Smithsonian Folkways

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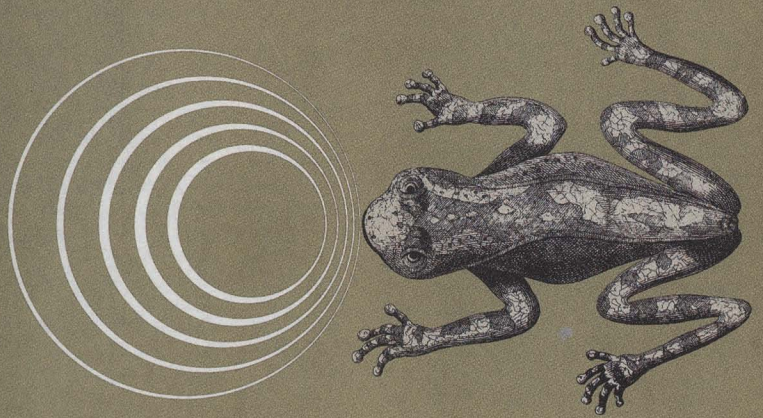
SOUNDS OF NORTH AMERICAN FROGS

The Biological Significance of Voice in Frogs

Conceived, Narrated and Documented, with Field Recordings by CHARLES M. BOGERT,
with the cooperation of The American Museum of Natural History



Ronald Clyne

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TRACKS

An annotated list of sounds in the order of their occurrence on the recording

1. Individual Barking Treefrog, *Hyla gratiosa*, recorded in soundproofed room at Archbold Biological Station, Highlands County, Florida; individual taken four miles south of the Station at 9:45 p.m. on the evening of July 16, 1957. *0:16*

2. Chorus of Barking Treefrogs, *Hylya gratiosa*, recorded four and a half miles south of Archbold Biological Station, Highlands County, Florida, between 8:45 and 9:05 p.m. on the evening of July 16, 1957. *0:20*

3. Mixed chorus recorded one-half mile south of Archbold Biological Station, Highlands County, Florida, at 10:15 p.m. on July 7, 1954. In addition to the Barking Treefrog other species discernible in the chorus are the Pine Woods Treefrog, *Hyla femoralis*, Cricket Frogs, *Acris gryllus dorsalis*, Oak Toads, *Bufo quercicus*, and the snore-like call of the Gopher Frog, *Rana capito*. Other species present in the chorus, but not close enough to the microphone to be easily distinguished, include the Southern Toad, *Bufo terrestris*, the Green Treefrog, *Hyla cinerea*, the Squirrel Treefrog, *Hyla squirella*, the Eastern Narrow-mouthed Toad, *Utricularia carolinensis*, Southern Leopard Frogs, *Rana gastrophryne*, Pig Frogs, *Rana grylio*, and quite possibly the Little Grass Frog, *pseudacris ocularis*, although this extremely small species may easily have been overlooked. *0:50*

4. The Southern Toad, *Bufo terrestris*, recorded at 8:10 p.m. on August 21, 1954, at East Lake, Putnam County, Florida. The hum discernible below the trill when the voice is amplified probably accompanies all calls of the species, although the hum is not ordinarily heard unless the microphone is close to the toad at the time it is calling. Probably it is the same hum heard when the warning vibration is produced along with the warning chirp. Aronson (1944) has demonstrated that this warning vibration is produced by some mechanism other than the vocal chords, although its precise origin remains uncertain. *0:38*

5. The Green Treefrog, *Hyla cinerea*, recorded at Orange Springs, Marion County, Florida, at 8:45 p.m., August 29, 1954, with the flow of water from the springs in the background. *0:18*

6. A continuation of the same call heard in No. 5, the call terminating in the accelerated, less musical sounds most often heard when these frogs are calling singly or in small choruses.It is uncertain why these treefrogs sometimes shift from one sort of call to another. *0:36*

7. Chorus of Eastern Narrow-mouthed Toads, *Gastrophryne carolinensis*, recorded at 10:55 p.m. on May 30, 1954, seven miles south of the Archbold Biological Station in Highlands County, Florida. *1:07*

8. Voice of *Acris gryllus dorsalis*, recorded at East Lake, Putnam County, Florida, at 1:45 a.m. on August 20, 1954. *0:21*

9. Mating call of Squirrel Treefrog, *Hyla squirella*, recorded at 11:45 p.m. on July 25, 1957, near Englewood, Sarasota County, Florida. *0:24*

10. Mating call of the Pine Woods Treefrog, *Hyla femoralis*, recorded two miles north of Orange Springs, in Putnam County, Florida, on the evening of August 23, 1954. The single grunt or territoriality call, of the Bronze Frog, *Rana clamitans*, can be heard in the background, along with another Pine Woods Treefrog. *0:25*

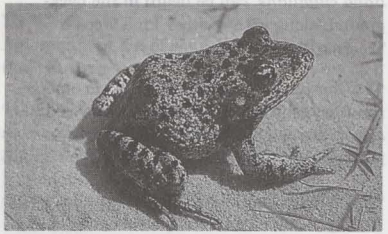
11. Chorus of Green Treefrogs, *Hyla cinerea*, recorded at 9:50 p.m. in a swampy area adjacent to the Oklawaha River, east of Silver Springs, Marion County, Florida. *0:23*

12. Barking Treefrog, *Hyla gratiosa*, taken at 10:05 p.m. four and a half miles south of the Archbold Biological Station and recorded the same evening in the laboratory at the Station on July 16, 1957. *0:34*

13. Mating call of the Pig Frog, *Rana grylio*, with Cricket Frogs, *Acris gryllus dorsalis*, in the background, recorded at 9:05 p.m. on May 31, 1954, four miles north of the Archbold Biological Station, Highlands County, Florida. *0:32*

14. Breeding chorus of Southern Leopard Frogs, *Rana utricularia*, recorded at 1:00 a.m., east of Hicoria in Highlands County, Florida, with Cricket Frogs, *Acris gryllus dorsalis*, in the background. *0:40*

15. A large breeding chorus of Florida Gopher Frogs, *Rana capito*, with one Barking Treefrog, *Hyla gratiosa*, and the Pine Woods Treefrog, *Hyla femoralis*, as well as Cricket Frogs, *Acris gryllus dorsalis*, in the background. Recorded eight miles south of the Archbold Biological Station at 9:45 p.m., July 18, 1957. *0:54*

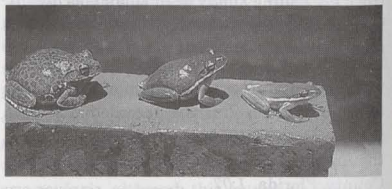


Florida Gopher Frog, *Rana capito*, tracks 15, 38, in chorus 3, 89, 92.

16. Mating trill of the Southern Toad, *Bufo terrestris*, recorded at 7:05 p.m., on May 25, 1954, at Tarpon Lake, Collier County, Florida. A barred owl in the distance and the Squirrel Treefrog, *Hyla squirella*, in the background. Recorded at 2:09 p.m., July 27, 1957, near Placida, Charlotte County, Florida. *0:39*

17. Breeding call of the Oak Toad, B*ufo quercicus*, with the Squirrel Treefrog, *Hyla squirella*, in the background. Recorded at 2:09 p.m., July 27, 1957, near Placida, Charlotte County, Florida. *0:25*

18. Mating call of hybrid treefrog, evidently the result of a cross-mating of the Barking Treefrog, *Hyla gratiosa*, and the Green Treefrog, *Hyla cinerea*. This hybrid was calling in a small chorus of Barking Treefrogs when found four and a half miles south of the Archbold Biological Station in Highlands County, Florida, at 8:30 p.m. on July 16, 1957. Although this frog joined the chorus of Barking Treefrogs, superficially it looks more like the Green Treefrog. However, it is much larger, being intermediate in size between the two parental species. After being captured on the evening of July 16, it was taken back to the laboratory at the Archbold Biological Station, where its voice was recorded in the laboratory. *0:47*



(left) Barking Treefrog, *Hyla gratiosa*, (right) Green Treefrog, *Hyla cinerea*, (center) Hybird Treefrog, (*Hyla gratiosa x Hyla cinerea*)

19. Green Treefrog, *Hyla cinerea*, recorded in the laboratory on July 17, 1957. Specimen taken in Highlands County, Florida, eight and a half miles east of the De Soto County line, on the road to Arcadia. *0:16*

20. The mating call of the Barking Treefrog is heard first, finally joined by the hybrid treefrog, *Hyla cinerea* x *Hyla gratiosa*, after both species were induced to call in the laboratory after their capture on the evening of July 16, 1957, by allowing them to listen to a recording of their own chorus through the earphones of a portable tape recorder. *0:26*

21. Mating call of the Red-spotted Toad, *Bufo punctatus*, recorded at an elevation of 5,000 feet in Cave Creek, Chiricahua Mountains, Arizona on the evening of July 3, 1953, between 10:30 and 11:00 p.m. *0:36*

22. The somewhat distinctive call of an individual Red-spotted Toad, *Bufo punctatus*, recorded at the AVA Ranch, Portal, Cochise County, Arizona, at 8:15 on the evening of July 10, 1955. *0:32*

23. Mating call of Fowler's Toad, *Bufo woodhousei fowleri*, recorded one mile east of Little Rock, Arkansas, at 8:45 on the evening of April 20, 1955. *0:22*

24. Mating call of Fowler's Toad, recorded one-half mile west of Henderson, North Carolina, at 11:00 p.m. on May 17, 1954. *0:28*

25. Mating call of the Southwestern Woodhouse's Toad, *Bufo w. australis*, recorded on the outskirts of Phoenix, Arizona, on the evening of April 24, 1955. Traffic from the city can be heard in the distance. *0:21*

26. Mating call of the American Toad, *Bufo americanus*, recorded at 10:45 p.m. on April 30, 1957, one-fourth mile south of Monett, Missouri. The Southern Leopard Frog, *Rana utricularia*, can be heard in the background. *0:51*

27. Mating call of the Southern Toad, *Bufo terrestris*, recorded at East Lake, Putnam County, Florida, at 7:45 p.m., August 20, 1954. *0:41*

28. Mating call of Eastern Gray Treefrog, *Hyla versicolor*, with the single note or "territoriality call" of the Green Frog, *Rana clamitans melonata*, in the background. Recorded in a pond on the edge of Tenafly, New Jersey, on the Palisades above the Hudson River, at 9:15 p.m. on May 25, 1955. *0:30*

