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RESEARCHES ON

THE AMPHIBIA
OF
OKLAHOMA

BY

ARTHUR N. BRAGG A. O. WEESE
HAROLD A. DUNDEE HELEN TALLEY FISHER
A. RICHARDS CAROL BERGTHOLD CLARK

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Foreword

THE STUDIES presented in this volume have been made over a period of years on various aspects of the lives of Amphibia in Oklahoma. They were produced under the auspices of the University of Oklahoma Biological Survey, on whose staff most of the authors represented serve. It is the hope of the Survey and of the individual contributors that these collected studies may afford useful information in a form which will prove convenient to students of this branch of scientific investigation in Oklahoma.

Contents

PART I. PAPERS ON TAXONOMY

I. The Identification of Salientia in Oklahoma	<i>Arthur N. Bragg</i>	9
Keys to Frogs and Toads of Oklahoma	<i>Arthur N. Bragg</i>	11
II. A Key to the Adult Salamanders of Oklahoma, Including the Forms Likely to Occur in the State	<i>Harold A. Dundee and Arthur N. Bragg</i>	30
III. Salientian Breeding Dates in Oklahoma	<i>Arthur N. Bragg</i>	35
IV. Salientian Range Extensions in Oklahoma and a New State Record	<i>Arthur N. Bragg</i>	39

PART II. PAPERS ON ECOLOGY

V. Observations on the Ecology and Natural History of Anura.		
XIV. Growth Rates and Age at Sexual Maturity of <i>Bufo Cognatus</i> under Natural Conditions in Central Oklahoma	<i>Arthur N. Bragg and A. O. Weese</i>	47
VI. Observations on the Ecology and Natural History of Anura.		
XVII. Adaptations and Distribution in Accordance with Habits in Oklahoma	<i>Arthur N. Bragg</i>	59
VII. Some Adaptations of Survival Value in Spadefoot Toads	<i>Arthur N. Bragg</i>	101
VIII. Frequency of Sex Calls in Salientia	<i>Arthur N. Bragg</i>	117

PART III. PAPERS ON SEX CYCLES

IX. The Annual Ovarian Cycle of <i>Acris Crepitans</i> Baird	<i>Helen Talley Fisher and A. Richards</i>	129
X. A Comparison of the Ovaries of Two Species of <i>Bufo</i> with Different Ecological Requirements	<i>Carol Bergthold Clark and Arthur N. Bragg</i>	142

PART I
PAPERS ON TAXONOMY

I

The Identification of Salientia in Oklahoma

ARTHUR N. BRAGG

KEYS for the identification of the fauna of each state or group of small states should be available. Due to lack of knowledge of the distribution, habits, ecological relationships, the eggs and larvae, and in several cases even the presence of many of the local forms, it has not been possible previously to construct a key to the Salientia of Oklahoma that is reasonably complete. As late as 1935, taxonomic and distributional matters were in confusion, and eggs, tadpoles or both of several forms were undescribed.

During the past ten years while concentrating on problems in ecological distribution and habits of Salientia of Oklahoma, I have always had in mind the construction of a key which would include eggs and larvae as well as adults of our local forms, and I have consistently made observations and collections toward this as an eventual goal. Unknown eggs and larvae have been described as opportunity permitted their study and a large number of specimens of species in Oklahoma have been preserved in my personal collection and in the University of Oklahoma Museum; these together form a good basis for a key because they are extensive enough to show most of the variations likely to be encountered.

In the meantime, workers in other regions have published descriptions of tadpoles or eggs of some of our local forms that happen also to occur in their areas of study; these serve to fill in some gaps in our knowledge, as well as to indicate other possible variations within the species based on ecological or zoogeographic factors. All told, therefore, there now are available basic descriptions of adults, eggs, and larvae of all except a very few of the twenty-seven species and subspecies known to occur in Oklahoma.

The purpose of this paper is to bring together all available information of whatever source bearing upon identification of the frogs and toads of Oklahoma, including their eggs and tadpoles. The keys are constructed partly from the literature and partly from my own observations, the former being used only wherever the latter are still inadequate or when statements by others are considered so appropriate to a given situation as to seem better than I could do. In a few cases direct quotations are given; in others I have paraphrased. I wish to acknowledge especially my dependence upon the works of Wright (1920), Wright and Wright (1942), Smith (1934, 1946), Youngstrom and Smith (1936), Tanner (1939), Walker (1946), and Goin and Netting (1940).

The key is complete for adults; as to eggs and larvae, those of one frog (*Rana areolata areolata*) and one tree toad (*Hyla versicolor chrysoscelis*) and

the eggs of one toad (*Bufo insidiosus*) are still unknown. The only reasonably complete key to the eggs of the Salientia of the United States has only recently appeared (Livezey and Wright, 1947). The tadpole of *Bufo insidiosus* included in the present key has never been found in Oklahoma, the differentiating factors being based on the statements of Smith (1934) for *Bufo debilis* of Kansas.¹

The identification of salientian eggs and of adults in Oklahoma presents no unusual difficulties except in a few instances; but the identification of tadpoles is especially difficult, particularly in some groups. Most descriptions and keys are based upon larvae in early metamorphic stages or at the stage when they are about to enter transformation, and younger tadpoles often cannot be identified without raising them to these stages before keying them out. Furthermore, some larvae do not follow the pattern typical of their group, as is seen in the Hylidae, where for example, the tadpole of *Acris crepitans* Baird superficially resembles the ranid type more than the hylid (i.e., frog more than tree toad). Variations in color in different regions and waters is the rule rather than the exception; and some characteristics of behavior tend to cut across taxonomic lines. Similar larval adaptations, color patterns, morphological structures, and behavior in securing food and protection of different species in a single pool at times may be confusing. Within *Bufo*, tadpoles of some species resemble each other closely at certain stages but differ at others, and many toad tadpoles resemble those of frogs in color, general appearance, and behavior in the face of danger.

Nevertheless, my whole experience indicates that characteristics of behavior at given places and conditions often can be used successfully in at least preliminary and tentative identification in the field; and in some cases when combined with known ecological requirements of the species, geographical distribution, and characteristics (and easily recognized markings or morphological structures) will identify tadpoles almost at a glance. If one uses such characteristics with judgment and caution they can be very valuable. But in case of doubt, careful study of morphological structures and proportions is the only safe procedure.

The key to tadpoles is constructed in the attempt to take advantage of these easily recognized characteristics in the field. Since many of them cannot be used for preserved animals, particularly whenever the water from which they came is unknown, the key presupposes two conditions: (1) The user is observing live tadpoles in nature, or (2) he has live or preserved animals before him in the laboratory with little or no knowledge of their source, except perhaps the general regions of the state where they were collected. The field key begins with No. 1, the general key with No. 18. Any tadpole should be identifiable by beginning with the latter number. Time can be saved under field conditions, however, by starting with the field key.

In addition to the keys there is a section in which each species is listed alphabetically, with summaries of data on distribution, ecological relations,

¹ *Bufo insidiosus* Girard was taken out of synonymy with *B. debilis* Girard by Taylor (1936). The form in Kansas and Oklahoma is *B. insidiosus*.

characteristic types of breeding sites used, typical behavior or attitudes of tadpoles, and other matters that may be of interest in themselves or as further aids in identification. For each form, one reference, or more, is given (when any exist) to a description of adults, eggs, and larvae. A glossary is included for those unfamiliar with technical terms used in the keys.

Keys to Frogs and Toads of Oklahoma

1. EGGS

1. Eggs deposited singly or (occasionally) a few together 2
1. Eggs deposited in groups of typically twenty or more 4
2. Single eggs light in color (brown or gray and cream or white), attached to vegetation 3
2. Single eggs dark in color (approaching black and white), attached to bottom. To be expected in rough mountainous areas, mostly in west. Rare.
Canyon Toad, *Bufo punctatus* Baird and Girard.
3. Single eggs with very sticky jelly; egg envelope single, more than 2.0 mm. in diameter. State-wide and abundant. Northern Cricket Frog, *Acris crepitans* Baird.
3. Single eggs with envelope not exceptionally sticky; egg envelope single but less than 2.0 mm. in diameter. Known only in the east.
Spring Peeper, *Hyla crucifer crucifer* Wied.
4. Eggs deposited in strings of jelly (Bufo) 5
4. Eggs not deposited in strings 10
5. Egg strings short, not exceeding about 15 cm. in length; egg size 1.0-1.3 mm.; envelope single, 3.2-3.6 mm. in diameter. Typically in rocky pools but probably sometimes in tanks in west. Rare. Canyon Toad, *Bufo punctatus* Baird and Girard.
5. Egg strings longer than 15 cm., usually very long 6
6. Eggs black and white; envelope wide (3.0 mm. or more) 7
6. Eggs brown and yellow; envelope narrow (about 2.0 mm.); western Oklahoma, east to Jefferson County in south; common southwest, rare northwest.
Desert Toad, *Bufo compactilis* Wiegmann.
7. Envelope double 8
7. Envelope single (*Bufo woodhousii*) 9
8. Egg size 1.0-1.4 mm.; egg number up to 8,000; eggs usually uncrowded with tube nearly or quite the same diameter throughout length; eggs in each string seldom in double rows; a straight partition visible between adjacent eggs. Eastern half of Oklahoma only. Abundant. American Toad, *Bufo terrestris americanus* Holbrook.²
8. Egg size 1.2 mm. (arithmetical mean); egg number up to 20,000; eggs often crowded; outer tube characteristically narrower between eggs than across eggs; eggs in each string sometimes in double rows (in whole or in part); each egg surrounded by an inner capsule, the walls of adjacent ones sometimes appearing as a partition but if so, not straight at outer edges. Western two-thirds of Oklahoma in grassland only.
Great Plains Toad, *Bufo cognatus* Say.
9. Egg number smaller (about 8,000); egg size smaller (1.0-1.4 mm.); tube diameter 2.6-4.6 mm.; eggs sometimes in double but almost never in triple rows. Eastern Oklahoma only, west to Coal County in south. Abundant.
Fowler's Toad, *Bufo woodhousii fowleri* Hinckley.
9. Egg number larger (about 25,000); egg size larger (about 3.5 mm.); tube diameter typically larger (about 4.0-5.0 mm.); eggs often in double, sometimes in triple rows; abundant in all of Oklahoma except where *B. w. fowleri* occurs. Present in

² Known until recently as *B. americanus americanus* but now proved to intergrade with *Bufo terrestris* Bonneterre and hence considered as a subspecies of this (see Netting and Goin, 1946).

THE AMPHIBIA OF OKLAHOMA

Craig County in north, Coal County in south but east of a line between these only along Arkansas River. Abundant from east central Oklahoma westward

Rocky Mountain Toad, *Bufo woodhousii woodhousii* Girard.³

10. Eggs floating free at surface of water 11
10. Eggs attached 16
11. Eggs black and white 13
11. Eggs not black and white 12
12. Eggs brownish and cream or yellow and produced in small packets; egg size 0.8-1.6 mm.; outer envelope 3.6-4.0 mm. in diameter, poorly defined; inner envelope 2.2-3.4 mm. and well defined. Extreme southeast only. Rare

Green Tree Toad, *Hyla cinerea cinerea* (Schneider).

12. Generally similar to above (12) but envelopes different; outer 4.0-8.0 mm.; inner 1.4-2.0 mm. in diameter; eastern half of Oklahoma. Abundant.

Common Tree Toad, *Hyla versicolor versicolor* (Le Conte).⁴

13. Individual eggs less than 1.0 mm. in diameter (0.8-0.9 typically); egg envelope 2.8-4.0 mm. in diameter; eggs occur scattered over surface singly or in small groups. (*Microhyla*) 14
13. Individual eggs more than 1.0 mm. in diameter (1.2-1.7 typically); egg envelopes wider (typically 3.0-5.0 mm.); eggs occur in continuous rafts sprawled on surface 15
14. Egg envelope truncate, flat above; west to Latimer County in south. Common.

Narrow Mouth Toad, *Microhyla carolinensis carolinensis* (Holbrook)⁵

14. Egg envelope not truncate, rounded above; state-wide except in east and possibly Panhandle. Very abundant.

Northern Narrow Mouth Toad, *Microhyla carolinensis olivacea* (Hallowell).⁵

15. Eggs in large numbers (up to 50,000) sprawled over surface to 2x3 feet; envelope single. Abundant in all parts of Oklahoma. Bullfrog, *Rana catesbeiana* Shaw.
15. Eggs in smaller numbers (up to 8,000) seldom covering more than 1x1 foot of surface (usually half this); envelope double. Eastern half of Oklahoma, rare except in southeast

Green Frog, *Rana clamitans* Latreille.

16. Eggs clearly black and white 17
16. Eggs not clearly black and white, typically brown or gray and white, cream or yellow 20
17. Egg mass a plinth, attached just below water surface 18
17. Egg mass not a plinth, irregular and loosely attached to vegetation 19
18. Diameter of egg not over 2.0 mm., usually less; outer envelope about 3.5 mm. in diameter; black and white regions distinct. Very abundant and state-wide.

Southwestern Leopard Frog, *Rana berlandieri* Baird.

18. Diameter of egg above 2.0 mm., sometimes 2.5; outer envelope wider than 3.5 mm. (typically 4.5-5.0 mm.); black and white regions indistinctly separated. Northeastern Oklahoma only. Common but seldom seen.

Northern Crayfish Frog, *Rana areolata circulosa* Rice and Davis.⁶

19. "Eggs in bands 6 mm. across or cylindrical mass on plant stems, the jelly rather firm, the eggs close together, black above and creamy white below" (Wright and

³ The eggs of Fowler's Toad and the Rocky Mountain Toad are very much alike. In the area of overlap of ranges the adults intergrade and the eggs are so alike that no constant differences will separate them.

⁴ Eggs of the closely related *H. v. chrysoscelis* (Cope) are unknown. This form replaces *H. v. versicolor* in some deep valleys in McCurtain and LeFlore counties.

⁵ Recent indications (Hecht and Matalas, 1946) are that the two forms of *Microhyla* of Oklahoma intergrade in Latimer County and in Texas and therefore henceforth should be considered subspecies. I have also seen intergrading specimens from Latimer County.

⁶ Data from Smith (1934) on the Kansas form. Eggs of *Rana a. areolata* (which occurs in southeastern Oklahoma) are still undescribed.

KEYS TO FROGS AND TOADS

Wright, 1942); egg diameter 1.4-1.6 mm.; southwestern Oklahoma, north to Custer County, east to Jefferson County; abundant.

Southern Spadefoot, *Scaphiopus couchii* Baird.

19. Eggs in loose masses roughly suggesting strings joined at various points but with no continuous tube as in *Bufo*; attached loosely near surface to vegetation; envelope single, 6.7 mm. in diameter; egg size 2.3 mm. Some masses superficially suggest exceptionally loose plinths of frogs, others loosely attached egg strings of toads. Eastern half of Oklahoma and on flood plains westward. Not uncommon but rarely seen. Savannah Spadefoot, *Scaphiopus huerterii* Strecker.

20. Eggs numerous (up to 3,000); mass globular and tight, 87-100 mm. in diameter; egg color brown and yellow; inner membrane elliptical. Eastern Oklahoma only, rare except in extreme southeast. Pickerel Frog, *Rana palustris* Le Conte.

20. Eggs less numerous (usually less than 300); egg mass neither globular nor firm; often quite irregular; inner membrane, if present, not elliptical 21

21. Eggs mostly floating free at or very near the surface, attached very loosely in a few places to vegetation 22

21. Egg mass attached beneath surface 23

22. Outer envelope 3.6-4.0 mm., inner 2.2-3.4 mm. in diameter; extreme southeast only. Rare. Green Tree Toad, *Hyla cinerea cinerea* (Schneider).

22. Outer envelope 4.0-8.0 mm., inner 1.4-2.0 mm. in diameter. Eastern half of Oklahoma. Abundant. Common Tree Toad, *Hyla versicolor versicolor* (Le Conte).⁴

23. Eggs produced in a mass of smooth outline, lobed, soft and very sticky; attached to vegetation or twigs, typically slanting rather than upright (some exceptions); envelope single; egg color grayish brown and quite dark shading to cream or white; egg size slightly variable (1.17-1.26 mm. diameter observed). All parts of state except eastern and western edges Texas Ornate Chorus Frog, *Pseudacris streckeri* Wright and Wright.

23. Not as above 24

24. Eggs attached near surface; color darker, brown or dark gray shading to yellowish, cream or white 26

24. Eggs not attached near surface (except in shallow water where they are seldom produced); color lighter (light brown or gray and cream or white); diameter of egg 1.0-1.61 mm. 25

25. Egg mass roughly cylindrical; western one-third of Oklahoma only. Rare.

Western Spadefoot, *Scaphiopus hammondi* Baird.

25. Egg mass elliptical; western two-thirds of Oklahoma, east to Tulsa in north. abundant. Plains Spadefoot, *Scaphiopus bombifrons* (Cope).

26. *Envelope double*; egg mass small (usually 10-50 eggs); produced not more than 2 inches beneath surface; typically attached to upright vegetation with one piece passing near center of mass (some exceptions); eggs noticeably variable in size seen without lens (0.65-1.03 mm. diameter); always in quiet water. Western two-thirds of Oklahoma in grasslands only east to Tulsa in north.

Spotted Chorus frog, *Pseudacris clarkii* (Baird).

26. *Envelope single*; egg mass small to medium (10-50 eggs); attached nearer surface than bottom except in very shallow water; often on slanting vegetation or twigs (some exceptions), usually with no piece passing near center of mass; eggs less variable in size (0.9-1.2 mm.), variation not noticed with naked eye; mostly in quiet water but occasionally in fast flowing streams; abundant in eastern one-third of state. Rare elsewhere. Striped Chorus Frog, *Pseudacris triseriata* (Wied).

II. TADPOLES

1. If in the field see 2
1. If in the laboratory see 18

2. Tail red or red and black mottled.

Common Tree Toad, *Hyla versicolor versicolor* (Le Conte)⁷

2. Tail without red	3
3. Tail tip intensely black	4
3. Tail tip not intensely black (fin may be clear or mottled)	5
4. Body flattened, not distinctly spotted with light, nearly circular marks on a greenish or olive background; older individuals tend to float at the surface (Microhyla)	20
4. Body rounded; greenish with light circular spots dorsally; no tendency to float at surface. Northern Cricket Frog, <i>Acris crepitans</i> Baird.	
5. Movement in a pool is almost continuous, when individuals pause to feed, their tail tips continuously move; not shy but easily captured; a generally "mouse like" appearance from shape of head and the eyes set fairly close together; tail tip rounded, tail fin clear; often but not always iridescent ventrally and sometimes dorsally; color very light to very dark. (Scaphiopus).	6
5. Not as above	10
6. Color light (almost white with iridescence) to medium gray or brown (with little iridescence); size at full development large (up to 65 mm. total length).	7
6. Color dark (sometimes nearly black) often with much iridescence; size at full development small (not over 30 mm. usually).	8
7. East central to west central Oklahoma.	

Plains Spadefoot, *Scaphiopus bombifrons* (Cope).

7. Western Oklahoma in short-grass plains or mesquite savannah	44
8. Body of peppered appearance with coppery or bronzy sheens, no light bar at dorsal tail base, southwestern Oklahoma. Southern Spadefoot, <i>Scaphiopus couchii</i> Baird.	
8. Otherwise or elsewhere	9
9. Body dark gray (rarely brown and often with some sheen), a light bar (cream or yellow) at dorsal tail base common especially if development has been in clear water and if sheen be present. Eastern half of Oklahoma in woodland pools usually quite shallow. Savannah Spadefoot, <i>Scaphiopus hurterii</i> Strecker.	
9. Not dark gray or brown, etc., as above	18
10. Tadpoles congregated in shallows but rush madly for deeper water on being approached. (Bufo or Rana)	11
10. Behave differently from above	14
11. Tadpoles not excessively large (25 mm. or less)	12
11. Tadpoles very large (25 to 75 mm.); color dark greenish often with some darker mottling or spotting; most common in deeper pools.	

Bullfrog, *Rana catesbeiana* Shaw.

12. In western Oklahoma north to Harper, east to Jefferson County in south. Particolored tadpoles with light line through eye and another light line along base of tail laterally. Desert Toad, <i>Bufo compactilis</i> Wiegmann.	
12. Elsewhere in state and/or differently colored	13
13. In extreme eastern Oklahoma; small tadpoles coarsely mottled dorsally in browns; in shallow water; weak swimmers; tend to stay close to bottom even when disturbed. Fowler's Toad, <i>Bufo woodhousii fowleri</i> Hinckley.	
13. Otherwise or elsewhere	18
14. Weak swimming; small tadpoles tending to occur in clusters on bottom in shallows; eastern half of Oklahoma only	15
14. Not as above, occurring elsewhere	18
15. In small streams, shallow pools, or shallow edges of larger streams; common in valleys, seldom high on mountains; color coarsely mottled in browns; extreme eastern Oklahoma only; most abundant in southeast.	

Fowler's Toad, *Bufo woodhousii fowleri* Hinckley.

⁷ Tadpoles of the closely related *H. v. chrysoscelis* (Cope) are unknown. This form replaces *H. v. versicolor* in some deep valleys in eastern Oklahoma, at least in McCurtain and LeFlore counties (probably does not occur north of the Arkansas River).

KEYS TO FROGS AND TOADS

15. In small streams, shallow pools, or rarely in shallow edges of larger streams and lakes; rarely in valleys, common on mountains (in eastern Oklahoma); color very dark (black, or nearly so, dorsally), eastern half of Oklahoma mostly in woodland or savannah. American Toad, *Bufo terrestris americanus* Holbrook.
16. Tail tip attenuated (Hylidae) 18
16. Tail tip not attenuated 17
17. Body flattened; eyes on lateral axis; general appearance like a small frying pan. (Microhyla). 20
17. Body rounded, eyes not on lateral axis; not pan-like. (Bufo, Rana, Scaphiopus) . . 30
18. Eyes very wide apart, at or near sides of head (Hyla, Microhyla, Pseudacris) . . 19
18. Eyes not exceptionally wide apart (Acris, Bufo, Rana, Scaphiopus) 29
19. Body depressed; eyes at extreme sides of head; tail often with black tip, rather short; no horny jaws; no labial teeth; general appearance like a tiny frying pan with a short handle. (Microhyla) 20
19. Body not depressed, rounded, not frying pan-like; horny jaws and labial teeth present; tail tip not intensely black. (Hyla, Pseudacris) 21
20. Eyes *just visible* from ventral surface. State-wide except eastern tier of counties
Texas Narrow Mouth Toad, *Microhyla carolinensis olivacea* (Hallowell).
20. Eyes *clearly visible* from ventral surface; extreme eastern Oklahoma only.
Southern Narrow Mouth Toad, *Microhyla carolinensis carolinensis* (Holbrook).
21. Tail fin *heavily* mottled (Hyla) 22
21. Tail fin *not heavily* mottled (Acris, Hyla, Pseudacris) 25
22. Much red in tail fin, often mixed with black when tadpoles are nearing transformation.
Common Tree Toad, *Hyla versicolor versicolor* (Le Conte).
22. Tail fin without red, pigment mostly black. 23
23. Some black pigment concentrated at fin margin. 24
23. No black pigment concentrated at fin margin. 25
24. Marginal concentration of pigment essentially in blotches; eastern Oklahoma only.
Spring Peeper, *Hyla crucifer crucifer* Wied.
24. Marginal concentration of pigment practically a continuous line (often with blotches on other portions of fin); younger tadpoles, not nearing transformation.
Common Tree Toad, *Hyla versicolor versicolor* (Le Conte).
25. Head-body a short broad ovoid, not quite so wide as long; eyes about as near to midline as to sides; dorsal color greenish to greenish brown marked with numerous, clear-cut, nearly circular cream or yellow spots; labial formula 2/2; tail tip commonly intensely black on nearing transformation of tadpoles.
Northern Cricket Frog, *Acris crepitans* Baird.
25. Head-body a longer ovoid, considerably longer than wide; eyes nearer sides than to midline; tail tip never extensively black. 26
26. Dorsal color greenish but not conspicuously spotted; eyes on lateral axis and visible from ventral surface; tail fin clear or with small black dots in smaller individuals and younger stages, the black in older animals tending to form blotches or larger spots; typically a lighter line through eye; extreme southeastern Oklahoma only; rare.
Green Tree Frog, *Hyla cinerea cinerea* (Schneider).
26. Dorsal color variable from gray to nearly black but almost never green; no line through the eye; eye dorsal to lateral axis and either not visible or barely so from ventral surface; labial formula 2/3. (Pseudacris)⁸ 27
27. Lower dorsal row of labial teeth not interrupted in the middle; western two-thirds of Oklahoma, grasslands only. Spotted Chorus Frog, *Pseudacris clarkii* (Baird).
27. Lower dorsal row of labial teeth interrupted in the middle 28
28. Labial papillae confined to the sides.
Texas Ornate Chorus Frog, *Pseudacris streckeri* Wright and Wright.

⁸ *Pseudacris clarkii*, *Ps. streckeri*, and *Ps. triseriata* are difficult to distinguish from each other and the younger tadpoles of *Ps. streckeri*, especially, resemble those of *Hyla v. versicolor*.

28. Labial papillae on ventral as well as sides.
Striped Chorus Frog, *Pseudacris triseriata* (Weid).
29. Labial formula 2/2; dorsal surface with several cream or light yellow nearly circular spots; tail tip attenuated and in larger individuals often intensely black.
Northern Cricket Frog, *Acris crepitans* Baird.
29. Labial formula not 2/2; dorsum without nearly circular cream or yellow spots; tail tip not attenuated and never intensely black. 30
30. Labial papillae confined to sides. (Bufo). 31
30. Labial papillae not confined to sides. (Rana, Scaphiopus). 39
31. Body coloration generally light. Body of at least two colors; a light hard line along tail base in musculature, another (smaller and fainter) through eye.
Desert Toad, *Bufo compactilis* Wiegmann.
31. Body coloration generally dark, mottling, common (though not universal) . . 32
32. Papillae on sides of ventral labium only (or with a very few scattered dorsally); inner papillae usually absent (if present, very few); rocky areas, especially west. Rare.
Canyon Toad, *Bufo punctatus* Baird and Girard.
32. Labial papillae not confined to lateral margin of lower labium; inner papillae usually present 33
33. Inner dorsal row of labial teeth entire, division at midpoint in right and left halves just discernible.
Northern Little Green Toad, *Bufo insidiosus* Girard.⁹
33. A distinct median space between the right and left halves of the inner dorsal row of labial teeth 34
34. Body color black (or very nearly so) dorsally; no mottling or spotting on body; eastern half of Oklahoma in wooded areas mostly.
American Toad, *Bufo terrestris americanus* Holbrook.
34. Body varicolored or mottled, not uniformly black 35
35. Body varicolored; a light line through eye and another on each side of tail base. Western Oklahoma, east in south to Jefferson County.
Desert Toad, *Bufo compactilis* Wiegmann.
35. Body mottled mostly in browns, often some gray or black 36
36. Mottling fine 37
36. Mottling very coarse, consisting of large patches of light and dark browns over total dorsal surface. Young tadpoles only; confined to eastern Oklahoma.
Fowler's Toad, *Bufo woodhousii fowleri* Hinckley.¹⁰
37. Lower row of ventral labial teeth short, extending only to the region of the labial papillae or just beyond this. Wide midspace between left and right sides of the lower dorsal row.
Great Plains Toad, *Bufo cognatus* Say.
37. Lower row of ventral labial teeth extending well beyond inner borders of labial papillae. Space between right and left sides of lower ventral row not very wide . 38
38. Found west of a line from northeastern Ottawa County to Red River in eastern Bryan County (except probably present in Arkansas River Valley).
Rocky Mountain Toad, *Bufo woodhousii woodhousii* Girard.¹⁰
38. Found east of this line. Fowler's Toad, *Bufo woodhousii fowleri* Hinckley.¹⁰
39. Labial formula typically 2/3 (sometimes 1/3). (Rana). 40
39. Labial formula not 1/3 or 2/3. (Scaphiopus) 43
40. "Beak narrowly pigmented with dark, the lower mandible dark for less than half its width; belly densely pigmented, the viscera usually not visible through the skin." (Walker, 1946) 41
- ⁹ The tadpole of *Bufo insidiosus* is uncertainly known. Smith (1934) described from Kansas a bufonid tadpole which he took to be of this species. Since that time the only other unknown bufonid tadpoles likely to be in Kansas have been described (*B. compactilis*, *cognatus*, *w. woodhousii*) and this by elimination makes the identification fairly certain. These tadpoles have never been seen in Oklahoma, but adults are known.
- ¹⁰ The two subspecies of *B. woodhousii* can easily be distinguished when young. Older ones are so alike that separation is difficult or impossible by means of a key. In the zone of intergradation separation will be impossible with this key.

40. "Beak broadly pigmented, the lower mandible dark nearly to its base; belly lightly pigmented, the viscera usually visible through the skin." (Walker, 1946) 42
41. When full grown, the largest North American tadpole, sometimes three inches in length; body color typically greenish (considerable variation); tail pigmented with roundish black spots, more numerous dorsally than ventrally; state-wide.
Bullfrog, *Rana catesbeiana* Shaw.
41. Maximum size much less than three inches; "tail with moderate to large spots as blotches which are not sharply outlined; lower half of tail often as densely pigmented as upper." Eastern half of Oklahoma, rare except extreme east.
Green Frog, *Rana clamitans* Latreille.
42. Tail crest light, clear or with scattered irregular bits of pigment; state-wide, abundant.
Southwestern Leopard Frog, *Rana berlandieri* Baird.
42. Tail crest dark, large blotches of pigment which tend to fuse; southeastern Oklahoma only. Rare.
Pickerel Frog, *Rana palustris* Le Conte.
43. Color iridescent light cream to medium gray or brown, never very dark; size at metamorphosis larger (up to 65 mm.) 44
43. Color very dark gray or dark bronze with coppery or golden sheen; whole appearance dark rather than light; small at metamorphosis (up to 35 mm.) 35
44. Upper jaw with prominent median beak, lower with corresponding deep notch; jaw muscles large and bulging; lips thick; western Oklahoma only.
Western Spadefoot, *Scaphiopus hammondi* Baird.
44. Jaws with no prominent beak and notch; jaw muscles moderate; lips not notably thick.
Plains Spadefoot, *Scaphiopus bombifrons* (Cope).
45. Ground color dorsally dark gray to nearly black, sometimes with slight sheen; often with a small cream or yellow bar at dorsal tail base; Eastern half of Oklahoma and on large flood plains westward an uncertain distance.
Savannah Spadefoot, *Scaphiopus hurterii* Strecker.
45. Ground color coppery or bronze with a marked sheen, or peppered light and dark with little sheen, sometimes with some golden spots; southwestern Oklahoma only, north to Custer County.
Southern Spadefoot, *Scaphiopus couchii* Baird.

III. ADULTS

1. Parotoid glands prominently present behind eyes. (Bufo) 2
1. Parotoid glands absent 8
2. Cranial crests very slightly developed or absent 3
2. Cranial crests present and well developed 5
3. Parotoid glands small and approaching a circular outline; color dorsally brown or greenish; tips of warts commonly red; toes, soles, and palms often salmon or pink; western Oklahoma mostly in rocky areas; rare except in Wichita Mountains.
Canyon Toad, *Bufo punctatus* Baird and Girard.
3. Parotoid glands not approaching circular 4
4. Parotoid glands nearly triangular, broader than long; body size small (maximum total length about 32 mm.); dorsal color typically green mixed with less amounts of black, sometimes brown with some light color; ventral, clear white; body flattened; short-grass plains and mesquite savannahs, western half of Oklahoma; not abundant.
Northern Little Green Toad, *Bufo insidiator* Girard.
4. Parotoid glands not approaching triangular, longer than broad; size of body large (up to 100 mm.); dorsal color gray with a few scattered large darker spots, ventral white; very abundant in short-grass plains and mesquite savannahs of southwest, rare in northwest.
Desert Toad, *Bufo compactilis* Wiegmann.
5. Cranial crests converging anteriorly between eyes to a boss in such a way as to form a distinct V, especially on medium sized individuals (in larger ones the boss is better developed and the apex of the V is open); dorsal color brown, gray or greenish with from four to six large approximately paired, dark spots, characteristically ringed with lighter color; grasslands in western two-thirds of Oklahoma, very abundant.
Great Plains Toad, *Bufo cognatus* Say.

5. Not as above 6
6. Parotoid glands tending toward kidney-shaped, nearer together near middle than at either end; ventral surface spotted or splotted with black; cranial crests converging slightly toward snout; most dorsal spots have only one wart; eastern half of Oklahoma; abundant. American Toad, *Bufo terrestris americanus* Holbrook.
6. Parotoids not kidney-shaped; ventral, white except for pectoral spot or spots and some darkening near insertion of arms in some; cranial crests parallel or nearly so. (*Bufo woodhousii*)¹¹ 7
7. Size smaller (up to 80 mm., usually about 60); usually with little or no yellow in groin; eastern Oklahoma only; abundant.
Fowler's Toad, *Bufo woodhousii fowleri* Hinckley.
7. Size larger (up to 125 mm., usually about 80-85); commonly with yellow in groin; all of Oklahoma except eastern third or less.
Rocky Mountain Toad, *Bufo woodhousii woodhousii* Girard.
8. Toes not webbed. (*Microhyla*). 9
8. Toes webbed (little to fully) 10
9. Venter lightly mottled with dark on light; eastern Oklahoma only.
Southern Narrow Mouth Toad, *Microhyla carolinensis carolinensis* Holbrook.¹²
9. Venter not mottled, its color white or nearly white; all of Oklahoma other than eastern part and possibly Panhandle.
Northern Narrow Mouth Toad, *Microhyla carolinensis olivacea* (Hallowell).¹²
10. Spades (sharp-edged metatarsal tubercles) on hind feet; pupil of eye vertical in light. (*Scaphiopus*) 11
10. No spades on hind feet; pupil circular in light 14
11. Spades elongate or sickle-shaped 12
11. Spades rounded, short; not sickle-shaped 13
12. Dorsal color commonly green, sometimes with darker spottings; pectoral glands present; tympanum distinct; no group of small, dark sharp-pointed tubercles just back of eyes; short-grass plains and mesquite savannahs in southwest, east to Jefferson County in south; abundant. Southern Spadefoot, *Scaphiopus couchii* Baird.
12. Dorsal color dark green to nearly black (sometimes lighter green), often with two curved white bands on back; pectoral glands absent; a group of small, dark, sharp-pointed tubercles just back of eyes; tympanum indistinct, savannahs and flood plain, abundant eastern half of Oklahoma, rarely on flood plains an uncertain distance westward. Savannah Spadefoot, *Scaphiopus hurterii* Strecker.
13. Interorbital osseous boss present; grasslands in western two-thirds of Oklahoma east to Tulsa in north. Plains Spadefoot, *Scaphiopus bombifrons* (Cope).
13. Interorbital osseous boss absent (sometimes a glandular area here appears like a boss); short-grass plains, western Oklahoma.
Western Spadefoot, *Scaphiopus hammondi* Baird.
14. Discs on toes present. (*Hylidae*) 15
14. Discs on toes absent. (*Rana*) 22
15. Discs large enough to be seen easily (*Hyla*) 16
15. Discs too small to be seen easily 19
16. X-like, thin, sharply defined mark on back; size small (up to 33 mm. total length); extreme eastern Oklahoma.
Spring Peeper, *Hyla crucifer crucifer* Wied.
16. No thin, sharply defined, X-like mark on back; size larger (up to 63 mm.) . . 17
17. Color quite variable but most commonly bright green, sometimes with a few spots

¹¹ The subspecies (*woodhousii* and *fowleri*) are difficult to separate. They intergrade in a narrow zone, from Ottawa County to Choctaw County except that both may be present in the Arkansas Valley of Sequoyah County.

¹² Intergradation occurs in Latimer County. Both subspecies are known in Cherokee County. An intergrade has a partly mottled venter. No other character than mottling will separate the two subspecies (Hecht and Matalas, 1946).

- on back; legs extremely long; body slender and flat; a light line normally occurs along jaw, passing backward and downward beyond insertion of arm; skin smooth; size up to 63 mm.; in moist woodlands along streams; known only from McCurtain County. Green Tree Toad, *Hyla cinerea cinerea* (Schneider).
17. Color also variable but most often gray or brown; a large irregular blotch of dark color on back often roughly approaching a ragged, broad X; no light line along jaw; size up to 48 mm.; skin commonly rough. (*Hyla versicolor*) 18
18. "Dorsal surface is smooth; a number of subcircular golden spots in the brown ground on rear of thighs; interspaces (on rear of femur) often reduced to small circular spots." ¹³ Habitat, deep valleys, southeastern Oklahoma.
Smooth Tree Toad, ¹⁴ *Hyla versicolor chrysoscelis* (Cope).
18. "Dorsal surface rough; ¹⁵ 'Brown reticulation on yellow ground of posterior face of the thighs; more fully mottled with yellow and brown even covering the whole inner face of the tibia and the light interspaces more or less angular.'" Habitat, woodlands and savannahs, eastern half of Oklahoma.
Common Tree Toad, *Hyla versicolor versicolor* (Le Conte).
19. Toe discs very small; light and dark alternating on rear of femur; light lines, sometimes interrupted with dark, along jaw; webbing on hind feet extensive but not complete on 4th toe; anal warts present; a large triangular mark back of eyes. Habitat, pond and stream sides except in deep woods. Probably state-wide and very abundant. Northern Cricket Frog, *Acris crepitans* Baird.
19. Toe discs small but not minute; triangular mark behind eyes and light line along jaw often present but seldom on same individual; webbing slight 20
20. Size larger (up to 42 mm.); body short, squat, toad-like; legs short; color gray or brown with few large dark spots dorsally, one of which is triangular and between eyes; a black band through eye; common except in extreme east and west.
Northern Ornate Chorus Frog, *Pseudacris streckeri* Wright and Wright.
20. Size smaller (up to 35 mm., usually about 30-33); body long and slender; legs long. 21
21. Light line along jaw present; back characteristically with three long dark stripes which may be broken into a series of spots; triangular mark behind eye very seldom present; common in eastern one-third, rare in western two-thirds of state.
Striped Chorus Frog, *Pseudacris triseriata* (Wied).
21. No light line along jaw; back characteristically with many spots which may partly or (rarely) wholly run together to form lines; triangular mark behind eyes rarely absent; grasslands in western two-thirds of state, going east to Tulsa and Washington counties in northeast. Spotted Chorus Frog, *Pseudacris clarkii* (Baird).
22. Dorsal color nearly solid green, greenish brown or (rarely) nearly black. Back with no markings or a few small irregular dark markings only 23
22. Dorsal surface definitely spotted. 24
23. Size larger (up to 200 mm.); dorsolateral folds short, bending around the tympanum; toes fully webbed. Habitat, edges of deep water, (juveniles sometimes in ditches); state-wide and abundant. Bullfrog, *Rana catesbeiana* Shaw.
23. Size medium (up to 100 mm., but usually smaller); dorsolateral folds long, extending to groin; toes not quite fully webbed. Marshes and muddy streams and pond sides; eastern half of Oklahoma, common only in east.
Green Frog, *Rana clamitans* Latreille.
24. Spots on back squarish; size smaller (up to 80 mm.). Known in eastern Oklahoma only, rare. Pickerel Frog, *Rana palustris* Le Conte.
24. Spots rounded (not squarish). 25

¹³ From Wright and Wright (1942).

