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THE STATUS OF
CALIFORNIA AND ARIZONA POPULATIONS OF THE WESTERN
SPADEFoot TOADS (GENUS *SCAPHIOPUS*)

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THE STATUS OF
CALIFORNIA AND ARIZONA POPULATIONS OF THE WESTERN
SPADEFOOT TOADS (GENUS *SCAPHIOPUS*)¹

By HERBERT A. BROWN²

ABSTRACT: Comparisons of morphology and mating calls of *Scaphiopus hammondii* populations from southern California and southeastern Arizona indicate a degree of evolutionary divergence between these geographical isolates that is indicative of reproductive isolation. I propose that the western populations retain the name *Scaphiopus hammondii* (Baird) and that the eastern populations be recognized as *Scaphiopus multiplicatus* (Cope).

An important difference between eastern and western populations is the structure of the male mating call. When mating call characters, normalized to 20°C, are compared, *S. hammondii* calls are short (0.51 sec) and rapidly pulsed (44.5 pulses/sec) while *S. multiplicatus* calls are long (1.12 sec) and slowly pulsed (20.3 pulses/sec.)

A comparison of the reproductive biology of *S. hammondii* and *S. multiplicatus* is presented. Time of reproductive activity, temperature of breeding pools, and thermal tolerances of embryos, larvae and adults indicate that *S. hammondii* are cold-adapted and *S. multiplicatus* are warm-adapted.

INTRODUCTION

Evolutionary relationships of allopatric populations are among the most difficult to determine, and the amphibians provide only a few well studied cases (Blair 1964, 1965; Littlejohn 1969). This study reports on the evolutionary divergence of allopatric populations of the spadefoot toad currently known as *Scaphiopus hammondii*, and it re-examines the systematic status of these two populations.

The geographical and ecological distribution of *S. hammondii* is extensive (Fig. 1), ranging from California to Texas and from Colorado to southern Mexico and occurring in diverse habitats of desert and grassland to chaparral and woodland into pine forest (Zweifel 1956; Lowe 1964). In California *S. hammondii* occurs in the San Joaquin Valley and southern coastal valleys, but it is absent from the arid southeastern regions. In Arizona another population occurs in the eastern and southern portions of the state, but it is absent in the arid western region. The California population is separated from the nearest Arizona population by nearly 300 miles. Thus, California *S. hammondii* constitute an isolate from the more continuously distributed populations occurring through Arizona across New Mexico into Oklahoma, Texas and Mexico.

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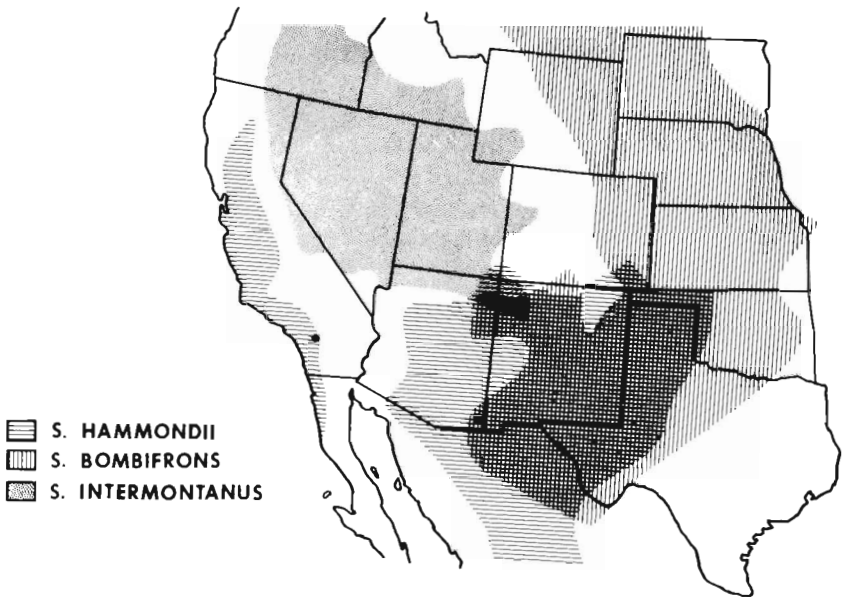


FIGURE 1. Distribution of species of the genus *Scaphiopus*, subgenus *Spea* in the southwestern United States (Stebbins 1966). Collection and study localities in southern California and southeastern Arizona are indicated by solid symbol.

There have already been some comparisons between these populations. Zweifel (1956) found no significant differences in cranial morphology between specimens from California and Mexico. Brown (1967a, 1967b, 1969) studied embryonic and larval adaptations to temperature and found that the summer breeding Arizona populations are warm-adapted and the winter breeding California populations are cold-adapted. The result of artificial hybridization between California and Arizona *S. hammondii* (Brown 1967b) indicated that the populations are genetically compatible since reciprocal crosses produce a high percentage of normal embryonic development; however, the fertility of F_1 hybrids was not determined.

The ranges of *S. hammondii* and *S. bombifrons* (Plains spadefoot toad) overlap in eastern Arizona, New Mexico, western Texas, and northern Mexico (Fig. 1), and this sympatry provides the opportunity of reproductive interactions between these two closely-related species. No such opportunity exists for the California populations of *S. hammondii*. The difference in reproductive environment may influence the evolutionary divergence of two disjunct, allopatric cognate populations (Porter 1968, Littlejohn 1969:462).