29. Mating call of Gray Treefrog, *Hyla chrysoscelis*, recorded one-half mile west of Henderson, North Carolina, at 10:15 p.m., May 17, 1954. *0:37*

30. Mating call of the Gray Treefrog, *Hyla chrysoscelis*, recorded near the Oklawaha River, Putnam County, Florida, at 10:15 p.m. on September 1, 1954. The Squirrel Treefrog,

Hyla sqirella, can be heard in the background. *0:32*

31. Mating call of the Gray Treefrog, *Hyla chrysoscelis*, recorded two miles south of Monett, Missouri, on the evening of April 30, 1957. *0:23*

32. Mating call of the Canyon Treefrog, *Hyla arenicolor*, recorded at the Painted Canyon Ranch, Cave Creek, Cochise County, Arizona, at 8:30 p.m. on July 8, 1953. Water flowing into a pool may be heard in the background. *0:31*

33. Mating call of the California Treefrog, *Hyla cadaverina*, recorded in Sentenac Canyon, San Diego County, California, with the Pacific Treefrog, *Hyla regilla*, heard in the background. Taped at 11:35 on the evening of March 24, 1956. *1:01*

34. Warning croak accompanied by "warning vibration" of the Southern Toad, *Bufo terrestris*, recorded at East Lake, Putnam County, Florida, on August 20, 1954. *0:54*

35. Warning chirp of the Boreal Toad, *Bufo boreas boreas*, without any warning vibration apparent. Recorded in the laboratory in New York with a specimen from Mendenhall Moraine, ten miles northwest of Juneau, Alaska. *0:31*

36. Warning croak of the Sonoran Desert Toad, *Bufo alvarius*, recorded at Wickenburg, Arizona, the day after the toad was collected on April 24, 1955, near Phoenix, Arizona. A fly hovering around the toad can be heard. *0:28*

37. Warning chirp of the California Treefrog, *Hyla cadaverina*, recorded in Andreas Canyon, Riverside County, California, on the afternoon of March 26, 1956. Normally uttered when one male is seized by another during the breeding season, the sound in this instance was issuing from a plastic bag containing several male treefrogs of the species, and the chirp was elicited when one frog got on the back of another. *0:31*

38. Warning croak of the Florida Gopher Frog, *Rana capito*, recorded on July 7, 1954, in the laboratory at the Archbold Biological Station, with a specimen taken one-fourth mile south of the station. This frog was held in a human hand. Under natural conditions, the sound would not be repeated so many times before the male would be released by another male that had seized it. *0:55*

39. The "territoriality call" of the southern race (the Bronze Frog, *Rana c. clamitans*) of the Green Frog. When these frogs are in the water, their territoriality calls sound somewhat more resonant than they do when on land, as this one was at the time it was recorded. The mating call of the Pine Woods

Treefrog, *Hyla femoralis*, can be heard in the background. Recorded at 9:10 p.m. on August 24, 1954, two miles north of Orange Springs, in Putnam County, Florida. *0:27*

40. "Rain song" of the Squirrel Treefrog, *Hyla squirella*, recorded at Tarpon Lake, Collier County, Florida, on the afternoon of May 27, 1954. A few Green Treefrogs, *Hyla cinerea*, can be heard in the distant background. These calls were recorded in the afternoon after a heavy rain earlier in the day. Squirrel Treefrogs are commonly heard calling from trees, or even from the walls of houses, under such conditions. The "rain song" of this species differs from the mating call largely in being less spirited, and uttered at less frequent intervals. *1:01*

41. Scream of the Southern Leopard Frog, *Rana utricularia*, from a specimen taken at the Archbold Biological Station and recorded in the laboratory, where it was simply seized in the hand. Under natural conditions, when seized by such enemies as the raccoon, the Southern Leopard Frog produces a far more bloodcurdling scream. *0:49*

42. Chorus of Pig Frogs, *Rana grylio*, recorded two miles north of the Archbold Biological Station on the evening of May 31, 1954. Also heard are Cricket Frogs, *Acris gryllus dorsalis*. *0:57*

43. The grunt-like sound produced by the Pig Frog, *Rana grylio*, with the rasping voice of a barred owl and Cricket Frogs in the background. This sound is sometimes heard during the day as well as at night. Thus far it has not been demonstrated that it actually serves as a warning to other Pig Frogs to keep their distance. However, in view of the apparent similarity of the conditions under which it is produced by the Green Frog (Martof 1953), it seems probable that it serves the same purpose as the "territoriality call" of *Rana clamitans*. *0:17*

44. The voice of the Pig Frog, *Rana grylio*, that corresponds to the scream of the Leopard Frog. This sound is produced with the mouth open, rather than closed, as it is when all other sounds are produced. The voice heard here is that of a large female Pig Frog that was maintained at the laboratory at the Archbold Biological Station. It got out of its enclosure in the laboratory, on June 6, 1954, and when it was picked up to be returned, it produced this sound. *0:39*

45. The mating call of the Bullfrog, *Rana catesbeiana*, with Cricket Frogs, *Acris g. gryllus*, in the background. Recorded 1.5 miles southeast of Swainsboro, Georgia, on the evening of May 18, 1954. Bullfrogs produce the same sort of call after the mating season is past, suggesting that the same call may serve as a "territoriality call." This remains

to be investigated, but when Bullfrogs are introduced into isolated ponds they space themselves at varying distances, seemingly with each frog at approximately the same place night after night. *0:33*

46. The mating call of the Pig Frog, *Rana grylio*, recorded four miles north of the Archbold Biological Station at 9:15 p.m. on May 31, 1954. The Cricket Frog, *Acris gryllus dorsalis*, may be heard in the background. *0:32*

47. Mating chorus of Southern Leopard Frogs, *Rana utricularia*, near Hicoria, Highlands County, Florida, with Cricket Frogs, *Acris gryllus dorsalis*. Recorded at 1:35 a.m. on the night of May 30, 1954. *0:34*

48. Mating call of the Pickerel Frog, *Rana palustris*, with the territoriality call of the Green Frog, *Rana clamitans melanota*, heard in the background. Traffic sounds from the highway a half mile away, including an automobile horn, can also be heard. Recorded in Tenafly, New Jersey at 9:30 p.m. on the evening of May 18, 1955. *0:29*

49. Mating call of the Giant Toad, *Bufo marinus*, recorded on Barro Colorado Island in the Canal Zone by Peter Paul Kellogg. The sound in the background is the call of the small Leptodactylid Frog, *Physalaemus pustulosus*. *0:43*

50. Mating call of the Sonoran Desert Toad, *Bufo alvarius*, with the New Mexico Spadefoot, *Scaphioupus mulitplicatus*, and Couch's Spadefoot, *Scaphiopus couchi*, in the background. Recorded in the Rillito on the northern outskirts of Tucson, Arizona, at 10:45 p.m. on July 18, 1953. *0:39*

51. Mating call of the Gulf Coast Toad, *Bufo valliceps*, with other toads of the same species to be heard in the background. Recorded approximately a mile west of Austin, Texas, at 10:10 p.m. on April 22, 1957. An airplane is also discernible in this recording. *0:48*

52. Mating call of the Arroyo Toad, *Bufo microscaphus californicus*, recorded in the evening near the Mojave River, near Victorville, California, April 1954, by Robert C. Stebbins. *0:41*

53. Mating call of the Red-Spotted Toad, *Bufo punctatus*, recorded at 11:10 p.m. on April 22, 1957 near Austin, Texas. Red-Spotted Toads in this Texas population are somewhat smaller than those in Arizona and Sonora and appear to have higher pitched voices. Water flowing in a stream alongside the toad is discernible in the background. *0:45*

54. Mating call of the Green Toad, *Bufo debilis insidior*, recorded ten miles north of Rodeo, New Mexico, at 9:55 p.m. on July 17, 1955. *0:42*

55. Mating call of the Oak Toad, *Bufo quercicus*, recorded near Placida, Florida, at 2:50 a.m. on July 27, 1957. The Pine Woods Treefrog, *Hyla femoralis*, may be heard in the background. *0:27*

56. The call of the Green Toad, *Bufo debilis insidior*, recorded ten miles north of Rodeo, New Mexico, on the evening of July 17, 1955. Another toad of the same species can be heard in the distance. The same call is reproduced at half speed. *0:34*

57. This is the same call heard in the previous recording but reduced to one-quarter speed. *0:40*

58. The mating chorus of the Eastern Narrow-mouthed Toad, *Gastrophryne carolinensis*, recorded near the Oklawaha River, east of Orange Springs, Marion County, Florida, at 10:20 p.m. on September 1, 1954. *0:38*

59. The mating call of the Great Plains Narrow-mouthed Toad, *Gastrophryne olivacea*, recorded at Alamos, Sonora, Mexico, on the evening of August 20, 1955. *0:33*

60. Mating chorus of the Plains Spadefoot, *Scaphiopus bombifrons*, with a duet discernible in the foreground. Recorded in Cochise County, Arizona, one mile west of Rodeo, New Mexico, on the evening of July 13, 1955. *0:41*

61. Chorus of the Lowland Burrowing Treefrog, *Pternohyla fodiens*, recorded 13 miles west of Hermosillo, Sonora, Mexico, on the evening of July 30, 1955. *0:27*

62. Mating call of the Pine Barrens Treefrog, *Hyla andersoni*, with a "reply" of another frog of the same species in the background. Recorded three miles south of Taunton Lakes, New Jersey, on the evening of May 13, 1955. *0:35*

63. Mating call of the Mountain Treefrog, *Hyla eximia*, recorded one mile south of Tepic, Nayarit, Mexico, on the evening of August 16, 1956. *0:36*

64. Mating call of the Mexican Treefrog, *Smilisca baudini*, joined by the Mexican Burrowing Frog, *Pternohyla fodiens*, recorded 25 miles south of Culiacán, Sinaloa, Mexico, on the evening of September 9, 1957. *0:35*

65. Mating call of the Spring Peeper, *Hyla crucifer*, recorded at the eastern edge of Tenafly, New Jersey, at 7:15 p.m. on April 18, 1957. *0:23*

66. Mating chorus of the pacific Treefrog, *Hyla regilla*, in Littlerock Creek, Littlerock, Los Angeles County, California, on the edge of the Mojave Desert at 10:20 p.m. on April 30, 1955. This call has been widely used as background sound in various Hollywood movies regardless of the part of the world being portrayed. *0:34*

67. The mating call of the Dwarf Mexican Treefrog, *Hyla smithi*, recorded four miles east of Tepic, Nayarit, Mexico, on the evening of September 1, 1957. The voices of the Sabinal frog, *Leptodactylus melanonotus*, can be heard in the background. *0:33*