¹⁴ This vernacular name is here proposed for the first time, since when the list of suggestions for such naming was published (Bragg, 1943), this subspecies was not included because then not known from the state.

¹⁵ Sometimes smooth in central Oklahoma.

25. Spots oval, each with a lighter area about it. 26
 25. Spots nearly circular, snout rounded. (*Rana areolata*). 27
 26. Snout pointed, animal *very* agile, state-wide and abundant.
 Southwestern Leopard Frog, *Rana berlandieri* Baird.
 26. Snout rounded, animal not especially agile, western Oklahoma only.
 Short Headed Leopard Frog, *Rana brachycephala* Cope.¹⁶
 27. Dorsal surface smooth; dorsolateral folds narrow and usually not well developed;
 legs fairly short (tibiae 40 mm. or less);¹⁷ crayfish burrows in southeastern Okla-
 homa. Southern Crayfish Frog, *Rana areolata areolata* Baird and Girard.
 27. Dorsal surface often rugose; dorsolateral folds well developed; legs rather long
 (tibiae more than 40 mm.).¹⁷ Crayfish burrows in northeastern Oklahoma.
 Northern Crayfish Frog, *Rana areolata circulosus* Rice and Davis.

Annotated List of Species and Subspecies

1. *Acris crepitans* Baird (Northern Cricket Frog)

Distribution: state-wide. *Habitat*: edges of pools, lakes, and streams except in deep woods, most abundant on mud-flats adjoining shallows, rare where tall vegetation goes to water's edge or where bank is steep. *Breeding*: April to September in waters adjoining habitat. *Call*: a series of rapidly repeated "kick-kick-kick" often slower and drawn out toward end of each series. *Eggs*: single with very sticky jelly attached to vegetation below water surface. *Tadpoles*: greenish, broadly oval, spotted dorsally with cream or very bright yellow, older ones often with intensely black tail-tip, very shy at all ages, tending to hide in algal mats or other cover most of the time; grow to rather large size and except for an attenuated tail-tip superficially resemble frog tadpoles just before metamorphosis. *Descriptions*: eggs not certainly and clearly dealt with as such, some data given by Smith (1934) and Walker (1946); tadpoles, Walker (1946); adults, Smith (1934), Walker (1946).

2. *Bufo terrestris americanus* Holbrook (American Toad)

Distribution: eastern half of Oklahoma, mostly in woodland and savannah. *Habitat*: in southeast tends to occupy the wooded hillsides rather than the valleys; farther west, in both situations. *Breeding*: April to July in shallow grassy pools or shallows of larger bodies of water, also in small streams (spring runs and tiny creeks where current is not swift). *Call*: a prolonged, high sweet-toned trill. *Eggs*: in long strings on bottom distinguished by a straight partition between adjoining eggs. *Tadpoles*: black or nearly so, tending to cluster in shallows or on bottom, weak swimmers. *Descriptions*: eggs, Wright and Wright (1942); tadpoles, Wright (1929, 1942); adult, Wright (1942), Smith (1934), Walker (1946).

3. *Bufo cognatus* Say (Great Plains Toad)

Distribution: western two-thirds of Oklahoma in grassland only. *Habi-*

¹⁶ *R. brachycephala* occurs in western Oklahoma. Its tadpoles are in all probability similar to those of *R. berlandieri* but are not well known.

¹⁷ Largely after Goin and Netting (1940).

tat: higher portions of grassland mostly, common on prairie roads at night. *Breeding*: in temporary shallow pools only, and only immediately after rains at temperatures above 12° C., any time March to September. *Call*: a long raucous rattle or fast high pitched clanking trill, quite distinctive. *Eggs*: in long strings in shallows distinguished by the diameter of the jelly being less between eggs than across eggs and by a circular capsule of jelly enclosing each egg within a continuous gelatinous tube. *Tadpoles*: brown, fair swimmers and shy, tending to hide on disturbance. *Descriptions*: eggs, Bragg (1937); larvae, Bragg (1936), Smith (1946);¹⁸ adults, Bragg (1940), Wright and Wright (1942).

4. *Bufo compactilis* Wiegmann (Desert Toad)

Distribution: about western third of Oklahoma, west of a line including Harper and Jefferson counties; rare in northwest (uncertain in Panhandle) very abundant southwest. *Habitat*: short-grass plains and mesquite savannahs. *Breeding*: after rains only, in almost any standing water, especially if shallow, may appear in deep and muddy cattle tanks. *Eggs*: in strings, their color brown and yellow. *Tadpoles*: light-colored, greenish-gray or brown, spotted with lighter brown and with light streak through eye and another along base of tail, laterally. Movements fast and quick, on disturbance each races along bottom for a few feet and stops quickly on bottom or beneath debris and remains still as though depending upon protective coloration which seems often to be effective. *Descriptions*: eggs, Wright and Wright (1942); larvae, Wright (1929); adults, Wright and Wright (1942).

5. *Bufo insidiosus* Girard (Northern Little Green Toad)

Distribution: western third of Oklahoma east to Murray-Carter County line and western Garvin County in south; not abundant. *Habitat*: short-grass plains, mesquite savannahs, and gypsum-hill regions. *Breeding*: imperfectly known but they have been found calling in shallow pools and ditches with *Bufo compactilis*, *B. cognatus*, *B. woodhousii woodhousii*, *Scaphiopus couchii*, and several of the smaller forms (*Pseudacris*, *Microhyla*). *Eggs*: unknown. *Tadpoles*: not described with certainty but probably the description of the larvae of *Bufo debilis* by Smith (1934) applies, since adults were differentiated from those of *Bufo debilis* by Taylor (1936), and Smith in Kansas must have been studying *Bufo insidiosus* as now known.

6. *Bufo punctatus* Baird and Girard (Canyon Toad)

Distribution: questionable, known from few specimens in western and southern Oklahoma and one record from the mountains of northern McCurtain County (Trowbridge, 1937). Rare except in the rougher portion of the Wichita Mountains of Comanche County. *Habitat*: almost all adults taken have been in rough, rocky areas. *Breeding*: in rocky pools of the habitat and probably in cattle tanks (young have been seen on shores of such in the west). *Eggs*: single or in very short strings, colored black and white, Wright

¹⁸ Smith's figure of the mouth parts is excellent.

(1929), Wright and Wright (1942), Bragg and Smith (1943), Strecker (1926). *Descriptions*: eggs, Wright and Wright (1929); larvae, Wright (1929); adults, Wright and Wright (1924), Smith (1934).

7. *Bufo woodhousii fowleri* Hinckley (Fowler's Toad)

Distribution: eastern Oklahoma only, west to Atoka County in the south, questionably in Ottawa County in north, almost certainly not west of this. *Habitat*: wooded areas, particularly in valleys and low areas generally. *Breeding*: from late spring (late April, May) to July in shallow pools, creeks, edges of larger streams and lakes. *Eggs*: up to 8,000 in a string, black and white with no visible partitions between adjacent eggs. *Tadpoles*: often coarsely mottled in browns when young, finely mottled later; tend to remain on bottom and to cluster in shallows when young; active, and hide in vegetation on disturbance when older. *Descriptions*: eggs and larvae, Wright and Wright (1942); adults, Walker (1946).

8. *Bufo woodhousii woodhousii* Girard (Rocky Mountain Toad)

Distribution: all of Oklahoma where Fowler's Toad (*q.v.*) does not occur. Very abundant in central and western Oklahoma, unknown in southeast where Fowler's Toad replaces it. *Habitat*: unrestricted but most abundant in valleys and on flood plains; also seems partial to areas of sandy soils. *Breeding*: from March to at least mid-August in almost any water available in local situations, typically in shallow pools but occasionally in metal cattle tanks fed by windmills, in concrete pools in gardens, and in shallow flowing streams. *Eggs*: in long strings often doubly or triply arranged, color black and white with no partition between adjacent eggs; in numbers up to 2,500. *Tadpoles*: mottled finely in browns and very active, very much like those of Fowler's Toad at later stages. *Descriptions*: eggs, Smith (1934); larvae, Youngstrom and Smith (1936), Johnson (1939); adults, Smith (1934), Wright and Wright (1943).

9. *Hyla cinerea cinerea* Schneider (Green Tree Toad), and

10. *Hyla crucifer crucifer* Wied (Spring Peeper)

Distribution: the former known only from McCurtain County, the latter from eastern Oklahoma generally. *Habitat*: trees along streams. *Breeding*: observed in Oklahoma only a few times. (See Wright and Wright, 1942, for general accounts.)

11. *Hyla versicolor chrysoscelis* (Cope) (Smooth Tree Toad)¹⁹

Distribution and habitat: only recently reported from two valleys in Oklahoma: (1) along Little River north of Idabel, McCurtain County, and (2) in valley north of Rich Mountain, LeFlore County. Its eggs are unknown. Its tadpoles indistinguishable with certainty from *H. v. versicolor* (may not have red in tail). Its breeding behavior in both valleys was observed to be much like that of its close relative *H. v. versicolor*. *Description*: adults, Wright and Wright (1942).

¹⁹ Vernacular name here proposed for the first time.

12. *Hyla versicolor versicolor* (Le Conte) (Common Tree Toad)

Distribution: eastern half of Oklahoma. *Habitat*: trees of both woodland and savannahs. Abundant. *Breeding*: from April to August (concentrated in May) in pools and creek-overflows of its habitat. *Eggs*: brown and cream, produced at surface, attached lightly to vegetation or, rarely floating freely. *Tadpoles*: young tadpoles easily confused with those of *Pseudacris streckeri* and *Ps. triseriata* and, morphologically, with those of *Ps. clarkii* but they are not likely to be found with the last mentioned (a grassland rather than a woodland form). Older tadpoles are absolutely distinguished from all others known in Oklahoma by the red or red and black mottled tail fin. Shy and fast at all ages and older ones have a tendency to float near surface. *Descriptions*: eggs, Wright and Wright (1942); tadpoles, Wright (1929); adults, Wright and Wright (1942), Walker (1946).

13. *Microhyla carolinensis carolinensis* (Holbrook) (Southern Narrow Mouth Toad)²⁰

Distribution: eastern Oklahoma only. Known at present from Delaware, eastern Cherokee, Adair, central Latimer, LeFlore and McCurtain counties. *Habitat*: imperfectly known, so far observed only in grassy valleys and in edges of woodlands along streams. *Breeding*: in grassy pools of shallow water after rains in late spring and summer. Breeding adults are shy, the most difficult to catch by hand of any Oklahoma form. *Eggs*: small, black and white, floating singly or in small groups on the surface. *Tadpoles*: flat, quick moving. *Descriptions*: eggs and adults, Wright and Wright (1942); tadpoles, Wright (1929).²¹

14. *Microhyla carolinensis olivacea* (Hallowell) (Northern Narrow Mouth Toad)

Distribution: probably state-wide except as replaced in eastern Oklahoma by *M. c. carolinensis* (*q.v.*). Intergrades with latter at least in Latimer County (Hecht and Matalas, 1946) and both species occur in Cherokee County (Bragg, 1947). Unknown and uncertain in the Panhandle. *Habitat*: abundant in all ecological zones except lower levels of large flood plains, at least in central Oklahoma. *Breeding*: from about May 1 throughout summer in temporary pools after rains of some extent (0.5 in. upward) but only at relatively high temperatures. *Eggs and tadpoles*: similar to the Southern Narrow Mouth Toad (*q.v.*). *Descriptions*: eggs and adults, Wright and Wright (1942); tadpoles, Wright (1929).²⁰

15. *Pseudacris clarkii* (Baird) (Spotted Chorus Frog)

Distribution: approximately western two-thirds of Oklahoma, but east

²⁰ The older names, *Gastrophryne carolinensis* and *G. texensis* ($\equiv$ *olivacea*), are used by some, including the author of the paper cited.

²¹ Many vernacular names are current for this animal. Inasmuch as *Narrow Mouth Toads* is frequently used for the family Microhylidae of which at least three members of the genus *Microhyla* and one of *Hypopachus* occur in the United States and adjacent northern Mexico, the above is proposed exclusively for this subspecies, specifically to distinguish it from its northern relative, *M. c. olivacea* which also occurs in Oklahoma.

to Washington County in north. *Habitat*: grasslands and very open savannahs, never in true woodlands and seldom in lower areas of large flood plains. *Breeding*: in shallow grassy pools, March to August, only after rain; not inhibited by near freezing temperatures. *Eggs*: in small masses attached just below surface on upright vegetation, usually notably variable in size. *Tadpoles*: a few days after hatching almost square in appearance with eyes seemingly on stalks (an illusion due to a very transparent skin). Older tadpoles are not easily distinguished from *Ps. triseriata* and *Ps. streckeri*. The former has a mottled tail, something not true of either *Ps. clarkii* or *Ps. streckeri*. *Ps. clarkii* has greater tendency to float at surface, whereas *Ps. streckeri* tends to work up plant stems and is more shy. *Descriptions*: eggs and larvae, Bragg (1943); adults, Smith (1934), Wright and Wright (1942).

16. *Pseudacris streckeri* Wright and Wright (Texas Ornate Chorus Frog)

Distribution: known in a broad diagonal band bounded by a line from Kay to Greer counties in the west and from Cherokee to Marshall counties in the east. Unknown elsewhere in the state, but may occur. *Habitat*: ecologically unrestricted where known. *Breeding*: late winter and early spring (observed from January 1 to early May); greatly favored by early rains, but not affected by rains in late spring and summer. Breeding sites include all sorts of temporary pools of shallow water as well as small tanks up to four feet in depth. *Eggs*: gray or brown and cream or white attached to twigs or other support, sometimes six inches or more beneath the surface, more often not more than two inches beneath it. *Tadpoles*: very shy at all ages, tending to hide in algal mats or other cover. Older tadpoles in warm pools tend to float lazily at the surface and to feed while working up plant stems. At the least disturbance, even by a shadow cast upon them, they flit downward to hide. *Descriptions*: eggs and larvae, Bragg (1942); adult, Wright and Wright (1933 the original description which is repeated in the second edition of the same work, 1942).

17. *Pseudacris triseriata* (Wied) (Striped Chorus Frog)

Distribution: probably state-wide but known only in eastern half of state. *Habitat*: very abundant in woodlands, common in tall grass prairie, rare in mixed prairie. Present in short-grass plains in Texas Panhandle and New Mexico, hence probably in similar ecological regions of Oklahoma, but if so it is rare for it is usually displaced by *Ps. clarkii* from central Oklahoma westward in grassland. *Breeding*: very versatile in breeding sites, typically shallow, temporary pools in which vegetation protrudes, but edges of deep tanks, lakes, rivers, and creeks as well as playas (in Texas) are also utilized. Recently in eastern Oklahoma, I found its eggs in a shallow, very clear, fast-flowing stream with a coarse gravel bottom. Breeding tends to follow rains from February to August, but some individuals breed in low swampy lands in early spring when no rain has occurred for weeks. *Eggs*: brown and white or cream (occasionally darker, according to Wright and Wright, 1942); masses attached to vegetation sometimes in small packets, often in larger

groups. Difficult to distinguish from eggs of *Ps. clarkii* but they differ typically as follows: (1) darker at animal pole, (2) little or no size variations of eggs as seen with the naked eye, (3) egg mass typically larger (exceptions), attached commonly to standing twigs or other support (also exceptions), (4) often in tall grass and woodland and rare elsewhere. Opposite tendencies are present in *Ps. clarkii* except in northeastern tall grass prairie (Osage County eastward) where both species occur fairly commonly and often breed in same pools. *Tadpoles*: shy and variable in color. Many have heavily mottled tails which is true of no other species of *Pseudacris* in Oklahoma. Young tadpoles appear squarish, and tend to swim near the surface (differing from all other Hylidae of Oklahoma). Older ones seldom float at surface like those of other *Pseudacris*, some *Hyla*, and *Microhyla*. *Descriptions*: eggs, Smith (1934), Wright and Wright (1942), Walker (1946); larvae, Youngstrom and Smith (1936), Bragg (1934); adults, Walker (1943), Wright and Wright (1942).

18. *Rana areolata areolata* Baird and Girard (Southern Crayfish Frog)

Distribution: southeastern Oklahoma, central Pontotoc County eastward and south eastward. *Habitat*: lower areas in and about crayfish burrows and in valleys in mountains. Adults shy, seldom seen except during breeding. *Breeding*: in waters adjacent to the habitat in early to mid-spring only (February to mid-May observed). *Eggs*: are little understood and tadpoles little known but are now being studied. *Descriptions*: adults, Wright and Wright (1942), Goin and Netting (1940).

19. *Rana areolata circulosus* Rice and Davis (Northern Crayfish Frog)

Distribution: northeastern Oklahoma, west to Osage and Tulsa counties. *Habitat*: lower areas in and about crayfish burrows. *Breeding*: March and April observed, typically in flooded areas of the habitat. *Eggs*: in large masses, tadpole just described. *Descriptions*: eggs, Smith (1934); adult, Smith (1934), Goin and Netting (1940).

20. *Rana catesbeiana* Shaw (Bullfrog)

Distribution: probably state-wide. *Habitat*: abundant about and in lakes, large quiet rivers, pools in creeks, cattle tanks and, in general, in and about deep, still water; sometimes young juveniles are found about ditches. *Breeding*: in deeper pools of permanent water. *Eggs*: produced as large rafts on surface. *Tadpoles*: greenish with some dark mottling; grow to a very large size before metamorphosis (more than three inches). *Descriptions*: eggs, adults, and larvae, Wright and Wright (1942).

21. *Rana clamitans* Latreille (Green Frog)

Distribution: eastern half of Oklahoma, rare except in extreme east. *Habitat*: muddy and marshy banks of streams and ponds. *Breeding*: has not been observed in Oklahoma. *Descriptions*: eggs, adults, and larvae, Wright and Wright (1942).

22. *Rana palustris* Le Conte (Pickerel Frog)

Distribution: recorded in Oklahoma only from McCurtain County. *Habitat:* has been seen in Oklahoma only in valleys of streams (as along Little River near Idabel and its tributary, Mountain Fork River). *Breeding:* unknown in Oklahoma. *Descriptions:* eggs, adults, and larvae, Wright and Wright (1942).

23. *Rana berlandieri* Baird²² (Southwestern Leopard Frog)

Distribution: state-wide. *Habitat:* about water courses, lakes, pools, and ditches, ranging widely from these in moist weather to feed. Very abundant. *Breeding:* February to September (perhaps later) most abundantly after rains typically in shallow water. *Eggs:* attached in an ovoid mass of jelly to vegetation just below water surface. *Tadpoles:* active, variable in color in different waters, but typically grayish to greenish. These larvae are active and like to feed in the shallows but many seek deeper water to avoid excessive heat. *Descriptions:* eggs, Wright and Wright (1942); larvae, Wright (1942); adults, Wright and Wright (1942).

24. *Scaphiopus bombifrons* (Cope) (Plains Spadefoot)

Distribution: western two-thirds of Oklahoma, rare east of Payne and Cleveland counties, very abundant to westward. *Habitat:* grassland only. *Breeding:* any time from March to September, but only after rains of 0.5 in. or more, and if temperature is not below 9° C. Violent rains induce breeding activity quickly. *Eggs:* attached below surface, typically in deeper temporary pools. *Tadpoles:* large, typically gray to brown but in some muddy tanks in western Oklahoma may be nearly white. Superficially like *S. hammondi* but difference in mouth parts distinguishes them easily, especially in the larger individuals, which are recognizable even in the field (for specific difference see No. 44 in the tadpole key). *Descriptions:* eggs, Wright and Wright (1942); tadpoles, Wright (1929) (under the name of *S. hammondi*, see Bragg, 1941); adults, Smith (1934).

25. *Scaphiopus couchii* Baird (Southern Spadefoot)

Distribution: southwestern Oklahoma, north to Custer County, east to western Carter County. *Habitat:* short-grass prairie and mesquite savannah. Abundant. *Breeding:* after rains only, in shallow temporary pools from at least late April to August. *Eggs:* black and white in irregular masses attached to vegetation. *Tadpoles:* small, dark colored and often very iridescent in golden and bronze, very distinctive as they approach metamorphosis. *Descriptions:* eggs, Strecker (1908), adults, Wright and Wright (1942); tadpoles, Wright (1929).

²² At least two kinds of leopard frogs occur in Oklahoma (Bragg, 1949), *R. berlandieri* and *R. brachycephala* Cope. The latter occurs only in the west, its range overlapping that of *R. berlandieri* in the Panhandle and in approximately the western tier of counties. Two specimens are known from western Major County, and a few from the Wichita Mountain area of Comanche County also. The common name for *R. berlandieri* is here proposed for the first time.

26. *Scaphiopus hammondi* Baird (Western Spadefoot)

Distribution: western Oklahoma east to Woods and western Greer counties. *Habitat*: short-grass plains and gypsum hill country only. *Breeding*: pattern like *S. bombifrons* (q.v.) *Descriptions*: eggs, Wright and Wright (1942); tadpoles, Smith (1934) under the name *S. hammondi* (see Bragg, 1941); adults, Smith (1934), Tanner (1939).

27. *Scaphiopus hurterii* Strecker (Savannah Spadefoot)

Distribution: eastern half of Oklahoma including eastern Logan and Cleveland counties and perhaps west of this on flood plains. *Habitat*: woodland and savannah only; abundant but rarely seen. *Breeding*: conditions of breeding somewhat obscure. Have been observed to breed only during periods of heavy rainfall, April, May, and September, but not uniformly. *Eggs*: black and white attached in irregular masses or strings to vegetation near shore or near surface in shallow temporary pools. *Tadpoles*: small, dark gray or brown, often with small cream or yellow bar at tail base, and with clear tail fin. Easily confused superficially with *Bufo terrestris americanus* because of small size and dark color. *Descriptions*: eggs and tadpoles, Bragg (1944); adults, Strecker (1910), Smith (1937), Tanner (1939).

Glossary²³

- Attenuated. Thin toward end, or brought to a sharp point (said of tail-tips of certain tadpoles.)
- Beak. (1) A median extension of the horny upper jaw of a tadpole, or (2) sometimes the whole upper jaw as distinguished from the lower.
- Boss. (1) A protuberance usually caused by an underlying outgrowth of bone, or (2) the bony outgrowth alone.
- Cranial Crests. Ridges on the head between the eyes of some species of toads (*Bufo*).
- Depressed. Flattened dorso-ventrally.
- Egg Envelope. A layer of clear gelatinous material about an amphibian egg which serves a protective function.
- Entire. Not interrupted by a space in the middle (said of labial teeth rows of tadpoles).
- Head-body. Tadpole exclusive of its tail.
- Iridescence. Coloring which gives a sheen at different angles. Common on the ventral surface of tadpoles and on some types it occurs dorsally.
- Labial. Referring to a lip.
- Labial Formula. A fraction whose numerator is the number of rows (whether or not any is interrupted in the middle) of labial teeth on the

²³ All definitions given here apply specifically to this key, and are not intended for all other possible uses, since some terms in the key are employed in special senses.

- upper labium, and whose denominator is the number of rows on the lower labium of tadpoles.
- Labial Papillae. Small protuberances on the labia of tadpoles, the arrangements of which are used as criteria in distinguishing species.
- Labial Teeth. Small horny tubercles on the lips of tadpoles, not homologous to "true" teeth of the jaws of vertebrates.
- Labium. Lip.
- Lateral. Referring to the side (right or left).
- Mandible. Lower horny jaw of a tadpole (or, as used in one quotation in the key, either jaw).
- Mesquite Savannah. Ecological community characterized by mesquite trees growing far enough apart for short grasses to form a sod among them. Common in southwestern Oklahoma.
- Parotoid Gland. A wart-like, integumentary gland on toads (*Bufo*), rarely on members of other genera, situated just posterior to the eyes on the dorsal surface.
- Particolored. With two prominent colors in the coloration. Smaller amounts of other colors (spots, streaks, etc.) may also occur.
- Savannah. Ecological community in which trees are widely enough spaced so that grasses can form a sod among them.
- Short-grass Plain. Ecological community in which the dominant vegetation under natural conditions is buffalo grass or other grasses of short stature. Typical of the Panhandle and some other regions of the west.
- Tail. Portion of body posterior to the anal or cloacal opening.
- Tail Crest. Dorsal portion of the tail fin.
- Tail Fin. The thin portion of the tail of a tadpole extending dorsally, posteriorly, and ventrally from the thicker, muscular portion along the median axis.
- Venter. The ventral (belly) surface.
- Viscera. Organs in the abdominal and thoracic cavities considered as a unit.
- Wart. A skin gland of a toad situated dorsally or laterally and markedly smaller than the parotoid gland.
- Web. A thin membrane extending between adjacent toes of amphibians.
- Woodland. Ecological community in which trees are so closely spaced that grasses cannot form a sod among them.

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II

A Key to the Adult Salamanders of Oklahoma, Including the Forms Likely to Occur in the State

HAROLD A. DUNDEE AND ARTHUR N. BRAGG

THE following key includes only the adults of salamanders known in Oklahoma or likely to be found within the state. The information on the eggs and larvae, at the present time, is insufficient to make feasible the construction of a key for immature forms. Ranges given apply to Oklahoma only. Many species, of course, occur in other states.

We acknowledge our considerable indebtedness to S. C. Bishop's manual, *Handbook of Salamanders*, with which we believe our work consistent, and to which reference should be made on problems involving the salamanders of the United States.

Key to the Families

1. Body elongated and eel-like; limbs very short 2
1. Body flattened and shorter, not eel-like; limbs longer and suitable for walking 3
2. Large external gills at base of head; hind limbs absent. SIRENIDAE.
Only the one species in the state, the siren or mud-eel.
Siren intermedia nettingi Goin.
2. A single pair of gill slits in the adult (larvae may have small gills); both anterior and posterior limbs present. AMPHIUMIDAE.
Only the one species, the congo "eel." *Amphiuma means tridactylum* Cuvier.
3. Adults with external gills or gill slits; always living in water. 4
3. Adults without gills or gill slits; found on land but may enter water. 7
4. External gills present in the adults. 5
4. External gills absent in adults but present in larvae. Adults with a single pair of gill-slits; a wrinkled fold of flesh along either side. CRYPTOBRANCHIDAE.
Only the one species, the hellbender. *Cryptobranchus alleganiensis* (Daudin).
Not known definitely from the state but it has been taken in the Neosho River just north of the Oklahoma line.
5. Five toes on hind feet; length usually less than 9 inches. 6
5. Four toes on hind feet; length often exceeding 9 inches. PROTEIDAE.
Only the one species, the mudpuppy or water dog.
Necturus m. maculosus (Rafinesque).
6. Length usually over 6 inches; body stout; dorsal fin continued on body to base of head; gills very large in comparison to head; costal grooves fewer than 14. AMBYSTOMIDAE.
Only one member of this family in Oklahoma conforms to this neotenic condition, the tiger salamander in the western half of the state.
Ambystoma tigrinum mavortium Baird.
6. Length under 5 inches; body slender; dorsal fin restricted to tail; gills small; costal grooves 16 or more. PLETHODONTIDAE.
7. No groove from lip to nostril; no parasphenoid teeth. 8

7. A groove from lip to nostril; both vomerine and parasphenoid teeth present. PLETHODONTIDAE.
8. Costal grooves indistinct (may appear visible in preserved specimens); vomeropalatine teeth in more or less longitudinal rows; a black bar in the eye; skin tuberculate. SALAMANDRIDAE.
Only the one species, the Louisiana newt. *Triturus viridescens louisianensis* (Wolterstorff).
8. Costal grooves prominent, although occasionally indistinct; vomerine teeth transverse; no bar through eye; skin smooth. AMBYSTOMIDAE.

Keys to the Genera of the Various Families

The following families contain but one genus and one form in Oklahoma. They are recognized by means of the family key alone: for the family PROTEIDAE, there is only the genus *Necturus*; for AMPHIUMIDAE, there is only the genus *Amphiuma*; SIRENIDAE, only the genus *Siren*; and SALAMANDRIDAE, only the genus *Triturus*.

The family AMBYSTOMIDAE contains only the genus *Ambystoma*, a key to which is found in the keys for the species of the various genera.

The family PLETHODONTIDAE, therefore, is the only one which requires a key for its genera.

Key to Genera of PLETHODONTIDAE

1. Toes four front and five back.	2
1. Toes four-four.	Genus <i>Manculus</i> .
Only one representative, the dwarf salamander.	M. quadridigitatus. ¹
Not definitely found in Oklahoma but likely along the eastern border in LeFlore and McCurtain counties.	
2. Tongue free at sides and behind only; external gills present in aquatic forms and absent in terrestrial genera.	3
2. Tongue with a central pedicle, free all around.	Genus <i>Eurycea</i> .
3. Without external gills in adults.	5
3. With external gills in adults.	4
4. Costal grooves never over 19 and usually 18; intercostal folds 6 or 7, usually 6; body chunkier and head more blunt; cleared and stained specimens show 20 rib-bearing vertebrae between the axis and sacrum inclusive; pterygoid teeth usually in patches.	Genus <i>Typhlotriton</i> .
4. Costal grooves 18 or more, usually 19-22; intercostal folds 7 or more, usually 8 or over; more slender and head less blunt; cleared and stained specimens show 21 or more rib-bearing vertebrae from axis to sacrum inclusive; pterygoid teeth in single row, or at most in two rows (neotenic species).	Eurycea.
5. Unpigmented and with reduced eyes; legs long and slender.	Typhlotriton.
5. Normally pigmented and with normal eyes; legs shorter; occasionally entering caves but never becoming light colored or unpigmented.	6
6. Without gills but usually found in water or at the edge of water; body short and stout; tail trigonal in section; a light bar from posterior corner of eye to angle of jaw.	Desmognathus.
Only in Ouachita Mountains, or just south of them. The only species is Brimley's Dusky Salamander.	D. fuscus brimleyorum (Stejneger).
6. Without gills, often found far from water in damp areas; tail round in section; no light bar from corner of eye to angle of jaw.	Plethodon.

¹ According to Mittleman (Herpetologica, 3:209-224, 1947) the form likely to occur here would be *M. q. uvidus*.

Keys to Species of the Various Genera

Only four genera have more than one species, so keys are given for *Ambystoma*, *Plethodon*, *Eurycea*, and *Typhlotriton*.

Genus *AMBYSTOMA*

1. Tongue without a median groove, the plicae radiating from the posterior part to the margins, or plicae narrow, nearly parallel and extending to anterior margin of tongue; costal grooves 13 or less but occasionally 14. 2
1. Tongue with median groove from which the plicae extend obliquely outward; costal grooves 14 or 15; the Texas salamander. *Ambystoma texanum* (Matthes).
2. With silvery gray cross bands on back; costal grooves usually 11; the marbled salamander. *Ambystoma opacum* (Gravenhorst).
2. Without silvery gray cross bands; bands, if present, black and yellow. 3
3. Ground color dark without vertical bars but usually with rounded spots of yellow or orange color; costal grooves 12 or less, rarely 13; eastern Oklahoma only. 4
3. Ground color dark with vertical yellow bars on sides and back; costal grooves usually 13 but occasionally 12 or 14; western Oklahoma; the western or Great Plains tiger salamander. *Ambystoma tigrinum mavortium* Baird.
4. Costal grooves 11 or more; yellow or orange markings on back. 5
4. Costal grooves 10; dorsal markings light lichen-like clusters; the mole salamander. *Ambystoma talpoideum* (Holbrook).
5. Dorsal spots in a dorso-lateral position and small and rounded in outline; the spotted salamander. *Ambystoma maculatum* (Shaw).
5. Dorsal spotting on sides and back; belly spotted; outlines of spots more elongate; abundant spotting; the eastern tiger salamander. *Ambystoma t. tigrinum* (Green).

Genus *PLETHODON*

1. With a median, dorsal band having definite edges; costals 15-20; often with red or chestnut-brown dorsally. 2
1. No median dorsal band; never any red on dorsum; costals not over 16; the slimy salamander. *Plethodon g. glutinosus* (Green).
2. Costal grooves 17 or more, usually 18 or 19; rarely over 4 inches. 3
2. Costal grooves 15 to 17, usually 16; large size, up to 7 inches 4
3. Dorsal band not too well demarcated; edges of dorsal band straight; in Ozark area (northeastern Oklahoma); Ozark red-backed salamander. *Plethodon cinereus angusticlavius* Grobman.
3. Dorsal band usually very distinct and serrate; in Ouachita area (southeastern Oklahoma); Ouachita red-backed salamander. *Plethodon cinereus serratus* Grobman.
4. In life, a very dark blue or black above with many small whitish specks on dorsum. The whitish flecks concentrated on the sides to form a band but this band without well marked edges; often over 5 inches; in both Ouachita and Ozark regions; the slimy salamander. *Plethodon g. glutinosus* (Green).
4. In life with chestnut-brown color above and golden splotches on back; bands on side and back well marked; rarely over 5 inches. In preservation the brown fades and this form may look like *P. g. glutinosus* but with experience one can note the distinctive lateral bands; found only on Rich Mountain in LeFlore County, and one in southeastern McCurtain County; the Ouachita salamander. *Plethodon ouachitae* Dunn and Heinze.

Genus *EURYCEA*

1. Costal grooves 17 or less; no gills. 2
1. Costal grooves 19-22; often neotenic, with external gills. 3
2. Venter immaculate; ground color of back yellow to orange or reddish-orange; spots not concentrated into a dorso-lateral dark line. Found only in northeastern Oklahoma; cave salamander. *Eurycea lucifuga* Rafinesque.
2. Venter more or less spotted or mottled; ground color mainly yellow; dark spots

KEY TO ADULT SALAMANDERS

concentrated to form a dorso lateral line on either side; found in northeast and southeast Oklahoma; Cope's cave salamander.

Eurycea longicauda melanopleura (Cope).

3. Terrestrial; no gills. 4

3. Aquatic and neotenic having external gills 5

4. Vomerine teeth 6-10 on either side but usually 7; venter immaculate; tail longer than body; found both north and south of Arkansas River; many-ribbed salamander.

Eurycea multiplicata (Cope).

4. Vomerine teeth 9-11 at type locality in Sequoyah County, but farther north as low as 4-5 on either side; venter usually with many small melanophores sprinkled over the surface; only north of Arkansas River; the gray-bellied salamander.

Eurycea griscogaster Moore and Hughes.

5. Dorsal pattern consisting of many pigment spots scattered diffusely over surface so as to give a peppered appearance but occasionally forming larger mottles; cleared and stained specimens have 21 rib-bearing vertebrae from axis to sacrum inclusive (neotenic specimens); the many-ribbed salamander.

Eurycea multiplicata (Cope).

5. Dorsal pattern more approximating a net-like appearance but occasionally most spotting fused so as to obscure ground color; 22 rib-bearing vertebrae; Oklahoma neotenic salamander.

Eurycea tynerensis Moore and Hughes.

Genus *TYPHLOTRITON*

The two species here mentioned are quite different as adults. The larvae of *T. spelaeus* resemble both the larvae and adults of *T. nereus* and often occur with them in a single habitat.²

1. Gills absent; color very light (cream approaching white); legs thin and weak; known only from caves; the Ozark cave salamander. *T. spelaeus* Steineger.

1. Gills present, color dark, usually in the open in small streams. 2

2. Costal grooves 16 or 17, including one each in the axilla and groin; intercostal folds 2-4; premaxillary teeth 17 or more, usually 20. *T. spelaeus* (larvae).

2. Costal grooves 18 or 19, including one each in axilla and groin; intercostal folds 6 or 7, rarely 5; premaxillary teeth 11-20 but usually 14 or 17; the Ozark neotenic salamander. *T. nereus* Bishop.

² These species may be distinguished by clearing and staining. *T. spelaeus* has 19 ribs bearing vertebrae from axis to sacrum inclusive. *T. nereus* has 20.

TABLE I

Breeding records by half months, Jan.-Sept., for several Salientia (1.1 = Jan. 1-15 inc., 1.2 = Jan. 16-31 inc., etc., for other months). All records from Oklahoma except a few just over state lines in adjacent states. The years are disregarded but all records are from 1935 to 1948 inclusive.