The purpose of this study was to evaluate the degree of evolutionary divergence between California and Arizona populations, currently referred to *S. hammondii*, by examining the differentiation of adult morphology and mating call in one population from each of the two areas. This would supplement previous studies and con-

tribute to understanding the development of potential reproductive isolation between California and Arizona populations during geographical isolation. In addition, further information on the reproductive ecology of California *S. hammondi* is presented.

STATUS OF WESTERN SPADEFOOT TOADS

ADULT EXTERNAL MORPHOLOGY

Comparative morphological studies frequently have been used to determine the extent of geographic variation or to evaluate evolutionary divergence between allopatric populations. Firschein (1950) and Zweifel (1956) studied geographic variation in morphology of *S. hammondi*, and both suggested that further study is needed before any taxonomic changes are made. Detailed description of the external features of *S. hammondi* was given by Stebbins (1951:207) and will not be repeated here.

Morphological comparisons were made between one California sample (San Jacinto Valley, near Moreno, Riverside Co., LACM 122867-91) and one Arizona sample (San Simon Valley, near Portal, Cochise Co., LACM 122840-64), each consisting of 25 sexually mature adult males collected during the breeding season. The following measurements were made with vernier calipers and recorded to the nearest 0.1 mm: snout-vent length, head width, interorbital width, tibia-fibula length, height of spade, and width of spade. Measurements of tibia-fibula length were expressed as a ratio of snout-vent length; head length and interorbital width were expressed as a ratio of head width; and the relative size of the spade was expressed by a ratio of spade height to spade width.

A comparison of these measurements (Table 1) suggests that the two populations are similar in most characters, but there are some important differences. The mean

TABLE 1

Morphological characteristics of breeding adult males of *Scaphiopus hammondi* from southern California and southeastern Arizona. Data are mean \pm twice standard error, and range. Sample size = 25 for each population.

	California		Arizona	
Snout-vent length (SV) mm	53.2 \pm 1.38,	45.3 - 58.5	46.9 \pm 1.28	41.0 - 51.9
Tibia length (TL) mm	20.1 \pm 0.38,	18.3 - 22.4	17.8 \pm 0.37,	16.0 - 19.8
Head width (HW) mm	20.6 \pm 0.55,	17.9 - 21.7	17.5 \pm 0.48,	15.2 - 19.1
Head length (HL) mm	11.7 \pm 0.48,	9.9 - 13.9	9.9 \pm 0.25,	8.9 - 10.9
Interorbital width (IW) mm	5.2 \pm 0.26,	3.8 - 6.5	4.4 \pm 0.20,	3.2 - 5.4
Spade height (SH) mm	2.5 \pm 0.24,	2.0 - 3.4	2.6 \pm 0.11,	2.2 - 3.1
Spade width (SW) mm	3.7 \pm 0.16,	2.9 - 4.0	2.8 \pm 0.13,	2.1 - 3.2
100X TL/SV	37.8 \pm 0.3,	34.5 - 40.4	37.9 \pm 0.3,	35.2 - 42.2
100X HL/HW	56.8 \pm 2.0,	45.1 - 65.3	57.1 \pm 1.4,	51.1 - 64.5
100X IW/HW	25.2 \pm 0.5,	21.2 - 29.6	25.1 \pm 0.5,	20.4 - 31.2
100X SH/SW	76.6 \pm 3.6,	60.6 - 103.0	95.5 \pm 3.2,	75.8 - 108.8

snout-vent length of California males is 53.2 mm while that of Arizona males is 46.9 mm; this difference is statistically significant $P < .01$; $t = 6.8$). Chrapliwy (1956: 68) also reported that California specimens (average, 53.3 mm) are larger than those in Arizona, New Mexico, and Texas (average, 47.4 mm). Another important difference (Table 1) is the shape of the metatarsal tubercle (spade). When spade height is expressed as a percentage of spade width, the mean of the California sample (76.6) is significantly less than that of the Arizona sample (95.5) ($P < .01$; $t = 7.9$).

Although there is some overlap in the morphological measurements the two populations are quite distinct in terms of color and color pattern, all individuals being easily allocated on the basis of this one character. In specimens from California, the color and pattern of the dorsum is dark gray-green with distinct, light gray or white, dorsolateral stripes diverging from the head and extending to the sacrum; the pigmentation of the eye (iris) is conspicuously variegated with bright yellow and black. This description is the same as the illustration of *S. hammondii* (from central California) presented by Stebbins (1966: plate 8). In specimens from Arizona the color of the dorsum is uniformly brown or dark tan, and dorsolateral stripes are usually not evident; the iris is slightly variegated and appears pale copper.

MATING CALL COMPARISONS

Recordings of mating calls of individuals at natural breeding sites were made with a battery-operated tape recorder (Stancil-Hoffman) at a tape speed of $7\frac{1}{2}$ inches per second and an Altec microphone (633A). At least six calls per individual were recorded. Water and air temperature were taken at one inch below the water surface and one inch above, respectively, using a Schultheis rapid reading thermometer. Analysis of the mating calls was made by using a "Sonagraph" (Kay Electric Co.) that produces a sound spectrogram with a frequency range to 8,000 cycles per second over a time period of 2.4 seconds. Four variables of the mating call were obtained from the spectrogram: duration of call in seconds, pulses per call, rate of pulse production in pulses per second, and dominant frequency. The tape-recordings have been deposited at the Natural History Museum of Los Angeles County.