68. Mating call of the Little Grass Frog, *Pseudacris ocularis*, with the Squirrel Treefrog, *Hyla squirella*, in the background. Oak Toads, *Bufo quercicus*, and the Eastern Narrow-mouthed Toad, *Gastrophryne carolinensis*, are also discernible. Recorded near Placida, Charlotte County, Florida, on the evening of July 26, 1957. *0:17*

69. Western Chorus Frog, *Pseudacris triseriata*, recorded two miles south of Monett, Missouri, at 9:05 p.m. on April 30, 1957. *0:24*

70. Blanchard's Cricket Frog, *Acris gryllus blanchardi*, with the Southern Leopard Frog, *Rana urticularia*, in the background. Recorded two miles south of Monett, Missouri, at 8:30 p.m. on April 30, 1957. The call of the Gray Treefrog, *Hyla chrysoscelis*, can be heard in the background. *0:28*

71. The Florida Cricket Frog, *Acris gryllus dorsalis*, recorded at East Lake, Putnam County, Florida, on the afternoon of August 20, 1954. *0:16*

Mexican Leaf Frog, *Pachymedusa dacnicolor*, track 72

72. Mexican Leaf Frog, *Pachymedusa dacnicolor*, recorded near Acapulco, Guerrero, Mexico, on the evening of August 12, 1956. The Sabinal frog, *Leptodactylus melanonotus*, can be heard in the background. *0:26*

73. Mating call of Couch's Spadefoot, *Scaphiopus couchi*, recorded nine miles north of Rodeo, New Mexico, at 9:40 p.m. on July 17, 1955. It is unusual to hear an isolated Couch's Spadefoot calling; this one was hidden under tumbleweeds in a depression at the side of the road. *0:35*

74. Mating call of the Plains Spadefoot, *Scaphiopus bombifrons*, a single individual calling from a pond on the afternoon of July 13, 1955. This individual was joined by a large chorus after dusk. It was recorded from a distance of approximately 50 feet, from the opposite side of a large temporary pool created by heavy rains earlier in the day. *0:19*

75. Mating chorus of the New Mexico Spadefoot, *Scaphiopus multiplicatus*, recorded seven miles west of San Antonio de las Alazanas, Coahuila, Mexico, on the evening of June 21, 1957, at 9:30 p.m. *0:32*

76. Mating chorus of three species of spadefoot, with the New Mexico Spadefoot, *Scaphiopus multiplicatus*, predominating. The voices of Couch's Spadefoot, *S. couchi,* and the Plains Spadefoot, *S. bombifrons*, can be heard in the foreground as individuals. Recorded on the state line between Arizona and New Mexico on the evening of August 31, 1955. *0:37*

77. Mating call of the Great Basin Spadefoot, *Scaphiopus intermontanus*, recorded in Sacajawea State Park near Pasco, Franklin County, Washington, in July 1954, by Robert C. Stebbins. *0:30*

78. Mating call of the Sabinal Frog, *Leptodactylus melanonotus*, with *Smilisca baudini* heard in the background. Recorded twenty miles south of Culiacán, Sinaloa, Mexico, at 10:20 p.m. on September 9, 1957. *0:31*

79. Mating chorus of the Great Plains Toad, *Bufo cognatus*, recorded three miles east of the Cienega Ranch, in Hidalgo County, New Mexico, at 9;17 p.m. on July 17, 1953. *0:28*

80. Mating call of the Yosemite Toad, *Bufo canorus*, recorded .2 miles northeast of the Kaiser Pass summit, Fresno County, California, between 1:00 and 2:00 p.m. on the afternoon of June 8, 1954, by Ernest L. Karlstrom. *0:33*

81. Mating call of the Sonoran Green Toad, *Bufo retiformis*, recorded seven miles south of Hermosillo, Sonora, on the evening of July 29, 1955. *0:26*

82. Mating call of the Green Toad, *Bufo debilis insidior*, recorded at 9:00 p.m. on July 17, 1955, ten miles north of Rodeo, New Mexico. *0:25*

83. Mating call of the Carpenter Frog, *Rana virgatipes*, recorded at Taunton Lakes, New Jersey, on the evening of May 13, 1955. *1:02*

84. Winter mating chorus of the Pátzcuaro Frog, *Rana dunni*, recorded in Lake Pátzcuaro, Michoacán, Mexico, on the evening of January 27, 1956. The recording was made near 11:00 p.m. from a dugout canoe, with air temperature at 9.5°C. And water temperature at the surface of the lake approximatly 14°C. *0:40*

85. Chorus of Bullfrogs, *Rana catesbeina*, four miles south of Yuma, Arizona, with an occasional Southwestern Woodhouse's Toad, *Bufo woodhousei australis*, heard in the background. Recorded at 11:30 p.m. on the night of April 6, 1956. *0:31*

86. Chorus of Sonoran Desert Toads, *Bufo alvarius*, Great Plains Toads, *Bufo cognatus*, Couch's Spadefoot, *Scaphiopus couchi*, and the New Mexico Spadefoot, *Scaphiopus multiplicatus*, recorded in the Rillito, at 10:30 p.m. on July 18, 1953, on the outskirts of Tucson, Arizona. *0:54*

87. Chorus of Spadefoot Toads, with the Plains Spadefoot, *Scaphiopus bombifrons*, in the foreground, and the New Mexico Spadefoot, *Scaphiopus mulitplicatus*, in the background, and the Green Toad, *Bufo debilis insidior*, occasionally in the foreground. Recorded in Cochise County, Arizona, approximately one mile northwest of Rodeo, New Mexico, on August 3, 1957. *0:34*

88. Frog chorus recorded four miles south of Brighton, on the Seminole Indian Reservation in Okeechobee County, Florida, at 1:15 a.m. on June 2, 1954. The Florida Chorus Frog, *Pseudacris nigrita verrucosa*, is in the foreground, and the Green Treefrog, *Hyla cinera*, is in the background. The Little Grass Frog, *Pseudacris ocularis*, was well represented in the chorus, but its voice is not easily discernible in the din of louder voices at lower pitches. *0:38*

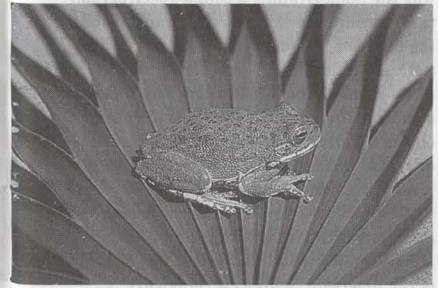
89. Large chorus recorded west of the Archbold Biological Station, Highlands County, Florida, at 8:40 p.m. on June 6, 1954. The general din is made up largely of the Pig Frog, *Rana grylio*, the Southern Leopard Frog, *Rana utricularia*, the Gopher Frog, *Rana capito*, and Cricket Frogs, *Acris gryllus dorsalis*, Squirrel Treefrogs, *Hyla squirella*, and Pine Woods Treefrogs, *Hyla femoralis*. Some Southern Toads, *Bufo terrestris*, were also calling. *0:26*

90. A breeding chorus of the Southern Toad, *Bufo terrestris*, with Pine Woods Treefrogs, *Hyla femoralis*, in the background. Oak Toads, *Bufo quercicus*, were also present and calling, although they are not readily heard against the background of the larger toad. Recorded near Placida, Florida, at 2:10 a.m. on July 27, 1957. *0:30*

91. Sounds issuing from the Oklawaha River east of Orange Springs, Marion County, Florida, on the evening of September 1, 1954. The growl-like call at the beginning of the recording, and repeated once later is that of the River Frog, *Rana heckscheri*. The single grunts are the territoriality calls of the Bronze Frog, *Rana clamitans clamitans*. The mating call, accelerated at the end, of the Green treefrog, *Hyla cinerea*, was issuing from a tree on the opposite side of the river. The relatively weak call of the Eastern Narrow-mouthed Toad, *Gastrophryne carolinensis*, is barely discernible. Sounds, perhaps inaptly described as the snapping of some orthopteran—possibly a katydid rather than a cricket can be heard throughout the recording. *1:03*

92. This is the same chorus reproduced as track 3, recorded one-half mile south of the Archbold Biological Station on the evening of June 7, 1954. Most conspicuous in this recording are the call of the Barking Treefrog, *Hyla gratiosa*, the voice of the Pine Woods Treefrog, *Hyla femoralis*, and the snore-like call of the Gopher Frog, *Rana capito*. However, eight other species were also calling, as explained in the notes to track three. The calls of the individual frogs in the chorus are reproduced separately elsewhere on this recording. *0:53*

Barking Treefrog, *Hyla gratiosa*, tracks 1, 2, 3, 12, 20, 92



CURATOR'S REMARKS

Sounds of North American Frogs is considered a classic by specialists and has also long been one of the most popular recordings in the "Science Series" that Moses Asch issued on Folkways Records between 1950 and 1986 (see discography). Asch wanted to document the world's sounds on his ruggedly independent record label, and he did not stop with human ones—the list includes sounds of dolphins, lyre birds, insects, and of course frogs. Nor was he content with animal sounds—he published recordings of airplanes and rockets, trains, race cars, junk yards, and offices. This at the same time as he was producing recordings of the last chanters of the Selk'nam Indians in Tierra del Fuego, and the avant garde musicians and beat poets of New York City. Folkways is a remarkable achievement.

We reissue *Sounds of North American Frogs* as part of the celebration of the 50th anniversary of Moses Asch's founding Folkways Records in 1948. As with most of our reissues, it has been carefully remastered, and the notes updated to reflect changes during the past 40 years. This release, however, comes at a time when an alarming decline of many amphibian species is encountered around the world, giving added importance and urgency to our understanding of these species. Thus the sounds on this recording, like those on many Folkways

releases, may be rarely heard today. But as with other Folkways recordings, we hope that your recognition of their uniqueness, their remarkable individuality and the reasons they are made will lead to new respect for, and concern about, the makers of the sounds—be they human or animal. Once you listen to this recording and read the extensive notes by leading herpetologists, you will never listen to the croaking of frogs and toads in the same way again.