Half Months	1.1	1.2	2.1	2.2	3.1	3.2	4.1	4.2	5.1	5.2	6.1	6.2	7.1	7.2	8.1	8.2	9.1	9.2
<i>Acris crepitans</i> Baird					1	1	14	34	21	32	22	10	3	3	3	1		
<i>Bufo t. americanus</i> Holb.				2	7	16	28	16	16	7	2			2	1			
<i>Bufo cognatus</i> Say				1	6	10	80	25	19	15	4	4	2	1	1			
<i>Bufo compactilis</i> Wieg.								3	1	2		1		6				
<i>B. w. fowleri</i> Hinck.									4	10	2							
<i>B. w. woodhousi</i> B&G					12	22	47	21	17	12	4	5	1	5	1			
<i>H. v. versicolor</i> LeC.				1	7	23	12	23	12	3	1	1						
<i>M. c. carolinensis</i> Holb.									5	5	1	1						
<i>M. c. olivacea</i> Hallow.							1	6	14	21	15	18	3	2	3	4	3	
<i>Ps. clarkii</i> Baird				1	4	38	39	15	23	14	7	6			2	1	1	
<i>Ps. streckeri</i> W&W	1		7	9	21	21	48	40	14	3								
<i>Ps. triseriata</i> (Weid)				4	8	9	21	9	7	15	14	3						
<i>R. berlandieri</i> Baird			2	10	17	21	30	39	17	10	13	3			2	2	1	1
<i>R. catesbeiana</i> Shaw								2	3	1	5	1	1	1				
<i>S. bombifrons</i> C.					6	20	23	25	16	14	3	3	1					
<i>S. couchii</i> Baird								3	1		1		3		4			
<i>S. huerfii</i> Strecker					1	1	8	2	3	2							2	
TOTAL	1	0	9	24	50	89	228	384	193	209	163	61	31	11	28	9	9	1

III

Salientian Breeding Dates in Oklahoma

ARTHUR N. BRAGG

DURING approximately thirteen years, records of the breeding activity among the Salientia each year about Norman, Cleveland County, have been kept and other data of the same sort from other regions of the state have been recorded at every opportunity. These have now accumulated to such an extent for several species that an analysis can be made of the range in the breeding periods characteristically used, and these can be related to the breeding patterns as outlined earlier (Bragg, 1944-45, 1946).

Of the twenty-eight forms known in Oklahoma, seventeen have been observed more than ten times. These are recorded in Table I. In the construction of this table the numbers of breeding congresses observed are given by half months, January through September. No records occur during October through December. In handling the dates, days 1-15 were considered the first half month, 16-30 or 31, the second half month. Years were disregarded as of no consequence to the purpose of the table. Table II gives the observed seasonal range for these same species. All are records of clear-cut breeding congresses in Oklahoma except a very few observed just over state lines in ad-

TABLE II

Seasonal breeding range for 17 forms recorded more than ten times. Years of observation of the extremes are indicated in parenthesis.

Species	Total	Earliest Date	Latest Date
<i>Acris crepitans</i> Baird	144	3/12 (1935)	8/17 (1939)
<i>Bufo t. americanus</i> Holb.	97	3/10 (1945)	8/26 (1946)
<i>Bufo cognatus</i> Say	143	3/28 (1935)	8/9 (1939)
<i>Bufo compactilis</i> Wieg.	13	4/16 (1940)	8/9 (1939)
<i>B. woodhousii fowleri</i> Hinck.	16	5/16 (1946)	6/10 (1948)
<i>B. w. woodhousii</i> B & G.	147	3/21 (1945)	9/4 (1940)
<i>H. versicolor versicolor</i> LeC.	83	3/16 (1945)	7/23 (1947)
<i>Microhyla c. carolinensis</i> Holb.	12	5/16 (1946)	7/14 (1947)
<i>M. c. olivacea</i> Hallow.	90	4/14 (1940)	9/4 (1940)
<i>Pseudacris clarkii</i> Baird	151	3/28 (1948)	9/14 (1940)
<i>Ps. streckeri</i> Wright & Wright	164	1/1 (1941)	5/21 (1940)
<i>Ps. triseriata</i> (Wied)	90	2/2 (1944)	6/23 (1938)
<i>R. berlandieri</i> Baird	168	2/9 (1942)	9/27 (1945)
<i>R. catesbeiana</i> Shaw	14	4/16 (1940)	7/20 (1943)
<i>Scaphiopus bombifrons</i> C.	111	3/16 (1945)	7/18 (1947)
<i>S. couchii</i> Baird	11	4/20 (1940)	8/8 (1939)
<i>S. hurterii</i> Strecker	19	3/16 (1945)	9/4 (1940)

patterns. April, 1947 was selected and the results are given in Table III. Rain-jacent states. Most of the observations were made by me personally, but a few came from other observers whom I know to be competent. I am especially indebted to Mr. Harold Dundee, and Dr. Charles C. Smith, both of whom have contributed to the data. All doubtful items have been eliminated, whatever their source.

There appears to be a clear-cut, over-all tendency for most breeding to occur during the period, April 16 to June 15, and for many species to breed together. Mixed congresses are the rule. However, some species do not conform. *Pseudacris streckeri*, for example, has been found breeding only three times after May 15 out of a total of 164 times. While the records are few, *Bufo woodhousii fowleri* has been recorded only in May and June. This is also true of *Microhyla carolinensis carolinensis* except for one record in the first half of July. These species seem to have some seasonal restriction in breeding. On the other hand, forms like *Bufo cognatus*, *B. w. woodhousii*, *Pseudacris clarkii* and, especially, *Rana berlandieri* show less restriction. Not only do they start earlier but they end later than many other forms.

Elsewhere, I have emphasized that the frogs and toads of Oklahoma are influenced differently by the amount and rate of rainfall. All are stimulated; but some respond only during certain periods of the year. Others breed during rain at any time when temperature is high enough to permit it. This must be taken into consideration in interpreting Table I. For example, the record for *Bufo cognatus* (143 items) is approximately the same as for *B. w. woodhousii* (147 items) and the over-all period utilized is about the same (March 28 to August 9 for *B. cognatus* and March 24 to September 4 for *B. w. woodhousii*). Most of the breeding for each occurs from April 1 to June 1 but the percentage difference is approximately 21 ($134 = 93.7 + \%$ for *B. cognatus*, $107 = 72.8 - \%$ for *B. w. woodhousii*). Inspection of Table I will show that some of this difference comes from more congresses in late March and August for *B. w. woodhousii* than for *B. cognatus*. Opportunity for convenient observation probably accounts for most of the remainder.

Field observations show that all of the 143 items recorded for *B. cognatus* have been after rain at temperatures, 12°C . or above. Those of *B. w. woodhousii* have also been after rain except twelve and at temperatures 13°C . or above. On several occasions, *B. w. woodhousii* has not called at 12°C . after rain when *B. cognatus* was breeding; and on eight occasions *B. cognatus* has failed to breed after rain below 12°C .

It is on the basis of such observations as these that I have suggested the breeding patterns, outlined without supporting data in earlier papers (Bragg, 1944-45, 1946). I have been particularly impressed by the distribution of these patterns in relation to ecological distribution of the various forms.

I thought that it would be instructive to select one month arbitrarily (out of the many for which I have adequate records) to illustrate the relation of breeding to rainfall. This was not selected to show this relation best, and I had no idea what the details would indicate except, naturally, the confidence that they would support my general impression as to validity of the breeding

TABLE III

Salientian breeding record in Cleveland County, Oklahoma for April, 1947. Dates not included are those when no observations were made, x = breeding after rain; y = breeding without rain at least 4 days prior to date of observation. Rainfall given in inches. Breeding patterns are indicated (X = Xeric, M = Mesic, I = Intermediate) after the names of each species (second column).

Rainfall	.03	.02	1.5	.5	1.1	1.4	1.35	.87	.21	17	18	19	20	23	25	26	27	28	.01	.15
Species																				
Day of Observation	3	7	8	9	10	12	13	14	15	16	17	18	19	20	23	25	26	27	28	29
<i>A. crepitans</i> (I)															y				x	
<i>B. t. americanus</i> (M)	y		x	x	x		x		x				y	y		x				
<i>B. cognatus</i> (X)											x								x	
<i>B. w. woodhousii</i> (I)											x			y					x	
<i>H. v. versicolor</i> (M)	y	y		x	x											x	x		x	x
<i>M. e. olivacea</i> (X)	(Starts late, hence no record for this month)																			
<i>Ps. clarkii</i> (X)			x	x	x	x	x	x				x				x	x	x		
<i>Ps. streckeri</i> (M)			x	x	x	x	x	x	x								x		x	x
<i>Ps. triseriata</i> (I)	y	y	x	x			x		x					y			x		x	
<i>R. berlandieri</i> (I)	y	y		x	x							x				x			x	
<i>R. catesbeiana</i> (M)	(Starts late, hence no record for this month)																			
<i>S. bombifrons</i> (X)				x													x			
<i>S. huerfii</i> (X)	(No record during April of this particular year)																			

Temp. too low to expect much breeding

7°C

13°C

fall data are taken from the United States Weather Bureau, University Station, Norman.

One unsuspected relationship was brought out for the xeric form, *Bufo cognatus*. On the 13th and 14th, 2.75 in. of rain is recorded, but the temperature was near freezing. During the next two days a drizzle with showers brought a total of 1.08 in. more, while the temperature still remained low. The animals bred in large numbers the night of the 17th at 13°C. This suggests that *B. cognatus*, like the prairie spadefoot, *Scaphiopus bombifrons* (Bragg and Smith, 1942), may receive the stimulus for breeding by heavy rainfall at low temperatures and have a delayed response to this as the temperature rises above the critical point.

Note also that *S. bombifrons* is recorded as breeding on the 14th, but not on the 13th. This was a very small congress at just about the critical point of temperature. A large congress of this species occurred with *B. cognatus* on the 17th, just as was expected from former observations.

The data presented, therefore, support my former general statements given without many supporting data, as to the breeding patterns and they further indicate that breeding *periods* are distinct from breeding *seasons*.

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IV

Salientian Range Extensions in Oklahoma and a New State Record

ARTHUR N. BRAGG

THE University of Oklahoma Biological Survey maintained a series of collecting trips in Oklahoma from mid-May to early July, 1946, and again during June and July, 1947. Between these dates each year I, as a member of this group, visited most of the major ecological and biological provinces within the state, many of them more than once, and collected Salientia as opportunity permitted. All collections of frogs and toads were recorded as collected by me, but many specimens were actually caught by my companions of 1946, Dr. A. O. Weese and Mr. W. L. Burger (and a few by Mr. U. T. Waterfall in 1947), to whom acknowledgment is due.

Although several hundreds of specimens were taken and deposited in the University of Oklahoma Museum (Division of Zoology), this paper reports only those which appear to be new county or state records. In a few cases it goes into more detail concerning the ranges of forms where doubt has existed or still exists. Notes on behavior and habits of some species are also given wherever these notes are thought to add enough to our understanding to justify their inclusion.

Five symbols indicate the type of records obtained, as follows: (1), at least one adult or juvenile taken where previously the form had not been recorded; (T), tadpoles but no adults or juveniles taken; (2), at least one adult or juvenile taken which confirms a former call or sight record; (C), the distinctive call clearly recognized; or (S), specimen seen in a region where heretofore the species has not been certainly known. The county is in all cases used as a convenient unit.

1. *Acris crepitans* Baird.

Blaine (2), Caddo (1), Jackson (1), Jefferson (1), Johnston (1), Kingfisher (1), Noble (2), Tillman (1). With these records only six counties in Oklahoma remain in which this species has not been collected. In three of these there are call records. There seems little doubt that it is state-wide in occurrence, since the counties where it is unknown are widely scattered. The two western counties of the Panhandle may be an exception, however.

2. *Bufo cognatus* Say.

Woodward (1). A single large adult taken at the western Woodward city limits.

3. *Bufo compactilis* Wiegmann.

Beckham (T). Adults and tadpoles of this toad were very abundant in the southwestern part of the state but were not found in the northwest. The presence of the species near Buffalo, Harper County (Bragg, 1946), makes it probable in Ellis, western Woodward, western Dewey, and Roger Mills counties, as well as in the Panhandle. It is, of course, possible that the Buffalo colony is an isolated population.

4. *Bufo insidiosus* Girard.

Beckham (I). A single adult female was secured from a dry cistern on a hilltop in the edge of the Gypsum Hills of this county in 1946. Despite a six-inch rain two weeks previously here, its tadpoles could not be found in two pools at the base of this hill, each of which contained thousands of spadefoot tadpoles (*S. bombifrons*) and larval salamanders. I am puzzled as to why I have never succeeded in securing tadpoles of this species in western Oklahoma, even in regions where some years ago I had collected calling males after rain. Former experience indicates that *B. insidiosus* commonly breeds with *Scaphiopus couchii* and *Bufo compactilis* in southwestern Oklahoma. In 1946, tadpoles of the latter were abundant but those of this spadefoot were not found, perhaps because of differential developmental rates. None of either was taken in 1947. Does *B. insidiosus* have an exceptionally high rate of development also?

5. *Bufo punctatus* Baird and Girard.

Greer (I). A single specimen, active after a heavy rain in the morning at Granite, Oklahoma, was taken at the base of a small mountain at edge of the city.

6. *Bufo woodhousii fowleri* Hinckley.

Haskell (T), Pushmataha (I). Adults and tadpoles of this species were common in southeastern Oklahoma in late May and in mid-June, 1946, and in June, 1947. Several breeding congresses were visited in eastern Oklahoma, especially in McCurtain County. No recently metamorphosed young were seen, although those of the earlier breeding American toad were locally abundant.

It is commonly stated that tadpoles of Fowler's toads are difficult or impossible to distinguish from those of *B. t. americanus* (Holbrook). (See Walker, 1946, pp. 35-36, for example). This is true of preserved animals. I find it not true of live tadpoles in eastern Oklahoma. Those of the American toad are nearly black dorsally whereas those of Fowler's toad are mottled in black and various shades of brown, even when quite young. Older tadpoles of Fowler's toad in some pools are very much like those of the closely related *B. w. woodhousii*, both in general appearance and in behavior, but neither of these need ever be confused with tadpoles of the American toad in natural waters, at least in Oklahoma.

7. *Hyla versicolor chrysoscelis* (Cope).

Le Flore (1), McCurtain (1).

On a humid afternoon in late May a single tree-toad was calling from the woods near the bridge over Little River on Highway 70 between Broken Bow and Idabel, McCurtain County. The call was recognized as an amphibian voice never before heard and every effort was made (without success) to secure the specimen. The call suggested that of *H. v. versicolor* in general type, in length, and in interval but differed in being much hoarser in tone. Rainfall brought out a large number of breeding individuals the following evening and a thorough search of the area from Idabel to the river was made. The hoarse-voiced *Hyla* was heard all along the river valley but not in the uplands above the river. Here, in contrast, the calls of typical *H. v. versicolor* were abundant. On the upper slopes the calls appeared to be intermediate in tone. At a pool almost on the bank of the river, several specimens of the hoarse-voiced form were stalked individually, by following their calls, and captured. Since they conform to the description of *H. v. chrysoscelis* (Cope) as given by Wright and Wright (1942), since they occupy a habitat given there as characteristic of this form, since this subspecies might be expected in this geographic region, and since the calls differ from those of *H. v. versicolor*, I conclude that the specimens represent *chrysoscelis* which have migrated up the valley of Little River from Arkansas where they are known. This, so far as I am aware, constitutes a new state record for the presence of this subspecies.

Some days later, *H. v. chrysoscelis* was heard again, this time in the valley between Rich Mountain and Black Fork Mountain near Page, Le Flore County. Before dark calls of *H. v. versicolor* were heard at intervals along Highway 270 between Heavener and the head of this valley about three miles northwest of Page; but only on approach to the valley itself were the calls of *H. v. chrysoscelis* heard. Here both forms were together at dusk moving into a roadside pool, calling from the trees as they came. I went into the woods and collected several by stalking calling males; taking care to keep them in separate containers as caught. The males of *chrysoscelis* taken here were smaller than the *versicolor* and were more difficult to secure because of their tendency to stay in the deepest cover, particularly on trees surrounded by vines of smilax. A mated pair was collected from an oak limb about six feet from the ground, the first hylas I have found mated in trees. The female was of normal size but the male was small. Later that evening, all down this valley following the highway to Mena, Arkansas, calls of *chrysoscelis* were abundant but no *versicolor* were heard all the way to Mena. One *H. v. chrysoscelis* was heard within the city of Mena itself.

All of this conforms to expectations as to the habitat of these two forms (Wright and Wright, 1942), *chrysoscelis* being essentially a *versicolor* differentiated in evolution in a valley habitat.

8. *Hyla versicolor versicolor* (Le Conte).

Haskell (T), Love (T).

9. *Microhyla c. carolinensis* (Holbrook).

Cherokee (2), Le Flore (C), Mayes (T), McCurtain (1).

The distribution of the two forms of *Microhyla olivacea* in Oklahoma (*olivacea* and *carolinensis*) has been uncertain till recently. I had supposed only the former to be present (Bragg, 1943) till 1946 (Bragg, 1946). Recently Hecht and Metalas (1946) relegate *olivacea* to a subspecies of *carolinensis* partly on the basis of specimens of intergrading color pattern from Latimer County, Oklahoma. They could find no structural characters other than color pattern which consistently will separate the two forms. Because of these uncertainties I have rechecked the specimens in the University of Oklahoma Museum (Division of Zoology) from the state as well as making special effort to secure more information while in eastern Oklahoma during the last two seasons.

Of sixteen museum specimens from Latimer County, fourteen, identified some years ago by Mrs. Helen P. Gaige as *Microhyla carolinensis*, are clearly of this form. Two appear to intergrade in ventral color pattern and a note with one of these specimens indicates that possible intergradation with *M. olivacea* was recognized by Mrs. Gaige. All specimens from McCurtain County are *carolinensis* and under favorable conditions for breeding in May, 1946, *carolinensis* was the form exclusively seen and heard near Idabel. In Le Flore County, this species was calling with the hylas northwest of Page (see above) and without them at the same pool in the afternoon; but a specimen could not be secured. Later in 1946, another small chorus was heard at dusk in a spring-fed pool on the bank of Tyner Creek in eastern Cherokee County. They were found calling at this same site in June, 1947, as well as elsewhere in this general region. I have formerly heard *olivacea* in western Cherokee County north of Fort Gibson. Since both forms are present at Fort Smith, Arkansas (Bragg, 1946) the band of territory separating the two in Oklahoma appears to follow closely that separating *Bufo woodhousii fowleri* and *B. w. woodhousii* (Bragg and Smith, 1943).

Some observations on the calls and slight differences in behavior of the two forms seem worthy of record. On each of several recent occasions the largest chorus of *M. c. carolinensis* has developed on warm bright afternoons with a lessening of the calls at night. With *olivacea* the reverse tends to be the case in all my experience. The calls of the two are different, that of *olivacea* appearing to me to be of slightly higher pitch and with greater carrying power. To Wright and Wright (1942) the reverse seems to be true. Both call from clumps of vegetation but males of *carolinensis*, on the twelve occasions when I have studied a chorus, invariably have called only from the tallest and thickest grass clumps. *Olivacea* often uses such places but does not invariably do so. This makes specimens of *olivacea* much easier to collect by hand than those of *carolinensis*. It will be interesting to observe these matters in intergrades.

10. *Microhyla c. olivacea* (Hallowell).

Jefferson (T), Okmulgee (I), Major (T).

The tadpoles from Major County constitute the only specimens from northwestern Oklahoma. There is, however, a sight record from Harper County, still farther westward.

11. *Pseudacris clarkii* Baird.

Harmon (1).

12. *Pseudacris streckeri* Wright and Wright

Blaine (2), Rogers (C), Greer (T).

The tadpoles from Greer County give us the first record in Oklahoma west of the Wichita Mountains of Comanche County. They were taken in a large, clear-water cattle tank in mesquite-savannah three miles west of Mangum on Oklahoma Highway 9.

13. *Pseudacris triseriata* (Wied).

Pushmataha (2), Okmulgee (T), Okfuskee (T).

14. *Rana catesbeiana* Shaw.

Greer (T), Jefferson (S), Bryan (S), Craig (1), Johnston (1), Kingfisher (S), Love (S), Major (S), Noble (S), Ottawa (1), Tillman (1), Haskell (S).

Twelve scattered counties in Oklahoma now remain without some kind of record of the bullfrog. It is almost certainly state-wide in distribution.

15. *Rana berlandieri* Baird.

Bryan (2), Canadian (S), Craig (1), Ellis (2), Haskell (1), McIntosh (S).

Valid records based on specimens now exist for all but four scattered counties in Oklahoma. In all of these we now have sight records. Hence it is now certain that this frog occurs in all counties of the state.

16. *Scaphiopus bombifrons* Cope.

Garvin (T), Harmon (T), Jackson (T), Love (T), Roger Mills (T).¹

17. *Scaphiopus hammondi* Baird.

Beckham (T), Greer (T), Texas (T).¹

Several pools in the gypsum hill regions of Beckham and Greer counties had tadpoles of both the above species of spadefoots, all far along in development. All pools on the clay soils to the east of this region that had spadefoot tadpoles contained only *S. bombifrons*. Since *bombifrons* has been known in this region for a long time (and is abundant) whereas this is the first record of *hammondi* south of the counties bordering Kansas, at least one hundred miles to the north, it may be that the western spadefoot is here limited mostly to these hills.

¹ Collected in 1940 by Dr. Charles C. Smith and presented to the author. These records are included here for convenience.

In one prairie region of Beckham County, however, a large collection of spadefoot tadpoles at and near metamorphosis contained a few individuals of *hammondii* and also a few with jaws intermediate in character between those of *bombifrons* and *hammondii*. Over 95 per cent of several hundred identified were of *bombifrons*. It is thought probable that the intermediates represent hybrids. Hybridization between these closely related species might be expected in this region since it is near the eastern limits of the range of *hammondii*. Presumably, therefore, in the breeding congress only a relatively few *hammondii* mixed with many *bombifrons* tended to break down the normal sexual isolation of the two.

It is of further interest to note that this same site yielded almost exactly the same proportions of tadpoles of the two species and of intermediates in each of the two years.

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PART II
PAPERS ON ECOLOGY

V

Observations on the Ecology and Natural History of Anura.

XIV. Growth Rates and Age at Sexual Maturity of *Bufo Cognatus* under Natural Conditions in Central Oklahoma

ARTHUR N. BRAGG AND A. O. WEESE

THE varying sizes of the toads found in the spring suggested to Dickinson (1913) that several years probably elapse between metamorphosis and sexual maturity in *Bufo cognatus* Say. Bragg (1940) noted, however, that the sizes of juveniles of essentially the same age, collected in October, 1938, varied sufficiently to indicate marked differences in individual growth rates during the first summer. This indicates that a juvenile toad's age cannot be successfully deduced from its size alone. Both Dickinson and Bragg commented on the probable age or size reached at sexual maturity but neither had data to substantiate his deductions. Actually, practically nothing is known concerning age or size at sexual maturity of *B. cognatus* and a search of the literature revealed little data on other species.

In central Oklahoma, particularly in the region about Norman, Cleveland County, the breeding habits, dates of breeding congresses, success in production of metamorphosed young each year, and general movements and reactions of these toads at all ages were under nearly continuous observation for twelve successive seasons, 1935-1947, inclusive. The principal breeding sites in this area are well-known and records have been kept of their use by the toads, and something learned as to the degree of success in breeding each year. Data on growth rates and observations on age and size at sexual maturity as interpreted on this rather extensive background of general observation are now available. A preliminary note has already been published (Bragg and Weese, 1942).

Since we wished to secure data on growth rates under natural conditions we did not, except incidentally, study captive toads. However, one group of fifty young toads of known age was confined in August, 1941, and measured at intervals thereafter for two years. Some of these were still alive in September, 1947, having never since capture lived elsewhere than in the artificial environment into which they were placed as very young toads. Another small group of captive juveniles was under observation during the summer of 1947.

Our principal method of studying growth rates consisted of collecting young toads in selected, restricted regions, measuring them, and releasing

them in the general area of capture. Some also were preserved for later study. By repeated collections in the same general area, data were secured as to size and variation of individuals in each population so treated. By interpreting the results in the light of observations on breeding dates, breeding sites, and habits of movement of the toads in feeding, a fair idea could be secured as to growth rates of the toads in each area for the seasons studied.

The age at sexual maturity was not so easily obtained. Several methods, none of them perfect, were utilized. (1) The smallest toads in breeding congresses were compared with others feeding but not breeding on the same nights. By examining hundreds of such toads we could at least find the smallest probable size attained before breeding activity commenced. (2) Male toads develop secondary sex characters by which they may be distinguished easily from females. By watching for the beginnings of such differentiations and comparing the sizes and stages of development of small toads taken from breeding congresses with those of others taken feeding but not breeding, some idea of age at sexual maturity of males could be obtained. Females do not show secondary sex characters clearly until maturity, but one behavior character of the male may be used beyond a certain size limit to distinguish the sexes. This is the protesting note which males, but not females, give when handled or otherwise disturbed. Any healthy and unfatigued individual beyond 60 mm. in size which does not "protest" when handled may safely be inferred to be a female. Below this size females cannot certainly be separated from males except, of course, as males may show the beginning of other secondary sex characters. It follows that males may be distinguished clearly at an earlier age and at a smaller size than females, and that our methods could teach us more about the former than the latter.

As background for our interpretations, data on sizes of adults are given in Table I. These came from measurements recorded over several years, some from preserved and others from living specimens. Table II treats breeding adults in the same manner except that all were alive when measured. A resumé is given below of our observations on breeding dates, characteristic breeding sites, the degree of success in breeding each year, and characteristic movements of both young and adults while feeding. Unless otherwise stated all data apply specifically to *B. cognatus* in Cleveland County and mostly from an area within four miles from the center of the city of Norman. For details of breeding habits here, see Bragg (1940).

Bufo cognatus breeds only after rains, typically of one-half inch or more, from March to August (observed) and perhaps later. Breeding activity is inhibited by air temperatures below 12°C. Therefore, the distribution of temperature and rainfall within the warmer months (rather than a limited breeding season) determines largely how much breeding there will be and also whether it will be successful. Spring rains in central Oklahoma are commonly accompanied by falling temperatures, often by temperatures too low for breeding.

Should a given spring be exceptionally dry during March, April, and early May, or if all early rains fall while the temperature is too low for breed-

ing to occur, large numbers of eggs are likely to be produced after rains from late May onward, just at the beginning of a period of high temperatures and hot, dry winds. Under such circumstances all, or nearly all, tadpoles may be killed by evaporation of pools before they have had time to complete the aquatic phase of their existence. Such a circumstance is by no means rare in Oklahoma and about Norman two or three years may elapse without successful breeding of *B. cognatus*. Part of this is a direct consequence of the selection of none but shallow pools (up to 8-10") for breeding. In this, *B. cognatus* differs from the other common toad here (*B. w. woodhousii*) which, by utilizing the deeper pools, has never failed completely to produce young during the past thirteen years. It is important to understand these relationships to see how we are better able to judge the ages of toads collected here, why we know in some cases that a small toad (*B. cognatus*) is older than its size would seem to indicate and why we cannot be so sure about *B. w. woodhousii*. During the period under observation, 1935-1947, the degree of success in breeding of *B. cognatus* has been as follows:

- 1935. Moderately successful breeding.
- 1936. Very successful breeding. Thousands of young toads emerging from pools in May.
- 1937. Breeding largely unsuccessful. A very few tadpoles, probably not more than 50, in *one* pool succeeded in the race with evaporation. All others, even in this one pool, were killed.
- 1938. Very successful breeding (Bragg, 1940), starting in late March.
- 1939. No successful breeding.
- 1940. No successful breeding in spring. Congresses in early July *may* have produced some young.
- 1941. Very successful breeding. Distribution of rainfall and temperature practically ideal for these toads (Bragg, 1942). Most toads breeding at this time have been at least three years old.
- 1942. Poor success in breeding—a few succeeded in metamorphosis (about like 1937).
- 1943. No successful breeding.
- 1944. Poor success in breeding. A few tadpoles emerged, however.
- 1945. No successful breeding.
- 1946. No successful breeding.
- 1947. Successful breeding but not equalling 1938 and 1941. In some pools, all tadpoles were killed but in others many survived. Young toads abundant in early July, but few seen the following spring.

Our data came largely from the population of young toads resulting from the most successful breeding year ever observed in this region, i.e., 1941. A glance at the foregoing list will show that two full years had elapsed since the last markedly successful breeding had occurred and that this season was

followed by five during which only a very few young toads were produced. Because of this, we are more sure that the small toads taken in the springs of 1942 and 1943 were produced in 1941 than we would otherwise be. It is evident that a small toad collected in this region in either 1942 or 1943 must have been of the 1941 reproductive period or be a stunted adult, at least three years old (i.e., metamorphosed in 1938 or before). For similar reasons, it is clear that all small to medium sized toads collected in the summer and fall of 1941 were wholly or largely products of the 1941 breeding period, having emerged in May or early June of that year. In case of any doubt, the immaturity of the males as shown by their beginning development of secondary sex characteristics could be relied upon to validate the data for this sex.

It seems wise to call attention to differences in behavior of these toads at different ages. Adults emerge in March or April (depending upon temperature) and feed till the coming of hot, dry weather, usually in late June. Thereafter, old females may be out but males usually are not. Often in September, even after rains, no adult toads of this species can be found in areas where fifty or more can be seen in a half-hour's search earlier in the year. This does not usually apply to juveniles. On emergence at metamorphosis the young toads remain about the pool for some weeks or until all water evaporates if this happens quickly. Eventually, they wander away but apparently do not scatter widely, but seek areas of soft soil in which to burrow. In central Oklahoma this usually means agricultural areas, such as corn and cotton fields, from which they come forth in large numbers at night to feed in adjacent roads and fields and to which they return each morning. Their movements are stimulated by any showers which may come but most individuals continue to feed each night through the summer and well into September whether it rains or not. We have collected young *B. cognatus* in nights between days of maximum temperatures of over 100°F. when the night temperatures were above 90°F. and when no precipitation had occurred for over a month.

Commonly in spring and occasionally in fall, rainfall in central Oklahoma is followed by a marked drop in temperature. It has been noted consistently through the years that even heavy rainfall fails to stimulate emergence of either *B. cognatus* or *B. w. woodhousii* if it is to be followed by such a cold wave. Many times we have failed to find a single toad in several hours' search after rain at temperatures high enough for one to expect them to be out. Invariably, when this has been the case, a severe cold wave has moved in before morning. A possibly related phenomenon is the fact that toads of all ages above two months are active almost in direct proportion to the numbers of insects which are attracted to light at night. It seems that *B. cognatus* is in nice adjustment to the conditions which will protect individuals from cold and insure an adequate supply of food. The physiological mechanism involved is wholly unknown.

Collecting areas (all about Norman, Oklahoma), were as follows (see Fig. 1):

A. A ditch between a roadway and the tracks of an interurban railway, 1.8

Fig. 1

miles north of West Main Street and on Berry Road, which served as a breeding site.¹

- A₁. South of 0.2 miles from Robinson Street along Berry Road (i.e., approximately 1 mile south of A) and east along Robinson 0.2 miles from the corner.
- A₂. Toads collected on 0.8 mile of Berry Road from Main Street north were assumed to have been produced at a breeding site in a pasture northwest of this corner. Toads collected from A₁ could have been from either breeding site.
- B. Polo Field south of the University of Oklahoma campus—now part of the South Campus of the University and adjacent thereto on the north. Until 1942 this area served as principal breeding site for *B. cognatus* in this region and had been watched closely for several years. Toads of several ages were found here in May and June, 1941, coming from breeding congregations at different times during the spring.
- C. Along Lindsey Road for 0.8 mile west from its junction with Berry Road 1.0 mile south of Main Street. The breeding site or sites near here in 1941 were unknown but young toads are always abundant whenever found anywhere about Norman.
- D. On Berry Road just south of Main Street. Breeding site in pasture some 0.1 to 0.2 mile from corner. This is so near the site mentioned in A₂ that mixing of the toads from the two sites is probable.
- E. Along West Boyd in the second half mile from Berry Road intersection. Breeding site here is unknown. This is approximately 0.8 mile across agricultural land from Main and Berry and approximately 0.5 mile from the west half of the section of W. Lindsey Road mentioned under C.

The first young toads to emerge in the spring of 1939 appeared on the evening of April 14. The season was very dry and individuals were not found feeding until after showers on May 10 and 13. Many were out on May 17. Adult males were calling but the young males, which probably had metamorphosed the preceding year but may have been older, failed to enter the breeding pools. Young females picked up from the grass adjacent to breeding pools and offered to calling males were clasped by them but struggled in a continuous attempt to escape. Apparently, young toads of neither sex were sufficiently mature to breed.

On the night of June 6, twenty-six young toads collected from Station A₂ ranged in length between 51 and 67 mm. None of these had developed the secondary sex characters of the male (they were presumably females), but six days later ninety-nine, of which seventeen were juvenile males, were collected. The juvenile males ranged between 51 and 75 mm. in length. Many adults in the roads with them were no larger than the largest of the juveniles. Thus a few males metamorphosing in the spring of 1938 had now reached a size

¹ This is now no longer available as such, due to the construction of the naval air training base during the war. The site is now located on the eastern edge of the North Campus of the University of Oklahoma and its character is completely changed. *B. cognatus* bred on the North Campus in 1947 but did not use this site.

comparable to that of some adults at least a year and probably two years older. These results were confirmed at a later date (June 21) when calling males 75 mm. in length and with fully formed functional vocal pouches were collected from breeding congresses at the same time that other males of this size and with incompletely developed pouches remained away from the breeding pools.

The year 1939 was a poor breeding year for *B. cognatus*. Rains were late and most egg-laying was in June. For this reason pools evaporated, killing all tadpoles. Despite constant search, we found evidence of the emergence of only ten young toads from a single pool in the Norman region. It was thus not possible to follow the young toads of the 1938 season into their third year.

After a light shower on May 20, 1940, twenty-two toads were collected and measured. Of these, six were judged to be of the 1938 brood, two were questionable, and the remainder were judged to be older. The next night, after a heavy shower in the late afternoon, twelve calling males were selected from a breeding congress because they seemed to be the smallest of hundreds in the pool. These ranged from 66 to 78 mm. in length. Only two males of this approximate size could be found on an adjacent roadway (62 and 64 mm. respectively). Both had immature vocal pouches.

Observations were discontinued shortly after this until September. The fall was dry, however, and no further information was secured until the following spring. It should be mentioned that very large breeding congresses were seen in early July by Dr. Charles C. Smith and that these are known to have been successful in the production of young metamorphosed toads. It is also practically certain that eggs laid in May produced young toads.

In the spring of 1941, therefore, young toads of two ages were to be expected in our collections, as well as young adults of the 1938 season. On April 14 and 27 fifteen individuals, obviously of the 1940 season, were taken. They ranged from 44 to 75 mm. in length, four of them certainly being males. One 55 mm. individual, probably from a late summer brood, chirped when picked up and was, therefore, classified as a male although no sign of the vocal pouch was present. Other toads collected at the same time were thought to be of the 1938 season, but they could not be distinguished with certainty from older individuals.

The spring of 1941 (April through June) was the wettest in many years, and *B. cognatus* responded by producing millions of young (Bragg, 1942). Accordingly, we had the best opportunity for observations on growth rates yet afforded.

So long as the young metamorphosed toads remained diurnal, we could collect them in numbers about the pools; but after they became nocturnal we were forced to make collections at night at what seemed to be the most favorable times. Accordingly, as the weather became hotter and drier, our data became more scattered and meager, but we succeeded in tracing their growth fairly well until they hibernated for the winter in late October.

Collections were made in several areas during late spring and early summer, but it soon became evident that we were dealing with several age

groups. Breeding had occurred in the many pools over and over again during this spring. However, in one place (Sta. A), the breeding site had obviously been used but once, and all of the tadpoles had metamorphosed within a period of one week. Fortunately, the nearest pool to this at which breeding was also successful was just less than two miles distant. Since our studies on the movements of young toads had indicated that these toads congregate in agricultural areas near the pool from which they emerged and since there were several such areas available nearby, we assumed that any young toad taken within a mile of this breeding site actually emerged from this pool during the time indicated. Because of occasional mass movements, there is probably some error introduced here, but that this is not great is indicated by the fact that we always found very many more toads adjacent to cultivated fields nearest the breeding pool (or in them) than elsewhere within the linear mile usually covered by our collections. In traversing one mile of roadway the night of August 4, for example, sixty-eight toads were collected, thirty-two of which were taken adjacent to a cotton patch 0.2 miles in linear extent along the road. Many such observations were made, always with consistent results.

The collections from this area furnish the data for Table III and Fig. 2. On May 17, tadpoles in the water and metamorphosing toads on the bank were present in about equal numbers. One week later, May 24, no tadpoles could be found. May 21 was taken as the average date of emergence of toads here. Collections were made about the pool as long as the toads remained. Thereafter, toads taken within a mile south of it along roads and in adjacent agricultural areas were assumed to have been produced in this pool.

The young toads of the May 24 collection were very uniform in size and grew but little during the following week. The next three collections showed a much greater variability but indicated a period of rapid growth, which was followed by a phase of decreasing growth rate coinciding with the appearance of the first external indications of sexual differentiation. From this population the first distinguishable males were taken on August 4, when they were approximately fifteen weeks old (from metamorphosis).

The last large collection of the year was on September 24 when both males and females had reached a length of over 60 mm. However, the average length of males at that time, as well as during the summer, exceeded that of the females. It is possible, of course, that smaller, undifferentiated males were designated as females because of the absence of the secondary sexual characters. The same condition persisted during the following spring, until collections were discontinued because of the inaccessibility of the area. Growth was very slow during the second spring and the toads collected had not reached full adult size by early June.

The initially slow rate of increase in length followed by more rapid growth and a final less rapid phase led us to attempt the computation of the formula of the logistic curve most nearly expressing the observed relationships. For the purpose of computation the data for September 15, September 19, and October 18 were omitted on account of the small numbers of indi-

viduals and the probability that the two males of September 15 may have belonged to another age class. The resulting formula, the curve for which is shown in Fig. 2 is:

$$L = + \frac{60.24}{1 + e^{2.03 - 0.0415t}}$$

where L is length in millimeters and t is time in days from May 24.

No theoretical significance is here assigned to the apparently close agreement between the computed curve and the observed data.