In addition to recording mating calls of *S. hammondii* in California and Arizona, mating calls of *S. bombifrons* and apparent hybrids between *S. hammondii* and *S. bombifrons* were also recorded in the San Simon Valley of southeastern Arizona. The structure of the mating calls of *S. hammondii* and *S. bombifrons* have been described for sympatric populations in western Texas (Blair 1955; Forester 1973) and southwestern New Mexico (Bogert 1960; Pierce 1976); apparent hybrids between *S. hammondii* and *S. bombifrons* were also recorded in southwestern New Mexico by Bogert (1960). There are no published accounts of the mating call of California *S. hammondii*.

I made tape-recordings of *S. hammondii* in California on three occasions at two localities in the San Jacinto Valley (Riverside Co.): (1) four males were recorded on 30 March 1965 in shallow pools along the San Jacinto River about two miles north of Lakeview when the water temperature was 12°C and the air temperature was 9°C ; (2) three males were recorded on 24 March 1966 in deep pools of a gravel

pit about three miles east of Moreno when the water temperature was 13.4°C and the air temperature was 8°C; (3) two males were recorded on 26 March 1966 at the gravel pit just described when the water temperature was 19°C and the air temperature was 13.8°C.

In southeastern Arizona and southwestern New Mexico tape recordings of *S. hammondi*, *S. bombifrons*, and apparent hybrids (*S. hammondi* X *S. bombifrons*) were made during July 1965 near the following localities: Portal and Wilcox (Cochise Co.) Arizona; Rodeo, Animas, and Lordsburg (Hidalgo Co.), New Mexico. Water and air temperatures at the time of these recordings were 18-24°C and 22-26°C, respectively.

The basic call structure of *S. hammondi* recorded in California and Arizona resembles the pattern described by Blair (1955); the call is distinctly trilled. Representative sonagrams of the calls of these two populations are presented in Fig. 2, and the physical characteristics are given in Table 2. Before comparisons were made, however, calls were adjusted for temperature. Previous studies have demonstrated that call length varies inversely with temperature while pulse rate varies directly (see Zweifel 1968a; Forester 1973). Arizona mating calls were recorded when water temperature was about 20°C, but California calls were recorded at 12, 13.4, and 19°C (Table 2). I analyzed the California data and calculated the following regression-

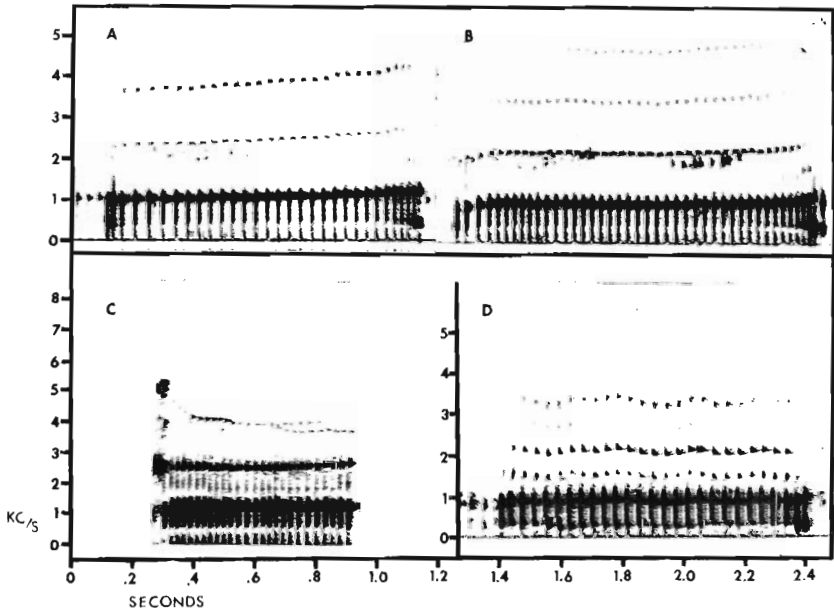


FIGURE 2. Sound spectrograms of *Scaphiopus hammondi* mating calls. California call recorded at 12°C (A), at 13.4°C (B), and at 19°C (C). Arizona call recorded at 20°C (D).

TABLE 2

Mating call characteristics of *Scaphiopus hammondi* from California and Arizona.
Data are mean and range

Number of Individuals	Temperature °C	Call Length (seconds)	Pulses per Call	Pulses per Second	Dominant Frequency (cycles per second)
California					
4	12	1.05 (0.86-1.18)	35.7 (27-45)	33.8 (29.5-37.2)	1450-1550
3	13.4	1.17 (1.05-1.25)	34.8 (32-38)	29.4 (27.8-31.5)	1370-1550
2	19	0.57 (0.50-0.65)	24.3 (22-26)	43.1 (39.7-47.2)	1490-1600
	20 ^a	0.51 (0.32-0.64)	22.7 (16.7-28.9)	44.5 (39.7-50.2)	
Arizona					
8	20	1.12 (1.05-1.25)	25.0 (21-28)	21.3 (20.2-24.5)	1400-1550

^aData adjusted to 20°C.

equations describing the influence of temperature on characteristics of the mating call: (1) call length on temperature, $Y = 2.1 - 0.08X$; (2) pulses per call on temperature, $Y = 56.8 - 1.7X$; (3) pulse rate on temperature, $Y = 10.8 + 1.7X$. The data of the California calls adjusted to 20°C are also given in Table 2. When compared at 20°C the mean call length for the California sample (0.51 sec) is significantly shorter than the Arizona sample (1.12 sec); values of mean pulses per call are similar (22.7 and 25 pulses per call), but mean pulse rate of the California sample (44.5/sec) is twice that of the Arizona sample (21.3/sec). In summary, California calls are short and rapidly pulsed but Arizona calls are long and slowly pulsed.