Anthony Seeger, 1998
Curator and Director
Smithsonian Folkways Recordings

NEW INTRODUCTION

by Richard G. Zweifel[1], 1998
Curator Emeritus, Department of Herpetology
American Museum of Natural History

Two technological innovations in the early 1950's had a large and stimulating effect on the scientific study of sounds made by free-living animals. One was the development of portable tape-recorders. Whereas prior to that time recording was limited to the radius of a microphone cable plugged into bulky equipment carried in an automobile, researchers now could seek out their subjects wherever they were. The second innovation was the Sona-Graph©, a sound-spectrograph that literally draws pictures of sounds, showing duration, frequency in cycles per second (Hz), and relative intensity (loudness). This enabled researchers to describe and illustrate sounds gathered in the field in accurate, objective terms: duration and pattern, frequencies and their variation, relative loudness and its change over time.

Charles M. Bogert was one of the earliest biologists to make use of the new technology. His recordings published in 1954 as *Sounds of the American Southwest* (Folkways Records and Service Corporation, Science Series, album FPX 122) preceded the more specialized *Sounds of North American Frogs*. The subtitle to the latter recording, *The Biological Significance of Voice in Frogs*, expresses the broad scope of the recording and its documentation, which includes an extensive essay. In the essay, Bogert sought to summarize and add to knowledge of the role of vocalization. Later he published a more extensive and detailed work on reptiles as well as amphibians (Bogert 1960). Bogert was not only a pioneer in the study of natural sounds, but also the founder of the archive of amphibian sounds at the American Museum of Natural History, which has continued to grow and diversify as a collection of international scope.

The essay that follows stands as originally written, excepting only that where required, scientific and vernacular names were replaced by their current equivalents to avoid confusion. Bogert studied many aspects of frog calls, and he directed attention to unstudied areas and to assumptions that were not well documented. Numerous researchers in subsequent years have, with increasingly sophisticated methodology and equipment, illuminated most of these once shadowy regions. I cite a few examples.

The question of whether calling by male frogs attracts females of the same species has been answered through many experiments that present females with a choice of two or more kinds of calls; typically, females in condition to breed respond by moving toward the source of the call (a loudspeaker) of their own species. The species-specific response is, of course, important in assuring that the female finds her appropriate mate and confirms the significance of calls as isolating mechanisms. Experiments with synthetic calls modified electronically show which are the more important elements (e.g. pattern, frequency level, rate of calling, loudness) in inducing a positive response.

Bogert was interested in a frog's ability to discriminate pitch and the role this might play in mate-finding. The hearing sensitivity of many species has been tested, and it turns out that frogs' ears tend to be most sensitive to the frequency levels broadcast by males of the species. This means that the ear in a sense filters out inappropriate noise. The cacophony you may hear in a chorus of mixed species probably sounds much simpler to the frogs themselves.

The term "mating call" used by Bogert and his contemporaries has been replaced by "advertisement call." This recognizes the fact that a call may serve more than one purpose: it may, for example, notify females that a male is present and available and also serve as a warning to other males to stay out of his territory. Many species, it turns out, have a considerable vocabulary. An advertisement call may elicit a different call from another male, and such conversations may escalate

1 Dr. Zweifel, now retired, worked at the American Museum of Natural History for 35 years. He still listens to and records frogs.

into actual fighting. Male bullfrogs, for example, engage in wrestling matches.

Following his major work (1960) on bioacoustics, Bogert published just two papers that used frog calls to discriminate species; he then went on to other areas of research. His earlier work provided a strong foundation for subsequent researchers.

Red-spotted Toad, *Bufo punctatus*, tracks 21, 22, 53.

THE BIOLOGICAL SIGNIFICANCE OF VOICE IN FROGS

by Charles M. Bogert, 1958

Frogs have been on earth for nearly two hundred million years. Their voices may have been echoing across Mesozoic landscapes for a hundred million years or so before "a mob of irresponsible and shifty-eyed little shrews swarmed down out of the trees to chip at stones, fidget around fires, and build atom bombs,"—to steal a phrase from Archie Carr.

But even before man had the wit to chip out an arrow point, much less contemplate the mass destruction of his fellow men, he could scarcely have escaped hearing the sounds that attend the breeding activities of frogs—the tailless amphibians known to all by such vernacular names as toads, treefrogs, spadefoots, or just plain frogs.

It is probable that the first voice in existence was that of a frog. To judge by what is now being learned about the sounds produced by fishes, (see Marie Poland Fish 1956) the ancestral stock that converted fins into limbs and ventured onto the land may have been able to make noises. Since it had lungs it's even possible that the ancestral amphibian had a voice. To qualify as a voice, however, the sound produced must be from the mouth, usually as the result of the forcible expulsion of air from the lungs over some sort of vocal apparatus in the throat. Fishes can scarcely

be described as being vocal even though they produce sounds. They do so by vibrating the walls or partitions of their balloon-like air bladders, or by having such mechanisms as that in the trigger fish, where the rays of the fin beat on a taut membrane to produce a drum-like sound. Still other fishes grind their teeth together, or somehow set particular groups of muscles to vibrating.

In a similar manner most toads (*Bufo*) produce a "warning vibration," an audible sound seemingly produced by muscular movements that cause one particular cartilage in the throat to vibrate. Even though the majority of the sounds produced by frogs can be classified as vocalizations, with only one exception these are produced with the mouth closed.

HOW FROGS CALL

The frog sounds we ordinarily hear, their mating calls, "sex-trills" or croaks, are those accompanying their breeding activities. Some treefrogs (those in the family Hylidae) may call from trees or bushes. Others call while on the ground, either some distance from the water or near the pool in which the mated pair will eventually deposit and fertilize their eggs. Some frogs call from the water, near the edge of the pool or near its center, the position chosen depending upon the habits of the individual species.

Air driven from the lungs passes over the elastic rims of the vocal chords, causing them to vibrate. However, except when a frog "screams," the air is not expelled through the nostrils or mouth, both of which are kept closed. Slits in the floor of the mouth allow the air to pass to a distensible throat. In many frogs the elastic skin of the throat balloons out as a translucent sac or a pair of sacs in some species, from which the air is shunted back to the lungs. Thus the same air is used repeatedly, although the vocal sac is not ordinarily completely deflated when some of the air is returned to the lungs. Thus a small portion of the trapped air is forced back and forth over the vocal chords, producing audible or even loud sounds as it is driven from the lungs. The inflated sac or vocal pouch serves as a resonator that reverberates with the sounds emanating from the vocal chords in the throat.

Not all frogs have vocal pouches that balloon out as resonators, but these external vocal pouches are characteristic of the smaller species with high-pitched voices. While producing its mating call the vocal pouch of the Little Grass Frog, *Pseudacris ocularis*, distends to greater bulk than its body. Among treefrogs (*Hyla*) and toads (*Bufo*) there is a general tendency for the larger species to have proportionately smaller vocal sacs, and the same is true to some extent of frogs (*Rana*), many of which have paired vocal sacs, one ballooning out from each side of the throat.

In some species, particularly such large frogs as the Pig Frog, *Rana grylio*, and Bullfrog, *Rana catesbeiana*, for example, or such sizeable toads as *Bufo marinus* and *Bufo alvarius*, there is no "external" vocal sac. The skin and muscle of the throat are not particularly distensible, and the throat merely assumes a swollen appearance when these large species call. Such vocal sacs are said to be "internal"; they are often found in species that call from the water. Frogs with internal vocal sacs can call from the surface of the water or while under it (the Leopard Frog, *Rana pipiens*, with external vocal sacs also has been reported to call from the bottom of the pond). Aquatic frogs such as the African Clawed Toad, *Xenopus laevis*, that rarely come out on land habitually produce their trills under water. The Tailed Frog, *Ascaphus truei*, an inhabitant of mountain torrents in the American Northwest lacks a vocal pouch, as well as a voice. In some frogs (both *Rana* and *Bufo*) inhabiting the western portion of the United States the mating call appears to have been lost, probably secondarily, even though the warning chirp is retained so that these frogs cannot be called voiceless. It is noteworthy that all the frogs inhabiting the wetter eastern portion of the United States have mating calls, and perhaps it will be shown that some of those in the West call for such brief periods that their mating calls have been overlooked.

THE FUNCTION OF AMPHIBIAN VOCALIZATION

There is reason to assume that at least some of the earlier amphibians of Carboniferous times had a tympanum or eardrum. Hence they probably also had ears and could hear. Whether any of them had voices we shall never know for certain, but its seems probable that the use of voice as an adjunct to mating activities evolved somewhat later, largely restricted to the tailless amphibians. Voice plays no part in the mating activities of the limbless (and probably voiceless) caecilians of the tropics, nor in the courtship of salamanders, even though the Pacific Giant Salamander, *Dicamptodon*, has been known to utter a short "bark," and some other salamanders, even those of lungless species, produce faint squeaks or squeals.

No one has ever tested caecilians to ascertain whether they can hear. Salamanders were long believed to be deaf, but in 1939 Ferhat-Akat demonstrated that they could not only hear, but were able to distinguish frequencies that differ in pitch as much as a musical interval of a fourth or fifth. It had generally been assumed that frogs could hear, principally because when one frog started to call it was often joined by others, or could be induced to call if suitable noises were produced in proximity. Not until Yerkes carried out experiments in 1905, however, was it actually proved that frogs could hear, and there is still no proof that frogs can discriminate between one pitch and another. Yerkes concluded that frogs were influenced by sounds ranging in rate of vibration form 50 to 10,000 cycles per second, but was careful to note that neither limit was accurately determined. Field observations suggest, but do not prove, that frogs respond to the mating calls of their own species. But there is some indication of discrimination, even though definitive experiments remain to be carried out.

MATING CALLS

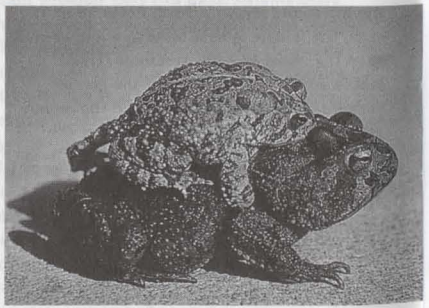
Not all of the sounds produced by frogs are vocal in nature, as pointed out above. The voice may be absent, present in both sexes, or restricted to the male, with the female mute. The male may not produce any mating call but may still produce other sounds. In the European Midwife Toad, *Alytes obstetricans*, the female is said to have a louder voice than the male. In some treefrogs (*Hyla*) and in some Mexican frogs of the genus *Tomodactylus*, both the male and the female produce what is apparently a mating call, but the pitch of the voice of one differs from that of the other. In some, possibly all, species the ability to call appears to depend upon hormonal control. Aronson (1944) found that sounds could not be produced by some toads after the breeding season ended.