Summary and Conclusions

1. Juveniles of *Bufo cognatus* in central Oklahoma vary considerably in growth rates during their first summer. This is true even of those emerging from pools at the same time. Those metamorphosing late in the summer may not be more than 30 mm. in length at the beginning of hibernation while those emerging early in the season may be as large as the smaller adults of broods of the preceding year.
2. Variation is also, in part, caused by differences in success in securing food. Some young toads are more aggressive than others. Toads which are injured are less adept at catching insects than their fellows. Some, also, may be more fortunate in finding areas in which suitable insects occur.
3. The rate of growth of young toads during their first season after emergence in early summer may be expressed at least roughly by a curve of sigmoid type.
4. Secondary sex characters of males tend to begin development toward the end of the first season. Males emerging from pools in mid-May begin to "protest" when handled in late August or early September at which time the dark-colored gular pouch may or may not have begun its development. By mid-October most males have developed the protesting note and have a dark smudge on the throat indicating the beginning of the pouch.
5. These secondary sex characters usually appear at this age irrespective of the size attained by the individuals.
6. On emerging from hibernation in the spring of the second year (approximately ten to eleven months after metamorphosis) all males "protest" when handled and all show some development of the gular pouch. The latter, however, is not fully developed. There is evidence that few, if any, males of this age frequent breeding pools or attempt to call females.
7. Late in the second summer some individuals (males) show practically complete development of the gular pouch and on emergence the following spring (second from the time of metamorphosis) practically all do so. In breeding pools, the sizes of the smallest males at this time compare favorably with the sizes of those taken in adjacent roadways, which indicates that the young males have now reached sexual maturity. A further indication of this is that in practically all young males the protesting note has now changed in pitch from the juvenile "peep" to the adult "quack."

Both these notes are distinctive and unmistakable to anyone familiar with them.

8. Sizes of mated females in breeding pools at the same time are not similar to those of small females on adjacent roadways. Mated females have always been found to be the larger. This seems to indicate that in the females sexual maturity is not attained at this time. We believe this to be the case, but our data, while consistent, are too meager to warrant a clear statement on the matter.
9. Toads feeding in fields and along roadways late in summer of their third year (and in breeding pools the following spring) are practically indistinguishable from older individuals, both in sexual development and in size. It is probably true that a selection of the smallest males (and certainly true of females) would contain more of the younger toads than of the older ones but there is no way to pick out individuals of known ages.
10. It follows from the above that: (a) most males of *B. cognatus* in central Oklahoma reach sexual maturity, regardless of the size attained, at the beginning of their third season; some females may do so but most probably do not; (b) most females reach sexual maturity and may breed one year later than their brothers; (c) by the end of their third summer younger toads of neither sex can certainly be distinguished by size from older individuals.

TABLE I

Snout to vent length of adult *Bufo cognatus* in Oklahoma. Range (R) expressed to nearest mm.; arithmetic mean (M) expressed to nearest 0.1 mm. N = Number in each category.

	N	R	M
Preserved Males—Cleveland County	227	62-90	74.5
Preserved Males—Elsewhere	108	63-95	77.1
Living Males—Cleveland County	394	63-103	82.7
Total Males—Cleveland County	621	62-103	79.7
Total Males	729	62-103	79.4
Preserved Females—Cleveland County	29	62-110	84.7
Preserved Females—Elsewhere	42	70-110	86.0
Living Females—Cleveland County	83	49-112	82.5
Total Females—Cleveland County	112	49-112	83.0
Total Females	154	49-112	85.8

TABLE II

Lengths of *B. cognatus* individuals at breeding—all specimens measured (snout-vent) while alive.

	N	R	M
Males—Calling when captured	205	66-103	80.7
Males—Clasping when captured	24	72-95	81.8
Males—Total	229	66-103	81.7
Females—Clasped when captured	24	65-98	81.8

THE AMPHIBIA OF OKLAHOMA

TABLE III

Lengths of *B. cognatus* individuals from a population metamorphosing during the week previous to May 24, 1941.

Date	Days from 5/24		N	Mean Length	Standard Deviation
5/24	0		50	17.02	1.37
5/31	7		86	18.86	2.05
7/5	42		33	47.24	5.27
7/12	49		8	44.00	5.22
8/13	81		60	58.28	4.90
8/24	92		27	59.41	3.38
9/4	103	m	14	58.21	3.49
		f	54	57.57	6.07
9/15	114	m	2*	69.50	0.25
		f	10*	63.20	3.94
9/19	118	f	4*	64.25	4.49
9/24	123	m	11	63.94	3.37
		f	86	60.56	4.80
10/18	147	m	1*	65	
		f	6*	62.17	2.27
1942					
4/14		m	7	69.43	4.36
4/23		m	15	69.92	4.47
		f	18	66.81	3.20
5/30		m	6	71.50	3.30
		f	22	68.91	3.66
6/4		m	3	69.33	3.86
		f	2	70.33	1.66
6/5		m	13	72.07	4.08
		f	13	68.04	4.68

* Data not used in the computation of the growth curve in Fig. 2.

Fig. 1. Breeding sites and collection areas near Norman, Oklahoma.

Fig. 2 Growth of *Bufo cognatus*.

The upper line indicates mean length plus standard deviation and the lower mean length minus standard deviation. Beginning at September 4, lengths of males and females are indicated separately, the former being represented by heavier lines. The crosses mark points on the curve drawn according to the formula given in the text.

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VI

Observations on the Ecology and Natural History of Anura. XVII. Adaptations and Distribution in Accordance with Habits in Oklahoma¹

ARTHUR N. BRAGG

IT HAS often been said that the goal of evolution is adaptation to a changing environment; from this it follows that any organism expresses in structure and in behavior the accumulation of adjustments throughout its phylogeny; and this is as true of a species, genus, or other taxonomic group as of an individual. Organisms must vary in order to remain in adaptation to the environment if they are to continue existence in any given place.

Most studies of phylogeny, taxonomy, and distribution of organisms tend to emphasize the morphological changes which occur as organisms come under varying environments. By comparing large series of specimens and emphasizing their differences in relation to distribution, the direction of dispersal, as well as anatomical trends in adaptation, are discovered and then expressed in a scheme of classification. These studies are of great value but even the best of them are apt to be weak in that (1) they tend to emphasize geographical as opposed to ecological distribution, and (2) they tend to overlook behavior and habits.

That habits especially have been neglected is easily shown by references to the Salientia. As pointed out elsewhere (Bragg, 1940d) many species (e.g., *Bufo compactilis* Wiegman and *Bufo cognatus* Say) had been known taxonomically for over a century and their geographic distribution fairly well worked out before anyone paid much attention to their ecological requirements or to their patterns of breeding behavior. *Pseudacris clarkii* (Baird) and *Ps. triseriata* Wied are still uncertain taxonomically but differ in ecological requirements and in habits (Bragg, 1943, 1943a). The leopard frogs of North America are very difficult to separate structurally and their specific or subspecific relationships have not been worked out satisfactorily (Burt, 1931; Kauffeld, 1937; Stejneger and Barbour, 1939; Wright and Wright, 1942; etc.) but the eastern forms differ from those of Oklahoma in habits in such a way as to indicate that there is a very distinct difference among them (Bragg, 1940, 1941).

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The emphasis on structure and the neglect of habits has given rise in some quarters to an unfortunate error, namely of expecting the habits of organisms always to correspond to their taxonomic arrangement. Because the better known eastern frogs and toads all have a definite breeding season, it is often assumed that most or all species in North America have one. Witness the peculiar interest among the earlier observers, sometimes approaching amazement, concerning the habits of the eastern spadefoot (*Scaphiopus h. holbrookii* Harlan) which does not behave in an "orthodox" manner. But once it was determined that this form is different, it was expected that other spadefoots are necessarily like it in its peculiarities; and some notions about these animals have developed which have no foundation in fact (see Bragg, 1944a, for a more extended discussion of this point.)

The almost universal reliance upon the experimental method has also caused some confusion. Davis (1936) gives emphasis to this fact as follows: "The most satisfactory approach to a study of the courtship behavior of animals is direct observation, preferably of undisturbed individuals in the field. Serious misinterpretations have not infrequently arisen from observation or experimentation on captive material, where unnatural associations almost inevitably alter behavior." What this author here states for courtship behavior, I hold to be true to some extent in *all* behavior. Animals segregated under experimental conditions do not always or *necessarily* behave in the same manner as in nature, and we never can be sure, even though in 90 per cent of the cases the field work may confirm the laboratory, that results obtained by these methods are valid in nature without field observations to check them. Furthermore, in the open, experimental control is at most very difficult and usually impossible to secure, and the experimental method, because it is based upon controlled conditions, is of very limited application in nature. Not only this, but control is often actually undesirable; for under natural conditions many factors work together to produce a given effect, each modifying the others in complex, interrelated ways. From an ecological point of view, it is exactly these interrelations of physiological and environmental conditions which we wish to know. In other words, experimentation, valuable as it is, like other methods, has its limitations, and, in the particular problem at hand, overemphasis or reliance upon it may lead one astray. Simple observation still has its place in science, even though it lacks the precision of experimentation.

The present series of papers, of which this is the seventeenth and last, has dealt with many phases in the lives of most of the frogs and toads in Oklahoma. Some have been rather extensive analyses of field observations upon a single species; others have dealt with some one phase in the lives of several species; still others have been mere notes on interesting points. All have emphasized habits in relation to environment and all have been essentially observational rather than experimental. The present contribution summarizes the work on adaptation to the various environments present in Oklahoma and adjacent regions. The intent is to generalize so far as seems justified by the observations without becoming confused by the multitudinous details. Habits

and habit patterns are emphasized, not because morphological changes are unimportant, but only because they have already received sufficient emphasis in studies of evolution. It is not intended to *overemphasize* habits, for this would be as unsound as the neglect of them has been.

Taxonomic Relationships

Twenty-seven species or subspecies of frogs and toads are known in Oklahoma as shown in the following outline.

Order Salientia (Anura)

Family Bufonidae (toads: garden toads)

Genus *Bufo*

1. *B. terrestris americanus* Holbrook, 1836
2. *B. cognatus* Say, 1823
3. *B. compactilis* Wiegmann, 1833
4. *B. insidiosus* Girard, 1854
5. *B. punctatus* Baird and Girard, 1852
6. *B. woodhousii fowleri* Hinckley, 1882
7. *B. w. woodhousii* Girard, 1854

Family Hylidae (tree toads)

Genus *Acris*

8. *A. crepitans* Baird, 1854

Genus *Hyla*

9. *H. versicolor chrysoscelis* (Cope, 1880)
10. *H. v. versicolor* (Le Conte, 1825)
11. *H. crucifer crucifer* Wied, 1838
12. *H. cinerea cinerea* (Schneider, 1892)

Genus *Pseudacris*

13. *Ps. clarkii* (Baird, 1854)
14. *Ps. streckeri* Wright and Wright, 1933
15. *Ps. triseriata* (Wied, 1838)

Family Microhylidae (narrow mouth toads)

Genus *Microhyla*²

16. *M. carolinensis carolinensis* (Holbrook, 1836)
17. *M. c. olivacea* (Hallowell, 1856)

Family Ranidae (frogs)

Genus *Rana*

18. *R. arcolata arcolata* Baird and Girard, 1852
19. *R. a. circulosa* Rice and Davis, 1833
20. *R. catesbeiana* Shaw, 1802
21. *R. clamitans* Latreille, 1802
22. *R. palustris* Le Conte, 1825
23. *R. berlandieri* Baird,³ 1859

Family Scaphiopodidae (Spadefoots: spadefoot toads)

Genus *Scaphiopus*

subgenus *Scaphiopus*

24. *S. (Scaphiopus) couchii* Baird, 1854
25. *S. (Scaphiopus) hurterii* Strecker, 1910

subgenus *Spea*

26. *S. (Spea) bombifrons* (Cope, 1863)
27. *S. (Spea) hammondi* Baird, 1859

² *Gastrophryne* of Stejneger and Barbour (1939).

³ Some question as to identity of this frog still exists: see later discussion.

Conditions of Existence in Oklahoma

Oklahoma is a peculiar region when considered as an environmental complex. Its area is close to 70,740 squares miles and its elevation varies between approximately 400 feet in the southeastern corner to about 4,500 feet on Black Mesa in the northwestern tip of the Panhandle. Physiographically, it is essentially a tilted plane roughened and cut by the valleys of its streams and by the presence of several old mountain masses, many of them now eroded to mere hills. Some of these are the Ozark highlands entering the state from Arkansas in the northeast, a part of the Ouachita uplift in the southeast, the Arbuckle Mountains in the south, the Wichitas in the southwest, the Glass Mountains or Gypsum Hills in the west, and the extensive sandstone hills running roughly north and south through the east central part (see map by Bruner, 1931, p. 103). Two drainage systems occur, that of the Red River in the south and that of the Arkansas River in the north. Approximately the southwestern fifth of the state is drained into the Red River by the Washita River to the north to the Wichita Mountains and the North, Elm, and Salt Forks of the Red River to the south and west of them. All of the central area is drained to the Arkansas by the Canadian, North Canadian, and Cimarron rivers, whereas the northern and northeastern portions drain more directly into the Arkansas through a series of larger (Illinois and Grand) rivers or smaller tributaries. In the southeast, the Kiamichi and Little rivers with their branches drain the southern and western Ouachita Mountains, the former entering the Red River in eastern Choctaw County, the latter crossing southwestern Arkansas first. Throughout the state, numerous creeks and gullies feed the larger streams, often with an intermittent flow. The larger rivers have wide valleys, those of the prairie regions being dry, sandy ribbons during summer from one-fourth mile to one mile wide and fringed with flood-plain forests far westward into the grasslands. Their banks in some places slope gently upward to the prairies, but at other places are sheer. Sometimes, after heavy rains, these streams become temporarily raging torrents.

The climate of Oklahoma varies greatly from east to west. Twenty inches of annual rainfall (distributed very irregularly through the year) in the Panhandle of the state is normal but thirty to thirty-five inches is usual in the central portion; the Northeast receives forty inches and the Southeast forty-five. Summers are hot and dry and the prevailing hot southwesterly winds of this season make rates of evaporation excessive, particularly in the southwestern part of the state. According to Bruner (1931), "The high evaporation rate is due to relatively high temperatures, high and almost continuous winds and low relative humidity. Tanks located in western Nebraska gave an evaporation rate of forty-one inches and in North Dakota only thirty-one inches (as compared with fifty to fifty-five inches in western Oklahoma). This great increase in evaporation southward causes the twenty inches of rainfall in the Panhandle to be only as efficient as fifteen inches in western North Dakota." These high evaporation rates affect greatly the lives of individual salientians and, through this, the ecological distribution of species.

Soils in Oklahoma are incompletely known. Sufficient information has been gathered to indicate several broadly different basic types; those based upon (1) weathered sandstone outcrops; (2) weathered limestone; and (3) clay deposited in ancient fresh water or marine basins. Smaller areas of other types exist, such as the alluvial loams and clay-sands on the flood plains of streams, and the sand dunes and salt plains which occur in the West.

Ecologically, the state is sometimes thought of as essentially prairie; but this is at best only a half truth. Most of the eastern half is wooded, with oaks and hickories dominant, either as scrubby thickets or as savannah. Bottom lands along the streams, except in the western portion of the state, have a forest of mixed deciduous woods; cottonwood, elm, willows, and redbud being particularly noticeable. Rather extensive patches of pine woodland occur locally on the Ouachita Mountains of the Southeast; and on the flood plain of the Red River and its major tributaries in this region, such southern trees as sweet-gum and cypress are common. The western half of the state is grassland, broken here and there by islands of oak-hickory woodland, and oak-shinnery, in addition to which are the flood-plain forests of the rivers and, in the west central part, the wooded ravines. In the Northwest, fairly extensive stands of sagebrush occur. Climatically, one would expect the true prairie (i.e., *Andropogon* or tall-grass prairie) to extend over much of the eastern half. Actually, except for "islands" of it farther south, only a relatively small tongue enters the Northeast from Kansas. This distribution is traceable primarily to the fact that soil type determines the present vegetative cover as much as climate does over most of Oklahoma. In general, limestone and clay soils favor climax grassland; and sandstone soils, sub-climax woodland or savannah in much of the state. This is the reason why larger or smaller islands of prairie in woodland and islands of oak-hickory woodland in prairie are so often encountered (for further detail of ecological relations see Bruner, 1931, and Bragg and Smith, 1943).

In fauna, Oklahoma varies greatly from east to west, less so from north to south. This might be expected inasmuch as the extreme southeastern corner is little more than a northward extension of the Gulf Coastal Plain whereas Black Mesa at the northwestern edge of the Panhandle is an eastern outlier of the Rocky Mountain Highland. Conditions of existence vary enormously from east to west and many components of the eastern, mesically adapted fauna and flora find their western limits in Oklahoma. Likewise, many of the western and southwestern, xerically adapted forms meet an ecological barrier here to further extension to the eastward. In short, no state of the United States except Texas offers more favorable opportunities to learn just what happens when two differently adapted faunas or floras meet.

Since Amphibia are dependent upon factors correlated with available moisture, both in their individual lives and in breeding, these factors are emphasized, especially among the salientians. Morphological variations might be expected within species and between species as conditions become gradually less favorable for any given group, west to east or east to west, the degree of variation dependent upon the interplay of genetic factors tending

toward variability on the one hand and environmental pressure, selecting only the most favorable individuals, on the other. Rigorous conditions anywhere almost always result in extermination of, or change in, the existing fauna and flora of a region.

There is a possibility, at least theoretically, that some organisms may meet and cross a partial barrier to dispersal by change in *habits* without essential change in *structure*; and it should be noted that, should this occur, the change need not be great in any one case. In passing to a progressively drier country, for example, so simple a variation as an average slight increase in developmental rate of tadpoles may make all the difference between extinction and survival through many seasons.

To determine such cases (or to test for their possible occurrence) involves the gathering of multitudinous observations. Even the smallest detail may be the key to the principle being sought although at the time when first observed it may seem so trivial as not to be recorded or remembered.

Habitat-Patterns

The salientians of Oklahoma, broadly considered, exhibit two general habitat preferences. All of the frogs (*Rana*) and the cricket-frog (*Acris crepitans*) are semiaquatic in that they tend to be restricted to pond sides or streams. On the other hand, all of the others range widely over the land paying little attention to the presence or absence of water except during breeding. Within each of these general types, however, there are varying adaptations to specific types of habitats.

Both subspecies of *Rana areolata* inhabit the burrows of crayfishes and are, therefore, restricted mostly to low-lying fields and ditches wherein burrowing crayfishes abound. *Rana clamitans*, here as elsewhere, is mostly restricted to muddy stream banks, swampy areas, and lake margins; the bull-frog (*R. catesbeiana*) is present most abundantly in and about permanent pools or lakes. The southwestern leopard frog (*R. berlandieri*) and also the pickerel frog (*R. palustris*), at least elsewhere, range widely from water in order to feed, particularly during moist weather, or at night. All of these semiaquatic organisms in Oklahoma seek other pools when the water upon which they are dependent evaporates. It is, therefore, a common thing to find frogs on roads at night. These movements tend to be seasonal; but this is more the result of seasonal rhythms in rainfall and in hot weather than of inherent drives in the animals, except during the time when they are migrating to breeding sites.

Members of the nonaquatic species tend in varying degrees toward both nocturnal and fossorial habits, although these two phenomena are not necessarily correlated. The individuals of various species of *Hyla* tend to rest in the trees during the day and, so far as known, never burrow. Members of *Microhyla c. olivacea*, *M. c. carolinensis*, and all species of *Pseudacris* rest beneath objects during the day and range widely at night to feed; and this is apparently true also of one of the toads (*Bufo punctatus*) since nearly all adult specimens, as well as some juveniles, that have been taken in Oklahoma

during daylight have been found beneath rocks or boards (Bragg and Smith, 1943). All of the remainder of the bufos and all species of *Scaphiopus* are definitely fossorial but some specimens of the toads may be diurnal during moist spring weather, and often at other times. In central Oklahoma this is true particularly of large females of *B. cognatus* and *B. w. woodhousii*. In the moister southeastern part of Oklahoma, *B. t. americanus* and *B. w. fowleri* are commonly out during daylight, especially in shaded areas.

The seasonal behavior of these organisms is interesting because it varies not only interspecifically, as is to be expected, but also intraspecifically with age, environmental conditions, and sex. This is especially true of the toads (*Bufo*) as has been shown earlier (Smith and Bragg, 1943; Bragg and Weese, 1942). The young of all of the species of *Bufo* in Oklahoma tend in their first season to be active and to feed both day and night for several weeks after metamorphosis, the exact time depending upon available moisture and interspecific differences in behavior. The young of *B. cognatus*, *B. compactilis* and *B. insidiosus* (all limited to prairies in distribution) remain about the parent pool for some time after metamorphosis and disperse from it only when it evaporates or when they reach an age of approximately two to three months, whichever occurs first. At the other extreme, *B. t. americanus* and *B. w. fowleri* disperse from the pool and scatter widely within a week or less; but *B. w. woodhousii* shows an intermediate condition, the individual young toads wandering gradually away from the region of the pool in moist periods but staying rather close to it if the weather is exceptionally dry during their first two or three months. The movements of young *B. punctatus* are largely unknown, although I have one specimen taken on a dry hillside during daytime and Jones and Derrick (1939) reported young ones active near a pool in daylight.

The food preferences and feeding habits of salientians in Oklahoma are imperfectly known. The hylas apparently feed in the trees, probably mostly upon insects. The ranas and the cricket-frogs (*Acris crepitans*) eat smaller organisms within their normal habitat, the latter being very adept at catching the insects which frequent the banks of pools and streams. The members of the commoner species of *Bufo* in Oklahoma show little food selection, except that they very rarely ingest vertebrates (Smith and Bragg, 1949) and this seems to be true also for the adults of most species of *Scaphiopus* (Bragg, 1944). The spotted chorus frog (*Pseudacris clarkii*) has been seen jumping among weeds, feeding upon small insects. Members of *Ps. streckeri* more commonly frequent road sides and flood plains searching for ground dwelling, nocturnal insects and probably spiders after the manner of toads.

From limited observations, it would seem that food (arthropods) is so abundant in most habitats during the warmer seasons that little in the way of special adaptations has evolved among these animals. All are alike in the essentials of food preference and methods of capture. What the average individual eats depends upon availability and relative size of the food object. It should be recalled, however, that toads are more selective than frogs, and that young spadefoots sometimes behave as though certain insects are dis-

tasteful (Trowbridge and Trowbridge, 1937; Bragg, 1941). Also, there is some indication that adults of all species limited to a prairie distribution do more feeding in the spring and early summer than later in the season.

Breeding Habits

For the study of the evolutionary development of habits during phylogeny the period of reproduction is of special interest, because success or failure at this point in the life of the organism actually determines whether there shall be a phylogeny, and if so, what kind it shall be. A species with unvarying breeding habits is at a distinct disadvantage if the environment changes or if it attempts to disperse to a different ecological community than that to which it is already adapted. On the other hand, habits not too rigidly fixed may gradually become modified (with or without change in the animal's structure) in adjustment to changing environments. Accordingly, the breeding pattern of a frog or a toad has considerable influence upon its distribution and upon the possibility of its dispersal to territory adjacent to its present range.

In Oklahoma, three patterns of breeding behavior among frogs and toads are recognized and clearly correlated with the ecological distribution of the organisms. They are not so clearly correlated with the taxonomic divisions, for they often cut across taxonomic lines in fundamental ways. In a former paper (Bragg, 1945: 52-53) two of these patterns were defined and named as follows:

"There are two principal patterns, one characteristic of those species especially adapted to drier habitats and manifested especially by those limited to the grasslands or other more xeric environment; the other shown by those organisms which inhabit moister environments (woodlands, savannahs, etc.) whether restricted to these habitats or not. . . . For convenience, I propose to call the breeding pattern characterized by a breeding season little influenced by rain the *mesic* pattern; that characterized by no breeding season with all breeding initiated by rainfall, the *xeric* pattern."

The third breeding pattern mentioned above may be called *intermediate* because it has some of the characteristics of both of the others.

It should further be noted that in saying that a species has a xeric breeding pattern I do not imply that it could never breed in a mesic environment, or, conversely, that one having the mesic pattern will not do so in a xeric environment. As a matter of fact, *mesic* and *xeric* are relative terms, each more or less dependent upon the other for meaning. The real point is that forms like *Scaphiopus bombifrons*, limited to prairies and deserts, have developed habits of breeding which adjust them to successful reproduction in these regions. A definite breeding season, for example, would be a distinct disadvantage to any amphibian attempting to live in a desert or grassland country because water would not always be available at the right time. In contrast, in the eastern woodlands, such a breeding season might be an advantage—at least, it would not be a definite disadvantage.

No part of Oklahoma may properly be called desert but several forms

inhabiting the clear-cut xeric environments of desert or semidesert character farther to the southwest extend into the state. It is very significant, however, that not a single western species showing the xeric breeding pattern ranges out of Oklahoma to the east. In all probability, the breeding pattern of the organisms is not the limiting factor, but, rather, is a reflection of habits of ancestors which have long inhabited a xeric region to the west where such a pattern is an advantage. On the other hand, without exception these species whose range merely extends from the east into Oklahoma, somewhere in the state apparently are blocked from further expansion westward partly because of the very habits which characterize their mesic breeding pattern.

Expressed in more physiological terms, one can say that those frogs and toads having the mesic breeding pattern have a physiological cyclic nature involving internal factors such as hormonal control of the reproductive cycle. By contrast, in those having a xeric pattern such internal control is modified. The xeric forms are actually physiologically adjusted to the sudden changes in conditions of moisture so characteristic of xeric regions. The contrast in the two principal breeding patterns is, therefore, a difference in cyclic and non-cyclic rhythms, the former fitting the organism to life in more moist (mesic), the latter to life in drier (xeric) regions. On this view, the intermediate breeding pattern may be considered as a partial adaptation to xeric conditions through an incomplete (or at least different) change in the cyclic rhythm; and thus, in evolution, may be interpreted as physiological adjustment to intermediate ecological conditions.

For convenience of reference, one may divide the reproductive period of individual frogs and toads into the following periods: (1) the initiation of breeding behavior, (2) migration to breeding sites, (3) sex recognition and mating, (4) reproduction and fertilization of eggs, (5) tadpole development, (6) metamorphosis, and (7) dispersal of the young from their natal aquatic environment. Each of these is discussed below in relation to the three types of breeding patterns given above.

(1) *The Initiation of Breeding Behavior*

Three principal factors seem clearly to be involved in the initiation of the breeding in frogs and toads in general: (a) hormonal control, (b) the cytological cycle in the gonads, and (c) environmental factors, especially prevailing temperature and amounts and distribution of rainfall. The mesically adapted species emerge to breed within a definite seasonal range, usually in early to mid-spring (Bragg and Smith, 1943). The breeding season is, therefore, clear-cut and definite. In Oklahoma the following species are in this group: *Bufo terrestris americanus*, *B. woodhousii fowleri*, *Hyla* (all species), *Microhyla c. carolineusis*, *Rana catesbeiana*, *R. palustris*, *R. clamitans*, both subspecies of *R. areolata* and *Pseudacris streckeri*. The xerically adapted species, on the other hand, tend not to have a breeding season (except as limited by temperature) but, instead, to follow the rains in breeding. This group in Oklahoma is composed of *Ps. clarkei*, *B. cognatus*, *B. compactilis*, *B. insidiosus*, *Microhyla c. olivacea*, and all four species of *Scaphiopus*. The intermediate group contains all of the other known species in Oklahoma. In

these (*Acris crepitans*, *Ps. triseriata*, *R. berlandieri*, *B. w. woodhousii*) breeding behavior is initiated by rainfall at times; at other times, however, by internal factors not too well understood, although probably wholly or partially hormonal in nature (see Rugh, 1935, 1937, 1937a). *B. w. woodhousii* and *R. berlandieri* are puzzling in this regard, for some individuals of both will breed from early to mid-spring, irrespective of rainfall but others in the same locality will await the rains of summer or fall. The common leopard frog of Oklahoma has been known to breed in every month from February to September inclusive; and in January, 1942, I found tadpoles of this species which had survived the winter and which must have come from eggs laid after rains the previous October or November. In February, 1946, tadpoles were found which came from a breeding congress observed the previous September. Tadpoles also over-wintered near Norman, Oklahoma, during the dry winter of 1946-47. The breeding pattern of *R. berlandieri* is so radically different from that of the mesically adapted *R. p. pipiens* Schreber of the eastern portion of the United States that I have consistently maintained that it must be taxonomically distinct from the eastern forms.⁴ *R. p. pipiens* as I have observed it in Maine, New Hampshire, Massachusetts, Maryland, New York, Michigan, Wisconsin, and northeastern New Mexico has a distinct breeding season whose early limit is modified by temperature (I have found eggs in February in Maryland whereas in Maine breeding usually does not begin until early April). By about May 15 in the East all breeding has ceased, the breeding season has closed, and even torrential rains in June, July, or August have no effect in stimulating further breeding (cf. Wright, 1920, and Wright and Wright, 1933, 1942).

Noble and Aronson (1942), in a valuable experimental study on the breeding behavior of the leopard frog of Vermont (presumably, *R. pipiens* Sch.) show that initiation of breeding behavior in this species involves ovulation under stimulation of the anterior pituitary hormones followed by a receptivity of the female to the male. They deduce from their laboratory study that, in nature, both male and female are simultaneously stimulated by a complex of environmental conditions at the proper time in the seasonal rhythm, that ovulation then ensues, and clasping and egg laying follow. They lay stress on this sequence of events and apparently think that their results are in conflict with some of my own interpretations (Bragg, 1941d). They say, "Bragg believed that rain and other environmental conditions during the proper season stimulate the pituitary. The sexually excited male, Bragg said, now clasps the female; amplexus in turn stimulates the female pituitary

⁴This form would be *R. brachycephala* according to Kauffelt (1937). Whether *brachycephala* is distinct from *pipiens* or not has no bearing on the question here discussed because both are mesically adapted forms essentially alike in breeding patterns. The Oklahoma frog has recently been referred to *R. pipiens berlandieri* Baird by Mittleman and Gier (1942), but Moore, (1946) still insists that it is *R. pipiens* Schreber, which he thinks to have indistinct ecological variants in various positions of its very wide range. So far as technical naming is concerned, he may be correct. I am certain that the forms in Oklahoma differ in habit patterns from their eastern and northern counterparts. I here follow Mittleman and Gier in part.

and ovulation ensues. This sequence is untenable for *Rana* where the female will not permit the male to retain his clasp unless ovulation is almost complete."

This outline fits perfectly my statement concerning those forms which *breed only after rain* (i.e., those having the xeric breeding pattern). Concerning others, in the same paper I said, "In other species wherein a breeding season occurs irrespective of rainfall, factors other than rainfall, of course, start the cycle of breeding activities; but in those (e.g., *Rana berlandieri* and *B. w. woodhousii*) whose breeding season is modified or extended by the coming of the rain, either some internal factor alone, or rain alone, or the two of them working together at times stimulate the pituitary of the male, the remainder of the cycle progressing as before." Whatever the details may be, the essential point is that what applies to a mesically adapted species like *Rana pipiens* does not necessarily apply to a xerically adapted form like *Bufo cognatus* or to a form like the leopard frog of Oklahoma, called by me *Rana berlandieri*, which behaves differently from either the mesically adapted or the xerically adapted species. I am convinced that Noble and Aronson are substantially correct for the frogs which they studied, but I am also convinced that their results cannot be applied to Salientia in general, particularly to xerically adapted forms. (For further discussion, including detailed evidence, see Bragg, 1937, 1940, 1940a, 1940b, 1940d, 1941, 1941d, 1942, 1942b, 1943, 1943a, 1944, 1944a, 1944b, 1945, 1945a; Bragg and Smith, 1942, 1943.)

(2) *Selection of and Migration to Breeding Sites with Diverse Habitats*

The frogs and toads of Oklahoma may be classified into (a) those which migrate little or none to reach a breeding site, and (b) those which characteristically migrate considerable distances. The first group includes those whose habitat is in or near water (all *Rana*, and *Acris crepitans*). The second, of course, contains the aboreal, fossorial, and, in general, the more nearly terrestrial species (in *Hyla*, *Bufo*, *Microhyla*, *Scaphiopus*, and *Pseudacris*). In the first group active selection of breeding sites is rare or nonexistent; in the second, it is common although not universal.

There is some evidence that so-called selection of breeding sites is, in some forms, no more than the chance result of the marked attraction of the calls of males which happen to arrive first at a given pool. In other species, there seems to be a clear selection of one or a few types of sites among several types which are equally available. (See Fig. 15.) In each case "selection" may or may not cut across taxonomic lines. The following discussion illustrates this:

In an earlier paper (Bragg and Smith, 1942) notes were given on the breeding sites of frogs and toads based upon four years of field studies in Oklahoma and immediately adjoining areas. Observations have continued each year since that time; now a total of about ten seasons gives a fairer basis for generalizations concerning many species inhabiting the area. Breeding congresses and pools inhabited by tadpoles have been examined in every county in the state but the most detailed data are available from the area within a twenty-five mile radius from Norman, Cleveland County. Some

species in Oklahoma have been seen hundreds of times whereas a few known to be present have not been seen at all during breeding. A few have been discovered only rarely but the majority of the twenty-seven forms known in Oklahoma have been studied in at least ten different pools, some in as many as fifty or more.

Recently it has become possible on approach to a given pool to predict the species of tadpoles to be found in it (or recently metamorphosed juveniles about it) with a fair degree of accuracy. At first the basis of prediction was vague and subjective, being derived from unconscious correlations made through experience. But since predictions must have an objective basis (even though a complex one), an attempt has been made to analyze the major factors in it. The results of this analysis are given below and some of the factors for several species illustrated in the figures.

In correlating field observations of this sort, care must be taken to avoid the many possible sources of error. For example, the tadpoles or juveniles may not be present at a given time and place for one of the following reasons: (1) The pool may have been formed under weather conditions inhibiting breeding of some species. This will often be true in prairie, for example, among those species (e.g., *Bufo cognatus*, *B. compactilis*, *B. insidiosus*, *Microhyla c. olivacea*) that have the xeric pattern of breeding. (2) A species may be rarely represented in the neighborhood of the pool and, through chance, all males may have happened upon other pools in the region rather than the one examined. (3) Males may have called here in small numbers only and all females may have been attracted by the louder clamoring of more males about adjacent pools and hence laid eggs in them (more especially true of species limited to prairie). (4) Breeding may have occurred but all tadpoles may have succumbed to predators in this pool. This condition must be rare but can occur wherever predators occur in large numbers. One case is on record where all of the thousands of tadpoles of *Bufo cognatus* in a buffalo wallow disappeared progressively as tadpoles of a known predator (*Scaphiopus bombifrons*) increased in dominance and individual sizes (Bragg, 1940). (5) There may originally have been many tadpoles, all of which were killed by evaporation of the water; subsequently, the pool may have formed again without further reproductive activity. (6) In several species (e.g., *Acris crepitans*, *Microhyla c. olivacea*, *Rana berlandieri*, *Bufo w. woodhousii*) not all females produce eggs at the first favorable condition within a given season. Should all females near a given pool fail to reproduce, no tadpoles of these species will be found here, even if breeding is known to have occurred elsewhere.

Of course, there may be other factors which should be considered; but enough has been noted to show that unsuitability of a pool for the breeding of any given species is not indicated merely by the absence of tadpoles, even when one knows that the species could have bred prior to a given date in the region indicated. Negative evidence does have some value, however, when consistently negative results can be correlated with one or more characteristics of a pool, such as depth, extent, vegetation, permanence, or contamination.

tion of a specific type; and it is especially useful when correlated with many data of a positive kind on a given species. It has been noted, for example, that *Scaphiopus couchii* and *S. hurterii* are found breeding almost exclusively in the shallower pools where both shallow and deep pools seem equally available as hundreds of the animals are breeding. Species of *Bufo* manifest the same tendency, but *Scaphiopus bombifrons* and *S. hammondi* show the opposite. Selection as to depth of water, therefore, tends to serve as an isolating mechanism among groups of species of spadefoots (*Scaphiopus*) but not among species of *Bufo* in regions where these selections are possible to the animals. In playas of the Texas and Oklahoma panhandles, however, species rarely found together may use various portions of a single pool, the spadefoots breeding in the deeper water, the garden toads in the shallows at the edges. *Pseudacris triseriata*, normally breeding in twig or grass strewn pools, also uses playas on the high plains, since these are the only places available in many regions. The adaptability of this species to these situations (and others) is probably one of the main reasons for its wide distribution, for no species of animals can long occupy an area in which its individuals cannot successfully breed.

Some positive observations also must be used with discretion. For example, if one finds tadpoles in a pool or juveniles about it, this affords no assurance in and of itself that the pool was used by the species for breeding. This is evident from the following considerations: (1) juveniles may have migrated here to escape desiccation as their natal pool evaporated. *Rana berlandieri*, *R. catesbeiana*, and *Acris crepitans* are known to have done so in several instances. (2) In streams (or in some pools) a current, not evident later, may have deposited tadpoles in the location where observed. One case involving *S. bombifrons* is known with certainty, and several involving *R. berlandieri*, *R. catesbeiana*, *Bufo t. americanus*, *B. woodhousii fowleri*, and *B. w. woodhousii* were probably of this type.

Some of the factors apparently influencing successful prediction of the use of water as a breeding site are depth, temperature, turbidity, shade (or lack of it), water movements, extent, permanence, type of bottom, presence and relative abundance of potential food (algae and other aquatic plants), associated invertebrate fauna, and nature of the terrain about the site. These factors are, of course, rarely independently acting agencies; all are or may be interrelated. The presence of some invertebrates (e.g., fairy shrimps) suggests temporary water; of others (e.g., clams), permanent water. Extent and depth together similarly indicate temporary or permanent pools, although the type of bottom often influences this. Turbidity influences the types of algae present, as well as the amount produced per unit time; but this also is modified by temperature as well as by the chemical nature of the pool which in turn is influenced by the terrain and the geological nature of the exposed rocks and soil.

