By contrast with the intermediacy of the call of hybrids between these closely related species, the call of sterile hybrids between the distantly related *B. woodhousei* and *B. valliceps* are imperfect but tend to resemble the call of the male *valliceps* parent (W. F. Blair, 1956 c).

SUMMARY

Analysis of the mating call is useful for the study of evolutionary problems in anuran amphibians because characteristics of the call are chiefly related to the functions of attracting a mate and of species identification in breeding congresses. Use of the sound spectrograph in recent years has made possible the measurement and objective comparison of calls.

Variations in call occur among individuals in local populations and between the calls of the same individual under different conditions. Frequency and repetition rate tend to increase with increased environmental temperature and to decrease with increased body size. The call may vary in relation to sexual excitement. The variation in call of a single *Hyla versicolor* recorded on nine different nights and the variations among 17 *Pseudacris streckeri* recorded from a breeding population on a single night are discussed. Variations not explainable in terms of environmental or ontogenetic factors or degree of sexual excitement are deemed to have a genetic basis.

Patterns of geographic variation in call are discernible in species which have been investigated. In *Pseudacris nigrita,* on present information the call races tend to correspond to subspecies described on morphological bases. In *Hyla versicolor,* the relationships of three call races seem best explained by the hypothesis of secondary interbreeding after Pleistocene separation of three segments of the population.

Each species of anuran has a call that differs from the call of every other species. Groups of species within a genus, however, show basic similarities in call structure, which, with other evidence, are indicative of evolutionary relationship. Species groups in the genera Scaphiopus, Bufo, and Hyla of the United States are suggested on the basis of call structure and other evidence.

Various allopatric and sympatric species pairs are discussed in relation to their bearing on the question of purely geographic speciation versus geographic separation with subsequent reinforcement of isolation mechanisms. Some allopatric species (*Pseudacris streckeri-P. ornata, Scaphiopus holbrooki-S. hurteri*) show little differentiation in call. Others (*Hyla femoralis-H. arenicolor* and various members of the *Bufo americanus* species group) show strong differentiation. Some allopatric species show as much differentiation in call as do sympatric species. Among sympatric species, *Acris gryllus* and *A. crepitans,* along with previously reported species

pairs, show reinforcement of call differences where they occur together. Some sympatric species pairs (*Bufo compactilis-B. cognatus, Hyla cinerea-H. gratiosa, Hyla versicolor-H. phaeocrypta*) have strongly differentiated calls but show no evidence of reinforcement where they occur together. The evidence from the allopatric and sympatric species pairs is interpreted as indicating that speciation has occurred either through the evolution of effective isolation mechanisms under geographical isolation or through reinforcement of partially effective mechanisms after ranges have become sympatric.

The mating call is weak or lacking in some anuran species. All instances of this in the United States are found in far western species of Bufo, Rana and Ascaphus and in which the identification function of call may be relatively unimportant because of the scarcity of species there.

Natural hybridization sometimes occurs between species with well differentiated calls. All well authenticated natural hybrids among U. S. toads involve crosses between *Bufo woodhousei* with representatives of the *B. americanus* group or with *B. valliceps*. This indicates that call differences are not necessarily sufficient to prevent interspecific hybridization when other isolation mechanisms are weakened or eliminated. Hybrids are also known in Scaphiopus.

The calls of hybrids between closely related species are intermediate in character between those of the parental species. The calls of hybrids between two distantly related species (*Bufo woodhousei* and *B. valliceps*) are imperfect and tend to resemble the calls of the male (*B. valliceps*) parent.

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