In general the sounds frogs make that are most often heard are the mating calls. These accompany their breeding activities, and have also been termed "male sex calls" or, particularly in toads, "male sex trills." In the northern portions of the United States many species breed only once, during the early spring or summer. In the southern part of the country, particularly in Florida, many species breed from early spring to fall. No one has ascertained whether any individual frog breeds more than once a year or whether the breeding of individuals comprising each local population is staggered. Almost any heavy rain is followed by large choruses of frogs, and in Florida a few can be heard during every month of the year according to Carr (1940). Others, such as the Chorus Frogs (*Pseudacris*) that breed during the early spring in New England, sometimes before ice is gone from the ponds, carry out their reproductive activities largely during the winter months in Florida. In the Pacific states, as well as in Mexico, breeding activities are largely keyed to the rainy season, during the winter in California, but during the summer in Arizona, Utah, New Mexico, and the west coast of Mexico. Most frogs in the tropics breed during the season of heaviest rainfall, but a few prefer the dry season when streams diminish in volume to form sporadic pools.

The early naturalists doubtless wondered why frogs gave vent to such loud cries. Not all naturalists realized that most frog calls

accompanied breeding activities, nor did anyone make a very serious effort to find out why frogs called until after 1905 when Yerkes demonstrated that frogs could hear. Only a couple of decades prior to this a naturalist in New Jersey had described what he called a "deafening epithalamium" produced by a chorus of Eastern Spadefoots (*Scaphiopus*). Seemingly he considered the breeding aggregation he described to be something similar to a party where the guests had gotten a little out of hand. He suggested that the noises emanating from the chorus were perhaps "expressions of delight at meeting." Such speculations were not particularly rewarding as biologists later realized when they reported more detailed observations. The picture that began to emerge made it seem obvious that frog voices had some adaptive significance, and this began to become more apparent as the data accumulated. By 1931, Noble was willing to state rather emphatically that "the chief function of the voice in frogs is to attract mates." As he visualized it, the advent of suitable weather brought frogs out of seclusion. The weather conditions that bring frogs to the surface vary somewhat from species to species, but it is plain that the advent of rain is important, especially for those living in arid regions. The first male that chances to reach a suitable breeding site begins to call. This sound serves to attract other males, and a chorus finally assembles at the pond or stream where the eggs are to be deposited. For reasons that remain obscure, there is a delayed response in females, but eventually they begin to show up at the breeding site. As they approach or come in contact with males of their own species, they are seized or clasped (*amplexus* is the technical term for the clasping of amphibians), and it may be either pectoral or inguinal, depending on the group to which each species belongs. The male's prepollex (i.e., each "thumb") is often provided with spines or enlarged during the breeding season to serve as a gripping organ. Ordinarily the male remains clasped to the female until she has deposited her eggs, which are fertilized as they issue from her body. (Variations

Southern Toad, *Bufo terrestris,* in axillary amplexus. The male grips the female until the eggs are deposited, after she carries him to the breeding pond.



in breeding behavior have recently been discussed by Jameson 1955).

To test Nobel's belief that voice is important in attracting toads to the breeding site, we ran a series of experiments at the Archbold Biological Station in 1954. We employed Southern Toads, *Bufo terrestris*; these were marked for future identification and liberated in a paved plaza. A loud-speaker, shifted from one end of the plaza to the other in successive experiments, was employed to broadcast a taped recording of a chorus of the species. The toads used were gathered at random around the Archbold Biological Station as well as elsewhere in the vicinity. Some were taken while calling, but most of them were not engaged in breeding activities when captured.

When toads were liberated in the plaza without any sound issuing from a loud-speaker, there was no marked tendency for toads to go in one direction in preference to another. When the taped chorus was reproduced over the loud-speaker, there was a negative response from a number of male toads liberated over a hundred feet away from it. In every experiment more male toads went away from the sound than went toward it.

Female toads behaved somewhat differently from the males. Well over half of them headed toward the sound source. Unfortunately, several of these taken in breeding choruses laid their eggs in the laboratory before they could be tested with the taped chorus. It seems doubtful whether a spent female (one that has already spawned) would necessarily respond to the call of the male, and we were inclined to attribute the limited success of the experiment to our inability to prevent females from depositing their eggs prior to being exposed to the conditions of the experiment.

We repeated the experiments in 1957. Results similar to those obtained in 1954 were obtained, (except that somewhat larger percentages of females went toward the source of the sound, whereas larger percentages of males went in the opposite direction, away from the loud-speaker where the chorus was being broadcast). Judging by these results it seemed extremely doubtful whether there was any positive response of one male to the call of another.

Then, on August 25, while at the Cape Haze Marine Laboratory, we encountered a storm that brought approximately 5.5 inches of rain. Sometime after midnight, we encountered a breeding aggregation of moderate size comprised of Southern Toads. We recorded the chorus (reproduced in part on the accompanying record) around 3:00 a.m. After that had been done, we caught all the toads in the aggregation that we could find. There were 39 males and 14 females.

These were taken back to the Archbold Biological Station the same day. Despite their

isolation from males, we found that as usual most of the females had deposited their eggs. There was a slight rain at 9:00 p.m. when the toads—both males and females this time—were released, with the chorus being broadcast at the north end of the plaza 130 feet away. After half an hour we ceased our broadcast of the sound and retrieved all the toads we could find, keeping records of the direction in which they had traveled. This time we found that 24 out of 39 male toads had gone toward the source of the sound. Even more convincing, however, was the fact that Miss Alice G. C. Grandison, who assisted in the work, found the majority of the males lined up in a semi-circle facing in the direction of the loud-speaker even though they were some ten or fifteen feet from it.

The outstanding differences between this experiment and those that preceded it lay in the fact that all the toads employed had been actively engaged in mating activities when captured at 3:00 a.m. the morning prior to the evening when the test was carried out. Presumably the majority of them were in suitable physiological condition to engage in breeding activities. It seems probable, therefore, that toads, at least those of the species employed, respond to mating calls only when they are in breeding condition. This reflects a physiological state involving secretions from the ductless glands. It is well established that the pituitary controls many aspects of the sex cycle, including ovulation in the female. It seems probable, at least in Florida, that many, but not all, toads are in suitable condition to breed throughout the summer. Precisely how the advent of heavy rains provides the stimulus for these toads to migrate to breeding sites remains obscure. There would seem to be an interaction of physiological and environmental factors, with some sort of mechanism to trigger sexual activity only under suitable weather conditions.

It is noteworthy that all frogs or toads abroad in any locality in Florida after a heavy rain are not necessarily breeding. Large choruses were often heard near the Archbold Biological Station when individuals of the same species (toads, frogs, and treefrogs) lacked any urge to participate. Some of these were immature, but many adults evidently were engaged in feeding activities and seemed oblivious to the sex calls emanating from the adjacent ponds. Noble and Aronson (1942) believe that female Leopard Frogs possess an estrous cycle analogous to that of mammals and are receptive to males only when they are in suitable physical and physiological condition to breed. They also suggest that there is perhaps some hormonal mechanism involved in the loss of the warning croak in female Leopard Frogs after they have deposited their eggs. To judge by the negative reactions of the majority of both male and female toads not in breeding condition when captured, there is a tendency for such amphibians to avoid breeding choruses.

Much remains to be learned concerning the role of frog voices in their reproductive activities. Nevertheless the one experiment, where the majority of male toads employed not only moved toward a loud-speaker artificially reproducing their calls, but were found clustered around the loud-speaker with their bodies oriented toward it, offers rather conclusive evidence to substantiate Noble's assumptions (1931: 404). It would appear that the first males to find suitable breeding sites begin to call, and that these calls do indeed attract other males and finally females. Once the females have deposited their eggs they depart, but the males remain on hand, sometimes for long periods depending in part on the weather or the continued existence of the breeding pool. In some species at least, the same male may mate with several females before the breeding season comes to an end. This difference between the sexes in their behavior readily accounts for the predominance of males in most mating choruses. In fact, no females may be present on occasion, perhaps because they have not yet arrived when individual ponds are observed, or because the supply of receptive females in the vicinity of the chorus has already been exhausted.

MATING CALLS AS ISOLATION MECHANISMS

Whereas we have evidence that the male sex trill of at least one species of toad serves to attract females to the breeding site, it should be noted at the outset of this discussion that thus far there is no proof of frequency discrimination in frogs or toads. Furthermore, it has been pointed out by Adrian, Craik, and Sturdy (1938) that nerve response varies with temperature, and hence frequency discrimination is dependent upon more precise body temperature regulation than that possessed by amphibians. But mating calls also differ in timbre, duration, and intensity, and the spacing of the calls or the trill rates may differ. Hence it is conceivable that frogs distinguish mating calls of other species from those of their own by characteristics other than pitch.

While differences in mating call have been referred to as "important isolation mechanisms," (W. F. Blair 1955), the evidence for this belief rests largely on field observations. Noble and Aronson (1942) note that their extended laboratory investigation of the Leopard Frog, *Rana pipiens*, "gave no indication whatever that either the male or female was attracted by the sex call." A.P. Blair (1942) released marked toads midway between two pools, one of which was populated with the American Toad, *Bufo americanus*, the other with Woodhouse's Toad, *Bufo w.*

woodhousei. Of ten American toads recaptured, six went to the pond where their own species was calling and four went to the pond where Woodhouse Toads were calling. Of ten Woodhouse Toads retrieved, seven went to the "right" pond, three to the other. Blair concluded that "call response is not a strong isolating mechanism between the two species."

Later A.P. Blair (1947a) carried out a similar and equally inconclusive experiment with Couch's Spadefoot, *Scaphiopus couchi*, and the New Mexico Spadefoot, *S. mulitplicatus*, noting that "it has not been experimentally demonstrated that anurans respond preferentially to the calls of their own species." However, nothing thus far reported either proves or disproves the importance of the mating call as an isolation mechanism. There can be little doubt that Southern Toads were attracted from a distance of 130 feet to a loudspeaker reproducing the mating call of the species at a place where no breeding pool existed. Still it is conceivable that any loud sound within the frequency range heard by these toads would have been equally attractive. Savage's (1935) work with the common European Frog, *Rana temporaria*, points to the strong possibility that olfactory cues are employed by frogs to reach breeding sites. It is plausible, therefore, that such cues (or other sensory data) are employed by some American species in addition to auditory stimuli.