In these complex situations it is impossible as yet to trace precisely the interactions of all factors, but those of major importance can usually be delimited roughly. However, a minor influence in one place may become a

TABLE I

Breeding Patterns, geographic and ecological distributions of the twenty-seven species of Salientia in Oklahoma

Species Number	Organism	Breeding Pattern	Geographic Distribution in Oklahoma	Ecological Restrictions	Taxonomic affinities with faunae of other regions
1	<i>B. t. americanus</i>	mesic	Eastern half	Limited to woodland, savannah, and tall-grass prairie (11 forms)	Eastern
6	<i>B. w. fowleri</i>	mesic	Southeastern third		Eastern
9	<i>H. v. chrysoscelis</i>	mesic (?)	Southeast		Eastern
10	<i>H. v. versicolor</i> ⁸	mesic	Eastern half		Eastern
11	<i>H. c. crucifer</i>	mesic	Southeast corner		Eastern
12	<i>H. c. cinerea</i>	mesic (?)	Southeast corner		Southeastern
18	<i>R. a. areolata</i>	mesic	Southeast fifth		Southern
19	<i>R. a. circulosa</i>	mesic	Northeast fifth		Southern
21	<i>R. clamitans</i>	mesic	Eastern third (?)		Eastern
22	<i>R. pulstris</i>	mesic	Southeast corner		Eastern
16	<i>M. c. carolinensis</i>	mesic	Extreme eastern		Southeastern
25	<i>S. huerfii</i>	xeric	Eastern half	Limited to short-grass plains (4 forms)	Western
3	<i>B. constrictilis</i>	xeric	Western third (mostly S.W.)		Southwestern
4	<i>B. insidor</i>	xeric	Western third		Western
27	<i>S. hammondi</i>	xeric	Northwest only		Western
24	<i>S. couchii</i>	xeric	Southwest fifth	Limited to short and mixed prairie	Western
2	<i>B. cognatus</i>	xeric	Western half		Western
13	<i>Ps. clar-kii</i>	xeric	Western half		Southeastern
26	<i>S. bombifrons</i>	xeric	Western half		Western
8	<i>A. crepitans</i>	mixed	Statewide	Semi-aquatic (pond sides, streams)	Southern
20	<i>R. catesbeiana</i>	mesic	Statewide		Eastern
23	<i>R. berlandieri</i>	mixed	Statewide		Eastern
5	<i>B. punctatus</i>	xeric (?)	Spotty in rocky regions		Western
7	<i>B. w. woodhousii</i>	mixed	Everywhere except southeast third	Widely distributed with little or uncertain restrictions ecologically (5 forms)	Eastern
17	<i>M. c. olivacea</i>	xeric	Statewide (?)		Southern
15	<i>Ps. triseriata</i>	mixed	Statewide (?)		Southeastern
14	<i>Ps. streckerii</i>	xeric	Statewide (?)		Southern

⁸ *H. v. chrysoscelis* is ecologically restricted to deep valleys.

major one in another, so no hard and fast rule can be established for any one which will apply to all species. Therefore, after as many data as possible have been gathered for a potential breeding site, the final conclusion inevitably must be based upon the experience and judgment of the observer.

Below are listed terms used in describing breeding sites, and definitions are given indicating quasi-quantitative meanings, where possible. Other less exact terms are used in their usual senses. Both types of terms are sometimes further modified by qualifying adjectives.

A. *Depth*:

- (1) *shallow* is used for water up to 1½ feet in depth.
- (2) *intermediate*—1½ feet but below 3 feet.
- (3) *deep*—above 3 feet.

B. *Temperature* (water or air):

- (1) *cold*—0° to 10° C.
- (2) *intermediate*—11° to 20° C.
- (3) *warm*—21° to 40° C.

C. *Turbidity*:

- (1) *muddy*—visibility through water as standing in the pool practically zero in good light.
- (2) *turbid*—visibility a few inches.
- (3) *semi-clear*—visibility at least 1 foot but with a haze noticeable.
- (4) *clear*—practically no turbidity.

D. *Permanence of water*:

- (1) temporary water—present not more than a few months—usually only a few weeks—site dry at least once a year on the average.
- (2) semi-permanent water—present in some quantity through rather long periods, usually two or more years, but varying with conditions.
- (3) Permanent water—never wholly absent through long periods—many years.

Below are repeated alphabetically the species of Salientia known in Oklahoma. For each is summarized (1) ecological relationships, (2) general region of the state where found, (3) characteristics of typical breeding sites, (4) breeding patterns, and (5) known exceptions. See also Table 1. For more detailed descriptions of the ecological communities, see Bruner (1931), Bragg and Smith (1943), and Blair and Hubbell (1938). For the ecological relations of *Bufo* in Oklahoma see Bragg and Smith (1943), of *Scaphiopus*, Bragg (1944a-45), of *Hylidae*, Bragg (1943).

1. *Acris crepitans* Baird (Northern Cricket Frog)

Geographically unrestricted; ecologically restricted to pool, lake, or stream margins but not often present in heavily wooded sections even near water; breeding in any water which is (1) standing, (2) shallow, and (3) intermediate in temperature; especially abundant if vegetation is protruding and algae are plentiful, hence most common in clear to semi-clear pools, lakes or stream margins, especially on mud flats; seldom about pools with steep banks. Not especially abundant in swamps. Breeding unknown in shallow, clear, buffalo wallows (although feeding and occasionally calling about them). Apparently never breeds in deep water but may use shallows in the edges of very deep lakes or streams. Breeding pattern, intermediate with

tendency toward the xeric pattern. (Figs. 2, 16, 23, 27, 28, 29, 30 show typical breeding sites.)

2. *Bufo terrestris americanus* Holbrook. (American Toad)

Ecologically restricted to woodland, savannah, and tall-grass prairie, hence to the eastern half of the state. Breeding sites are (1) shallow and (2) intermediate in temperature; otherwise, breeding largely unrestricted. Often in very shallow, slow flowing streams as well as in very muddy ditches; may occur in very little water or in edge of large lakes, but uncommon in swamps and other exceptionally low regions. Breeding pattern, mesic. (Figs. 1, 14, 16, 17, 28, 29, 30, 31.)

3. *Bufo cognatus* Say (Great Plains Toad)

Ecologically restricted to grasslands; especially abundant on higher areas of mixed-grass prairie, rare in the tall-grass prairies, but abundant in lower reaches in short-grass plains. Breeding sites are (1) shallow to intermediate, (2) clear to semi-clear, (3) temporary, (4) of intermediate temperature. Very common in buffalo wallows, flooded fields, ditches (if not deep or muddy); unknown in streams in Oklahoma and very rare in sloughs on flood plains. Uses playas in the Texas and Oklahoma Panhandles. Tadpoles are occasionally found in water which was roiled after eggs were produced. Breeding pattern, xeric. (Figs. 10, 15, 18, 23, 26.)

4. *Bufo compactilis* Wiegmann (Desert Toad)

Ecologically restricted to short-grass plains, although rare even in this community in northwestern Oklahoma. Elsewhere more abundant in the higher regions of its habitat than in the lower where it is partly replaced by *Bufo cognatus* (see above). Breeding sites almost exactly like those of *B. cognatus* except (1) often in muddy pools (including the artificial pools known locally as cattle tanks), and (2) more often in water of intermediate depth. Breeding pattern xeric. (Figs. 24, 25, 26, 35.)

5. *Bufo insidiosus* Girard (Northern Little Green Toad)

Ecologically restricted to short-grass plains and to the ecotone between this and the mixed prairie. Most numerous in the mesquite savannah of the Southwest but not really abundant anywhere. Breeding sites seen are exactly like those of *B. compactilis* (except unknown in cattle tanks); the two are commonly found breeding in other common sites. Breeding pattern xeric. (Figs. 8, 26.)

6. *Bufo punctatus* Baird and Girard (Canyon Toad)

Little known; rare in western and northwestern Oklahoma in short-grass plains. Common in rocky regions, especially in Wichita Mountains. Only sure breeding sites, rocky pools, clear, very shallow, in stream beds. Juveniles taken twice near cattle tanks (semi-clear, one deep, the other intermediate, both semi-permanent). Breeding pattern unknown, but probably xeric. (Fig. 9.)

7. *Bufo woodhousii fowleri* Hinckley (Fowler's Toad)

Ecologically limited to woodland and geographically limited to eastern Oklahoma. Abundant in southeast, rarer to the north, tends to inhabit lower areas of its region and to be replaced higher up (especially on mountains) by *B. t. americanus*. Tends to intergrade with *B. w. woodhousii* along a narrow zone from Ottawa County southwestward to western Choctaw and eastern Bryan counties, except in Sequoyah County where it is largely replaced along the Arkansas River by *B. w. woodhousii*. Breeding sites are (1) shallow, and (2) high intermediate to warm. Common in all sorts of pools, ditches, river and lake margins, small creeks, and flooded fields which are shallow and warm. Breeding pattern, mesic.

8. *Bufo woodhousii woodhousii* Girard (Rocky Mountain Toad)

Ecologically generally unrestricted over most of the state although replaced by *B. w. fowleri* in the east, especially in southeast. In prairie, it finds its best habitat in lower regions, including flood plains of rivers, and is imperfectly replaced in high areas by *B. cognatus* in the northwest. Breeding sites almost unrestricted in general type. Best sites are (1) shallow, (2) intermediate in temperature, (3) semi-clear to turbid, (4) temporary to semi-permanent. Tadpoles have exceptionally been found in shallow flowing creeks nearly saturated with lime, in very muddy cattle tanks, and even in artificial, concrete or metal containers, in water from two inches to three feet in depth. Breeding pattern, intermediate. (Figs. 10, 11, 12, 15, 23, 26, 28, 33, 34.)

9. *Hyla cinerea cinerea* (Schneider) (Green Tree Toad)

In Oklahoma known only from the valley of the Mountain Fork River, McCurtain County. Breeding pattern, mesic, as observed elsewhere; unobserved in Oklahoma.

10. *Hyla crucifer crucifer* Wied (Spring peeper)

In Oklahoma known only from the east. Breeding observed only a few times in Oklahoma. Breeding pattern mesic.

11. *Hyla versicolor chrysoscelis* (Cope) (Smooth Tree Toad)

Replaces *Hyla v. versicolor*, at least partly, in the valley of Little River, McCurtain County, and in the valley north of Rich Mountain, LeFlore County. Breeding observed once each in these, in shallow heavily vegetated pools. Breeding pattern unknown; probably mesic, like its close relative, *H. v. versicolor*. (Fig. 6.)

12. *Hyla versicolor versicolor* (Le Conte) (Common Tree Toad)

Ecologically restricted to woodland and savannahs, tending to follow flood-plain forests westward into grassland, especially in the south. Breeding sites in pools which are (1) shallow to medium depth, (2) intermediate to warm, and (3) typically but not always shaded. Most abundant if pool has

many plants protruding through surface. Permanence and turbidity seem to have no influence. Seldom in flowing water, never in water with strong current, although sometimes in shallows along edges of creeks or rivers. Exceptionally in prairie pools near woodland or ravines connecting to woodland. Breeding pattern, mesic. (Figs. 16, 27, 28, 29, 30.)

13. *Microhyla carolinensis carolinensis* (Holbrook) (Southern Narrowmouth Toad)

Restricted in Oklahoma to the eastern portion from Delaware and central Cherokee counties, central Latimer to eastern Choctaw counties and eastward of these. Uncertain in the Arkansas River Valley of Sequoyah County but present at Fort Smith, Arkansas. Intergrades with *M. c. olivacea* at least in Latimer County. Breeding has been observed in Oklahoma, in warm, shallow, well vegetated pools in May and June; once its tadpoles were found in a turbid, shallow cattle tank. Several congresses have been heard or seen in bright afternoons although nocturnal congresses also occur. Breeding pattern mesic. (Figs. 6 and 7.)

14. *Microhyla carolinensis olivacea* (Hallowell) (Northern Narrowmouth Toad)

This subspecies replaces *M. c. carolinensis* west of the latter's range in Oklahoma but is present with it at Fort Smith, Arkansas. Within its range it seems little restricted ecologically except that it rarely or never occurs on lower levels of extensive flood plains. It breeds in any water which is (1) temporary, (2) shallow to intermediate, (3) intermediate to warm, and (4) with no current. It is most abundant in well-vegetated pools, especially if vegetation is protruding through the surface. Breeding pattern, xeric. (Figs. 10, 16, 18, 19, 23, 28, 29, 30.)

15. *Pseudacris clarkii* (Baird) (Spotted Chorus Frog)

Ecologically restricted to the grasslands community or present in smaller numbers in very open savannah or in islands of prairie in thicker savannahs. Never present in real woodland. Rarer in tall-grass prairie than in mixed and short-grass prairies. Absent or rare on large flood plains. Breeding in pools which are (1) shallow to intermediate, (2) warm to cold, (3) typically well vegetated (never has been found in completely barren pools), (4) temporary, (5) often, but not always, intermediate to clear. Never in permanent water; not in flowing water. Breeding pattern, xeric. (Figs. 10, 23, 30.)

16. *Pseudacris streckeri* Wright and Wright (Northern Ornate Chorus Frog)

Probably unrestricted ecologically but uncertain in the high plains of Northwestern Oklahoma and unknown in the southeastern low areas. Breeding sites varied: typically (1) shallow to intermediate, (2) cold to intermediate, (3) temporary, (4) well vegetated. Often in sloughs on flood plains, ditches, and flooded fields. *Never* in flowing creeks. Sometimes breeding in ice water and males have been collected calling during a sleet storm at an

air temperature of 0° C. Breeding pattern, mesic. (Figs. 5, 10, 12, 14, 16, 19, 23, 28, 29.)

17. *Pseudacris triseriata* (Wied) (Striped Chorus Frog)

Ecologically unrestricted but tends to be abundant as *Ps. clarkii* tends to be absent; hence, common in woodlands, savannahs, and tall-grass prairies, rarer in mixed-grass and short-grass prairies. Breeding in almost any sort of pools or creeks (buffalo wallows in prairies, ditches, sloughs, flowing or still). Uses playas in Texas Panhandle. I have found males calling at the edges of very fast flowing streams (and have taken eggs from such waters) and at pools at temperatures from near freezing to about 80° F. Breeding pattern, intermediate. (Figs. 4, 7, 14, 16, 19, 21, 30.)

18. *Rana arcolata arcolata* Baird and Girard (Southern Crayfish Frog)

Relatively little known. Has been seen calling in extensively flooded fields and ditches in southeastern Oklahoma in April after extensive rain (observation of Dr. Chas. C. Smith) and in February and March; was not calling in same region after heavy rains in June. Breeding pattern, probably mesic.

19. *Rana arcolata circulosa* Rice and Davis (Northern Crayfish Frog)

Known (in Oklahoma) only in the northeast. Breeding seen only rarely. Reports from others suggested a mesic breeding pattern and general habits similar to *R. a. arcolata*.⁵ I have recently confirmed this.

20. *Rana catesbeiana* Shaw (Bullfrog)

Geographically unrestricted but ecologically restricted to edges of deep pools, river sides, and lakes. Breeding in slightly deep water (never in shallows). Juveniles sometimes about shallow ditches in which they were not produced. Breeding pattern, mesic.

21. *Rana clamitans* Latreille (Green Frog)

Known in eastern Oklahoma (one record in the literature also from Lincoln County) where it is mostly restricted to swamps, muddy banks of streams or pools, and other swampy areas. Breeding observed in June in Oklahoma; some were heard calling along two swampy creeks one night in June just *before* an extensive rain. Breeding pattern probably mesic here as elsewhere.

22. *Rana palustris* Le Conte (Pickerel Frog)

Known in Oklahoma only from three specimens taken in McCurtain County. Breeding here unobserved, probably has mesic breeding pattern here as elsewhere.

⁵I am indebted principally to my student, Mr. Harold Dundee, for notes on the breeding of this form.

23. *Rana berlandieri* Baird (Southwestern Leopard Frog)

State-wide in distribution and present in all habitats permanently or temporarily moist. Breeds in standing or very slow flowing water of all sorts up to three feet in depth, and at all seasons from February to September (observed) or later (inferred from indirect evidence). Breeding pattern intermediate with a tendency toward the xeric. This is different from its counterpart farther north (*R. pipiens* Schreber) which has a clear-cut mesic breeding pattern. (Figs. 1, 4, 5, 10, 12, 14, 16, 19, 23, 28, 29, 30.)

24. *Scaphiopus bombifrons* (Cope) (Plains Spadefoot)

Distributed both geographically and ecologically essentially as *Bufo cognatus* Say, but known slightly farther east. A grassland form only; absent from or uncommon on river flood plains. Breeding in pools (1) temporary to no more than semi-permanent, (2) intermediate and warm, (3) typically intermediate to deep (*rarely* in shallow water). Turbidity and water temperature (within reasonable limits) have no effect in the selection of breeding site, as do extent and depth. Shallow pools of small extent not used if deeper and larger ones are available in the same region. Shallow and extensive areas preferred to shallow and smaller pools, but of these, deeper regions are more attractive than the shallower portions. Breeding pattern, strictly xeric. (Figs. 3, 17, 20, 21, 23, 32, 35.)

25. *Scaphiopus couchii* Baird (Southern Spadefoot)

Distributed essentially with *Bufo compactilis* but not extending quite so far north; hence, limited in Oklahoma to short-grass plains and mesquite savannah in southwest. Breeds in pools (1) temporary, (2) shallow to intermediate (most commonly the latter, almost never in deep water). Commonly breeds with *B. compactilis*, sometimes with *B. cognatus* but seldom with *S. bombifrons* because it tends to select shallower pools than the latter. Breeding pattern strictly xeric. (Fig. 26.)

26. *Scaphiopus hammondii* Baird (Western Spadefoot)

In Oklahoma known in western portions only including the eastern and western Panhandle and Greer and Beckham Counties. Breeding in Oklahoma unobserved. In New Mexico, using same sorts of sites as *S. bombifrons*. Tadpoles found in Beaver County in playas and in Beckham County in a ploughed field with those of *S. bombifrons*. Breeding pattern, xeric. (Figs. 13, 22, 32, 35.)

27. *Scaphiopus hurterii* Strecker (Savannah Spadefoot)

Ecologically limited to woodland and savannah but extending westward in the flood-plain forests fringing the larger rivers. Breeding in pools (1) temporary, (2) very shallow to intermediate (unknown in deep pools and in five instances found in the shallower of two adjacent pools). Turbidity has no effect but amount of vegetation may have (more commonly breed where vegetation protrudes but this may be only because more shallow). Tempera-

ture relations uncertain. Observed only a few times. Breeding pattern, xeric. (Figs. 14, 16, 19, 30.)

Some Details of Breeding Habits

A return to the consideration of the behavior of *Bufo* and *Scaphiopus* as they approach a breeding site proves especially interesting. Individuals of *Scaphiopus* are outstanding in the marked attraction of the male's breeding call for individuals of either sex. The first spadefoot male to reach a pool begins calling and others of either sex within hearing distance hurry toward the sound. In studying *S. bombifrons* and *S. hammondi*, I have frequently observed pools in late afternoon without evidence of a single animal but at ten to eleven o'clock the same night there were hundreds present and others still migrating in. Not only this, but in at least ten instances with *S. bombifrons*, I have watched the progressive development of such a congress. In all cases, there were only a few males to be found in the early phases; later, here and there a new voice was heard and individuals could be found on the bank and by another half hour the area within two hundred yards of the pool in all directions was swarming with spadefoots migrating toward the water. Claspings pairs are often found in such large aggregations as early as ten P.M. and most eggs that will be laid at any one site under the influence of a single rain are produced on the first night. Less extensive observations of the same type have been made upon *S. couchii* and *S. hurterii*, but they indicate that these species undoubtedly follow the same general pattern.

Members of the genus *Bufo* in Oklahoma differ more, interspecifically, than members of *Scaphiopus* in these matters. As stated above, all tend to use shallow water and the calls of the first males to arrive at a pool attract other individuals. It has been shown, however (Bragg, 1940), that, with *B. cognatus*, the place where eggs are to be laid is largely determined by the behavior of the female rather than by the place where the male calls. Males call from any temporary water that they may find but females pay little attention to them unless the water is six inches to one foot in depth. When males about shallow pools fail to find females, they migrate to larger pools where others are calling. Thus, during the first night a huge chorus consisting of most of the adult male population of an area of some acres becomes congregated in one or a few pools. Females during this time are often inactive, sometimes in nearby pools (Bragg, 1937) although a few may go to the males and actually produce eggs. Most often daylight comes with hundreds of males, and at most only an incidental female, in the congress. In cases where several pools of the proper types are available within a given area, several correspondingly smaller congresses may, of course, develop. In any case, the typical result of the first night's activity is (1) huge numbers of available males in a small area, (2) females in abundance near the pool (usually not in it), and (3) a very small amount of actual reproduction, often none at all.

The approach of daylight typically stops the calling, although several

daylight choruses have been observed. Toads of both sexes remain in the vicinity of the pool through the day, sometimes in the pool itself, more often buried near its edge or resting in shallow burrows such as have earlier been described (Bragg, 1937). With the coming of twilight (or even of more rain in late afternoon) the chorus breaks out rather suddenly and within a half-hour or so reaches its full development. Females react by entering the pool, clasping occurs, and eggs are laid.

Thus, most eggs are laid during the second night (Bragg, 1942b) and on into the following day. During the third night or even the fourth, a few males which have not succeeded in attracting females may call and, should another heavy rain occur in the interim, males are further stimulated. It seems probable that females are also affected, for during very frequent and heavy rains in May and June, 1941, in central Oklahoma, large choruses of *B. cognatus* were heard practically every night for a month; and, later, young recently metamorphosed toads of at least three different ages were collected in several single breeding areas (Bragg, 1942e).

Peculiarities in the physiological adjustment of females in this prairie toad are shown by the fact that even on the nights of heaviest breeding activity some females continue to feed along the roads apparently not attracted by the loud clamoring of the males. This probably explains why periods of breeding activity continue to occur after rains throughout the summer—not all females are ready to lay eggs nor are they receptive to males at the same time. This again indicates a sort of eccentric rhythm in this xeric form (and possibly others).

This typical pattern of the breeding behavior of *B. cognatus* is reviewed here in some detail in order to compare it with that of other species. *Ps. clarkii* Baird behaves in much the same manner as *B. cognatus* in producing eggs on the second night after a rain (Bragg, 1942e), often developing huge congresses of males on the first night. *Microhyla c. olivacea*, *Ps. streckeri*, *B. w. woodhousii*, *B. t. americanus*, and *Hyla v. versicolor* differ radically from it. *M. c. olivacea* develops large congresses after rains but clasping pairs (and females migrating into the pools) may be found within an hour after the first calls are heard in a given place. Since in unmated females, captured as they are entering pools and retained overnight, eggs do not ooze from the cloacal opening, whereas in those taken from clasping males in a pool they usually do so, it is probable that ovulation does not occur in this species except under the influence of the male's clasp (contrary to Noble and Aronson, 1942, on *Rana pipiens*). Nearly all eggs are laid the first night. However, not all females enter pools during one night and, for this reason, reproduction is prolonged through the summer, males calling and some females laying eggs during or immediately after each rainy period, as in *B. cognatus*. I have frequently taken clasping pairs and found eggs in pools containing well-developed larvae of at least two ages and have found active breeding taking place in a pool simultaneously with the emergence and metamorphosis of young on two occasions. One would not find such a situation as this with a mesically adapted frog such as *R. pipiens* or *R. catesbeiana*.

Ps. streckeri is like *B. cognatus*, *Ps. clarkii*, and *M. c. olivacea* in developing huge congresses after rains, but is unlike them in not being dependent upon the stimulus of rain for initiation of breeding behavior of males. Males call in winter and spring, in greatest numbers after rains of considerable volume (1–2 inches). Females, however, seldom join males except during or just after rainfall (Bragg, 1942), and even the males fail to call in exceptionally dry years. Members of *B. t. americanus* and *H. v. versicolor*, while greatly stimulated by rain during spring, nevertheless breed only within a definite breeding period. Except that this both starts and ends later in the season, they resemble *Ps. streckeri* in this. *B. w. fouleri* has a breeding season beginning only after nights have become quite warm and ending toward midsummer. Its close relative, *B. w. woodhousii*, breeds intermittently, some individuals as early as in March, others as late certainly as in August and perhaps in September (Bragg, 1940a).

In summary, in Oklahoma there is much variation between species in the initiation of breeding behavior and in the migration to breeding sites. There is no simple universal pattern such as is often implied for many species of Europe and for most forms living in the eastern United States. Some species manifest a breeding season, others do not; some breed only after rain of one-half inch or more; others, irrespective of rains; still others, mostly after moderate to heavy rain, although some individuals breed each year whether rains come or not. Some closely related species, even in the same subgenus (*Scaphiopus*), differ in sensitivity to so great an extent that they react differently to the amount of rain and to its rate of fall. This is true, for example, of *S. hurterii* and *S. couchii*, the former being stimulated more by the volume of rain, the latter by its rate of fall. (Bragg, 1944a, 1945a.)

(3) *Sex Recognition and Mating.*

The problem of sex recognition may be expressed in the form of questions: How does a male, usually calling in the dark, recognize the object clasped as a female? What sensory cues are used? A partial answer to the first question is that he does not always do so. Various objects, other than females, may be clasped and retained for long periods; I have even seen a male of *B. cognatus* hang tenaciously to a chunk of mud. But no male salientian ever retains his sexual clasp on another normal adult male in a breeding pool. It would seem, therefore, that some behavior, secretion, differential in the sense of touch, or the sound made by a clasped male always stimulates the release mechanism of the clasping male. Also as pointed out by Noble and Ferris (1929), the sensory cues used by the males of one species need not necessarily be utilized by another, particularly when variation rather than constancy appears to be the rule in so many other phenomena in breeding behavior. Even so, one might expect greater uniformity in this matter than in other phases of the breeding pattern, because environmental factors operating during sex recognition are, and apparently always have been, more uniform than those operative outside the water of the breeding site. If constant interspecific variations in behavior are adaptive, as they may well be,

it follows that habit patterns change most during evolution in a varied, as opposed to a uniform, environment.

Noble and Aronson (1942) have reviewed much of the literature on sex recognition. It seems that, of the possible factors considered, most workers are agreed that sight and special secretions have been ruled out for all forms studied so far. Voice of the male and girth or firmness of the female are the factors most constantly favored by the evidence of most workers; but differential behavior of the sexes seems to be of some importance in some species. See Bragg (1940) for observations on *Bufo cognatus*.

Voice plays an important part in many of the Oklahoma species, particularly in *Bufo* and *Scaphiopus*. All species of *Bufo*, except *B. punctatus*, and all of *Scaphiopus* within the state have been studied from this viewpoint. In *B. cognatus* and *B. compactilis*, sexually stimulated males congregate in large numbers in a limited area and behave as though trying to attack each other; each actively tries to clasp those near him. Sometimes there are so many thus engaged that a pool may be a seething mass of struggling males. I have seen as many as five males piled on top of one another, each struggling to retain its sexual clasp upon the one next below. Such piles of clasping males always separate into their component individuals within a period of two to three minutes. However, if a *single* male clasps another in a pool, their separation typically comes about in less than one-half minute. Why should there be this marked difference in time between the two types of cases?

Six seasons of close observation of thousands of individual toads breeding in nature have convinced me that it is largely a matter of voice. When clasped, each male utters a protesting note characteristic of its species and, upon this note's being recognized by the clasping male, is immediately released. But if three or more males are involved, each, except the bottommost and the topmost, are acting under two stimuli at once. They are actively attempting to hold another toad while protesting vigorously to being held themselves. Since each is making so much fuss, it does not immediately recognize the protesting note of the individual directly below it and hence toads in a pile do not separate as quickly as two individuals will do. The protesting notes of these toads are also accompanied by a rapid movement of the sides of the body, caused by rapid alternating contraction and relaxation of the muscles of the body wall. Possibly the sense of touch is involved here instead of (or in conjunction with) hearing. But it seems likely that hearing is by far the more important of the two possible factors, since, in *Bufo cognatus* in nature, males which have not yet developed this protesting note are held by adult males as tenaciously as are mature females, although they may move their sides vigorously as though trying to protest. Some mature and most sexually undeveloped females also do the same thing when picked up by an observer and they may do so when clasped by a male.

I do not believe rigidity of the female's body, which appears to be significant in some frogs (Noble and Ferris, 1929; Noble and Aronson, 1942) to be important in *B. cognatus* nor *B. compactilis*, and I question it for other species of toads (*Bufo*). It is often emphasized that the female's body be-

comes rigid and swollen with eggs and thus has greater girth or firmness. The female is supposed to be released by the male's sensing a greater flabbiness or a lesser girth after eggs are laid. This may well apply to some ranas, as Noble and Ferris have shown, although I do not see how the increase in jelly about the ovulated eggs in the uterus (Noble and Aronson, 1942) can be a factor, since there is no such jelly in any significant amount until the secretion of the oviduct swells to form it after the eggs are laid. Also, if ovulation occurs only after clasping in these species (as I have thought probable) then there are no eggs in the uterus when the male clasps.

Females and juveniles of both sexes of *B. cognatus*, *B. compactilis*, *B. t. americanus*, *B. insidiosus*, *B. w. fowleri*, and *B. w. woodhousii*, when picked up by an observer, and often when clasped by a sexually excited male of any species, typically take large quantities of air into the lungs and sometimes become so rigid and rounded that a common three-celled flash light may be sufficient illumination to see the outline of the viscera through the skin of small to medium-sized individuals. This is primarily a protective mechanism. I am not certain whether this rigidity is retained during normal egg laying; but I am certain that it is by females which have laid their eggs and are subsequently clasped. Under these conditions, I cannot believe that rigidity or girth of the female's body has any but the most minor effect on sex recognition in these toads.

In *Hyla v. versicolor*, the male also "protests" when clasped or trodden upon during breeding activities, but the male of *Microhyla c. olivacea* apparently does not. (However, I have had only limited opportunity to observe the latter at this stage). I have also failed to note a warning croak in the female of *Rana berlandieri* such as described for *R. pipiens* by Noble and Aronson (1942). This, plus the many other detailed differences in breeding habits in these two frogs already reported above (see also Bragg, 1941, 1941b, 1941d.) makes it at least possible that the mechanism of sex recognition is somewhat different in these two closely related forms.

In Scaphiopus, voice appears to be the principal factor, at least in *S. bomifrons*, *S. hammondi*, *S. couchii*, and *S. hurterii* (Bragg, 1945). My observations on the remainder of the Oklahoma species of Salientia are inconclusive on this point.

(4) *Production and Fertilization of Eggs.*

My observations have shown less about this phase of reproduction than about any other, but the following should at least be noted: (a) Individuals of some species take a much longer time for egg-laying than others. Thus, *Bufo cognatus* commonly requires from ten to twelve hours and *Pseudacris clarkii*, six to eight; whereas *Microhyla c. olivacea*, *Rana berlandieri*, *Hyla v. versicolor*, and all species of Scaphiopus in Oklahoma require much less time, whether in a pool or in the laboratory. (b) Some species produce all of the eggs of a clutch at one time and place; others lay a few eggs here, some more there, scattered about in a pool. To the first group belong all of the

bufos and ranas⁶ of Oklahoma, *M. c. olivacea*, *H. v. versicolor*, and typically *S. hurterii* and *S. couchii*. To the second belong *S. bombifrons*, *S. hammondi*, *Ps. clarkii*, *Ps. triseriata* and probably *Ps. streckeri* as well. Since females of *Acris crepitans* lay their eggs singly or in small masses (Smith, 1934), this species should also be classified with the second group. In general, those species which attach their eggs in a definite arrangement to submerged vegetation belong to the second group. *Ps. clarkii* is especially interesting from this view point. The eggs are laid in very small masses, ten to twenty or so in a bunch, attached to grasses or sedge leaves (sometimes to weeds and other such objects) and placed just beneath the water surface, almost never more than three inches below it, irrespective of the depth of the water. I have never observed the actual laying of the eggs in nature but I have found pools in which hundreds of such small masses of eggs could be seen after a large breeding congress. Since the egg complements of the females are invariably large (in round numbers about 1,000; Bragg, 1943b, 1943c), it follows that the mated pairs must move about during egg deposition, depositing these small groups of eggs here and there on the vegetation. *Ps. streckeri* (Bragg, 1942) and *S. hurterii* (Bragg, 1944a) also lay eggs near the surface of the water attached in irregular masses to vegetation. Both of these, however, merely crawl about in a limited area as the eggs come, much as paired toads do on the bottom, rather than move definitely from one place to another after the manner of *Ps. clarkii*. *S. bombifrons* has similar habits but typically attaches its eggs deeper in the water. In very shallow pools, however, *S. bombifrons* may lay its eggs in small masses widely scattered, (Bragg, 1941, 1943). In one case, such a small mass hatched six out of only seven eggs that had been laid. *S. hurterii* also sometimes scatters small bunches of eggs about.

(5) Tadpole Development.

The most striking thing in tadpole development in Oklahoma is the marked variation in developmental rates manifested at different times and places. Two factors are operative here, one of which is entirely environmental, the other protoplasmic. The principal environmental factor is temperature, low temperatures retarding development markedly, and high temperatures, within physiological limits, greatly speeding the process. The protoplasmic factors are not well understood but their effects are perfectly obvious where developmental rates differ in a single pool, as is often the case. An example of this follows.

The pool chosen for illustration had been formed during heavy rains by a road which, serving as a dam, had backed water into the oak-hickory woodland forming a muddy pool of about one-half acre in extent which varied in different parts of it from a few inches to about three feet in depth (Fig. 30). During and immediately after the rains the following species were found breeding here: *Bufo t. americanus*, *Hyla v. versicolor*, *Pseudacris streckeri*, *Microhyla c. olivacea*, *Scaphiopus hurterii*, and *Rana berlandieri*. Later, other breeding congresses of some of these species occurred here and,

⁶ *R. berlandieri* is a possible exception. See Bragg (1944).

eventually, tadpoles of at least three ages were developing simultaneously. Close watch was kept of this pool till midsummer when all water had disappeared through evaporation. The tadpoles of the first breeding congress were large enough before other eggs were laid to distinguish them at a glance from the younger individuals. The pool was originally formed in April and the last tadpoles metamorphosed in late June. During May the weather gradually warmed, until by June 1 and thereafter water temperatures in early afternoon were quite high (30° – 35° C.) and on exceptionally warm days even higher. We are principally concerned here with those tadpoles which resulted from the first breeding congress.

Metamorphosis of these tadpoles was finished as follows: (1) *S. hurterii*, on the twenty-first day after eggs were laid.⁷ At this time young were found on the bank and no tadpoles could be captured with a dip-net in the water; (2) *M. c. olivacea* on the twenty-eighth day (first young out of the water on the twenty-sixth); (3) *B. t. americanus*, on the thirty-first day (first young on the eighteenth); (4) *H. v. versicolor*, on the forty-first day (first young on the thirty-ninth); (5) *Ps. streckeri*, on the forty-eighth day (first young on the fortieth); and (6) *R. berlandieri*, on the sixtieth day (first young on the fifty-third). Tadpoles of this species grew exceptionally large before metamorphosis in this pool and several of them died without metamorphosing, probably because of too high temperatures in the pool or from lack of oxygen. That it was temperature is indicated by the facts that when the water at the pool's edge approached 35° C. all sought deeper and cooler portions of the pool; and further, that there was little of the rising to the surface to gulp air that I have often observed in other pools. It should also be noted that at no time did other tadpoles show distress and that only a few even of the frogs were involved, something not to be expected if lack of oxygen were the primary operating factor. During the same time, another pool of intermediate character nearby was also under observation. (Fig. 29.) In it, *B. t. americanus*, *Ps. streckeri*, and *H. v. versicolor* which metamorphosed by June 1 came through beautifully and hundreds emerged. But younger individuals on this date soon began to die and very few succeeded in metamorphosis. There were no frog tadpoles in this second pool with which to compare those in the first. Such observations as these have been made sufficiently often during the past six years to warrant the following conclusions: (1) Intrinsic specific developmental rates are the rule among Oklahoma frogs and toads. (2) Metamorphosis is hastened in all species observed⁸ except *R. berlandieri* (see *infra*) by higher temperatures under comparable natural conditions. (3) In general, members of the genus *Scaphiopus* lead all others in develop-

⁷ That there is an innate protoplasmic factor is especially apparent from observations on the early development of *Scaphiopus*. This is not based merely upon a rapid rate of development of the tadpoles but goes back to the embryonic stages, at least in *S. bombifrons*. This was observed by Trowbridge and Trowbridge, 1937, who reported a fast cleavage rate as compared to the usual conditions in North American Salientia.

⁸ *R. berlandieri* and *H. v. versicolor* are the only ones of their genera observed sufficiently from this point of view. Insufficient observation has also been made on *Ps. triseriata*, *B. insidior*, and *B. punctatus* to warrant generalization.

mental rate, *Microhyla c. olivacea* is next, the bufos a close third, *Ps. clarkii* almost as fast as the bufos (faster than some of them), with *Pseudacris streckeri*, *Hyla v. versicolor* following somewhat later and *R. berlandieri* taking the longest time of any observed sufficiently⁹ for conclusions to be drawn.

Rana berlandieri is especially interesting as well as somewhat puzzling. Elsewhere (Bragg, 1940b) I reported that in a fast evaporating pool, half-grown tadpoles may go into metamorphosis and behave as though seeking the bank rather than the deeper water still available. Since those observations were made, I have noticed many times that in deeper pools these tadpoles grow larger and remain longer in a pool before metamorphosis than in more shallow pools. This could be due to temperature differences (in general, the deeper the water the lower the temperature) or it might be an effect of salt-concentration due to evaporation in the more shallow pools. The observations reported above give evidence against temperature as the major factor, for in the deep pool under investigation the animals became large and failed to metamorphose under temperatures sufficiently high to kill some of them.

The behavior of some kinds of tadpoles as they feed in a pool shows nothing of peculiar interest, but there are some in which it does so, especially in Scaphiopus. Recent observations on this genus (Bragg, 1944a, 1945a, 1946) have shown that social aggregation, with or without an accompanying active cannibalism commonly observed in certain species, may have a direct bearing upon survival in a dry climate. As the pool evaporates, developmental rate increases just at the time that food resources tend to run low. In the intense struggle for survival as the water becomes dangerously low, aggregation with its tendency to cut down evaporation rate may save the lives of many tadpoles. If aggregation is accompanied by cannibalism, food is insured for at least a few individuals which in this way have a chance to survive and to metamorphose before all the water disappears. (For detailed evidence of this, see the papers cited.) I have thus far searched in vain among other genera for these phenomena.

(6) *Metamorphosis and Dispersal.*

Once out of water, the behavior of the young differs interspecifically in two significant ways, (a) in methods of protection from desiccation and (b) in time of dispersal. The second of these has already been covered in other connections but the first needs further presentation.