There is additional information on the structure of the mating call of *S. hammondi* from other regions (central California, Arizona, New Mexico and western Texas). These data are summarized in Table 3. The mating calls recorded by Stebbins near O'Neals in central California (about 260 miles north of my study in the San Jacinto Valley) are shorter in call length (0.7 and 0.8 sec), but length of call is often variable and may reflect the degree of sexual excitement of the calling male (Porter 1964, Zweifel 1968a); in comparing pulse rates, however, the central California calls (30 and 32/sec) are similar to those from southern California (33.8/sec).

Tape-recordings of *S. hammondi* from Arizona at Avra Valley and Sierra Vista were provided by W. F. Blair (Univ. of Texas, Austin), and I made sonagrams of some of these calls for comparison with my recordings. The sample from Avra Valley (160 miles west of the San Simon Valley site of my study) was recorded at a water temperature of 28°C. Considering this high temperature and the positive influence of

TABLE 3

Mating call characteristics (call length and pulse rate) of *Scaphiopus hammondi* from other localities in California, Arizona, New Mexico, and Texas

Locality	Call			Source
	Temp °C	Length (sec)	Pulse Rate (pulses/sec)	
California				
San Joaquin Experimental Station, O'Neals (Madera Co.)	12.8	0.70	30	R. C. Stebbins, (Mus. of Vert. Zool., Berkeley, California)
	12.8	0.80	32	
Arizona				
Avra Valley, West of Marana (Pinal Co.)	28	0.70	30.5	W. F. Blair (Univ. of Texas, Austin)
Sierra Vista (Cochise Co.)	19.5	1.20	22	
New Mexico				
Rodeo (Hidalgo Co.)	20	0.97	26	Bogert (1960)
Texas				
Valentine (Jeff Davis Co.)	23	0.95	20.1	Blair (1955)
Tulia (Swisher Co.)	18	1.09	18.4	Blair (1955)
Lubbock (Lubbock Co.)	20	0.95	22.5	Forester (1973)

increasing temperature on pulse rate, the value of pulse rate in this sample (30.5/sec) is higher than my Arizona sample (21.3/sec) but still lower than the California sample (43.1/sec) recorded almost ten degrees lower (19°C). The mating calls from the Sierra Vista locality (about 80 miles west of the San Simon Valley) are similar to those in southeastern Arizona.

Mating calls of *S. hammondi* recorded in New Mexico by Bogert (1960) and in Texas by Blair (1955) and Forester (1973) are similar to those of the San Simon Valley of southeastern Arizona.

Forester (1973) also studied the effect of temperature on call length and pulse rate of mating calls of *S. hammondi* from northwestern Texas. When his data are adjusted to 12°C for comparison to my data on California calls, the value of call length is 1.01 seconds and pulse rate is 18.3/second; in the California sample call length is 1.05 seconds and pulse rate is 33.8/second. In Forester's study the pulse rate increased 0.5 pulses per second per degree centigrade increase but my data on California calls indicate that this increase is 1.7 pulses per second per degree centigrade increase. Thus, pulse rate in California calls is more sensitive to temperature change than that of northwestern Texas calls.

The mating call of *S. hammondi* in Mexico is poorly known, but Bogert (1960: 285) reported that "there are few important differences between calls of a population at Chapala, Jalisco, Mexico . . . and those of populations in Arizona . . ."

The reproductive environment of *S. hammondii* in southeastern Arizona differs from the population in California in that *S. bombifrons* in the San Simon Valley breed in the same temporary pools as *S. hammondii*. This sympatric distribution extends across New Mexico into western Texas. A limited amount of hybridization occurs between *S. hammondii* and *S. bombifrons* in southeastern Arizona (Bogert 1960), southern New Mexico (Creusere and Whitford 1976), and western Texas (Forester 1973); this is indicated by the incidence of interspecific amplexus and the presence of calling male hybrids in the breeding pools.

On the basis of mating call analysis two distinct call types of *S. bombifrons* are recognized (Pierce 1976): fast trill and slow trill. Table 4 compares the mating calls of two populations of *S. hammondii* sympatric with *S. bombifrons* and the disjunct, allopatric population of *S. hammondii* from California. In southeastern Arizona *S. bombifrons* represents a fast call type, and in western Texas the populations represent the slow call type. There are no differences in call structure between Arizona and Texas populations of *S. hammondii*. However, the California population of *S. hammondii* has a call pattern different from that of *S. hammondii* in Arizona and Texas. The California calls are more similar to those of *S. bombifrons* of western Texas. Porter (1964) suggested that "... in completely allopatric situations, in which no selection for call differentiation would be present, relatively distantly related species might possess similar calls, like that of their common ancestor." The similarity in mating call between the fast trill (California) *S. hammondii* and the slow trill (eastern) *S. bombifrons* suggests that these populations may have retrained the ancestral, or primitive, mating call pattern for the two species. The very different mating calls in southwestern New Mexico and southeastern Arizona could be considered the result of more recent evolution and be described as advanced.