In each of A.P. Blair's experiments it is pertinent to note that he removed animals from breeding choruses and introduced them into ponds where no members of their species had been calling. In the case of the spadefoots Blair notes that while Couch's Spadefoot was calling from numerous ponds in the vicinity, only a single pool contained a chorus of the New Mexico Spadefoot. Individuals of one species did not occur in the chorus of the other. That this is not due to the specificity of call response is indicated by the fact that the two species commonly breed simultaneously in the same pond elsewhere, and may even be joined by a third species, the Plains Spadefoot, *Scaphiopus bombifrons* (all three may be heard together in one of the sample choruses on the recording). Hence the fact that one species avoided the ponds sought as breeding sites by the other suggests that more subtle means were employed in making the selection.

Even though both toads and spadefoots did resume their calling when introduced into uninhabited ponds, the possibility remains that such sites are unattractive, even when mating calls of their own species are emanating from them. Indeed, frogs of various species may seek out breeding sites in terms of olfactory or other sensory cues, with voice playing a significant role in the selection of mates only after their arrival. Such assumptions would account for the confusion that Blair's toads and spadefoots exhibited, but

they are not in accord with the results obtained in Florida where no breeding site at all was available at the spot where toads were induced to assemble by means of an artificial chorus.

Information for other species offers evidence bearing on the problem. Noble (1931: 409) mentions female Cricket Frogs, *Acris gryllus*, sitting in a circle with their heads directed towards a calling male. Near Archbold Biological Station we observed a female Oak Toad, *Bufo quercicus*, nudging a calling male of her own species as though to attract his attention. The maneuvers were successful and the pair wound up in amplexus. Noble (1923) reports female treefrogs of two species leaping on the backs of males of their own species. Unfortunately such observations do not preclude the female's use of visual cues in seeking out males of her own species. However, the experience of a collector in Maryland is somewhat more convincing. He placed a male Narrow-mouthed Toad, *Gastrophryne carolinensis*, in a can where it continued to call. Even though the male could not have been seen, females continued to approach the source of the sound and five females were thus obtained.

That the voice is of importance is also suggested by our observation of twelve pairs of *Hyla gratiosa* taken in amplexus on the night of June 7, 1954. The individual pairs were separated as they were placed in a plastic aquarium approximately a meter in both length and width. Some of the males soon started calling, whereupon individual females would leap to the vicinity of such males and then sidle up to them, invariably facing in the same direction. In many instances the female virtually crawled beneath the male, although some movement on his part was necessary. Pairs in amplexus in various parts of the aquarium were repeatedly separated so that in all we were able to observe the approach of the female twenty or more times (unfortunately the exact number of times was not recorded). In only one instance did a female approach a male that was not calling.

The first male to arrive at a breeding site and start calling may employ olfactory cues in selecting the place. Whether he is joined by others of his species may depend upon cues other than, or in addition to, auditory cues. If the latter proves to be so it would explain the failure of A. P. Blair's experiments. But once females have reached the breeding site it seems fairly plain that in many species they actively seek out the male. Possibly vision plays some part in the behavior, but the few bits of evidence available point to voice as a factor of greater importance.

Tentatively we are forced to conclude that there is no adequate evidence to prove that voice differences are of importance as isolation mechanisms, even though field observations strongly suggest that they are for some

species. Nevertheless, interbreeding between species living side by side does occur. Hybridization of many amphibians has been accomplished under laboratory conditions with varying degrees of success (see Moore 1955 for a summary), and numerous instances of cross-mating under natural conditions have now been reported. Because a complex of several isolation mechanisms, rather than any single one, ordinarily discourages one species from mating with another, it is difficult to determine which is of greatest importance. That mating calls play an important part in the reproductive activities of many frogs and toads can scarcely be questioned. That there is a specificity of response to mating calls seems probable even though it remains to be scientifically proved.

TAXONOMIC LEVELS AND VOICE DIFFERENCES

The classification of frogs, like that of all animals, is based on a system that recognizes structural differences as well as similarities. All surviving amphibians (many groups are extinct) are placed in the Class Amphibia. Members of this group are backboned animals with moist, glandular skins. They are divided into three subgroups or Orders: (1) caecilians, eel-shaped creatures of the tropics that lack limbs; (2) salamanders, with limbs and a tail; (3) frogs, with limbs but without tails (even though they all pass through a larval or tadpole stage where a tail is present, it is invariably lost during transformation to the adult stage).

These tailless amphibians, or frogs and their relatives, belong to the Order Salientia. This subdivision of the Amphibia is further divided into families on the basis of similarities and differences in skeletal characters and other peculiarities. Each family in turn is comprised of genera (singular *genus*), each of which contains several species that have characteristics in common with species in other genera of the family. In addition, these species have additional similarities not shared by those in other genera that point to close relationships. All toads (Family *Bufonidae*, Genus *Bufo*), for example, have horizontal pupils, a distensible pear-shaped tongue, and no teeth.

But there are differences between the various species in each genus. Each species contains individual animals that are more or less alike, with due allowance being made for differences between the sexes and in stages of growth. There may be individual variations in such minor characters as color, pattern, or proportions. Just as in the human species there may be dark-skinned and light-skinned individuals, fat ones or thin ones, or even such abnormalities as extra toes. But the vast majority of those in any species will look pretty much alike. Ordinarily, each member of a species is potentially capable of mating with any other member of the opposite sex. While there are occasional exceptions, individuals of one species do not ordinarily mate with those of another.

This is not the place for a detailed discussion of the problems (see Dobzhansky, 1951), but when two or more species live in the same region, interbreeding is inhibited or prevented by various means. Each species may breed at a different time, or in a different sort of place. Some frogs prefer quiet pools for example, others running streams. Mating may be mechanically impossible; an adult male Southern Toad, *Bufo terrestris*, would be unable to clasp a female of the much smaller Oak Toad, *Bufo quercicus*, and hence could not remain with her to fertilize her eggs when they are laid. Or, as we have seen, it is possible that there is a specificity of response to the mating calls of amphibians. Females may be attracted only to males of their own species. Usually there are several isolation mechanisms to discourage or prevent interbreeding of species under natural conditions.

There is another aspect of the species that we must consider. Animals, like human beings, are not evenly distributed over the lands they occupy. Some kinds of frogs are restricted to lower elevations and never occur on mountains. Others are confined to mountains. The Yosemite Toad, *Bufo canorus*, for example has never been found below elevations of 6,000 feet in the Sierras of California. Other species are largely restricted to wooded areas and may shun open plains. Aside from the fact that many frogs need water, pools, or streams in which to breed, they may be absent from some areas but present in abundance in others.

Sonoran Green Toad, *Bufo retiformis*, track 81

Those in any small area are referred to as a population. The individuals comprising it may be geographically isolated or partially isolated from other groups or populations of individuals with similar characteristics. Taken together all the animals in the various populations, which may be scattered over a more or less extensive region, comprise the species. The region occupied is known as the range of the species.

There are often small differences between most individuals in one local population and those in another, particularly if they are widely separated geographically, or if environmental conditions are very different. Thus, the population of Red-Spotted Toads, *Bufo punctatus*, at Austin, Texas, consists of individuals that tend to be grayish in color and smaller than those in the population at Cave Creek in the Chiricahua Mountains, where the toads tend to be reddish in coloration rather than gray. Perhaps correlated with the difference in size is a difference in the pitch of the voice. W. F. Blair (1956) provides figures for those at Austin, indicating that the frequency varies from 2510 to 2700 cycles per second, whereas analysis of calls for those at Cave Creek indicates that the frequency varies from approximately 2000 to 2300 cycles per second.

As we have demonstrated on the recording, there may be differences between individual toads in voice characters. Most of the Red-spotted Toads in Cave Creek appeared to stop their calls abruptly, but one of them tapered off the trill at the end as though "running down." Analysis of the calls, using a Sona-Graph, shows that there is a tendency, not readily apparent to the human ear, for the voices of other toads in Cave Creek to taper off rather than stop abruptly as the toads of the species do near Austin, Texas.

Aside from individual differences in voices, frequencies as well as the trill rates, or the spacings of the individual calls, are affected by temperature. At higher temperatures voices are higher pitched and faster in animals in the same populations or subspecies, some of which may have a genetic basis. Altitudinal differences, doubtfully attributable directly to temperature, have been reported by Hoffman (1946) for the Gray Treefrog, *Hyla versicolor*. Walker (1946) reports that two voices can be heard side by side in the same species in parts of Ohio.

There are, therefore, individual variants in voice characteristics as well as local populations with voice peculiarities. Or several local populations in one part of the range of the species, usually where there are environmental differences, may be more or less alike in characters that distinguish them from other members of the species. These have often been recognized as subspecies. One of the common amphibians in the eastern part of the United States is Fowler's Toad, *Bufo woodhousei* fowleri. It differs from toads of the same species in the western, more arid portion of the country in minor respects, most notably in size. The larger western subspecies, particularly *B.w. australis* in the desert regions, appears to have a lower pitched call, but the mating trills of local populations of each subspecies are so variable that the nature of the differences remains to be worked out. Recordings

obtained thus far suggest that differences between subspecies in voice characteristics usually are not great. Ordinarily anyone acquainted with the mating call of one subspecies would readily recognize others of the same species.

At the species level, very conspicuous differences between mating calls seem to be the rule, but there are exceptions. Most students would be hard pressed to distinguish between the mating trills of the American Toad, *Bufo americanus*, and the Southwestern Toad, *Bufo microscaphus*. The few data now available indicate an overlap in variations in the pitch, and other differences are minor. In this instance, however, it may eventually be shown that the western populations are representatives (subspecies) of the American Toad, despite possible disjunctions in the range.

The situation is not vastly different in other North American toads. With the notable exception of the Oak Toad, *Bufo quercicus*, the voices of the various species differ principally in pitch or duration of the mating call.

Voice, like the structural characters more commonly employed in the classification of frogs, provides clues to relationships. While conspicuous differences in voice are indicative of the specific distinctness of populations, similarities in voice do not necessarily reflect close relationships. The data thus far available offer little hope that voice characters will be of much value in defining generic groups. On the contrary, when two species of a genus occur side by side they usually have totally different mating calls. Within families there may be great diversity in mating calls, although it is possible that characteristics common to several genera may in some instances be demonstrated.