The semiaquatic forms (*Rana*, *Acris*), some of the fossorial forms (*Bufo cognatus*, *B. compactilis*, *B. insidiosus*, *B. w. woodhousii*), and some of the nocturnal species which seek protection beneath objects (*Ps. clarkii*) remain about their natal pool for some weeks. Others of the fossorial species (*B. t. americanus*, *B. w. fowleri*, all species of *Scaphiopus*, *Pseudacris streckeri*, and *Microhyla c. olivacea*) do not. Should the pool disappear immediately after

⁹ It should be especially noted that I am not comparing *R. berlandieri* with the green frog (*R. clamitans*) nor with the bullfrog (*R. catesbeiana*) whose larvae typically do not transform during their first season.

metamorphosis (a very common occurrence in Oklahoma), the young of frogs (*Rana*) and of cricket frogs (*Acris*) migrate overland to other pools, creeks, or rivers. (This applies to the bullfrog in this habitat also.) The toads, however, seek softer ground and become fossorial even if very young. Individuals of *S. bombifrons* burrow immediately upon emergence but those of *S. hurterii* often do not do so for at least two weeks (Bragg, 1944a, 1945a). Thus, habits of dispersal and methods of protection from drying differ inter-specifically even in closely related taxonomic groups, differing sometimes within genera (*Bufo*, *Scaphiopus*, *Pseudacris*). It should also be noted that there is some correlation between these reactions in time and method of dispersal and the breeding pattern of adults. This is to be expected since both types of behavior have evolved in gradual adjustment to environment.

Habits and Taxonomy

The habits of an animal in its normal environment are as characteristic of it as any other phase of its nature. Behavior patterns, since they are a product of evolution, tend (like morphological patterns) to be distributed among organisms in several ways. Broad trends in behavior can be recognized comparable to morphological patterns used in distinctions between orders, families, and other taxonomic groups. We are not surprised, therefore, to find the behavior, habits, and habit-patterns of individuals of a given species overlapping, in some particulars, those of others closely or even distantly related to it, just as morphological patterns overlap. For example, nocturnal feeding is a characteristic of many Salientia just as truly as is the morphological fact that some have dermal plicae.

It should, therefore, be possible to erect a reasonably sound classification of organisms on the basis of habits and habit-patterns alone, consisting of higher and lower categories analogous to those based upon morphology. Practical considerations have prevented the theoretically possible classification from being worked out except in a few instances. See, for example, Plath's (1934) attempts along this line with North American bumblebees.

It is true that morphological characters should serve as the basis of taxonomic distinctions wherever they can be used. But what of the cases in which they fall short? Habits and habit-patterns should be considered wherever they are known to aid in understanding the life of the animal and of its phylogenetic development. If habits and habit-patterns are also products of evolution, these should be used with morphology in classifying organisms and in studying phylogeny, which is, I believe, the goal of taxonomy.

I do not believe that the study of habits has gone far enough as yet to permit their use as more than an aid in taxonomy; but a few illustrations may show some of the possibilities among the Salientia.

(1) *Bufo woodhousii woodhousii* and *B. w. fowleri* are so closely allied that they are "practically indistinguishable except for size" (Smith, 1934). Yet, habits based upon real physiological differences will partly separate them. The former breeds sporadically throughout the spring and summer at

temperatures of 13° C. upward. The latter has a late but consistent breeding season (late April through June in Oklahoma) at temperatures seldom below 21° C. Therefore, in any region where both species may occur, if one is heard calling when the temperature is below about 20° C., it is almost certain to be *woodhousii*. At temperatures above 20° C. or 21° C. in March to mid-April and after July 1, it is again *woodhousii*. Of course, in the height of the breeding season of *fowleri* (about mid-May) and at temperatures above 20° C. the two could not be separated on this basis.

(2) In the leopard frogs, as emphasized previously in other connections, the Oklahoma form differs radically in breeding behavior from its counterpart, *Rana pipiens pipiens* of the East and North, although differing little if any morphologically.

(3) Groups of spadefoots may be separated partially by their breeding reactions; so, also, may species of *Pseudacris*.

(4) Behavior and movements of tadpoles as seen undisturbed in pools are also sometimes distinctive. Most larval Hylidae, and, to a lesser extent, larvae of Microhyla, tend to spend considerable time lying at the surface, especially in late larval life. Ranids, scaphiopodids, and bufonids seldom do so. Bufonids and ranids often feed in the shallows along the edge of the water and scatter widely into the deeper water on disturbance. Scaphiopodids, hylids, and microhylids (at least in Oklahoma) seldom do this. As is well known, young tadpoles are often difficult to distinguish morphologically and I have for several years used such behavior as an aid in recognition. While these methods are not perfect, I have found them to be fairly efficient for provisional naming of tadpoles and then following their development and metamorphosis till they can be recognized by more usual methods.

Let me emphasize again that I do not advocate substituting physiological and ecological characteristics or peculiarities of habits and habit patterns for the usual morphological criteria. But we must study the *whole* organism, including its habits; where morphological characteristics fail us, then we must use the less tangible distinctions as aids in making determinations.

Summary

- (1) Salientia in Oklahoma tend to be ecologically as well as geographically distributed. Some species are essentially unrestricted ecologically (within the borders of the state); others are quite restricted; still others, partially so.
- (2) Those that are unrestricted geographically are, nevertheless, sometimes restricted ecologically, *Rana catesbeiana* Shaw, *R. berlandieri* Baird, and *Acris crepitans* Baird being typical examples.
- (3) Those which are ecologically restricted live in grasslands only, woodlands or savannah only, or in "islands" where one type of community is surrounded by another. Ecologically unrestricted species range geographically more or less indiscriminately through radically different

types of habitats. Those only partially restricted seem equally at home in some different environments but seldom if ever occur in others.

- (4) The habits of the animals tend to vary with their ecological restriction. This is especially true of their reproductive activity. All prairie limited species tend to be more like each other than any of them resemble others which are ecologically unrestricted or which are limited to woodland. Similarly species limited to the woodland-savannah are mostly more like each other than any one of them is to others not so limited.
- (5) It is obvious from the above (4) that even though variations in habit and structure often occur at the same time, habit patterns tend to follow ecological restrictions in habitat rather than change of structure during evolution and dispersal. This means that habits may develop differently in closely related taxonomic groups and that deductions concerning the habits of one species may not apply to a closely related species; and this is more likely to be the case if the two species in question are differently restricted ecologically. A single, versatile, wide-ranging, and ecologically unrestricted species may even have slightly different habits in two ecological communities, especially if these are widely separated geographically so that breeding individuals from one extreme of the range are effectively isolated from those at the other. Trends of this kind are suggested by leopard frogs, by *Bufo w. woodhousii*, and by *B. cognatus*, for example.
- (6) In breeding habits, the Oklahoma frogs and toads fall into three groups, fairly closely correlated with their individual ecological limitations. Each species differs somewhat from all others in the details of behavior, but similarities are discoverable which are termed patterns of breeding behavior and are to be considered as traits or broad tendencies toward adjustment and adaptation to life in ecological niches.
- (7) These patterns are (a) the xeric pattern, exhibited by all species limited to grasslands, by one species of woodland-savannah (*Scaphiopus huerterii*), and by a few less ecologically restricted forms (*Microhyla c. olivacea*); (b) the mesic pattern, shown by all other species of the woodland-savannah, and by the same species limited to ecological islands (*Rana catesbeiana*, *R. clamitans*); and (c) a mixed pattern intermediate between the other two shown principally by *B. w. woodhousii* Girard, (ecologically essentially unrestricted over much of Oklahoma) and by *R. berlandieri*, *Ps. triseriata* and *A. crepitans* (partially restricted to ecological islands).
- (8) The contrasts between the xeric and mesic patterns are the most clear-cut the most closely correlated with life in specific ecological communities. The patterns differ essentially as follows: the xeric pattern is characterized by the following tendencies: (a) use of temporary water only, (b) breeding initiated only by rainfall at proper temperatures (no clear-cut breeding season), (c) calls of males attractive to other males as well as to females, (d) huge breeding congresses and much individual

excitement conditioned by social factors during breeding, (e) a greater tolerance of heat among developing tadpoles in pools, and (f) inherent faster rate of tadpole development (shown clearly only by the spadefoots). The mesic pattern shows the opposite tendencies although in degrees varying with individual species and sometimes with special local conditions.

It is to be noted that these patterns of behavior are subject to individual and specific variations over a considerable range; they are not to be taken as absolutely rigid and fixed in all situations, but rather as traits of behavior, whose relative constancy in the total pattern in any one species is notable.

- (9) Breeding habits, habit patterns, and tadpole behavior are useful to a limited degree as aids in taxonomy and identification.
- (10) These facts are open to the following generalizations:
 - (a) From the nature of the Amphibia, we expect the mesic pattern to be the more primitive.
 - (b) On this assumption, the species of grassland and desert arose from mesically adapted ancestors.
 - (c) In the dispersal to progressively more xeric environments, the various factors in the xeric pattern were developed in evolution where partial barriers in the environment were reached.
 - (d) Those groups (genera or species) that became xerically adapted tended (with some exceptions) to be restricted to xeric environments thereafter; those that became only partially adapted (*B. w. woodhousii*) often were able, later, to have a wider geographic range than their more closely adapted relatives; those that failed to become xerically adapted were either stopped in their dispersal by the environmental barrier (e.g. *B. t. americanus*, *H. v. versicolor*, *B. w. fowleri*) so that their geographic range coincided with ecological range; or they continued to spread to, and to live in, ecologically favorable islands within larger, more xeric, ecological communities (e.g. *Rana catesbeiana*, *R. clamitans*, *Acris crepitans*), and thereby extended their geographic range much more widely than their ecological range would otherwise permit.

There are some points which are still unexplained by the observations above reported. Why should some xerically adapted forms (e.g. *Bufo cognatus*, *B. insidiosus*, *B. compactilis*, *Pseudacris clarkii*) not spread eastward into woodland? If xeric adaptation prohibits this in some groups, why not in all? The genus *Scaphiopus* as a whole manifests the xeric pattern in its extreme form yet two of its species (*holbrookii* and *hurterii*) have invaded and are now limited to non-xeric environments. It is easy to understand why progressive dryness might stop the dispersal of Amphibia in places, but why progressive moistness (or conditions associated with this) should do so in the other direction is still unexplained.

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An Atlas of Breeding Sites for the Salientia of Oklahoma and Adjacent Regions

The following figures illustrate typical breeding sites used by species of Salientia in Oklahoma and adjacent regions. In every case the sites were selected as typical of this or that species or group of species. In many instances data are given concerning the region and ecological picture presented. The species known to have used the pool at least once are listed for each site. Naturally, some wide-ranging and less ecologically restricted species have breeding sites represented several times whereas a few species, which have not been seen breeding in Oklahoma, are not represented at all.

- Fig. 1. Shallow, temporary pool in a pasture near Braggs, Muskogee County, Oklahoma. Photo by Chas. C. Smith, April 29, 1939. Breeding site for *Rana berlandieri* and *Bufo t. americanus*, whose tadpoles were abundant when picture was taken.
- Fig. 2. Rocky pool near Soldier Lake, Wichita Wild Life Refuge, Comanche County, Oklahoma. Picture taken by author, May 6, 1939. Breeding site of *Acris crepitans*.
- Fig. 3. Ditch along Santa Fe R.R. three miles south of Las Vegas, New Mexico. Photo by author, August 17, 1940, illustrating a breeding site of *Scaphiopus bombifrons*. Water is turbid and about three feet in depth continuously replenished from a leaking dam (background of Fig. 32) and overflowing to the short-grass field shown to the right. The trees along the embankment to the left are small willows.
- Fig. 4. A small shallow seepage pool on a hillside in oak-hickory savannah, eastern Cleveland County, Oklahoma. *Rana berlandieri* laid eggs here in a rainy period during the last week in September, 1945. Tadpoles here on February 25, 1946, well developed. Metamorphosed in early May as *Ps. triseriata* was producing eggs in pool. Photo by A. O. Weese, April 7, 1946.
- Fig. 5. Very shallow pool in creek valley at Little Axe, Cleveland County, Oklahoma, in oak-hickory savannah. Breeding site of *Pseudacris streckeri* and *Bufo t. americanus* through at least two seasons. All breeding known here has resulted in loss of all tadpoles from evaporation of the pool.

Fig. 6. Temporary, clear pool, 3-3½ feet maximum depth in valley of Little River near Idabel, McCurtain County, Oklahoma. Breeding site of *Hyla versicolor chrysoscelis* and *Microhyla c. carolinensis*. Photo by A. O. Weese.

Fig. 7. Edge of a small tank, 2.4 miles south of Idabel, McCurtain County, Oklahoma. *Pseudacris triseriata* and *Microhyla c. carolinensis* were calling here when picture was taken May 19, 1946. Photo by A. O. Weese.

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Fig. 8. Shallow, newly formed turbid pool beside road through an extensive buffalo grass pasture, near Kenton, Cimarron County, Oklahoma, in which males of *Bufo insidiosus* were calling, mid-forenoon of July 29, 1945, after heavy showers the previous evening (Bragg, 1946a). Photo by A.O. Weese.

- Fig. 9. One of several adjacent tiny pools in solid rock (see lower right) from which hatching embryos of *Bufo punctatus* were secured on May 6, 1939. (See Bragg and Smith, 1943.) Stream bed below dam holding Soldier Lake, Wichita Wild Life Refuge, Comanche County, Oklahoma. Photo by the author.
- Fig. 10. Shallow, extensively flooded area in sedge meadow on the Canadian River flood plain, just southwest of Norman, Cleveland County, Oklahoma. For several years this area was studied intensively until it was destroyed by flood waters of the river. The following bred here repeatedly: *Bufo w. woodhousii*, *Pseudacris streckeri*, and *Rana berlandieri*. The prairie species *B. cognatus* and *Ps. clarkii* invaded this area occasionally (Bragg, 1942a), but no spadefoots were ever found. Compare with Fig. 12. Photo by the author, spring, 1939.
- Fig. 11. The Aroyo de Pecos, eastern edge of Las Vegas, New Mexico. Breeding site of *Bufo w. woodhousii* in shallow, running water (see Bragg, 1941).
- Fig. 12. Slough on Canadian River flood plain just beyond that shown in Fig. 10. Breeding site of *Rana berlandieri*, *B. w. woodhousii* and *Pseudacris streckeri*. Photo by the author, April, 1939.
- Fig. 13. Temporary pool just northwest of Las Vegas, New Mexico, in which *Scaphiopus hammondi* were first found breeding (Bragg, 1941). A very few *S. bombifrons* occurred here also.
- Fig. 14. Pool in the oak-hickory savannah just west of Little Axe, eastern Cleveland County, Oklahoma, wherein the following species are known to have bred: *Bufo t. americanus*, *Pseudacris triseriata*, *Ps. streckeri*, *R. berlandieri*, and *Scaphiopus hurterii*. This is pool B (Bragg, 1945a) in which social metamorphic aggregations of the tadpoles of the savannah spadefoot were observed in 1945. They did not use this pool in 1946. Photo by A. O. Weese, April 7, 1946.
- Fig. 15. Deep ditch with shallow pools in the field beyond in the valley of Hog Creek, west of Little Axe, Cleveland County, Oklahoma. In late June, 1939, after heavy rain *B. w. woodhousii* were calling along the ditch and *B. cognatus* about the shallow pools with no mixing of the two species. For a similar situation illustrating the marked tendency toward breeding-site selection in these two species see Bragg (1940, Fig. 5). Photo by Chas. C. Smith, June, 1939.
- Fig. 16. Borrow pit in clearing in oak-hickory savannah six miles east of Norman, Cleveland County, Oklahoma. This pool has been watched for eight consecutive seasons and the following species are known to have bred there: *Bufo t. americanus*, *Hyla v. versicolor*, *Acris crepitans*, *Pseudacris streckeri*, *Scaphiopus hurterii*, and *Rana berlandieri*. This is the pool described by Bragg (1944b) where social aggregations of tadpoles of *S. hurterii* was first observed; also, pool A of Bragg (1945B). Photo by Chas. C. Smith.
- Fig. 17. Small turbid tank in oak-hickory savannah southeast of Norman, Cleveland County, Oklahoma. Breeding site of *B. t. americanus*. One male of *Scaphiopus bombifrons* is the only spadefoot ever observed calling here. Photo by Chas. C. Smith, June 19, 1939.
- Fig. 18. Shallow, temporary, clear pool in mixed grass prairie at Norman, Oklahoma. Breeding site of *Bufo cognatus* and *Microhyla c. olivacea*. Photo by Chas. C. Smith, June 28, 1939.
- Fig. 19. Ditch along Oklahoma Highway 9, two miles east of Little Axe, eastern Cleveland County, Oklahoma, in the oak-hickory savannah. Pool D of Bragg (1945a) is shown in the foreground. Pool C is formed in the background after rains. Breeding site of *Pseudacris triseriata*, *Ps. streckeri*, *R. berlandieri*, *Microhyla c. olivacea*, *Acris crepitans* and *Scaphiopus hurterii* (in both pools, 1946, but only Pool C in 1945). *Ps. triseriata* (as tadpoles) were extremely abundant here when the picture was taken but all failed to metamorphose before the pool dried up. Later rains refilled the pool and successful breeding of all of the other species occurred in the late spring. Photo by A. O. Weese, April 7, 1946.

Fig. 20. Temporary, turbid, very shallow pool near eastern edge of Las Vegas, New Mexico, in which "stalked eggs" of *Scaphiopus bombifrons* were observed in 1940 (Bragg, 1941). This is the shallowest water ever known to have been used by this species. The pool was "alive" with their tadpoles when the picture was taken. This pool was not used by the related *S. hammondi*. Photo by the author, August 17, 1940.

Fig. 21. Temporary, clear pool about 2-2½ feet maximum depth in northern portion of Las Vegas, New Mexico. *Scaphiopus bombifrons* but not *S. hammondi* produced tadpoles here in 1940. Calling males and one mated pair of *Ps. triseriata* were also found (see Bragg, 1941). Photo by the author, August 17, 1940.

- Fig. 22. Temporary pool at entrance of Kearney's Gap, about three miles southwest of Las Vegas, New Mexico, in the ecotone between short-grass plains and the pinyon-juniper community. *Scaphiopus hammondi* but not *S. bombifrons* bred here in 1940. The spadefoot tadpoles of the same age in this pool when the picture was taken varied enormously in size. Photo by the author, August 17, 1940.
- Fig. 23. Extensively flooded but shallow pool in field, south edge of Norman, Cleveland County, Oklahoma. A large congress of *Scaphiopus bombifrons* and *Bufo cognatus* (including many mated pairs) was present when picture was taken in spring of 1940. Other species commonly breeding here each year include *B. w. woodhousii*, *Ps. clarkii*, *Ps. streckeri*, and *M. c. olivacea*. On two occasions a single male *Hyla v. versicolor* has been found indicating, probably, stray individuals which have followed wooded ravines from the oak-hickory savannah, four miles to the eastward where this species is very abundant. It was in this area that the crossed pair of *Bufo cognatus* (male) and *B. w. woodhousii* (female) was taken (Bragg, 1939). Photo by Chas. C. Smith at the time of greatest flooding.
- Fig. 24. Temporary, shallow, grassy, clear pool in sand hills bordering the valley of the North Fork of Red River near Granite, Greer County, Oklahoma. Breeding site of *Bufo compactilis*. Compare Fig. 25. Photo by A. O. Weese, June 11, 1946.
- Fig. 25. Clear, shallow, sedge-grown pool (sandy bottom) on flood plain of North Fork of Red River, just east of Granite, extreme eastern Greer County, Oklahoma. Breeding site of *Bufo compactilis* (compare Fig. 24). Photo by A. O. Weese, June 11, 1946.
- Fig. 26. Tank at Duke, Jackson County, Oklahoma. On the night of August 8-9, 1939, this area was extensively flooded and had the following species calling there: *Bufo insidiosus*, *B. cognatus*, *B. compactilis*, *B. w. woodhousii*, and (a few) *Scaphiopus couchii*. (See Bragg, 1940a for a description of segregation of species here.) Conditions had changed in the intervening years. No tadpoles were present here in July, 1945, but in June, 1946, those of *Scaphiopus bombifrons* were abundant. Photo by A. O. Weese, June 8, 1946.
- Fig. 27. Portion of an extensive clear pool near the Red River, southern Love County, Oklahoma, in oak-hickory savannah. Typical breeding site of *Hyla v. versicolor* and *Acris crepitans*, both of whose tadpoles were abundant when photo was taken by A. O. Weese, June 6, 1946.
- Fig. 28. Tank in oak-hickory savannah, about six miles east of Norman, Cleveland County, Oklahoma, very near pool shown in Fig. 16. This water is semi-permanent (dry just once since 1937). The following breed here each year: *B. t. americanus*, *Hyla v. versicolor*, *Pseudacris streckeri*, *Rana berlandieri*, and *Acris crepitans*. Occasionally males of *Microhyla c. olivacea* and *Bufo w. woodhousii* have been seen calling here but no tadpoles of these have ever been found. Also, this pool in contrast to the nearby temporary one (Fig. 16) has never been used by *S. hurterii* from 1939 to 1949 inclusive. Photo by Chas. C. Smith, spring, 1939.
- Fig. 29. Small tank in oak-hickory savannah, $7\frac{1}{2}$ miles east of Norman, Cleveland County, Oklahoma. Breeding site of *Bufo t. americanus*, *Pseudacris streckeri*, *Microhyla c. olivacea*, *Acris crepitans*, and *Rana berlandieri*. Photo by Chas. C. Smith, spring, 1939.
- Fig. 30. Depression in woodland with very small amount of water in it when photo was made but which forms an extensive temporary pond with water flowing back into the woods after heavy rains. Location about $7\frac{1}{2}$ miles east of Norman, Cleveland County, Oklahoma. Breeding site of *B. t. americanus*, *Ps. clarkii* (from small population in an adjacent prairie island not shown in picture), *Ps. triseriata*, *Ps. streckeri*, *Hyla v. versicolor*, *Microhyla c. olivacea*, *Rana berlandieri*, and *Scaphiopus hurterii*. This is the pool in which differential developmental rates among species were observed (see above). Photo by the author, spring, 1945.
- Fig. 31. Small tank in artificial clearing $\frac{1}{4}$ mile into oak-hickory savannah, $4\frac{1}{4}$ miles east of Norman, Oklahoma. The westernmost observed site of the breeding of *Bufo t. americanus* is at this point. Photo by Chas. C. Smith, spring, 1939.

Fig. 32. Large tank with shallow margins and turbid water draining from buffalo grass prairie (pinion-juniper in distance) three miles south of Las Vegas, New Mexico. Breeding site of two species of *Scaphiopus*. *S. bombifrons* used this pool twice in the summer of 1940, whereas *S. hammondi* used it only once and in relatively small numbers. Water seeping through the dam in the background collected in a ditch used by *Pseudacris triseriata* for breeding. From here water passing beneath a railroad and gathered in the ditch shown in Fig. 3. *Rana brachycephala* Cope may also use this pool sometimes. A mated pair was seen on its bank but no chorus was observed nor were its tadpoles found here. Photo by the author, August 17, 1940.

Fig. 33. Gallinas Creek just above its emergence from the mountains onto the plains at Montezuma, about seven miles northwest of Las Vegas, New Mexico. Breeding site of *Rana brachycephala* Cope and *Bufo w. woodhousii*. Photo by the author, August 18, 1940.

- Fig. 34. Small shallow, turbid tank (dam at right) in oak-hickory savannah, $7\frac{1}{2}$ miles east, two miles south of Norman, Cleveland County, Oklahoma. Hundreds of recently metamorphosed toads (*Bufo w. woodhousii*) were present about this pool when photo was taken in June, 1939, by Chas. C. Smith.
- Fig. 35. Flooded field and ditch, water turbid, temporary, and shallow, 2.5 miles west of Plain View School, western Greer County, Oklahoma, in short-grass plains near the gypsum hills country. Breeding site of *Scaphiopus hammondi*, *S. bombifrons*, and *Bufo compactilis*. Larval *Ambystoma tigrinum mavortium* Baird were also found. Rain forming this pool had occurred approximately two weeks earlier and the spadefoot tadpoles were well along in development. Photo by A. O. Weese, June 12, 1946.

VII

Some Adaptations of Survival Value in Spadefoot Toads¹

ARTHUR N. BRAGG

FOR several years I have been reporting on various phases of the distribution, behavior, and habits of spadefoot toads (genus *Scaphiopus*) as observed principally in Oklahoma during periods of breeding and tadpole development from year to year. In the more recent papers, peculiar behavior of tadpoles of *Scaphiopus hurterii* Strecker has been emphasized (Bragg, 1944, 1945, 1945a, 1948) and somewhat similar behavior noted in some pools among other species of this genus (Bragg, 1946, 1948).

These studies have clearly demonstrated the following as facts: (1) Spadefoot tadpoles maintain a very fast intrinsic rate of development (cf. Trowbridge and Trowbridge, 1937) but it is modified by factors in the environment so that the actual rate at any one time and place may be quite different from that at any other time and place. (2) The rate of growth (increase in size) is not always correlated with the rate of development (progress toward metamorphosis), at least in *Scaphiopus hurterii*. This is shown by the fact that the size of the animals of the same age at metamorphosis varies widely from pool to pool and, indeed, may be quite different in different years at the same poolsites, although this is not so usual. (3) During some developmental periods at a given pool, tadpoles of the spadefoots show marked social behavior; during other developmental periods they may not do so; during still others, their behavior, although still social, may differ in detail from that shown in other pools at different times and places or at the same place at different times. (4) This social behavior always involves aggregation of the tadpoles, either during feeding (very commonly seen) or at metamorphosis (more rare). (5) Some feeding aggregations in *S. hurterii* at metamorphosis (but apparently not at other developmental periods) take the form of active cannibalism based primarily on the attack upon the shrivelling tails of transforming individuals. More rarely this phenomenon also occurs in mixed groups of *S. hammondi* Baird and *S. bombifrons* Cope (Bragg, 1946, 1948). (6) Metamorphic aggregations of the type first described by Bragg (1944) in *S. hurterii* have never been known to develop cannibalism despite the further fact that such aggregations occur at about the same stage of development as cannibalistic aggregations at other times and places. (See Ball, 1936, for cannibalistic behavior of *Scaphiopus*

¹ These studies were made possible through an arrangement by Dr. J. Teague Self, Chairman, Department of Zoological Sciences, with the approval of Dean Laurence H. Snyder, Graduate College, and Dean E. D. Meacham, College of Arts and Sciences, whereby the author's teaching load was reduced.

holbrookii holbrookii in Connecticut at metamorphosis.) (7) All such phenomena, whatever the variations in detail from place to place may be, occur in pools often containing tadpoles of several other species (of *Bufo*, *Rana*, *Pseudacris*, *Hyla*, *Acris* and *Microphyla*) none of which behaves in these ways.²

Such distinctive and unusual behavior of tadpoles, as well as the variations in it in place and time, must have some explanation. Elsewhere (1946) I have pointed out that this is likely to be found in adaptations to xeric conditions in the environment characteristic of most spadefoot species, these adaptations supplementing the xeric breeding pattern of the adults (Bragg, 1944a, 1945), both types of phenomena probably developing through Darwinian selection in the evolution of these amphibians in the dry plains and xeric savannahs of the West.

But to stop here is scientifically unsatisfactory. We need to know (1) why the tadpoles vary in behavior in different times and places, (2) what factor (or factors) in the environment accounts for differential rate of growth and development, and, in general, (3) what the effect of each factor in the environment is (in quantitative terms) in correlation with the behavior observed.

Data are not yet available for a complete analysis. This paper, therefore emphasizes only one broad factor concerned. This is food. It was early noted (1944) that tadpoles of *S. hurterii* eat large quantities of the bottom materials, especially in pools largely devoid of microscopic algal growths. Such pools always have little "normal" food of other types (Bragg, 1946). This suggested that a study of the bottom materials correlated with behavior of the animals in given pools might throw further light on the problem. Could the food supply be correlated, at least broadly, with the occurrence of aggregational phenomena and cannibalism?

Observations

Mud from the bottom of pools, collected while animals (*S. hurterii*) were feeding, was examined under a microscope and materials from the stomachs and intestines of tadpoles collected at the same times and places were compared. Several hours of search of such materials revealed no visible significant differences in the different types of samples. Each was an amorphous mass, the only recognizable items being these: (1) a single empty diatom shell, (2) a single three-celled fragment of a filamentous alga, (3) a few bits of clay, and (4) an occasional plant fragment. Staining with several biological stains proved only that the main bulk of the materials was organic in nature and that it contained many very tiny rod-like particles which I took

² *Weak* feeding aggregations in artificially confined tadpoles of *Rana berlandieri* Baird have been seen (Bragg, 1948) and one case of hastened metamorphosis accompanied by a sort of aggregation in this same frog has been reported (Bragg, 1944). Neither of these cases was quite the same, at least in intensity, as in the spadefoot toads; and, perhaps more significant, neither has occurred through several years of observations in pools of natural water when spadefoot tadpoles were present and exhibiting social behavior.

to be bacteria. It made no difference whether these materials were unfixed; or fixed in any of several commonly used reagents (Bouin's picro-formal, 65 per cent or 70 per cent ethyl alcohol, or formalin in various dilutions up to 10 per cent). Since the bulk of bacteria was obviously insufficient to serve as the major food supply, it was concluded that the tadpoles were acting as scavengers, the essential food being obtained from organic materials accumulated during cycles of evaporation on the pools' bottoms.

Field observations were then made in the region east of Norman, Oklahoma, described in earlier papers as containing pools designated A, B, C, D, E, and F (Bragg, 1945, 1948) all of which at some time have been utilized by tadpoles of *S. hurterii*. The observations were made during tadpole development in the spring and early summer of 1948; and extensive notes taken in this region during the past six years (ten years for Pool A) were also reviewed. Pools A, D, E, and F were each used by this species in 1948, Pool E twice, and Pool F three times during the season.

Differences in the six pools were sufficient to make possible the following general classification into three types:

In type 1 (pools A, B, D, and F) the water varies from 5 to 10 inches in maximum depth after rains sufficient to stimulate breeding activity and it totally evaporates in from three to five weeks (if not replenished) during the usual season of tadpole development (May through June). Very few algae occur and (except for a few sedges growing from the bottom of Pool D, and sometimes of Pool F) there is little plant growth. Water is turbid at first but gradually clears if undisturbed. Pool F is the smallest in extent and shallowest of pools of type 1 and therefore tends to disappear soonest during any given period.

Pools of type 2 (Pool C) are very shallow (4 inches maximum) but extensive. Pool C measures approximately 70 by 30 feet and has an essentially flat and level bottom (small depressions, in the order of the size of one's cupped hands, occur). Water has never been known to stand for more than two weeks after a single rain. Almost no algae develop but seed plants (principally grasses, sedges, and a few other coarser types) grow in great profusion from the bottom, often hiding the water just before it completely evaporates. In winter, the pool site is a tangle of dead plants which, each year, disintegrate as new growth occurs in the spring. Water is at first turbid but clears within a week as the water level falls. Evaporation cycles pass rapidly; it is not uncommon for two, three, or even more to occur during a single spring and summer. This depends entirely upon the distribution of seasonal rainfall and upon evaporation rates.

Pools of type 3 (Pool E) are quite different. The water is clear at all times and its level depends upon seepage into and out of the pool as well as upon run-off and evaporation. How long water will remain (as well as its level at any one time) depends primarily upon the total precipitation of the season prior to a given date, since seepage from above is controlled by the amount of water absorbed by a sandy hill. After periods of considerable rainfall, seepage from the pool and evaporation from the surface often counter-

balance replenishment by seepage from above, so that a nearly constant water level may be maintained for as long as two months. Algae of many species are abundant and a growth of smartweed (*Polygonum fluitans* (Eaton) Green, (as kindly identified by Dr. Aven Nelson) springs from the bottom early in the season, shading the pool and often nearly covering the water before total evaporation occurs.

It should be recalled that pools C and D lie immediately adjacent to each other and receive their water from essentially the same source (Bragg, 1945) and that pools E and F are only a few hundred feet away, occupying higher portions of the same slope. Pool A lies ten miles, and Pool B, two miles, to the west of the others. All these pools are in the oak-hickory savannah as defined by Bragg and Smith (1943) and all are exposed to direct sunlight except Pool B which was not studied in 1948.

Pools of type 1 obviously tend, on the average, to develop less organic matter than those of types 2 and 3. During the dry phase of the evaporation cycle, the bottoms of pools B, D, and F are commonly bare, sun-cracked clay (scattered sedges in D and sometimes in F excepted). A thin film of darker organic residue commonly covers the bottom. The soil in the region is loose, sandy clay loam (known locally to be poor farming land) which gives little evidence of influencing the pools, from the viewpoint of tadpole development.

Not uncommonly water evaporates so rapidly from these pools (except Pool E) that all of the tadpoles are caught in pockets of water, flounder there for a few hours in soft mud, and die. This may happen two or three times during a season or not at all in any one place, depending upon local conditions of temperature, wind, and rainfall. It is very common in late spring and summer to find dead tadpoles dried up on the bottoms of former pools, and of course, this includes tadpoles of all species present, not just those of spadefoots. Despite the activity of scavengers (birds, ants, etc.) which eat some of these, dead tadpoles add materially to the organic matter in the bottom of the pools when these are again filled.

In pools of type 1, dried tadpoles appear to be the major source of organic materials. In pools of type 2, they supplement plant remains. In pools of type 3, they are of minor significance since they so rarely are killed by total evaporation.

Where water is very shallow, as in pools C and F, the evaporation cycle passes quickly and more tadpoles are killed than in other types, thus rapidly building up organic matter at these pool sites. Where water is deeper, as in pools A, B, and D, in contrast, these cycles pass less quickly and more tadpoles undergo metamorphosis. Their transformation has the effect of taking organic matter from the pool rather than adding to it, and thus of depleting the limited supply. Eventually, there comes a time in these pools when organic matter is insufficient in amount (or kind) to supply the nutritional needs of thousands of tadpoles and it may take several evaporation cycles (months or years depending upon local conditions) to furnish again the necessary food sources of the proper kinds for tadpoles to develop successfully.

This explains several facts earlier quite puzzling. Pool A supported tad-

poles of *S. hurterii* and they emerged in large numbers in 1941 (Bragg, 1944); but tadpoles of this species, transferred here from Pool E in 1945, became emaciated and weak. Many died and very few transformed (Bragg, 1946). This pool again supported tadpoles in the spring of 1948, during its second evaporation cycle of the season, the brief first one having caught and killed all tadpoles of several species developing here. Similarly, transferred tadpoles from Pool C developed poorly in Pool D in 1945 but this pool supported thousands which transformed normally in 1948, after a longer than usual period of development, however.

It also partially explains the difference in rates of development and growth mentioned earlier. In Pool F in 1947 tadpoles increased in size at an unusually rapid rate, eventually becoming twice the size of those of the same age in Pool C. In the latter pool, however, the tadpoles transformed a week earlier than those in F at the smallest size ever seen (mean length = 2 mm.) on the thirteenth day after water had first filled the pool (Bragg, 1948). This is the fastest developmental rate known to me among amphibians of any type. It is significant to note that all tadpoles had been caught and killed in Pool C by evaporation at nearly this same age in 1945 and again in 1946. Obviously conditions in the pool had made the difference. The observations certainly suggest that the number of cycles during which tadpoles have been killed is the deciding factor through the accumulation of organic matter (and perhaps some special substance) in their bodies. It is, for example, well known that the thyroid gland is active in metamorphosis. It is conceivable that the dried glands of dead tadpoles or something that they contain (iodine or thyroxine, for example) may so accumulate in the pool as to allow the tadpoles of the proper cycle to emerge at a small size, just as the water disappears. It should be noted, too, that this would apply only to the spadefoots. Several other species have used Pool C for breeding but not a single tadpole of other species here has succeeded in emerging from this pool since at least 1944 when I started watching it through all of its evaporation cycles.

Having determined broadly the source of organic materials which these animals secure from the bottom, I thought it wise to check some of the more obvious physical and chemical conditions of the water for possible factors which may effect the rates of development and growth. These data are not presented in detail because they were consistently and unquestioningly negative. Variation in temperature in pools (and diurnal-nocturnal fluctuation of temperature), in hydrogen ion concentration (pH and methyl orange and phenolphthalein alkalinity) and total carbonates and bicarbonates in the water³ obviously were not the determining factors, singly or collectively, in behavior or in growth and developmental rates of the tadpoles. For temperature this confirms the conclusion earlier reached (Bragg, 1948). It should

³ Analyses were made by Mr. William Thompson and his assistants of the State Game and Fish Department working in the laboratory of the Oklahoma Biological Survey, with which both he and I are connected. I express my appreciation for this aid by Mr. Thompson.

be noted, however, that not all possible factors were tested. Oxygen determinations were omitted deliberately since the prevailing water temperatures (25–33° in all pools) during most of the time indicated that not much could be held by the water. That oxygen was deficient was also indicated by the fact the tadpoles often gulped air at the surface.

The behavior of tadpoles in forming huge feeding aggregations in limited areas suggested that they might react to concentrations of organic matter locally on the pool's bottom. Some very simple observations were made, both in the pools and in the laboratory, to check this possibility.

At Pool D at a time when huge feeding aggregations were forming and breaking up into agitated schools, I scratched away the upper layer of organic matter on the bottom in an area approximately one inch square or less. This was done in a region of non-aggregation. Almost immediately two tadpoles found this and began feeding here voraciously. Others joined them in increasing numbers till within ten minutes thousands of agitated, struggling tadpoles had piled up in an aggregation, all attempting to feed from this small disturbed area of the bottom. The scratching had been done with my finger and there was a possibility the tadpoles were reacting to me rather than to the bottom materials. I slowly lowered my finger into the water, being careful not to touch the bottom. It was immediately attacked by tadpoles and an agitated aggregation formed about it nibbling so effectively that they could easily be felt. (At other times tadpoles of *S. hurterii* have attacked my bare feet as I waded a pool.) But when the bottom was disturbed with a small stick, an aggregation formed as before. These observations were repeated several times with comparable results. It was concluded that, under conditions in this pool at this time, the tadpoles reacted positively both to a disturbance of the bottom and to my finger suspended in the pool. In contrast, tadpoles of several other species, abundant in this same pool, did not so react.