The call differences in sympatric populations of *S. hammondii* and *S. bombifrons* apparently function as effective premating isolation mechanisms. Forester (1973)

TABLE 4

Comparisons of call length and pulse rate in *Scaphiopus hammondii* and *Scaphiopus bombifrons*. All data (mean and range) adjusted to 20°C

Population	Call Length (seconds)	Pulse Rate (pulses/second)	Source
southern California			
<i>S. hammondii</i>	0.51 (0.32-0.64)	44.5 (39.7-50.2)	Present study
southeastern Arizona			
<i>S. hammondii</i>	1.10 (1.00-1.20)	22.3 (19.2-24.3)	Present study
<i>S. bombifrons</i>	0.12	250.0	Bogert (1960)
western Texas			
<i>S. hammondii</i>	0.95 (0.77-1.21)	22.5 (18-25)	Forester (1973)
<i>S. bombifrons</i>	0.53 (0.39-0.72)	63.0 (54-75)	Forester (1973)

reported that in northwestern Texas females of both species can respond to the homo-specific male mating calls and that females can also discriminate between homospecific and heterospecific male mating calls. In southwestern New Mexico and southeastern Arizona where the call differences appear the greatest, hybridization is infrequent. Apparent male hybrids can be recognized by their distinctive mating call (Table 5 and Fig. 3); the call is short (0.39 sec) with a high pulse rate (50.7/sec) but the trills are discernible. These data support the values reported by Bogert (1960:285) where call length is 0.42 seconds and pulse rate (calculated from his data) is 52/second. Jack R. Pierce reported (see Wasserman 1970: 244) that male hybrids (recognized by their mating calls) are sterile in backcrosses to parental forms (in southwestern New Mexico). Forester (1975) reported, however, that male hybrids from northwestern Texas are fertile in backcrosses. The difference in fertility of hybrids would be explained by accepting the suggestion that the southwestern New Mexico populations of *S. bombifrons* are really a third undescribed species (see Pierce 1976).

CALLING POSITION AT BREEDING POOL

While sympatric populations of *S. hammondi* and *S. bombifrons* may breed in the same temporary pool, there are distinct differences in the position of males calling at the breeding pool. Males of *S. hammondi* call while floating and swimming at some distance from the pool's edge, but males of *S. bombifrons* call at the edge of the pool while sitting in shallow water (Lowe 1954, Gehlbach 1956, McAlister 1959). I observed these different behaviors in the San Simon Valley of southeastern Arizona. In California, however, males of *S. hammondi* have a preference to call from a concealed position near the edge of the pool; on several occasions males were found sitting and calling at the edge of the pool with only a part of their body immersed. Calling males were seldom observed in an open area of the pool. Gehlbach (1965) reported that in northwestern New Mexico, where *S. hammondi*, *S. bombifrons* and *S. intermontanus* occur together, *S. hammondi* males may call from shallow water or from shore; no *S. bombifrons* were found calling at this site even though they were present in this region. These field observations indicate that males of *S. hammondi* may prefer a more peripheral calling position when other closely-related spadefoot toads are not present in the breeding chorus.

TABLE 5

Mating call characteristics of three apparent hybrids, *Scaphiopus hammondi* X *S. bombifrons*, recorded near Rodeo, New Mexico

Individual	Water Temperature °C	Call Length (seconds)	Pulses per Call	Pulses per Second
1	17.8	0.36-0.41	19-21	50.0-52.8
2	19.6	0.36-0.40	18-20	50.0-52.6
3	18.4	0.38-0.40	19-21	50.0-52.5

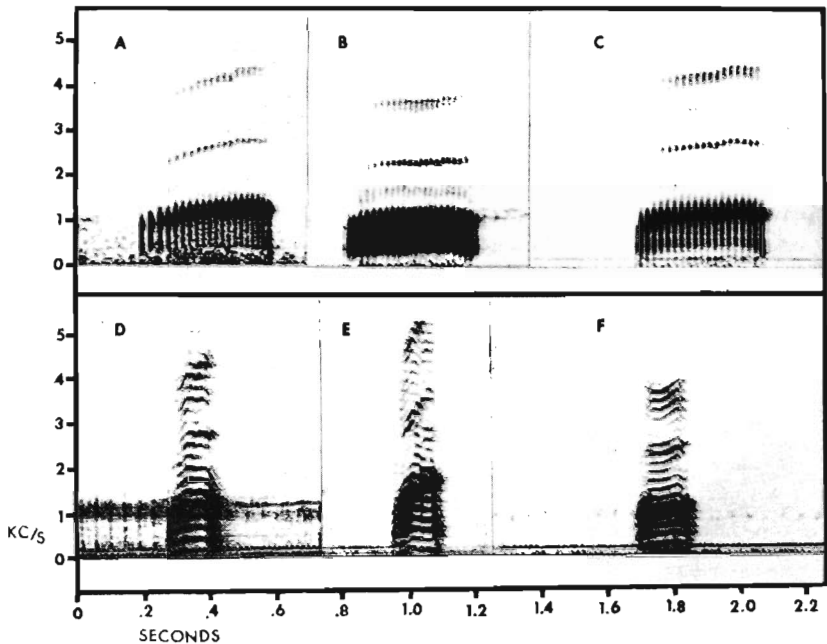


FIGURE 3. Sound spectrograms of mating calls of three apparent hybrids, *Scaphiopus hammondii* X *Scaphiopus bombifrons* (A, B, C) and three *Scaphiopus bombifrons* (D, E, F) recorded near Rodeo, New Mexico at a water temperature of 18.4°C.