SOUNDS PRODUCED UNDER SPECIAL CONDITIONS

Sounds other than mating calls fall into five categories: warning vocalizations, warning sounds, rain calls, screams, and territoriality calls. They will be taken up in order:

Warning Vocalizations: These are the "warning chirps" of most toads, and the "warning croaks" of many frogs and treefrogs. They have also been called "release sounds." In the species most intensively studied, they appear (along with the warning vibrations; see below) to be the principal means employed by males to distinguish the sexes. When large breeding aggregations of toads assemble, sexual excitement appears to reach a high pitch. Under such conditions it is not unusual for males to attempt to clasp virtually anything of appropriate size. (A correspondent writes that he found a small pond in North Dakota where several male toads were clasping axolotls, the large larvae of the tiger salamander, Ambystoma tigrinum.) If one male attempts amplexus with another, the one seized struggles to get away, emits a croak or

chirp and is promptly released. However, if a female is seized, she offers little if any resistence and remains silent. The male ordinarily stays in amplexus with her until the eggs have been deposited and fertilized.

It is uncertain whether the chirps or croaks induce the release of males or whether it is the respiratory movements that accompany their production. Noble and Aronson (1942) found that both male and female Leopard Frogs, *Rana pipiens*, produced warning croaks. The croaks of the female were not as loud as those of the male and were uttered only when the female was not in breeding condition. There are indications that the ability to produce the warning chirp is under hormonal control. During the breeding season it can be elicited in most species by touching them on the back or sides. Males ordinarily chirp repeatedly if seized in the human hand. In several species, including some treefrogs, frogs, and spadefoots, the warning croak is little more than an explosive rendition of all or part of the mating call.

Warning Sounds: These are not vocalizations, but sounds produced in some obscure fashion, perhaps as a result of accentuated respiratory movements that cause a cartilage in the throat to vibrate, with the vibrations transmitted to the body musculature, as Aronson (1944) suggests. Something of the sort, perhaps the same sound, may accompany the mating call of toads; it is discernible in recordings, particularly when the microphone has been close to the toad uttering the trill.

Ordinarily, however, the "warning vibration" is a sound produced when a male toad is clasped by another male. It has also been called the "preventive sex vibration" by Rengel (1949), who reports its presence in two South American toads as well as in the Mountain Pond Frog, *Telmatobius schreiteri*, and a treefrog, *Hyla raddiana*. In American toads it commonly accompanies the warning chirp, with the vocalizations possibly produced incidentally to the vibration. A.P. Blair (1947b), who carried out detailed studies with five species of toads, suggests that it conserves the reproductive potential of the species by insuring the quick release of clasped males. During the breeding season it can be elicited when the male is touched on the back or sides, or occasionally when touched on the top of the head and hind legs, according to Blair, who adds that contact of the throat
or undersides does not evoke the vibration.

Aronson found that discrimination of males from females when amplexus was attempted depended almost exclusively on the warning vibrations of the toad being clasped. In two species of American toads, Aronson found that warning vibrations were most easily elicited
at the height of the breeding season but disappeared following the loss of the warning

chirp, with the mating call being lost prior to that. Rengel states that, outside the mating season in South America, it is possible to observe a very reduced warning vibration in several species and that it occurs in females as well as males of some species. Blair notes that it cannot be elicited in juveniles unless they have been treated with male hormones and concludes that in adults it is probably under hormonal control.

Rain Calls: Various tailless amphibians call sporadically when they are not engaged in breeding activities. The sounds produced are often feeble renditions of the mating calls, or they may be recognizably different. For lack of a better name, these have become known as "rain songs." The name presumably stems from the fact that such calls from treefrogs often accompany the onset of showers during the daylight hours in Florida. Possibly it is the sound of the rain splattering on the leaves, rather than the rain itself, that elicits the vocal activity. In the Everglades, Mr. Richard Archbold and I thought at first it was merely bad luck that every time we tried to record the rain song of the Green Treefrogs, *Hyla cinerea*, an airplane could be heard in the background. Later we noted that the sound of a plane overhead was enough to induce the frogs to call, regardless of whether it was raining.

Not all species require auditory stimulation, however. Some species are reported to call whenever there is a sudden rise in the relative humidity. Usually following a thunderstorm during the day, but before breeding choruses assemble after dark, the Red-Spotted Toad, *Bufo punctatus*, produces a call that is slower, lower pitched, and more resonant than its strident mating trill. Dickerson (1906) observes that after its breeding season, the American Toad, *Bufo americanus*, produces a feeble call, about the same pitch, but more guttural and not as long, as its mating call.

The adaptive significance of such calls is obscure. Goin and Goin (1957) comment on the rain call of the Squirrel Treefrog, *Hyla squirella*, noting that it is heard throughout the summer months in warm, humid weather, uttered sporadically by resting individuals at any time during the day. Nobel (1931), observing that with the ripening of the sex cells in the fall many frogs begin to call, suggests that it is merely a "premature awakening of the sex instincts." The possibility has not been investigated, but the miscellaneous calls now designated "rain songs" in some instances may be manifestations of a primitive sort of territoriality.

Screams: If startled or injured, frogs give vent to a loud cry that in many species is aptly described as a scream. Carr (1940) tells of placing a large female Bullfrog, Rana catesbeiana, in a box containing a half-grown Ribbon Snake, *Thamnophis sauritus*. "After a brief time the frog set up a screaming that could be heard all over the premises; on inves-

tigating I found that the snake had fixed its tiny jaws on the enormous calf of the frog, whose first toe the little creature could hardly hope to swallow. The frog continued to cry and shake its leg—until the snake was thrown out of the box."

One dark night near the Archbold Biological Station in Florida, I heard not far behind me what writers of mystery stories usually describe as a bloodcurdling scream. I turned my flashlight toward the source of the scream, and about twenty feet from where I stood, a raccoon was wading at the edge of a shallow pool with a Southern Leopard Frog, *Rana utricularia*, in his mouth. While Noble (1931) suggests that screams uttered under similar conditions "may at least warn other frogs in the neighborhood," in this instance I was impressed by the fact that other frogs within a few feet of the raccoon continued calling as though completely unaware of the raccoon or the scream of their ill-fated neighbor.

Whether frogs in a less frenzied state of sexual excitement would have reacted to the scream, I can only guess. Leopard Frogs and Pig Frogs, *Rana grylio*, will often scream if merely seized although the sound produced by the latter species is a sound too low-pitched to be called a scream. It is more like the sound that in America has become known as a "Bronx cheer." Sounds produced by other frogs have been described as squeals, or loud clatters. All such cries that appear to be manifestations of pain or fright are produced with the mouth widely opened; frogs produce all other sounds with the mouth closed.

Yerkes (1905) found that loud sounds alone failed to induce any motor reactions in frogs although they reinforced reactions elicited by other stimuli. Hence the scream of a frog seized by an enemy may not produce any overt response in neighboring frogs, but under ordinary conditions it may put them on the *que vive*, so to speak. The may be prepared to jump faster and farther if an enemy comes into view. A croak or grunt, usually high-pitched, commonly accompanies the splash of frogs seeking safety in the water, and this too may serve to alert nearby frogs of approaching danger.

TERRITORIALITY CALLS

Frogs, particularly those of the genus *Rana* that spend much of their time feeding in shallow water or around the edges of streams and pools, sporadically give vent to grunts or similar sounds. They are commonly heard around ponds or streams inhabited by the Green Frog, *Rana clamitans*, the Pig Frog, *Rana grylio*, and the Leopard Frog, *Rana pipiens*. Frogs give vent to such sounds without any apparent stimulus, and to the casual observer they appear to have little if any biological significance.

The recent studies of the Green Frog by Martof (1953) suggest, however, that such

calls are associated with a primitive sort of territoriality. In the areas where Green Frogs were breeding near Ann Arbor, Michigan, he found that males were spaced at astonishingly uniform distances of about six to nine feet. Moreover, when the whole aggregation shifted, several individual frogs made approximately the same movements at the same time. Certain frogs tended to remain together, with some sort of orientation that permitted them to maintain the same general spatial relationships with one another. Frogs in any cluster tended to remain in it for periods of about two months. Martof suggests that this may have been accomplished by means of auditory or visual cues, and notes that calls were heard from April 13 until October 18. But after the breeding season, calls were often issuing from frogs underground—in muskrat burrows, from beneath overhanging sods, or in root entanglements of trees undercut by streams.

Under such conditions, and they are typical of many frogs, visual cues could scarcely have been employed to maintain the same general pattern of spatial relationships. The use of auditory cues seems far more likely; with each frog sporadically uttering its grunt it would be entirely feasible for other frogs in the vicinity to orient themselves in relation to the various sources of the calls in their vicinity.

Pending more detailed studies, this is a little more than a tentative explanation of the maintenance of the spatial configurations reported by Martof. If it proves valid, it will account for the sounds uttered by Green Frogs as well as other species. It may also be the explanation for the calls indistinguishable from breeding calls that some frogs produce after the breeding season is over.

In May 1930, at the request of the owner of a small isolated pond at Lovejoy Springs, near the western edge of the Mojave Desert, I introduced twelve Bullfrogs. During the next few years visits to the pond disclosed frogs widely distributed at various positions around the lake. They were never in compact groups. Moreover, frogs were found repeatedly calling at the same sites, long after the breeding season was over. There is no certainty that the same frog was at the same place, nor is it safely assumed that voice played any part in the spacing of the frogs. Nevertheless, the data assembled by Martof for Green Frogs suggest a possible connection between such vocalizations and the spacing. The maintenance of territories would be advantageous during the breeding season in permitting males to detect the presence of females, as Martof indicates. After the breeding season, when frogs seek out any moving prey that comes in sight, the spacing of individual frogs would ensure a more efficient coverage of the available prey.

PITCH IN RELATION TO BODY SIZE

Pitch, our auditory sensation of the highness or lowness in the musical scale, is a reflection of the frequency of the vibrations that constitute the physical tone. Timbre, or the quality of the sound, depends on the harmonics and the intensity of the sound. In the simpler calls of amphibians there is ordinarily a dominant frequency and its harmonics. W. F. Blair (1956) has shown this to be characteristic of many North American toads, finding it most practical to make comparisons of calls in terms of the dominant frequency.

While it has been apparent to field naturalists that the larger species of toads and frogs tend to have lower pitched voices than the smaller species, it is no simple matter to make precise comparisons. Individual variations, differences between local populations within the species in adult size, and other characters imply that comparisons have to be made in terms of mean differences. Aside from this difficulty, it has been shown by W.F. Blair that frequencies as well as trill rates in toad calls vary with the temperature. The dominant frequencies and adult sizes will illustrate the principle. Data for calls are taken from W.F. Blair (1956). Dimensions are those supplied by Wright and Wright (1949) and Stebbins (1951).