Comparable observations made in the laboratory support these observations in the field. About five hundred tadpoles of *S. hurterii* collected from Pool D, six days from egg laying were placed in a large, flat glass culture dish filled with clear tapwater. Here they swam almost continuously for several hours each apparently paying no attention to the others. This behavior conformed to the typical pattern observed many times earlier when no food was available.

A very small amount of Hartz-Mountain Fish Food (representing a mixed organic food source) was lightly sprinkled on the water surface near the center of the dish. The animals became more active immediately and began to concentrate in the region of the particles, spread by surface tension over the water's surface. Originally, two happened to be near the surface. In thirty seconds, six were there and more were coming up. In one minute fifty-six were concentrated at the surface. In five minutes so many were concentrated that they could not be counted. In twenty minutes I estimated that one-half of the total were at the surface.

Another sprinkle of the fish food caused the animals to become greatly agitated, swimming along the surface sometimes in small schools and clumps,

gnawing violently in the region of the surface film. It was concluded that these tadpoles had reacted positively to Hartz-Mountain Fish Food when hungry, and this fact supports the presumption that they would do so to other organic materials.

Simple experiments were devised to test these observations.

Experiment 1. Into each of two clean finger bowls, exactly alike, were placed 200 cc. of tap water from a single tap. After the dishes had stood for a few minutes to equalize temperatures (26° in each), ten tadpoles of *S. hurterii* were added to each. Ten minutes were allowed for stabilization. At the end of this time the behavior of the tadpoles in both bowls was the normal random swimming observed previously. The bowls were labeled A and B, experimental and control respectively. To A, I added a sprinkle of the fish food as before. In thirty seconds, one tadpole had found the food at the surface. In forty-five seconds, eight were violently moving at the surface, the other two attempting to feed at the bottom. In two minutes, one group of three and another of four were attacking small particles at the surface with violent movements. In six minutes, all were at the surface violently attempting to ingest the particles of food. Temperature = 25° C. at the end of the experiment.

In the meantime, the behavior in the control dish (B) had not changed. The normal slow random swimming had continued. Temperature = 25° C. at the end of the experiment.

It was concluded that the previous observation regarding the positive reaction to this fish food was confirmed; these *S. hurterii* tadpoles reacted positively to diffusion of chemicals and to physical disturbances, or both when this fish food was added to the water containing them.

Experiment 2. After the agitation had ceased in A, a small amount of carmine powder (relatively insoluble in water) was sprinkled on the surface. For the first few seconds, the tadpoles increased their movements, but within one-half minute all had settled to the normal, slow random swimming still being maintained in B. None approached the carmine and there was no suggestion of agitated movements as when comparable amounts of fish food had been added.

I then prepared two small squares of a porous cotton cloth cut to the same size. On one I placed a small amount of carmine, on the other, a comparable amount of the fish food. Each cloth was then folded in the same manner and tied with cotton thread from a single spool in such a manner to form a bag of material. These bags were lowered simultaneously into bowl B (the former control), so that the one was directly opposite the other and as far away from it as possible.

Within thirty seconds, eight of the ten tadpoles were attacking the bag containing the fish food, all in the folded area nearest this material. Two were attacking the carmine bag, but in a region of it well away from the carmine. In ten minutes all of the tadpoles were agitatedly attacking the bag of fish food. At the end of fifteen minutes, two tadpoles were about the carmine

bag but paying it no attention and eight were still behaving as though attempting to get food from the other bag.

It was concluded that (1) these tadpoles were essentially unstimulated by the presence of a small amount of carmine; (2) since carmine is relatively insoluble in water, this is presumptive evidence that other non-soluble substances might not stimulate the tadpoles, if as finely divided as was the carmine and present in equal amounts; (3) the results further suggest but do not prove that chemical rather than physical influences are the more important in stimulating the tadpoles.

Experiment 3. Four finger bowls were prepared as in above experiment and into each were placed ten tadpoles. The dishes were labeled A, B, C, and D. The temperature in the main culture on removal of the tadpoles was 23° C. In each of the experimental dishes it was 22.1° C. Dish A was retained as a control. The other dishes were treated as follows:

B. I added a *very* small pinch from a bouillon cube to the center of the dish. Contents as given on the can were salt, hydrolyzed plant protein, beef extract, sugar, rendered beef fat, spices, and flavoring. Proportions were not stated. The particles dissolved completely in four minutes forming a region of concentration of chemical substances in the center of the bottom of the dish.

In three minutes after this material was added the tadpoles became slightly agitated moving faster than those in the control. But even when they came into direct contact with the added material (whether dissolved or not) showed no tendency to ingest it.

About ten minutes after the complete disappearance of solid matter I added approximately three times as much of the bouillon cube as before. During its dissolution bubbles arose from it. In five minutes only a small bit had not dissolved and this was surrounded by a brownish spot of concentrated bouillon. The tadpoles avoided this area but elsewhere had taken up the slow random swimming of the controls.

C. A single raisin was broken into fine pieces of approximately equal size (to increase surface area) and put in the center of the bottom. In one minute four tadpoles were gathered about the raisin but none were feeding upon it. At two minutes, one tadpole investigated the raisin, gnawed briefly but soon left. Two minutes later this was repeated. For the next ten minutes a tadpole or two "investigated" the raisin from time to time in a similar manner but did not ingest much of it. There was no agitation such as noted in Experiment 1 and no schooling. This bowl was left undisturbed for several days and eventually the tadpoles ate the raisin.

D. A small fragment from the dried bottom of Pool A with six dried tadpoles on its surface was placed in the center of the bottom of the dish. (Species of the dried tadpoles is unknown but were probably of either some or all of *Hyla v. versicolor*, *Pseudacris streckeri*, or *Rana berlandieri*. They were known not to be *S. hurterii* or *Bufo t. americanus*.) Within a few minutes several tadpoles were ingesting the mud but there were no mass movements and no agitation such as caused by the fish food. None attacked the

dead tadpoles in thirty-five minutes of continuous observation and at the end of this time all were like the controls in behavior. However, eventually the tadpoles in this dish, which was left undisturbed, fed readily on the mud and the dead tadpoles disappeared in several days. All ten eventually transformed with no tendency toward cannibalism at any time.

One other observation should be noted. Whenever the thermometer was lowered into any of these dishes, some tadpoles invariably came to nibble briefly at the bulb as though finding it by sight and testing it as a possible food source.

It was concluded that (1) the substances in the bouillon cube in the concentrations and proportions used elicited a negative reaction from the tadpoles (a wholly unexpected result); (2) the raisin caused a reaction which was at first only weakly positive; however, it later became stronger; (3) bottom mud with dead tadpoles in it elicits a weak positive response, or none at all, at first but later serves as a satisfactory food source; (4) whether food materials are found by response to chemicals or not, sight plays a part in "investigation" of possible food sources.

An observation made in the laboratory concerned the tadpoles' reaction to a larger animal. A juvenile *Scaphiopus bombifrons* in the Biological Survey laboratory was noted to be in need of water. As a quick source, it was placed into a culture of *S. hurterii* tadpoles. Immediately it was attacked by hundreds of tadpoles, which swarmed about it nibbling at all its submerged parts. The little spadefoot was too large to be harmed, but it acted as though annoyed, brushing tadpoles away with its front legs and occasionally changing its position. This shows that *S. hurterii* tadpoles, if hungry, may attack quite large living vertebrates and recalls the attack on my finger at Pool D.

A further series of observations bear upon the same method of behavior. A large mass of tadpoles had been transferred from Pool D to my home and placed in clear water in the small artificial pool mentioned in a recent paper (Bragg, 1948). Here they behaved typically, including schooling and formation of feeding aggregations till they underwent metamorphosis.

About two hours after first placing these tadpoles into the pool, I held a small mass of ground beef (about $\frac{3}{4}$ inch in diameter) in the water near feeding tadpoles. None at first paid it any attention. After about three minutes, a tadpole swimming at random and obviously not attracted, blundered into it and immediately began feeding voraciously. I dropped the meat to the bottom of the pool and watched the behavior of the tadpoles closely for the next half hour and at intervals thereafter. At first only a few found it, but soon it was covered by a dense mass of agitated tadpoles. All evidence of it had disappeared late that night except a few pieces of fatty tissue floating on the surface. The most interesting thing observed was that the response seemed to be more to sight than to chemical diffusion from the food. I had a very definite impression that when one tadpole finds a food object others note it and come; the more tadpoles that accumulate, the greater the stimulation so that a great mass is thus built up. This simple observation, therefore,

substantiates field observations in several pools during which I have watched social behavior during the formation of great feeding aggregations, often when nothing could be found which might have started such an aggregation.

Experiment 4. This was designed to determine definitely how effective bottom materials from pools of types 1 and 2 may be as a total food source for *Scaphiopus hurterii* from the time of total absorption of the deutoplasm of the zygote till just after metamorphosis.

Source of materials: On August 21, 1947, I had collected a portion of the dried bottom of Pool C. This had been kept in a closely tied canvas bag till used. A similar sample of the dried bottom of Pool A was collected on April 17, 1948, at the end of the first evaporation cycle of the season here. The sample from Pool A had no obvious fibrous materials but did have large numbers of dead tadpoles. On the night of May 10, 1948, a mated pair of *S. hurterii* was observed in Pool F. They were left undisturbed. The next forenoon I visited the pool and found that one clutch of eggs had been laid. Some of these (now young embryos, of course) were collected and taken alive to the laboratory. They were immediately placed into a fingerbowl of clear tap water and set aside. They eventually hatched normally but were never fed prior to setting up the experiment.

On May 17, 1948, the experiment was set up as follows: Two clean aquaria, each approximately 37.5×14.5 cm. inside measurement were labeled A and B. In A, the soil sample from Pool C, ten of the young tadpoles, and tap water to a depth of 10 cm. were placed. In B, the treatment was exactly the same except that the bottom sample from Pool A was used. A larger quantity of bottom materials was used in A than in B because it was suspected that the dead tadpoles in the latter might be more effective than the materials without them in A. The tadpoles used were so uniform in size and shape that no differences were discernible to the naked eye. Accordingly, only one, taken as typical of all, was measured. This had a head-body length of 5 mm. and a tail length of 10 mm. (15mm. total length). All growth from the egg stage must have come about by utilization of deutoplasm and absorption of water (with the unlikely exception that the egg jellies might have been utilized). At the end of two days the water in each aquarium was clear. Most of the tadpoles in both aquaria were thinner than before and moved slowly. They apparently were not feeding (none had been seen to do so). But a few in each aquarium were larger, more active, and round bodied. These were at least twice the bulk of their fellows but did not equal the size of tadpoles of the same clutch left undisturbed in Pool F.

The next morning (three days from the start) many of the tadpoles had increased surprisingly in size. Some details set down in notes: "A. Water temperature = 23° C. All tadpoles, larger than yesterday and with little variation in size. All active but now look to be well fed. Several, feeding on the bottom mud and all appear to have ingested such materials (known from the color of the intestine seen through ventral body wall)." There was no social behavior. "B. Water temperature = 23° C. One tadpole is small, weak, and inactive at the surface. Another is active, round bodied, and about

twice the size of the first (very much like the majority in A). At least six are very large, very active and feeding on the bottom mud. These compare very favorably in size with others (much older) in Pool D and they are fully as large as those of the same clutch still in Pool F." (It perhaps should be noted that Pool F is the one in which growth rates were very rapid and the size attained was very large in 1947.—Bragg, 1948). There was no social activity.

On the fourth day, sizes of tadpoles in B exceeded those of the older ones in Pool D now just entering metamorphosis but they were no larger than their brothers and sisters still in Pool F. They were maintaining an extremely fast growth rate. There was one exception. A single tadpole was still small and inactive. In A, all tadpoles were still small but showed a slight increase over the day before. All seemed healthy but they were maintaining a slow growth rate. Water temperature in each aquarium = 24° C.

On the fifth day, the contrast between A and B was even more striking. Nine of the tadpoles in B were the largest of their species ever seen except a few developing in Pool F in 1947. Up to this time no measurements had been made for fear of disturbing the animals. Two from B were caught and measured at this time. One = 28, the other = 37 mm. total length.

Contrasts continued during ensuing days and on May 29 at 12:45 P.M. the first one in B to develop forelegs was seen. This was on the seventeenth day from hatching. Tadpoles in A were still small.

On May 31, nineteen days from hatching, all the animals were measured as follows:

A.	(1)	Body	9 mm.	Tail	11 mm.	Total	20 mm.
	(2)	"	9	"	11	"	20
	(3)	"	6	"	8	"	14
	(4)	"	9	"	11	"	20
	(5)	"	9	"	10	"	19
	(6)	"	7	"	9	"	16
	(7)	"	9	"	11	"	20
	Mean	"	8.3—	"	10.1+	"	18.5—

Three of the original ten were no longer present. None of the seven remaining showed the slightest signs of metamorphosis.

B. All ten were present. Nine had forelegs and the tenth had hind legs well developed. Three had died because they could not leave the water when ready to do so. It is to be noted that these were *not* eaten by their fellows. There was no evidence of cannibalism in this culture at any time. All were measured and then preserved for future study. The measurements were:

(1)	Body	11	Tail	9 mm.	Total	20 mm.	(tail shriveled)
(2)	"	13	"	8	"	21	" "
(3)	"	12	"	7	"	19	" "
(4)	"	11	"	8	"	19	" reduced

THE AMPHIBIA OF OKLAHOMA

(5)	"	12	"	9	"	21	"	"
(6)	"	12	"	9	"	21	"	"
(7)	"	12	"	8	"	20	"	"
(8)	"	12	"	12	"	24	(Tail full; all legs functional)	
(9)	"	9	"	9	"	18	(Tail reduced)	
(10)	"	6	"	9	"	15	(The smallest, and only one without forelegs)	
Mean	"	11.0	"	8.8	"	19.8		

Because of changes at metamorphosis in the B series but not in the A series, the figures somewhat belie the really great difference between the two. It is to be noted, however, that even after the shrinkage in size which is a normal part of transformation, those of the B series exceeded those of the A series by approximately 2.7 mm. (mean) in head-body length.

As a further minor check on the bottom materials, large amounts of which were still present in each aquarium (the dried tadpoles in B had disappeared) I changed the water in both A and B, bringing them to the same level. Then I distributed the tadpoles from A in the two as follows: In A were placed Nos. 1, 2, and 3 (11.3+ = mean length); in B, Nos. 4, 5, and 6 (mean = 15.0 mm.). No. 7 was preserved to illustrate conditions at the time.

On June 16, they were examined briefly. Little change was noted; but the next day those now in B seemed larger than those in A. In the former but not in the latter, dorsal markings and hind limbs were developing, indicating the approach of metamorphosis.

On July 2, the experiment was terminated. Conditions were as follows:

B. Two tadpoles were present: They measured 11.0, 16.0, and 27.0; and 12.5, 12.5, and 25.0 mm. (head-body, tail, and total lengths, respectively). In the first, the forelegs had just come through, in the other they appeared just about to do so. The tail fin had not yet shrivelled.

A. One tadpole (measuring 13.0, 14.0, 27.0 mm.) was present. This one was about like the second one in B.

From this experiment the following conclusions were drawn:

(1) Bottom material from some former pools may serve as an adequate total external food supply for development of tadpoles of *S. hurterii*.

(2) The materials from some poolsites (at a given time) are more adequate than others.

(3) Both growth rates and developmental rates depend at least in part on the nature of the food available, i.e., on the nature of the bottom materials.

(4) Individual rates, both of growth and development, may vary in the same environment and with an abundance of adequate food. Presumably this is due to the differential behavior in feeding among individuals.

The experiment indicates strongly but does not prove that dried tadpoles in the bottom mud if present in sufficient bulk may (1) contribute to the speed of both growth and development, (2) contain substances necessary for quick metamorphosis, and perhaps (3) prevent cannibalism during metamorphic stages.

A few new observations on the prairie spadefoot, *S. bombifrons* Cope, should also be noted. In most pools utilized by tadpoles of this species, water is deep enough to allow development of algae and other food sources. In shallow water, however, these tadpoles may also utilize bottom mud. I have checked the intestinal contents of several tadpoles from such pools and find the same conditions as in *S. hurterii*.

Social feeding aggregations of tadpoles of this species have not been recorded previously except cannibalistic aggregations at one site where food was scarce (Bragg, 1946, 1948). On June 4, 1948, my assistant in the University of Oklahoma Biological Survey, Mr. Harold Dundee, and I found a long, shallow ditch of clear water in northern Creek County, Oklahoma, swarming with large tadpoles of *S. bombifrons*. At the southern end where the water was very shallow, several large feeding aggregations were present, the animals in them feeding voraciously on the bottom materials in exactly the manner noted many times in *S. hurterii*. These were not cannibalistic aggregations. The ditch was approximately 150 feet long by 5 feet in width (maximum), and the maximum depth of water at the time was $6\frac{1}{2}$ inches. The temperature of the water was 33° C., both in the region of the aggregations and near the center of the pool where there were no aggregations. A small number of grass blades protruded from the surface but there were no algal mats present. I would classify the pool as of Type 1 (i.e., similar to pools A, B, D, and F of the *S. hurterii* studies).

Later in the season (early July) we found several stations in western Oklahoma where tadpoles of *S. bombifrons* occurred in water from $\frac{1}{2}$ inch to 2 inches in depth. These pools, however, were the remains of formerly extensively flooded, planted land. In all of these places the water was turbid, thus little detail could be seen as to behavior of the tadpoles; but there was no evidence of aggregations. In this shallow water, behavior of that kind, had it occurred, could scarcely have been missed, especially since I was acutely aware of its possibility. These tadpoles had also ingested large quantities of bottom mud which, indeed, seemed the only source of food. In former years, I have seen these same phenomena many times. It seems, therefore, that mere shallowness of water does not necessarily result in feeding aggregations in the prairie spadefoot, even when desiccation is imminent and bottom mud the main or sole source of food.

There is still another aspect of this problem which needs consideration. It has been noted many times that where few tadpoles of *S. hurterii* occur (either in nature or in laboratory cultures) social aggregations never develop. It seems, therefore, that the number of individuals present has some influence on behavior. It has also been noted that spadefoot tadpoles are often crowded in natural waters but no data have been presented which would indicate this quantitatively. Since several of the pools studied most intensively are fairly regular in shape and of reasonably uniform depth it is possible to figure, with a small degree of error, the volume of water available to each tadpole, provided, of course, the approximate number of tadpoles at any one time and place is also known.

The number of eggs in a single clutch of *S. hurterii* had not been determined. Through the years, I have seen egg masses of single females that, because I wished later to study the tadpoles in the pools, were not disturbed. All of these have appeared to be comparable in size and to contain comparable numbers of eggs. It seemed safe, therefore, to assume that any one clutch would be representative of the species so far as approximate numbers of eggs is concerned. Therefore a single clutch of eggs laid by the female of a pair found in amplexus in Pool F was collected, every care being taken to get all of the eggs. They were preserved in formalin as collected and later counted twice, in groups of fifty to minimize the chance for error. The number of eggs was 3,586. Some variation is to be expected but it seems reasonable to assume that, in round numbers, 3,600 eggs is representative of a clutch in *S. hurterii*.

In Pool F a single clutch has been produced on several occasions; nearly all these young have hatched. This pool measures close to $41 \times 3.5 \times \frac{3}{8}$ feet, a volume of 119.6 cubic feet maximum, assuming dimensions the same throughout. Since the depression in which the pool forms is actually somewhat shallower and narrower at the two ends, 100 cubic feet will probably be nearer its maximum volume. If we assume 3,500 of the potential 3,600 eggs of a single clutch to hatch, this gives thirty-five tadpoles per cubic foot of water. Within a week the water level usually falls to five inches or less and the tadpoles are at least twice their size at hatching. Even though these figures give only the approximate condition, it is easy to see that the animals may become very crowded. Similar calculations at Pool C, which is more uniform, and hence the figures more accurate, indicate conditions somewhat similar. The pool will contain not over 700 cubic feet of water which gives five tadpoles per cubic foot initially. However, the water level here drops rapidly and in a week's time the depth is not over two inches, usually one and one-half. If we assume a mean depth of 1.75 inches, then the amount of water is $306\frac{1}{2}$ cubic feet, each containing approximately eleven tadpoles. This is on the assumption that only one clutch of eggs is produced. Since two and sometimes three clutches of eggs are often laid here on the same night, it takes no great imagination to see that these animals are usually very crowded, especially as they increase in size. Their numbers are actually depleted somewhat by predators, especially larval beetles (Hydrophilidae and Dytiscidae principally) but not nearly enough to affect the principle that each tadpole has progressively less room as the water level falls. It should be noted also that crowding is also enhanced by the presence of many tadpoles of other species.

Discussion

The whole pattern of tadpole development in these spadefoot toads suggests an adaptation to development in shallow, temporary pools in a xeric environment. Even the breeding habits of the adults, at least of *S. hurterii*, fit this hypothesis and on the average work toward the survival and metamorphosis of maximum numbers of young.

Adults are involved in the following manner. They breed after rain of one inch or more at any time between March and September and only in temporary water (Bragg, 1944-45). This means that at any one time and place, several breeding periods may occur (as in the region studied most intensively in 1948). During or immediately after any one rain, males may call from any of several pools, but not all secure females. In 1948, for example, twenty-nine calling males were counted in Pool E one night but no eggs were laid. At the same time only two males were calling at Pool F, one of which secured a female that laid eggs. At another time, forty to fifty males in a pool failed to attract a single female, although several females were seen feeding near the pool. Near by at other pools a clutch of eggs was produced here and there. I have seen many other such instances. It would seem that the gonadal or hormonal cycle in females is an irregular one in the sense that not all females are ready at the same time to produce eggs. Therefore, at the beginning of each evaporation cycle in a given pool, some females are likely to be ready to produce eggs if found by a male. This has the effect of staggering the laying of eggs throughout the warm months, depending upon local rainfall, and of allowing some pools to "rest" through one or more evaporation cycles while organic matter may be built up.

Once tadpoles are in a pool their behavior depends upon the nature and amount of the food supply. When they are doing nothing else they swim continuously; usually their concentration is so great that they easily cover the bottom of the pool. If the pool is of type 3, food is abundant and they eat voraciously of what algae, plant debris, and animal matter is to be found, seldom eating the bottom materials. If in a pool of type 1 or 2, the bottom debris is the principal food source. When one tadpole finds a concentration of food, others commonly are attracted, apparently by sight of its accelerated feeding, and a great feeding aggregation is soon formed. Such aggregations in *S. hurterii* apparently never change to cannibalistic feeding.

In pools of type 1, where organic materials tend to be rare or inadequate, as the tadpoles approach metamorphosis they become cannibalistic, especially on the shrivelling tails of transforming individuals (Bragg, 1948). In pools of all types, if the food source is adequate, the tadpoles do not show cannibalism. However, as the water level falls dangerously low, they may form a dense metamorphic aggregation (Bragg, 1944) which tends to conserve the fast disappearing water by deepening a depression in the soft bottom, thus draining water into the area containing the animals and at the same time reducing materially the surface exposed to evaporation. Fifteen minutes to an hour saved in this way may make all the difference between death and survival of all tadpoles in a given place, so close is the race between development and evaporation in many cases.

In at least half of the instances, this race is lost and all of the tadpoles die. But even in their deaths they serve their species by building organic food for the next lot of tadpoles in the pools. This much the observations seem to demonstrate.

Whether or not some special substance is accumulated in the bodies of

dead tadpoles which functions to hasten metamorphosis in oncoming generations is not known. Hypothetically, a substance of this kind is strongly suggested by the observations in Pool C where the fastest developmental rate known has been seen (Bragg, 1948). Further progress seems to lie in searching for this hypothetical substance and, if found, in determining its source.

It should be noted that the usually observed differences in behavior of tadpoles of *S. bombifrons* and *S. hurterii*, so puzzling when first noted, seem to be merely a matter of breeding site, selected by the respective adults. It has been stated earlier (Bragg, 1944-45) that *S. bombifrons* always utilizes deeper water than *S. hurterii*, if available. When tadpoles of *S. bombifrons* do occur in shallow pools, especially of type 1, they show the same behavior as *S. hurterii*.

The total observations, therefore indicate the general conclusion that, in at least two species of spadefoots, all phases of reproductive activity of the adults (including the xeric breeding pattern) and the behavior of tadpoles in any one pool (including social aggregation of several types and cannibalism at times) are phases in a nice adjustment tending to secure the survival of the greatest numbers of tadpoles, on the average, under the adverse conditions of their environment, the dry grasslands and savannahs of the West.

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VIII

Frequency of Sex Calls in Some Salientia

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THE following facts are very well recognized: (1) that male salientians, under the influence of proper stimuli, use a call (usually distinctive for each species) in their attempts to secure females at breeding sites; (2) that there is some variation in the lengths of individual calls under different environmental conditions and physiological states of the organism; (3) that only males give such sexual calls; (4) that females respond to these calls as though attracted to the male by them; (5) that males often are affected by the calls of other males (usually taking the form of further stimulation of them); and, (6) that in some species the female also has a voice which is used during sexual activity (its functions differ from the breeding call of the male); in other species, females are completely silent during breeding. In addition, males of certain species (and both sexes of others) make different sounds at various times. The so-called protesting notes of various species of *Bufo* and *Scaphiopus* are example of one type, and the scream of certain frogs (*Rana*) when injured represent another.

Various observers have concluded that the sexual call of the male varies in rate according to temperatures, social factors, and physiological states. Thus, Harper (1937) reported that air temperature influenced this rate in *Pseudacris ornata* Holbrook practically as a straight line function for the few records that he could obtain. Bragg (1940, 1942, 1943, 1944-45) has shown that, in several forms, males are stimulated by the calls of their own kind and that in some, at least, the rate of calling is affected by the numbers calling at any one time and place. To me, this has seemed clear-cut in *Bufo cognatus* Say, *B. w. woodhousii* Girard, *B. compactilis*¹ Wiegman, *Pseudacris clarkii* Baird, *Ps. streckeri* Wright and Wright, *Ps. triseriata* Wied, *Hyla versicolor versicolor* LeConte, and all four of the species of *Scaphiopus* studied in Oklahoma and New Mexico. I strongly suspect it in all other species which I have often heard calling and the phenomenon may well prove to be universal in the group.

One of the difficulties in studying the calls of Salientia has always been the next to impossible task of describing differences in calls. To one familiar with the characteristic call of a given species, a variation may be striking but when he tries to put this in writing he usually ends up with unconvincing, vague statements, apparently based on mere impressions. Quantitative data have been needed.

¹ The only form of this species seen by the author at breeding is that called *B. compactilis speciosus* by Smith (1947).

Harper's paper on *Ps. ornata* (1937), appearing while I was actively engaged in studying the closely related *Ps. streckeri*, stimulated an attempt to secure data on rate of calling. The results demonstrated that temperature of both air and water influenced this rate as well as the interval between calls; but neither seemed to affect the duration of individual calls. It was clearly evident that other factors also were involved (Bragg, 1942).

Since that time, I have kept a record for all species heard, based upon (1) the number of calls per unit time, (2) the interval between calls, and (3) the duration of each call at the air and water temperatures prevailing. This has been done by timing with a stop watch at many of the breeding congresses being studied for other purposes. Time of day has also been noted, the record being based upon the time when observations at a given place were started. It has usually taken from ten minutes to two hours to complete each set of observations, depending upon conditions.

In the present paper, I present in Tables I–VII a summary of data so obtained. Additional similar data for *Pseudacris triseriata* have recently been published (Bragg, 1948) and also a smaller number for *Microhyla* (Bragg, 1949).

It is inherently more difficult to secure reliable data on some species than upon others by the method used. In some breeding congresses the calls of one species may make data on others difficult to secure. Also, timing of intervals presents a more difficult problem than timing of calls. For these reasons more data have been secured on some species than on others, as is reflected in the tables.

Those for which data adequate for analysis on calling rate have been secured are *Hyla v. versicolor*,² *Microhyla carolinensis olivacea*, *Pseudacris clarkii*, *Ps. streckeri* and *Ps. triseriata*.

For *H. v. versicolor* little need be said. The mean rate on 144 individuals was just over three calls per ten seconds, the range, 2–4 and the mode, 3. Within the range of the temperatures observed (16.5°–20.0° for air, 17.0°–22.0° for water, with the respective means, 17.5 and 19.3) there is very little departure from the modal value 3 irrespective of the size of congress. The duration of each call is short but the variation is considerable (Table VI). It is clearly not wholly a matter of temperature, however. For example, when AT = 16.5° and WT = 17.0° C. (item 8), R = 1.0–1.5, varying about a mean of 1.1, the mode, 1.0. But with only fifteen minutes difference (in time of day) in starting observation, item 10 does not compare well at all, both the mode and mean being only 0.4 with both AT and WT only slightly higher than in item 8. If item 7 is compared with these, the discrepancy is all the more apparent. The interval between calls is still more variable (Table VII), the extreme fairly comparable, in individual cases, with the over-all range for sixty-six observations. While we need further data (at lower temperatures, particularly) the facts as they stand show a short rhythmic call, varying in duration and interval irrespective of either air or water temperatures within the limits observed. General observation indicates for this species

² As interpreted recently in Oklahoma (Bragg, 1948a.)

a considerable influence of one individual on another, the size of the congress, therefore, having great influence on the calls.

The data given for *Microhyla c. olivacea* shows almost exactly the same tendencies as those for *H. v. versicolor* but these appear a little more clear-cut because all records on rate happened to be obtained at the same air temperature (Table I, items 8, 9, and 10). The variation of 0.3 in the means when water temperatures were also the same indicate a not quite perfect rhythm. Comparing durations (Table VI, items 13, 15, and 16) and intervals, Table VII, items 8, 9, and 11) in these same congresses, we see a greater variation in the last two phenomena than in the first. Here again, the size of the congress, with consequent effect of each individual on others present, is indicated by general observation.

The most adequate data have been secured on the three species of *Pseudacris* known in the Oklahoma fauna, *Ps. clarkii*, *Ps. triseriata*, and *Ps. streckeri*. This is especially fortunate because it enables one to see more clearly the difference in calling between these members of the same genus as well as to elucidate further these differences in the closely related and often confused forms *clarkii* and *triseriata*. Data on numbers of calls per ten seconds observed on 188 individuals of *Ps. clarkii*, 278 of *streckeri* and 262 of *triseriata* are presented in Tables II, III, and IV (cf. Bragg, 1948, Table II, for more data on *Ps. triseriata* taken by this same method).

In both *Ps. clarkii* and *Ps. streckeri* the breeding call is so short a call that durations and intervals are difficult to obtain, and I have not included any of my attempts in the tables because I have been uncertain of their accuracy. The number of calls for unit time average rather high (14.6 for *clarkii*, 20.5 for *streckeri*) and the variability is great in both ($R = 5 - 33$ for *clarkii*, 8-50 for *streckeri* (Table II and III). However, if we omit the one questionable series (Table III, item 11), the range in *Ps. streckeri* is from 8-30, making the two nearly comparable in variability.

Both these forms call at low temperatures and I early noted that the call of *Ps. clarkii* was slow at near freezing temperatures. I have not noted this particularly in *Ps. streckeri*. But other factors are involved: (note Table II, items 1 and 2). On the same date and within fifteen minutes of each other, means of 12 and 8 were obtained in different congresses at the same temperatures. While only six records were taken at the second of these congresses, I could note no difference in the rhythm with considerable listening. To check, I occasionally counted calls at random later while at the site and always got eight per ten seconds. Item 3 is of interest also, because of special conditions. The day had been bright and warm for the season after a heavy rain the day before. At about 4:00 P.M. a cold wind bore down from the north, sending temperatures down sharply. At 5:00 P.M. an almost constant rate of twenty calls per ten seconds was recorded for a small congress of *Ps. clarkii* at the edge of a terrace ditch. The falling air temperatures had not slowed the rate of call against the still warm water. When both water and air are cold, however, (item 9) the rate seems to be affected markedly.

With *Ps. streckeri*, two congresses on the same night varied by 4.8 calls

per unit of time between their means (Table III, items 6 and 7), but the number of observations was inadequate to show much. Where two or more items record the same water temperatures but different air temperatures (or *vice versa*), one variable is controlled; if, therefore, the rate varies directly with the other variable this should be evident. In items 2 and 9, $WT = 11.00$ and the difference in $AT = 2.5^\circ$. The mean call rate is 2.1 higher at the higher temperature. This corresponds to an average of $1.5+$ increase in call rate per degree rise in AT . But with only one degree less in water temperature (items 2 and 9) the corresponding figure is only $0.1-$ and other items (e.g. 10, 13, 14) correlate poorly with this. If we arrange means according to increasing air temperatures, disregarding temperature of water, we come out with the following sequence: 10.6, 13.4, 9.9, 12.4, 18.3, (14.5 and 23.9), (14.6 and 16.2), 22.2, and 24.2. A similar sequence for water temperature disregarding that of air is: 13.4 (14.5 and 12.4), (18.3 and 10.6), (19.0, 14.5, and 16.2), (22.2 and 23.9), and (24.2 and 29.0). Neither of these sequences of means nor similar sequences of modes indicates that rate of call is wholly a result of either air or water temperature taken alone. If we assume that the rate rises with increase in both air and water temperatures and that these have equal effects, then in a sequence of means of air and water temperatures, means in rate should also consistently increase. Such a sequence is 13.4, 10.6, 12.4, 18.3, 14.5, 19.0 (14.6 and 16.2), 22.0 (24.2 and 29.0), and 23.9. This is also negative. But if one take the means of each successive three of this sequence, thus further smoothing out individual variations, we do come out with an increasing rate as follows: 12.1, 17.3—, 17.3, 25.4—. It is very questionable whether 252 cases (omitting items 1 and 11 in the table) are sufficient data to justify conclusions based upon this result.

We therefore conclude that prevailing temperatures (within certain ranges, at least) do influence the call rate of *Ps. streckeri*, that this influence is probably differential as between water and air, that other factors operating in individual cases in congresses modify these effects, and that many more data are needed before a more adequate analysis can be made. These are substantially the conclusions reached earlier (Bragg, 1942) where social factors were emphasized as involved materially.

As stated above, the duration of calls and interval between calls in *Ps. streckeri* are so short that I have been unable to record them accurately by the method used. To my ear they usually seem to be of about equal length for any one individual, varying of course with the rate of calling at any one time and place. At lower temperatures, however, I have sometimes suspected that the rate of call was lower than usual because of a slightly lengthened interval, the duration remaining nearly constant. I hope to secure data to test this matter in the future.

The data for *Ps. triseriata* essentially substantiate conclusions drawn in an earlier paper (Bragg, 1948) and hence are not discussed in detail. It is well to emphasize again, however, the marked difference in the calls of *Ps. clarkei* and *Ps. triseriata*.

In later papers I expect to present further data on these species and upon others based upon mechanical recordings.

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TABLE I

Rates of Breeding Calls of *Hyla v. versicolor* and *Microhyla carolinensis olivacea* in eastern Cleveland County, Oklahoma, at various temperatures. AT & WT = atmospheric and water temperature respectively in °C.; T = total; Mo = mode; R = range; M = arithemetical mean number of calls per 10 seconds, expressed to nearest 0.1; N = number of items; time is p.m., T = summary, mean or totals, for species.

SPECIES	ITEM	DATE	TIME	AT	WT	MO	R	M	N
<i>H. v. versicolor</i>	1	4/23/46	9:30	16.5	17.0	3	2-4	3.0	21
	2	4/29/46	9:10	19.0	18.0	3	2-3	2.7	30
	3	4/29/46	9:30	19.0	18.0	3	3-3	3.0	6
	4	4/ 7/47	8:45	19.0	20.0	4	3-4	3.7	26
	5	4/28/47	9:15	20.0	18.0	3	2-4	3.0	31
	6	5/16/47	8:30	19.0	22.0	3	3-4	3.2	10
	7	7/23/47	9:30	19.0	22.0	3	2-4	2.7	20
	T			(17.5)	(19.3)		(2-4)	3.0	(144)
	8	4/29/46	9:10	19.0	18.0	1	1-1	1.0	72
<i>M. c. olivacea</i>	9	5/16/47	8:30	19.0	22.0	1	1-2	1.5	19
	10	7/23/47	9:30	19.0	22.0	2	1-2	1.8	19
	T			(19.0)	(20.7)		1-2	1.2	110

THE AMPHIBIA OF OKLAHOMA

TABLE II

Data on number of breeding calls of *Pseudacris clarkii*. Symbols and arrangement as in Table I. Item 3 taken in Payne County, Oklahoma; item 4 in Perryton, Texas; items 12, 13, 14 in Love County, Oklahoma. All others are from Cleveland County, Oklahoma.

ITEM	DATE	TIME	AT	WT	MO	R	M	N
1	5/ 2/46	10:15	17.5	16.5	12	12-13	12.2	27
2	5/ 2/46	10:30	17.5	16.5	8	8-8	8.0	6
3	5/10/46	5:00	12.0	21.0	20	19-21	20.0	20
4	7/ 5/46	5:00	28.0	27.0	32	30-33	31.6	10
5	4/10/47	Evening	11.0	16.0	9	7-9	8.4	24
6	4/ 8/47	11:45	16.0	16.0	11	10-11	10.8	23
7	4/ 9/47	9:00	20.0	18.0	15	14-17	15.7	20
8	4/ 9/47	9:30	20.0	18.0	14	12-15	14.4	12
9	4/12/47	10:15	6.0	8.0	6	5-6	5.5	41
10	4/26/47	2:30					20.0*	1
11	4/26/47	4:45					20.8*	1
12	4/27/47	6:30					13.3*	1
13	2/28/48	8:45	14.0	14.0			12.0*	1
14	2/28/48	8:45	14.0	14.0			11.2*	1
T			(16.0)	(16.8)		(5-33)	(14.6)	(188)

* Observation by Mr. Harold Dundee, to whom my thanks are expressed for securing for me what valid data he could when opportunity presented itself, more or less unexpectedly.

TABLE III

Data on number of breeding calls of *Pseudacris streckeri* in 10 seconds. Symbols and arrangement as in Table I and II. Items 1, 2 and 3 are from McClain County. All others from Cleveland County, items 4 and 7 and 11 to 14 from the western part, the others from the eastern part (oak-hickory savannah).