REPRODUCTIVE ECOLOGY OF *SCAPHIOPUS HAMMONDII* IN CALIFORNIA

Field observations on the breeding activity of *S. hammondii* in the San Jacinto Valley suggest that reproduction only occurs in late winter and spring. During the fall and winter from October to December the adults and immature toads may emerge after periods of wet weather, but no reproduction occurs at this time. The period of June through September corresponds to the hot, dry season and the toads are usually inactive and assumed to be beneath the soil.

Reproduction of spadefoot populations in the San Jacinto Valley was observed during four years (1963 to 1967), but the years 1964 to 1966 were studied more intensively. During November and December of 1964 a total of 2.36 inches of rain fell in the San Jacinto Valley and toads emerged, but they did not breed. Then a warm, dry period (January and February 1965) followed and the pools formed by the earlier winter rainfall became dry. During March and April of 1965 storms deposited 6 inches of rain and toads began chorusing in the refilled breeding pools. Calling males were heard from March 13 to April 23 when water temperatures ranged from 6° to 15°C. Gravid females were found near the breeding pools on March 15, 17, and 31. Intermittent rain was common between March 13 and April 11, but following this period no measurable rain was recorded in the San Jacinto Valley. Despite the absence of rain the toads continued to chorus in the temporary pools.

On 28 April 1965 I found spadefoot tadpoles in the temporary pools along the San Jacinto River near Lakeview; the tadpoles had developed to stages 30-34 of Gosner (1960) with well developed hindlimbs. On May 1 at the pools near Moreno I found tadpoles in stages 28-41. By May 10 the Lakeview tadpoles were at stages 40 and 42, some with front legs protruding. On May 30 the Lakeview pools contained many tadpoles with all four legs but still with long tails; in addition many recently transformed juveniles were hiding in the deep mud cracks of the drying pools. The average snout-vent length in a sample of twenty juveniles was 28 mm (range, 23-33). Oviposition probably began about March 13, and presumably took place several times later because metamorphosing tadpoles were found from May 10 to May 30. The period from oviposition to metamorphosis was about 55-60 days.

Further observations on the breeding activity of the San Jacinto Valley populations were made during the 1965-1966 season. In the fall and winter of 1965 from November 14 to December 31 the San Jacinto Valley received considerable rainfall (10.2 inches), and the usual breeding pools formed. Despite the abundant rainfall, available breeding pools, and moderate water temperatures (11 to 15°C) the spadefoot toads did not breed. Adult and immature toads were found on the wet roads and near the breeding pools, but I found only one small chorus on November 22. On subsequent visits (December and January) to this site no tadpoles were found in the pools.

During the following three months only 2.2 inches of rainfall was recorded in the San Jacinto Valley: January, 0.71; February, 1.01; March, 0.47. On February 5, I found a gravid female and a small group of calling male toads at the breeding pools near Moreno. On February 8 chorusing activity continued at the Moreno pools. On March 24 a convectional storm produced a series of light showers in the San Jacinto Valley, and a large group of about thirty calling toads were observed at the Moreno pools; water temperatures ranged from 13° to 19°C for the next several days, and toads continued to chorus at this site until April 14. However, no rainfall was recorded at this site after the light showers of March 24. The pattern of continued chorusing activity in the absence of rainfall is similar to spadefoot behavior observed the previous year. Storer (1925:156) reported similar observations on populations of *S. hammondi* near Banning (Riverside Co.), California. Zweifel (1956:42) reported that *Scaphiopus intermontanus* may chorus in the absence of rain also.

The following summary of terrestrial and reproductive activity of California populations of *S. hammondi* is based upon personal field observations and examination of museum specimens and field notes of the following institutions: Museum of Vertebrate Zoology (Berkeley); California Academy of Sciences (San Francisco); and the former collection of the Stanford Natural History Museum (Palo Alto) now transferred to the California Academy of Sciences. Spadefoot toads have been collected in every month of the year except August. While chorusing activity may occur from November to July, eggs have been found only during February, March and April, and tadpoles during January to June. Metamorphosing tadpoles have been found from March through June. These observations suggest that the usual period of reproduction is January to April.

The breeding season of California *S. hammondi* occurs during the months of high and frequent rainfall and low temperatures. In the San Jacinto Valley most rainfall

occurs from December to March with the maximum during February. The period when rainfall is frequent is January to April when there are six rainy days per month (U.S. Weather Bureau records). In contrast, Arizona populations of *S. hammondi* breed following the heavy rain and high temperatures of the summer months of July and August (Brown 1967b). Thus, California populations of *S. hammondi* are cold weather breeding, while Arizona populations are warm weather breeding or they breed when it rains at temperatures above 10°C.