Table 1

Dominant Frequencies of Toad Calls and Average Adult Sizes

Species	*Approx. body length of males in inches*	*Dominant frequency of call in cycles per second*
Bufo marinus	6.7	600
Bufo alvarius	6.2	1100
Bufo valliceps	4.0	1400
Bufo microscaphus	2.7	1500
Bufo punctatus	2.6	2700
Bufo debilis	2.0	3300
Bufo quercicus	1.1	5200

Truly satisfactory comparisons would entail the use of means for frequencies as well as dimensions for toads restricted to local populations, with due compensation made for differences in temperature. Also, in view of the strikingly different call of the Oak Toad, *Bufo quercicus*, as compared to the trills of other species in the United States, it is doubtful whether its call can legitimately be included in the table. Nevertheless, it seems probable that differences in frequency between calls of toads are partly a reflection of the mechanical limitations imposed by the size of the toad.

Reproduction of the calls of the smaller species at reduced speeds lends support to this interpretation. The call of the Green

Toad, *Bufo debilis insidior*, sounds like little more than a buzzing sound to the human ear. Reproduced at half speed it bears a fair resemblance to the calls of medium-sized toads, and at one-fourth the normal rate it is an approximation of the largest toad in the Western Hemisphere, *Bufo marinus*.

The great diversity in the mating calls of frogs (Ranidae) and the treefrogs (Hylidae), often with variations in the dominant frequency in various parts of the call, results in a more complex situation. Even here the correlation of large sizes with low frequencies appears to be the rule, but there are probably exceptions to all groups of frogs. The variations from frog to frog in the pitch of the call of virtually all species may be partly dependent upon the sizes of the individuals calling. Duets and trios, such as those of the Spring Peeper, *Hyla crucifer*, mentioned by Goin (1949) may reflect the sizes of the participants.

DIVERSITY IN MATING CALLS

The diversity in the mating calls of frogs is a reflection of the differentiation in size, structure, behavior, and other attributes. Frogs, like other groups of widely distributed animals, are represented by a vast number of species (nearly 5000), each of which is adapted for some particular combination of environmental conditions. As a corollary, toads (*Bufo*) and spadefoots (*Scaphiopus*), creatures not particularly dependent upon permanent water, are well represented in the arid southwestern portion of the United States, with few species in the East. In contrast there are many more frogs (Rana) and treefrogs (Hyla) in the humid Atlantic States than in the Southwest.

The habits of each species have evolved along with structural characteristics that fit them for some more-or-less specialized mode of existence. Natural selection tends to retain characters advantageous to the species and to weed out those that, either alone or in combination, inhibit the survival of the species. In the long run, selection favors the retention of combinations of characters that enhance the survival of the species. But the species is made up of individual animals, and since these evolve as integrated machines, so to speak, the addition or subtraction of any single part has its effects on the creature as a whole. Thus, call differences may reflect the evolution of structural differences that arose in groups of animals isolated from other groups of similar animals. For those in each group are slowly but continuously changing to meet the changes in their respective environments.

Whether mating calls have evolved their peculiarities directly as a result of natural selection, or whether they have evolved as parts of a complex of isolation mechanisms, which seems more probable, it is significant that ordinarily no two species inhabiting the

same area have mating calls that are not easily distinguishable at least to human ears, and quite possibly to amphibians that produce them.

SAMPLE CHORUSES

Characteristically, frogs call as breeding aggregations or mating choruses. Indeed, the vocalizations of these amphibians seem to be of considerable importance in bringing together the males and females ready for reproductive activities. Mating calls may even be looked upon as a sort of courtship, perhaps more necessary as an antecedent of the actual deposition and fertilization of the eggs under natural conditions than laboratory experiments would lead us to believe.

Whatever adaptive value the mating calls of amphibians may have, most frogs call in choruses. A few can be heard as isolated individuals, but these are the exceptions. Usually many individuals of the same species assemble within a relatively limited area; its extent and the number of participants depends upon several factors, notably rainfall and the size of the population. Temperature may be of importance in some instances, as suggested by the sequence of calls to be heard in more northerly climates such as that of New England. Harper (1926) some years ago worked out a "timetable" for ten New England frogs and toads. Spring Peepers, *Hyla crucifer*, called first, in March, followed in a sequence that was much the same from year to year, terminating with the Bullfrog, *Rana catesbeiana*, which was not ordinarily heard in the region until well along in May. It is noteworthy that the smaller species in each genus call earlier than their larger relatives.

The composition of mixed choruses varies because of several factors. With the varied habitats in the American Southwest, species confined to the mountains or the less arid coastal region are unlikely to be found calling in the same ponds as the species in the deserts. Partly for this reason, it is exceptional to find as many as six species calling from the same pond. In Florida, where the less varied topography results in less sharply defined habitats, each species manifests a preference for one calling site or another—from shrubs, or while hidden in the grass or climbing on it, or from the center of the pool in preference to the edge, or on the shore where other species call. Under such conditions, as many as fourteen species may be breeding simultaneously in the same pond. In the marshy areas around the shores of Lake Okeechobee, literally thousands, perhaps even millions, of frogs scattered over many square miles may be calling simultaneously following heavy rains.

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The following organizations are dedicated to recording and conserving natural sounds. Both hold field recording workshops and publish newsletters with information on recording:

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BIOGRAPHICAL SKETCH

Charles M. Bogert was born in 1908 on a cattle ranch near the town of Mesa in western Colorado. When he was in the seventh grade his family moved to Los Angeles, California, where he continued his education in the public schools. Later he attended the University of California at Los Angeles, serving as a teaching assistant from 1935 to 1936 while working toward his Masters Degree. (The University awarded him an honorary doctorate [L.L.D.] in 1966.) He was appointed Assistant Curator in the Department of Amphibians and Reptiles at the American Museum of Natural History in 1936, and the following year married Martha M. Ruby. In 1942 he became Curator of Amphibians and Reptiles, and from 1945 to 1968 was Chairman of the Department. He contributed 215 articles (a short story, book reviews, scientific reports and monographs) to numerous journals, magazines, and books. He also taught summer sessions at the University of California at Los Angeles and at the University of Virginia's Mountain Lake Biological Station.

Dr. Bogert carried out field projects in various parts of North America, particularly the arid regions of the American Southwest, and in Mexico and Central America. He made numerous trips to Mexico, and during his tenure of a John Simon Guggenheim Fellowship he and his wife spent the winter of 1955-1956 working in Michoacán, Nayarit, and Baja California. His studies dealt with the systematics and biogeography of amphibians and reptiles, their habits and behavior, in particular the ecological and behavioral aspects of thermoregulation. He also carried out investigations of the senses employed by rattlesnakes in their recognition of ophidian enemies, the adaptive modifications of fangs of cobras, the homing ability of toads, and the adaptive significance of voice in amphibians. One of his most noteworthy publications was *The Gila Monster and its Allies*, a monograph of the world's only venomous lizards, written jointly with Mexican herpetologist Rafael Martín del Campo.

Dr. Bogert retired at the end of 1968 and he and his wife moved from their long time residence in Englewood, New Jersey, to Santa Fe, New Mexico, where he continued to work on scientific projects almost to the time of his death at age 84 in 1992.

ACKNOWLEDGMENTS

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Pig Frog, *Rana grylio*, tracks 13, 42, 43, 44, 46, in chorus 78

CREDITS

Original production of Folkways 6166 directed by Moses Asch, 1958
Originally recorded on Magnamite
Transfer engineer: Mel Kaiser, Cue Recordings
Compensation engineer: Peter Bartok
Original cover design by Ronald Clyne
Introductory essay and updated annotations by Dr. Richard G. Zweifel
Mastered by Richard Lescallette, Disc Mastering, Nashville, TN
Sound supervision by Pete Reiniger
Smithsonian Folkways reissue production supervised by Anthony Seeger and Amy Horowitz
Production coordinated by Mary Monseur and Michael Maloney
CD layout and design by Visual Dialogue, Boston, MA.
Tray card photo: Mexican Treefrog, *Smilisca baudini*, track 64, in background 78.
Editorial assistance by Peter Seitel and Dr. Richard G. Zweifel
Additional Smithsonian Folkways Staff assistance: Tom Adams, engineer; Carla Borden, editing; Dudley Connell, fulfillment manager; Lee Michael Dempsey, fulfillment; Kevin Doran, licensing; Brenda Dunlap, marketing director; Judy Gilmore, fulfillment; Matt Levine, fulfillment; Heather MacBride, financial assistant; Jeff Place, archivist; Ronnie Simpkins, fulfillment; Stephanie Smith, assistant archivist; Chris Weston, marketing assistant.

Couch's Spadefoot, *Scaphiophus couchi*, tracks 73, 76, in chorus 50, 86, and 87.

ABOUT SMITHSONIAN FOLKWAYS

Folkways Records was founded by Moses Asch and Marian Distler in 1948 to document music, spoken word, instruction, and sounds from around the world. In the ensuing decades, New York City-based Folkways became one of the largest independent record labels in the world, reaching a total of nearly 2,200 albums that were always kept in print.

The Smithsonian Institution acquired Folkways from the Moses Asch estate in 1987 to ensure that the sounds and genius of the artists would be preserved for future generations. All Folkways recordings are available on high-quality audio cassettes or by special order on CD. Each recording is packed in a special box along with the original LP liner notes.

Smithsonian Folkways Recordings was formed to continue the Folkways tradition of releasing significant recordings with high-quality documentation. It produces new titles, reissues of historic recordings from Folkways and other record labels, and in collaboration with other companies also produces instructional videotapes and recordings to accompany published books, and other educational projects.

The Smithsonian Folkways, Folkways, Cook, Paredon, and Dyer-Bennet record labels are administered by the Smithsonian Institution's Center for Folklife Programs & Cultural Studies. They are one of the means through which the Center supports the work of traditional artists and expresses its commitment to cultural diversity, education, and increased understanding.

You can find Smithsonian Folkways Recordings at your local record store. Smithsonian Folkways, Folkways, Cook, Paredon, and Dyer-Bennet recordings are all available through:

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phone (202) 287-7298
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For further information about all the labels distributed through the Center, please consult our internet site (http://www.si.edu/folkways), which includes information about recent releases, our catalogue, and a database of the approximately 35,000 tracks from the more than 2,300 available recordings (click on "database search").

Or request a printed catalogue by writing to: Catalogue, Smithsonian Folkways Recordings, 955 L'Enfant Plaza, SW, Suite 7300, Smithsonian Institution MRC 953, Washington, DC 20560, USA. Or use our catalogue request phone: (202) 287-3262, or e-mail folkways@aol.com

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The Biological Significance of Voice in Frogs

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