In previous studies (Brown 1967a, 1967b) I compared the embryonic temperature adaptations of California and Arizona *S. hammondi* and found that California embryos have lower limits of tolerance (9° and 30°C) than Arizona embryos (13° and 32.5°C), and that California embryos have rapid developmental rates at low temperatures. Although I did not find eggs in the natural pools in California, Robert C. Stebbins (field notes) found embryos exposed to water temperatures of 7.7° to 15.6°C in the morning, 19.9°C in the afternoon, and 11.3°C in the evening at the San Joaquin Experimental Station on 11-13 March 1951; eggs deposited on the evening of March 10 hatched by the morning of March 13. I also studied the temperature adaptations of control and hybrid tadpoles made from crosses between California and Arizona *S. hammondi* (Brown 1969). These data suggest that Arizona tadpoles are more resistant to high temperatures than California tadpoles. Brattstrom (1968:103, Fig. 3h) reported that the critical thermal maximum of adult *S. hammondi* is higher for individuals from Sonora, Mexico than those from southern California. These data indicate that California *S. hammondi* have a cold-adapted physiology allowing them to take advantage of the winter and spring rainfall.

Another spadefoot toad, *Scaphiopus couchi*, occurs in California but it is restricted in distribution to the extremely arid, southeastern part of the state (Mayhew 1962). Although most rainfall comes to this region during the winter months, *S. couchi* does not respond to this rainfall but breeds only following the very infrequent heavy rains of the summer months (Mayhew 1965). While *S. hammondi* in California is a cold-adapted toad, *S. couchi* is an apparently warm-adapted toad that breeds in warm weather and has high embryonic thermal limits (15.5° and 34°C) and the most rapid rate of development of any North American anuran (Zweifel 1968b).

EVOLUTIONARY DIVERGENCE AND TAXONOMY

This study of allopatric populations of *S. hammondi* indicates considerable evolutionary divergence in morphology, breeding habits, mating calls, and physiological temperature adaptations (Table 6). The populations have presumably been separated at least since some time in the Pleistocene (Brown 1967b). The differences are presumably adaptive and attributable to selection in different climatic and biotic environments. The color differences may represent matching of different backgrounds and the shape of the metatarsal tubercle may relate to differences in the physical characteristics of the soil where the toads burrow (Wasserman 1957). Divergence in temperature tolerances is consistent with the rainfall patterns in the two areas. While the differences in mating calls and breeding behavior may be important potential pre-

TABLE 6

Summary of the characteristics of two species of western spadefoot toads, *Scaphiopus hammondii* and *Scaphiopus multiplicatus*

Character	<i>S. hammondii</i> (California)	<i>S. multiplicatus</i> (Arizona)
1. Morphology		
Coloration of body	Green	Brown
Coloration of eye	Yellow and black variegation	Copper
Body length of adult males	53.2 mm	46.9 mm
Shape of spade (SH/SW)	0.77	0.96
2. Reproductive Biology		
Breeding season	January-April	July and August
Embryonic temperature tolerance	9-30°C	13-32.5°C
Developmental rate (hr, 28°C)	25.1	21.7
Tadpole temperature tolerance	Hybrid > Control	Control > Hybrid
3. Genetic Compatibility		
Intraspecific crosses ^a	CH × AH, normal	AH × CH, normal
Interspecific crosses ^a	CH × AB, normal	AH × AB, normal
	CH × I, normal	AH × I, normal
Fertility of hybrids	Not known	Male hybrids (AH × AB) may be sterile.
4. Breeding Behavior		
Mating call duration at 20°C	0.51 seconds	1.12 seconds
Mating call pulse rate at 20°C	44.5/second	21.3/second
Calling position of male at breeding pool	Swimming-floating near shore	Swimming-floating away from shore

^aCH = California *S. hammondii*; AH = Arizona *S. multiplicatus*; AB = Arizona *S. bombifrons*; I = *S. intermontanus* from eastern California.

mating isolation mechanisms, the two populations are interfertile and have no apparent postmating isolation mechanisms. This pattern of evolutionary divergence follows that described by Blair (1964) where differentiation of the mating call and development of ecological isolation mechanisms have preceded the development of genetic incompatibility.

The taxonomic status of the North American pelobatine toads, *Scaphiopus* (Holbrook) and *Spea* (Cope), and their phylogenetic relationships have been reviewed by Zweifel (1956), Kluge (1966) and Estes (1970). These studies recognize three species of the subgenus *Spea*, *Scaphiopus hammondii*, *Scaphiopus bombifrons* and *Scaphiopus intermontanus*. It is my opinion, after studying male mating calls, adult morphology, breeding behavior, and physiological temperature adaptations (Table 6), that the biological differences found between western and eastern populations of *S. hammondii*, are the same order of magnitude as that observed between related

sympatric species. I therefore suggest that the western population retain the name *Scaphiopus hammondii* (Baird) and that the eastern population be recognized as *Scaphiopus multiplicatus* (Cope).

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LITERATURE CITED

- BLAIR, W. F. 1955. Differentiation of mating call in spadefoots, genus *Scaphiopus*. *Texas J. Sci.* 7:183-188.
- . 1964. Isolating mechanisms and interspecies interactions in anuran amphibians. *Quart. Rev. Biol.* 39:334-344.
- . 1965. Amphibian speciation. In *The Quaternary of the United States* (Ed. by H. E. Wright, Jr., and David G. Frey), pp. 543-556. Princeton Univ. Press, Princeton, New Jersey.
- BOGERT, C. M. 1960. The influence of sound on the behavior of amphibians and reptiles. In *Animal Sounds and Communication* (Ed. by W. E. Lanyon and W. N. Tavolga), pp. 137-320. *Amer. Inst. Biol. Sci. Pub. No. 7*, Washington, D. C.
- BRATTSTROM, B. H. 1968. Thermal acclimation in anuran amphibians as a function of latitude and altitude. *Comp. Biochem. Physiol.* 24:93-111.
- BROWN, H. A. 1967a. High temperature tolerance of the eggs of a desert anuran, *Scaphiopus hammondii*. *Copeia* 1967:365-370.
- . 1967b. Embryonic temperature adaptations and genetic compatibility in two allopatric populations of the spadefoot toad, *Scaphiopus hammondii*. *Evolution* 21:742-761.
- . 1969. The heat resistance of some anuran tadpoles (Hylidae and Pelobatidae). *Copeia* 1969:138-147.
- CHRAPLIWY, P. S. 1956. Taxonomy and distribution of the spadefoot toads of North America (Salientia: Pelobatidae). Thesis: University of Kansas, Department of Zoology, May, 1956.
- CREUSERE, F. M. AND W. G. WHITFORD. 1976. Ecological relationships in a desert anuran community. *Herpetologica* 32:7-18.
- ESTES, R. 1970. New fossil pelobatid frogs and a review of the genus *Eopelobates*. *Bull. Mus. Comp. Zool., Harvard Univ.* 139:293-340.
- FIRSCHIN, I. L. 1950. A new record of *Spea bombifrons* from northern Mexico and remarks on the status of the *hammondii* group of spadefoot anurans. *Herpetologica* 6:75-77.

- FORESTER, D. C. 1973. Mating call as a reproductive isolating mechanism between *Scaphiopus bombifrons* and *Scaphiopus hammondi*. *Copeia* 1973: 60-67.
- . 1975. Laboratory evidence for potential gene flow between two species of spadefoot toads, *Scaphiopus bombifrons* and *Scaphiopus hammondi*. *Herpetologica* 31:282-286.
- GEHLBACH, F. R. 1956. Annotated records of southwestern amphibians and reptiles. *Trans. Kan. Acad. Sci.* 59:364-372.
- . 1965. Herpetology of the Zuni Mountain region of northwestern New Mexico. *Proc. U.S. Nat. Mus.* 116:243-332.
- GOSNER, K. L. 1960. A simplified table for staging anuran embryos and larvae with notes on identification. *Herpetologica* 16:183-190.
- KLUGE, A. G. 1966. A new pelobatine frog from the Lower Miocene of South Dakota with a discussion of the evolution of the *Scaphiopus-Spea* complex. *Los Angeles County Mus. Contr. Sci.* 113:1-26.
- LITTLEJOHN, M. J. 1969. The systematic significance of isolating mechanisms. In *Systematic Biology*, pp. 459-493. *Nat. Acad. Sci. Pub.* 1692, Washington, D.C.
- LOWE, C. H. 1954. Isolating mechanisms in sympatric populations of southwestern toads. *Tex. J. Sci.* 6:265-270.
- . 1964. The amphibians and reptiles of Arizona. In *The Vertebrates of Arizona* (Ed. by C. H. Lowe), pp. 153-174. *Univ. of Arizona Press*, Tucson.
- MAYHEW, W. W. 1962. *Scaphiopus couchi* in California's Colorado Desert. *Herpetologica* 18:153-161.
- . 1965. Adaptations of the amphibian, *Scaphiopus couchi*, to desert conditions. *Amer. Midland. Natur.* 74:95-109.
- MCALISTER, W. H. 1959. The vocal structure and method of call production in the genus *Scaphiopus* Holbrook. *Tex. J. Sci.* 11:343-347.
- PIERCE, J. R. 1976. Distribution of two mating call types of the Plains spadefoot, *Scaphiopus bombifrons*, in southwestern United States. *Southwest. Natur.* 20:578-582.
- PORTER, K. R. 1964. Morphological and mating call comparisons in the *Bufo valliceps* complex. *Amer. Midland. Natur.* 71:232-245.
- . 1968. Evolutionary status of a relict population of *Bufo hemiophrys*. *Evolution* 22: 583-594.
- STEBBINS, R. C. 1951. *Amphibians of Western North America*. *Univ. of California Press*, Berkeley.
- . 1966. *A Field Guide to the Western Reptiles and Amphibians*. Houghton-Mifflin, Boston, Mass.
- STORER, T. I. 1925. A synopsis of the Amphibia of California. *Univ. California Pub. Zool.* 17: 1-342.
- WASSERMAN, A. O. 1957. Factors affecting interbreeding in sympatric species of spadefoots (*Scaphiopus*). *Evolution* 11:320-338.
- . 1970. Chromosomal studies of the Pelobatidae (Salientia) and some instances of ploidy. *Southwest. Natur.* 15:239-248.
- ZWEIFEL, R. G. 1956. Two pelobatid frogs from the Tertiary of North America and their relationships to fossil and Recent forms. *Amer. Mus. Nov.* 1762:1-45.
- . 1968a. Effects of temperature, body size, and hybridization on mating calls of toads, *Bufo a. americanus* and *Bufo woodhousii fowleri*. *Copeia* 1968:269-285.
- . 1968b. Reproductive biology of anurans of the arid Southwest, with emphasis on adaptation of embryos to temperature. *Bull. Amer. Mus. Nat. Hist.* 140:1-64.