ITEM	DATE	TIME	AT	WT	MO	R	M	N
1	3/ 5/46	5:00			21	20-23	20.8	6
2	3/ 5/46	9:30	13.5	11.0	15	14-16	14.5	26
3	3/12/47	9:45	12.0	12.0	19	16-19	18.3	25
4	3/20/47	10:15	7.0	12.0	11	8-12	10.6	8
5	4/ 8/47	8:45	16.7	16.0	20	18-25	22.2	23
6	4/ 9/47	9:00	20.0	18.0	25	21-26	24.2	14
7	4/ 9/47	9:30	20.0	18.0	29	28-30	29.0	3
8	4/10/47	8:45	13.5	16.0	23	22-26	23.9	30
9	4/13/47	9:00	11.0	11.0	16	15-18	12.4	40
10	4/15/47	6:00	9.9	14.0	19	19-19	19.0	20
11	2/26/48	8:45	18.0	14.0	50*	40-50*	48.5*	20
12	3/11/48	8:30	8.0	9.0	12	12-15	13.4	22
13	3/15/48	8:00	15.0	14.0	15	12-16	14.6	20
14	3/15/48	8:15	15.0	14.0	17	15-18	16.2	21
T			(13.8)	(13.8)		(8-50)	(20.5)	278

* This record appears so much at variance with other similar items that I doubt its validity. My notes indicate that these animals were calling very fast in a very large chorus. I can find nothing to indicate that the record is mistaken and therefore include it. I still think it should be considered tentative until confirmed.

FREQUENCY OF SEX CALLS

TABLE IV

Data on number of breeding calls of *Pseudacris triseriata* per 10 seconds. Symbols and arrangements as in Table I. Item 13 taken at the southern border of Rogers County. All others from eastern Cleveland County. For other data on this species see Bragg (1948).

ITEM	DATE	TIME	AT	WT	MO	R	M	N
1	3/ 5/46	10:40	13.5	12.0	4	4-4	4.0	20
2	4/22/46	9:15	22.0	18.0	6	5-6	5.9	20
3	4/23/46	8:30	16.5	18.0	5	4-5	4.9	20
4	4/ 3/47	9:15	21.0	21.0	5	4-5	4.9	17
5	4/ 7/47	8:45	19.0	19.0	3	2-4	3.1	20
6	4/10/47	10:45	16.8	16.0	5	4-5	4.8	24
7	2/26/48	8:45	18.0	14.0	4	4-5	4.1	20
8	2/28/48	11:00 AM	11.0	6.0	4	3-5	4.1	15
9	3/ 1/48	8:15	8.0	9.0	2	1-3	2.2	19
10	3/15/48	8:00	15.0	14.0	3	3-4	3.4	21
11	3/15/48	8:45	15.0	12.0	3	3-4	3.2	20
12	3/24/48	8:25	22.0	18.0	4	3-5	4.1	16
13	4/ 3/48	8:30	17.0	17.0	3	2-4	3.3	30
T			(16.5)	(14.9)		(1-6)	(4.0)	(262)

TABLE V

Data on number of calls per 10 seconds on three species: Item 1 for *Acris crepitans*, item 2, *Bufo w. woodhousii*, and item 3, 4, and 5 for *Scaphiopus hurterii*. All were recorded near Norman, Oklahoma, those on *Bufo* from the Canadian River flood plain, the others in the oak-hickory savannah 16 miles east of Norman. Symbols and arrangement as in Table I.

ITEM	DATE	TIME	AT	WT	MO	R	M	N
1	4/23/46	9:30	16.5	17.0	28	18-37	28.5	11
2	4/30/46	10:00	20.0	22.0	2	2-3	2.7	120
3	4/29/46	10:00	19.0	18.0	2	2-3	2.9	60
4	4/30/46	8:15	19.0	24.0	2	1-2	1.9	42
5	5/16/47	8:30	19.0	22.0	3	2-5	3.5	35
T (3, 4, 5)			(19.0)	(21.3)			(2.8)	(137)

THE AMPHIBIA OF OKLAHOMA

TABLE VI

Duration in seconds expressed to nearest 0.1 of breeding calls for the species indicated. Data symbols as in Table I.

SPECIES	ITEM	DATE	TIME	AT	WT	N	MO	R	M
	1	4/23/46	10:00	16.5	17.0	20	10.0	9.2-15.0	11.3
<i>Bufo t.</i>	2	4/ 8/47	10:45	16.8	16.0	13	16.0	10.0-33.4	16.8
<i>americanus</i>	3	4/13/47	9:30	11.0	11.0	6	16.0	13.0-21.0	15.8
	T			(14.8)	(14.7)	(39)		(9.2-21.0)	(14.6)
<i>B. cognatus</i>	4	5/ 2/46	10:00	17.5	16.5	14	17.0	10.2-20.0	16.4
<i>B. w.</i>	5	5/15/46	Evening	18.5		15	2.0	2.0- 3.1	2.4
<i>fowleri</i>	6	5/19/46	10:30	21.0	22.0	24	2.0	1.8- 3.2	2.1
<i>B.w.woodhousii</i>	7	4/30/46	10:00	20.0	22.0	20	3.2	2.0- 4.2	2.9
	8	4/23/46	9:30	16.5	17.0	9	1.0	1.0- 1.5	1.1
<i>Hyla r.</i>	9	4/29/46	9:10	19.0	18.0	10	3.0	3.0- 3.0	3.0
<i>versicolor</i>	10	4/28/46	9:15	20.0	18.0	35	0.4	0.3- 0.5	0.4
	11	7/23/47	9:30	19.0	22.0	20	1.0	0.6- 1.1	0.5
	T			(18.6)	(18.8)	(74)		(0.3- 3.0)	(1.3)
<i>M.c.carolinensis</i>	12	6/25/46	7:15	29.0	30.0	11	1.0	1.0- 1.6	1.2
	13	4/29/46	9:10	19.0	18.0	13	3.5	2.0- 6.0	4.0
<i>M. c. olivacea</i>	14	4/30/46	8:00	19.0	24.0	20	2.4	1.3- 4.5	2.7
	15	5/16/46	8:30	19.0	22.0	28	4.0	2.5- 4.0	3.5
	16	7/23/47	9:30	19.0	22.0	20	4.0	3.9- 5.0	4.3
	T			(19.0)	(21.5)	(81)		(1.3- 6.0)	(3.6)
	17	4/13/47	9:25	11.0	11.0	20	1.1	0.9- 1.5	1.1
	18	4/28/47	9:30	20.0	18.0	25	0.9	0.3- 1.0	0.7
<i>Ps. triseriata</i>	19	2/26/48	8:45	18.0	14.0	6	1.0	0.5- 1.8	1.0
	20	3/ 1/48	8:15	8.0	9.0	30	1.6	1.4- 2.2	1.6
	21	4/ 3/48	8:30	17.0	17.0	60	1.0	0.7- 1.3	1.5
	T			(14.8)	(13.4)	(141)		(0.3- 2.2)	(1.2)
<i>R.berlandieri</i>	22	4/ 9/47	9:00	20.0	18.0	4	2.5	2.0- 3.0	2.5
<i>S.hurterii</i>	23	4/29/46	10:00	19.0	18.0	15	0.3	0.2- 0.5	0.3

FREQUENCY OF SEX CALLS

TABLE VII

Mean Interval between breeding calls in seconds for the species listed. Symbols as in previous tables.

SPECIES	ITEM	DATE	TIME	AT	WT	N	MO	R	M
<i>B.t.americantus</i>	1	4/23/46	10:00	16.5	17.0	20	12.0	9.0-13.0	10.7
<i>B.cognatus</i>	2	5/ 2/46	10:00	17.5	16.5	2		12.0-18.0	15.0
<i>B.w.fowleri</i>	3	5/19/46	10:30	21.0	22.0	17	4.0	3.1- 8.0	5.2
	4	4/30/46	8:00	19.0	24.0	20	4.0	3.0- 6.0	4.1
<i>Hyla v.</i>	5	4/28/46	9:15	20.0	18.0	34	3.0	2.1- 6.1	3.3
<i>versicolor</i>	6	7/23/47	9:30	19.0	22.0	12	3.6	3.0- 7.0	4.8
	T			(19.3)	(21.3)	(66)		(2.1- 7.0)	(4.1)
<i>M.c.carolinensis</i>	7	6/25/46	7:30	29.0	31.0	8	21.0	18.5-23.5	21.3
	8	4/29/46	9:10	19.0	18.0	7	9.7	7.0-11.0	9.6
	9	4/30/46	8:10	19.0	24.0	16	6.0	3.9- 7.0	5.4
<i>M.c.olivacea</i>	10	5/16/47	8:30	19.0	22.0	19	7.0	5.0- 8.1	6.0
	11	7/23/47	9:30	19.0	22.0	14	6.8	6.0-17.0	9.1
	T			(19.0)	(21.0)	(56)		(3.9-17.0)	(7.5)
	12	4/ 7/47	8:45	19.0	20.0	28	1.2	1.0- 2.2	1.4
	13	4/10/47	8:45	13.5	16.0	24	1.8	1.0- 2.2	1.8
	14	4/13/47	8:15	11.0	11.0	20	3.0	2.0- 3.9	2.9
<i>Pseudacris</i>	15	4/15/48	6:10	9.9	14.0	6	3.0	3.0- 4.0	3.3
<i>triseriata</i>	16	2/26/48	8:45	18.0	14.0	20	2.5	1.8- 2.9	2.5
	17	3/ 1/48	8:15	8.0	9.0	12	4.3	3.9- 5.3	4.6
	18	4/ 3/48	8:25	22.0	18.0	24	2.6	2.1- 3.2	2.6
	T			(14.5)	(14.6)	(134)		(1.0- 5.3)	(2.7)
<i>S.hurterii</i>	19	4/29/46	9:10	19.0	18.0	10	7.0	4.0- 7.9	6.3

PART III
PAPERS ON SEX CYCLES

IX

The Annual Ovarian Cycle of *Acris Crepitans* Baird

HELEN TALLEY FISHER AND A. RICHARDS

STUDIES on the sex cycles of warm-blooded animals are numerous, but few investigations of similar character have been reported for the cold-blooded vertebrates. Investigators in this general field have followed several lines of research, including the determination of the processes of spermatogenesis and oögenesis, morphological studies of the genital organs, determination of breeding periods and periods of hibernation, the effect of environmental factors on sex cycles, and more recently the relation of the endocrines to germ cell cycles. Studies made of the sex cycles of amphibians are very limited and no work has been published on the species *Acris crepitans*, although an unpublished investigation was carried on in this laboratory by Whaley on the male of the species. The investigations recorded here were concerned principally with the annual morphological changes in the ovaries of mature specimens of *Acris*, and minor emphasis only is placed upon other phases of the reproductive process.

In 1905 and 1908 King reported observations on the oögenesis and morphology of the ovaries of *Bufo lentiginosus*, following an earlier work (1902) on the follicle sacs of the ovaries of several amphibians, *Rana palustris*, *Hyla*, and particularly *Bufo lentiginosus*. Her account of the morphological features of the ovaries of these forms in the period preceding the maturation of the oöcytes agrees in all essential respects with the observations here described for specimens of *A. crepitans*. Smith (1912) reported a similar study of females of *Cryptobranchus allegheniensis*. He found that eggs about to become mature are readily distinguishable by their much greater size and yolk content, a criterion which may be applied to the oöcytes of specimens of *A. crepitans* also. There is a similarity in morphological features and cyclic activity of the ovaries of specimens of *Cryptobranchus allegheniensis*, as Smith described them, with those of specimens of *A. crepitans*. Alexander in 1933 reported on the seasonal variation in the general morphology of the gonads of a tropical toad, *Bufo melanostictus*. He found, in mature females examined, ovaries in all conditions of growth and maturity at all times of the year, with the exception of October and November. He regarded reduced ovaries in mature females as an indication that the spawning period had occurred a relatively short time previously, and thought the breeding season of the form might thus be determined. More general descriptions of amphibian ovarian changes and the morphological features accompanying them are found in the accounts of Morgan (1897), McEwen (1928), Korschelt and Heider (1902), Noble (1931), and others. Kingery (1917) worked on oögene-

sis in the white mouse and discussed features similar to those found in amphibian forms, particularly the appearance and behavior of the nucleoli just previous to the period of maturation in the ova. Clark (1934) followed the annual cycle in the California sardine, *Sardina caerulea*, and determined the time of maturity in the female by measuring the diameters of ovarian ova at various seasons of the year.

Notes on the life history of *Acris* are found in the papers of Dickerson (1908), Wright and Wright (1933), Wright (1932), and Stejneger and Barbour (1933). Numerous investigators have reported within very recent years the effect of rainfall, temperature, humidity, periods of light and darkness, and hormonal products on the annual sex cycles of animals.

Material and Methods

The cricket frog, *Acris crepitans*, common throughout a large part of the United States, is one of the few non-hibernating frogs and toads, and may be found in central Oklahoma during all months of the year. According to Wright (1932), this frog at breeding has the least size of any, with the exception of individuals of *Pseudacris ocularis*; males mature at a length of 15–29 mm. and females at 16–33 mm.

All observations reported in this paper were made on fixed specimens. Those frogs upon which the study was largely based were collected during the years, 1931–1939, principally from the vicinity of Norman, Oklahoma.¹ At the time of collection, ventral incisions were made in the specimens, they were fixed in Bouin's fixative, and stored in 70 per cent alcohol. Females in the collections number 108 individuals, and collections from all months are represented. In addition, specimens of *Acris* in the Museum of Zoology of the University of Oklahoma were available for supplementary study. These had been fixed in a 10 per cent solution of formaldehyde and preserved in 70 per cent alcohol. Seventy-one female frogs are included in this collection and represent the months of March, May, June, July, August, and October, from the years 1924 through 1933. Only frogs of mature size were used, specimens smaller than 16 mm. not being considered. It was not found that the method of fixation made any noteworthy difference in the measurements of the specimens or ovaries.

Several methods of study were employed. The first consisted of a measurement of the entire volume of the body of each of the 179 females, and the dissection and measurement of the volume of their ovaries. From these data the ratio of the ovarian volume to that of the entire body for each frog was estimated. Volume of the body was determined by suspending the specimen by a fine wire hook in alcohol in a 100 cc. graduated cylinder with calibration of 1 cc. Readings were taken while the frog was suspended therein and after its removal, and the difference calculated to give the volume, allowance being made for the volume of the hook.

¹ The work of Miss Whaley, previously mentioned, upon the males of this species was also based on animals collected in this vicinity. They were mistakenly identified as *A. gryllus*.

The ovaries were then dissected and a fine-meshed copper basket was used to suspend each in alcohol in a graduate burette of 25 c.c. volume and calibration of 0.1 c.c. Readings were taken as before, allowance being made for the volume of the basket. All measurements were recorded in cubic millimeters. The ovarian volume in percentage of the volume of the entire body was estimated and recorded with the number of the frog, date of its collection, body length, volume of the entire body, and volume of the ovaries. The average percentage of ovarian volume to total volume of the specimens fixed during each month was figured, as shown in Table I. As noted before, all months are represented in the collections, although the collections of January consist of only a few females whose ovaries had been removed and embedded in paraffin previous to this part of the study; no data are available, therefore, on the size of the ovaries for specimens fixed during this month. Collecting during January is usually difficult because of low temperatures.

Observations on the shape, color, and general features of the ovaries were made at the time of their removal. Notes were taken on all unusual specimens, and in some few cases the gonads were left intact for further observation. With the aid of a dissecting microscope a careful study of all external features of the ovaries was made, with especial attention to the changes occurring in their appearance from month to month.

Representative ovaries from each month were embedded in paraffin, sectioned at eight micra, and stained with Heidenhain's iron-hemotoxylin.

OBSERVATIONS

Ovarian Volume

The calculation of the volumes of the ovaries relative to the volumes of the entire bodies of the frogs, given in percentages (the percentage of ovarian volume), shows a significant variation during the year. (See Table I.) Frogs collected in September have a low average of ovarian volumetric percentage and the variation among individuals is slight. The average percentage for frogs of October collections is lower than any since March, and the decline of average percentages continues through December. As stated previously, no frogs of January were available for measurement of their ovaries. The average for February continues low and the variation among individuals is not noteworthy. A small decrease in the average percentage was found in the frogs collected during March. The range of percentages among individuals here is wider, however. A distinct rise was noted in the average percentage of volume for frogs fixed in April, and a still greater individual variation was evident. The average percentage for frogs of May is the highest of the year, both among Bouin-fixed specimens and formalin-fixed frogs. The June average remains high, although it is slightly less than that of May. The July average is also among the highest of the year. It is interesting to note that the average for this month was lowered by a group of frogs collected during the drouth year of 1936, which suggests a probable effect of rainfall and humidity on the

development of the ovary. Likewise, frogs collected during August, 1936, had lower percentages than did those collected during August of other years. The general average for August is slightly lower than that of July, with a rather wide range among individuals. Thus the average ratios of ovarian volume to that of the body of frogs collected during the months of October through March represent the lowest of the year, while the peak is reached in May.

External Changes in the Character of the Ovaries

The female genital system of specimens of *Acris crepitans* is similar in all essentials to that of the typical frog. A detailed description of the same will not be included in this report, the interest of the observations made lying solely in the changes of the ovaries during the year.

Ovaries of frogs collected in September and October are shrunken, unpigmented, and contain few well-developed oöcytes. As will be noted later, a significant difference is found in the appearance of these ovaries and those of frogs in the August collections, a difference which marks the end of the breeding season and the beginning of the new generation of oöcytes. The small oöcytes, entirely lacking in pigmentation, which are found in ovaries of specimens collected and fixed during September and October are almost translucent, although the nuclei are distinctly visible. Ovaries of frogs taken during November and December are quite similar externally to those of October. Although the oöcytes vary slightly in size, no advanced stages are seen in the average specimen.

Ovaries of frogs collected during January were not available for gross study. The ovaries of those specimens fixed in February are entirely lacking in pigmentation, and when seen under a dissecting microscope show no well-developed oöcytes. Their shape and general appearance is much like that of a mulberry, small oöcytes causing slight protrusions over the entire surface of the ovary.

The ovaries of frogs in collections of March are quite similar in appearance to those which are typical of February, development externally showing little progress. Pigmentation is lacking and the increase in size of the oöcytes is almost negligible. Ovaries of specimens taken during April are slightly advanced in development over those of March. Although of varying sizes, none of the oöcytes show marked development. Changes in both pigmentation and size occur at the end of April, and many well-developed, deeply pigmented oöcytes are found in ovaries of animals collected in May. The range of size is great, indicating the presence of various stages of development within a single ovary.

Frogs collected during June have ovaries so greatly increased in volume by the rapidly developing oöcytes as to fill the entire body cavity, although of the 179 frogs examined there was none in which eggs were found free in the cavity either during this month or other months, as had been reported for *Bufo* by King (1905) in numerous cases, and for *Cryptobranchus* by Smith (1912) in very few.

Specimens of *Acris* fixed during July and August have ovaries which vary little in external appearance from those of June. Ovulation occurs during late July, August, and September, and it may be of interest to note the general features of an oöcyte at the period just preceding ovulation. When removed from the ovary and observed beneath the dissecting microscope, the typical oöcyte is found to be pigmented on approximately two-thirds of its surface; the remainder is much lighter in color, a manner of pigmentation which gives the ovaries a speckled appearance. When dissected, the oöcyte is found to be covered by a thick membrane, the egg membrane or the "zona pellucida." The yolk layer is approximately one-third the diameter of the ovum in thickness. Due to the great abundance of yolk within this portion of the egg, it is thick and opaque. The nucleus, located in approximately the center of the oöcyte, has a white, gelatinous appearance.

Microscopical Structure of the Ovaries

When ovaries are studied microscopically and in section, both shape and size are found to vary markedly at different seasons of the year. At no time does an ovary seem to have a definite form, but it is made up of a varying number of irregularly shaped lobes. The size of the ovary is determined, of course, by the degree of development of the oöcytes contained therein.

The entire ovary is covered by the mesovarium, which attaches it to the body wall. This membrane is thin, transparent, and dotted by numerous deeply staining spots of pigment. The mesovarium is seldom seen in sections, and is apparently destroyed during the preparation of the ovary for staining.

The wall of the ovary is double, the two layers being made up of small cells whose boundaries are not visible, but whose nuclei are deeply stained by hematoxylin. Between these layers lie scattered blood vessels which supply the ovary with blood.

The developing oöcytes, with their membranes, fill practically the entire volume of the ovary. A few groups of cells, similar in all respects to those composing the outer ovarian wall, are found between the follicles. Due to their crowded condition, the oöcytes are irregularly polygonal in shape, with the exception of those in the outer portion of the ovary, which are rounded on the outer side.

In mature females of *Acris* the ovaries contain only germ cells in the period of growth preceding the first maturation division. No oöcytes with a maturation spindle are found before the time of ovulation in this species. Since the study did not include the rupture of the ovarian wall by the oöcyte, definite cytological information concerning spindle formation is not available. King (1905), however, described the formation of the first maturation spindle in *Bufo* as synchronous with the rupture of the wall of the ovary by the oöcyte, and the first polar body as given off during the passage of the oöcyte down the oviduct. The chief emphasis of this study of the mature ovaries of specimens of *Acris* is not, therefore, on the behavior of the chromosomes, but on the seasonal changes in the morphological features of the ovaries.

Oöcytes of many stages of growth and development are found within a single ovary. (See Figs. 2-4.) It is obvious, therefore, that all the oögonial cysts in the preceding period do not advance in development at the same rate, and some oöcytes reach maturity long before others. In general, the larger oöcytes are found in the center of the ovary, while the less advanced and the very young ones are located near the periphery.

Only one oögonium of an oögonial cyst continues development. The remaining oögonia of the cyst become flattened and combine to form the follicular membrane, which surrounds the developing oöcyte. (See Fig. 1.) The follicular cells have deeply staining nuclei and even more darkly staining nucleoli. Their walls are not visible, but in some places the follicular membrane appears to be two or more cells in thickness, judging by the number of nuclei seen. A thick inner membrane closely invests all larger oöcytes, but is rarely seen within the follicular membrane of oöcytes less than 0.14 mm. in diameter. This is the future "vitelline membrane," usually termed at this stage the "zona pellucida." It is anucleate and almost clear in appearance. (See Fig. 1.) The presence within the "zona pellucida" of a "zona radiata," which is described for some amphibians, is not apparent in the ovaries of individuals of *A. crepitans*. A suggestion of this layer is found in certain sections, but is so indistinct as to make its existence uncertain.

Although the membranes remain fairly constant during the year, the cytoplasm and nucleus of an oöcyte show striking changes. The cytoplasm of very young oöcytes exhibits no differentiation, and cytoplasmic inclusions are apparently lacking. (See Fig. 3.) In later periods of growth, however, "yolk nuclei," described by King (1908) for *B. lentiginosus*, are found. These "yolk nuclei" are thickened areas which stain more deeply with hematoxylin than the remainder of the cytoplasm. When first noted, they are scattered throughout the outer two-thirds of the cytoplasmic portion. At a still later stage, when the yolk has accumulated in the oöcyte, the "yolk nuclei" lose their identity. Whether they play a direct role in yolk formation is not certain. King, in her report of *Bufo*, suggested this might be true, and believed that the "yolk nuclei" are probably developed from the "vitelline bodies" which are found at an earlier stage. She described the latter as small, darkly staining spots in the cytoplasm which multiply by a form of fission. A careful study of sectioned ovaries from specimens of *Acris* fixed during all months failed to reveal the presence of "vitelline bodies." These are described, also, for the genus *Cryptobranchus* by Smith (1912). Smith stated that "the disappearance of the 'vitelline bodies' at the time of yolk formation suggests a correlation between the two phenomena; but so far as I have been able to observe, the final stages in the disappearance of the 'vitelline bodies' are not closely associated with the formation of yolk granules, nor have I found any undoubted 'yolk nuclei' such as described by King for *Bufo*." Smith thought that this is not surprising in view of the diverse methods of yolk-formation found in different amphibians. Whether "vitelline bodies" are actually lacking in individuals of *Acris*, or whether the methods of fixation and staining used failed to reveal them, cannot be stated.

Between the "zona pellucida," or "zona radiata," if the latter is present, and the yolk region is an area of yolk-free cytoplasm (See Fig. 4.) This is seen in oöcytes of all periods of development. Within this, in those stages where yolk is present, lies first a narrow region of very fine yolk, and then a dense layer of cytoplasm filled with large yolk spherules; the region immediately surrounding the nucleus carries less yolk. The comparative density of these regions varies during development. The cytoplasmic portion is approximately two-thirds the diameter of the entire oöcyte. This proportion is less, of course, in the smaller oöcytes where yolk is either lacking entirely or present in small quantities. (See Figs. 2-4.)

The nuclear membrane of the oöcytes is seen distinctly in all series studied. The shape of the nucleus is in general oval, although quite irregular in the larger oöcytes. Darkly staining nucleoli are present in varying numbers in the nucleus of the smallest oöcytes found in ovaries of mature specimens of *Acris* and persist throughout the growth period. (See Figs. 4 and 6.) The origin of these nucleoli has not been adequately explained by those who have described them for other forms. Pratt and Long (1917), studying the egg of the white rat, *Mus norvegicus albinus*, thought these "chromatin nucleoli," as they have been designated in some instances, to be merely closely compacted clumps of chromatin which have migrated back along the linin threads to one or more common points. An adequate determination of their origin and function in these oöcytes necessitates further work. Their staining capacity is the same as that of the chromosomes, however. The nucleoli vary in size, and, as noted earlier, change their position relative to the chromosomes as growth proceeds from month to month.

The behavior of the chromosomes during the period of growth, as suggested above, is of little interest. The chromosomes stain very lightly and are inconspicuously grouped in the center of the nucleus, apparently in more or less reticular form, but in some instances they have a feathery appearance.

Monthly Changes in the Ovaries

Ovaries of frogs collected and fixed during September are of such character as definitely to mark the end of the old cycle and the beginning of the new. (See Fig. 2.) Few evacuated or degenerating follicles are present. The cytoplasm of the small oöcytes is undifferentiated, lacking in yolk and "yolk nuclei." In the average oöcyte of frogs of September, the cytoplasm occupies no more than half the diameter of the entire oöcyte, while in the months just passed the proportion of cytoplasm is markedly greater. The follicular membrane is present, of course, but the "zona pellucida" is seen around only the very largest of the oöcytes. A pigmented membrane bearing what seems to be particles of fat often lies beside the ovary. This is doubtless a portion of the mesovarium. The position of the chromatin nucleoli is distinctly different from that found in oöcytes of frogs collected during the active breeding months. The nucleoli here are sparse and lie close to the nuclear membrane; none are found in the central region of the nucleus, as in the ovaries of frogs during the summer.

Ovaries of specimens collected during October (see Fig. 3) differ little in general features from those of September. There is a small increase in the average size of the oöcytes. The only other change noted is a movement of the chromatin nucleoli closer to the centers of the nuclei.

An increase is found in the diameters of the largest oöcytes and of the predominant size of oöcytes in the ovaries of frogs of November. (See Fig. 4.) A slight differentiation of cytoplasm is seen at this stage. "Yolk nuclei" are few in number, but are occasionally found in the outer region of the cytoplasm; no general peripheral yolk concentration is seen, however. The chromatin nucleoli lie closer to the nucleus than in the oöcytes of frogs collected in October.

No outstanding differences are seen between the ovaries of frogs fixed in November and those of individuals of December collections. In the sections studied of the latter a slight retrogression in development is apparent. Reference to comparative ovarian volumetric percentages of the two months shows also a similar slight decrease for December. Cytoplasmic differentiation is likewise a little less marked here.

Ovaries of frogs collected and fixed during January contain oöcytes in a stage of growth and development approximately midway between those of frogs taken in September and those taken during the summer months. The range of variation in the sizes of oöcytes of these frogs is not so great as in those collected during the months closer to or during the breeding season. (See Table II.) The cytoplasm in the larger oöcytes of frogs of January is more dense around the periphery than in the inner region, due to the gathering of yolk spherules in the former. No "yolk nuclei" are distinctly seen. The cytoplasm of smaller oöcytes, of course, shows no differentiation and no sign of the presence of yolk. The nuclei, numerous at this time, are grouped approximately midway between the periphery of the nucleus and the chromosomes. These darkly staining nucleoli are of various sizes, the larger several times that of the smaller. The chromosomes fit the general description given in the preceding section, that is, they are feather-like in appearance, lightly stained, and lie in the center of the nucleus.

The mean diameter of oöcytes of frogs fixed in February (see Fig. 5) differs little from that of oöcytes of frogs of January, although the range of size is greater. The cytoplasm of the larger oöcytes is becoming more dense near the periphery. Cytoplasmic differentiation has not advanced far, but the outer region is heavier with yolk than the region immediately surrounding the nucleus. No change is noted in the appearance of the chromosomes, but the chromatin nucleoli are more numerous and lie closer to the chromosomes.

The general increase in size of the oöcytes is considerable. As in all months, however, very young oöcytes are present. (See Fig. 6.) The yolk in the larger oöcytes found during February, and the region of heavy yolk extends closer to the nucleus. Chromatin nucleoli lie slightly closer to the chromosomes.

The increase in the average size of oöcytes in ovaries of frogs collected during April over those found in March is less than was seen in the month

preceding. The size range during the month is approximately the same as during March, although there seem to be fewer very small oöcytes. Little change is seen in the appearance of the cytoplasm; it stains darkly with the exception of the region immediately surrounding the nucleus.

The average size of the oöcytes of frogs collected in May increased definitely, for very small ones are fewer in number, and the larger ones have accumulated yolk near their periphery. Here, as in other months, the larger oöcytes are found in the center of the ovaries. The chromatin nucleoli at this period lie very close to the chromosomes and vary considerably in size.

The average size of the oöcytes is increased still more in ovaries of frogs fixed in June. The majority are yolk-laden and in an advanced state of growth. Very few small oöcytes are present. No change was noted in the appearance of the chromosomes from those of the preceding months.

It is necessary in describing ovaries of July frogs to consider two stages of development, that of frogs collected early in July (see Fig. 7) and that of frogs collected late in the month. The former resembles very closely that of specimens fixed in the preceding month, the only difference being a slight increase in size of the oöcytes at the later date. Few small oöcytes are present. Ovaries of frogs collected late in July, however, contain comparatively few large oöcytes, many young ones, a considerable number of follicles from which the oöcytes have escaped, and others in which a process of degeneration is taking place. Degeneration of the follicular membrane begins shortly after the escape of the oöcyte. The cells forming the membrane which surrounds the mature oöcyte before its escape move into the evacuated follicle in an irregular manner. A similar condition was found in oöcytes which were undergoing degeneration, as described below. The collection and study of ovaries of frogs fixed at more frequent intervals during this period should prove to be of much interest in respect to the specific manner in which degeneration of the follicular sac in this form occurs. King (1902) reported the manner of degeneration of the follicular sac in specimens of *Bufo*. This degeneration must occur, of course, to make room for the new generation of oöcytes. Left in the follicle after an oöcyte escapes is a reticular framework and in some instances the follicle cells which are moving in from the broken follicular membrane. The "zona pellucida" is not seen, of course, since it becomes the "vitelline membrane" of the egg in later development and remains with the oöcyte as it leaves the ovary.

In those follicles in which the oöcyte is degenerating (see Fig. 8) the reticular framework is present, supporting the remaining yolk which varies in amount with the stage of degeneration. Degeneration seems to occur first in the outer regions of the oöcyte, and the last remaining portion of the oöcyte is found in the very center of the follicle. The presence of follicles undergoing degeneration substantiates the theory of Hargitt (1930) drawn from his study of the sex glands and germ cells of the female of the albino rat, that many ova degenerate and never come to ovulation.

The ovaries of frogs collected during August (see Fig. 8) resemble in all general respects those just described for frogs of late July. The number

of yolk-laden oöcytes which remain is smaller, however, in proportion to the many small oöcytes present. Those in an intermediate stage of growth are practically lacking. Evacuated follicles are seen in greater numbers than in the ovaries of specimens fixed during July, and a considerable number of oöcytes are in some stage of degeneration.

Discussion

The foregoing account of the changes occurring monthly in the ovaries of mature female specimens of *Acris* indicate a definite annual ovarian cycle. A consideration of the changes in the size of the ovaries in proportion to the total body size, the growth of the oöcytes, the accumulation of yolk, and the behavior of the various component parts of the oöcytes all point to a yearly cycle beginning late in September and ending with the close of the breeding season in late August and early September.

Little change is seen during the year in the membranes of the ovary. The follicular membrane is present during the entire period of growth of the oöcyte and is the last remnant of the follicle after the oöcyte has escaped. Degeneration and resorption of this membrane occur at the close of the breeding season to make room for the new generation of oöcytes which start development in September.

"Yolk nuclei" are first observed in ovaries of frogs fixed in November. No formation of yolk spherules is found until January, when there is a slight thickening of the outer region of the cytoplasm. In ovaries of frogs taken during February the oöcytes are found to have a definite cytoplasmic differentiation, although there is no region of dense yolk. At the time of yolk formation, the "yolk nuclei" lose their identity; it would thus seem that they play a role in the formation of the yolk.

The exact mode of the formation and the derivation of yolk is a question of speculation and doubt among workers on amphibian forms. King (1908) in her discussion of the problem remarked that "investigators have seemed to show that yolk is derived directly from nucleoli, or from chromatin, or from follicle cells, are all open to question, and until they have been confirmed by further research, I shall be inclined to believe that yolk formation is one of the anabolic processes in the cells which, although it is directly or indirectly controlled by the nucleus, does not depend upon the nucleus for its material substance." She wrote further, "It may be that during the earlier stages in the development of the ova 'yolk is present in the cytoplasm in the form of diffused, unstainable fluid' as Montgomery has suggested, and that this fluid is first collected into rounded vitelline bodies and later changes into yolk spherules." There is no indication in the study of females of *Acris* that yolk is derived in any way from the nucleus or from the follicle cells, and although "vitelline bodies" are not found in this material, it seems from all indications that the "yolk nuclei" may in some way give rise to the first yolk, since these nuclei disappear almost completely when yolk formation begins.

The nuclei of the oöcytes of mature specimens of *Acris* present only one

feature of cyclical activity. The nuclear membrane is intact throughout the entire growth period, and the chromosomes remain in a state of inactivity; the behavior of the nucleoli, however, is of considerable interest. Nucleoli are present in all stages of oöcytic growth, their number increasing as the oöcyte grows. No definite cyclic change in the proportion of large and small nucleoli has been noted. The most striking feature in connection with them is their gradual movement from the periphery of the nucleus to the immediate vicinity of the chromosomes. This movement begins in September and is completed at the time the oöcytes reach their greatest development in the summer. King thought this arrangement of nucleoli in the egg previous to maturation to be characteristic of all amphibian eggs.

A careful study of the comparative sizes of oöcytes from frogs of each month of the year leads to the conclusions which follow. The ovaries of those specimens collected from any month of the year contain oöcytes of varying stages of growth. The least variation is found in the ovaries during late September and October. An increase in the size of the oöcytes is found month by month, December excepted, until the onset of the breeding season. Sizes of those fixed during the month of December, as noted previously, fluctuated irregularly, although this fact is probably of little significance in the characterization of the annual cycle. During July and August the ovaries contain oöcytes of approximately the same average size, although more very small oöcytes were noted in the ovaries of frogs collected in the latter part of July and in August than in the early part of July. Young oöcytes which are to remain in the ovaries and constitute the next generation of oöcytes are seen in late July and August and constitute the bulk of the ovaries in September, while the well-developed oöcytes in ovaries of frogs fixed during August are either breaking out of the ovary or are degenerating and being resorbed. Few large ones remain in a whole condition at this time. The very small ones are found grouped around the periphery of the ovaries and this represents the earliest period at which new oöcytes are seen as they move into the ovary to replace those degenerating or being lost through ovulation. The marked difference between the predominant stage of oöcyte growth in July and that of late September clearly marks the close of the breeding season in late August and early September.

Changes in the average percentages of ovarian volume correspond quite closely to other changes taking place in the annual cycle. The percentages increase during the spring months, reaching a maximum in May, June, and July. A decline begins gradually in August, which may be accounted for by the occurrence of ovulation and degeneration of oöcytes. Averages in the late fall and winter months are the least of the year.

A study of the length of the body, volume of the entire body, volume of the ovaries, and the percentage of ovarian volume of mature females of *Acris* suggests several general relationships. Correlation between the size of the ovaries and the body length is slight, but the volume of the body, exclusive of the ovaries, is correlated with the body length. Considerable variation is found among mature frogs of any month in the percentages of ovarian

to total volume, and while the ovarian volumetric percentage does not always seem to indicate the stage of development of the oöcytes, the trend of changes is very clear.

Summary

One hundred and seventy-nine females of *Acris crepitans* were studied both macroscopically and microscopically with regard to changes occurring in their ovaries during the course of a year. An annual cycle in the development of the ovaries, beginning in late September and terminating in late August or early September, is indicated by the curve of average monthly percentages of ovarian volume, the relative sizes of the oöcytes during each month, the time and manner of yolk formation, the movement of the nucleoli from the periphery of the nucleus in September to a position of close proximity to the chromosomes in the center of the nucleus in the breeding months, and, in order to make room for the new generation of oöcytes beginning development, the degeneration and resorption during the breeding season of all well-developed oöcytes which do not escape from the ovary. The breeding season, as determined from this study, extends during the years of these observations from the latter part of July to the early part of September.

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ANNUAL OVARIAN CYCLE

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TABLE I

Ratios of Percentages of Ovarian to Total Volume

Time of Fixation	Bouin Fixation		Formalin Fixation	
	AVERAGE PERCENTAGE	RANGE OF PERCENTAGES	AVERAGE PERCENTAGE	RANGE OF PERCENTAGES
January	—	—	—	—
February	4.72	4.17– 5.92	—	—
March	4.68	2.50– 5.56	1.43	0.63– 2.16
April	5.77	3.08–10.43	—	—
May	13.96	5.37–21.63	14.23	12.28–16.81
June	6.04*	6.04– 6.04	12.08	3.62–27.18
July	8.72	1.24–22.00	9.81	4.94–28.86
August	5.74	2.68– 7.53	7.29	3.96–11.11
September	6.64	2.06– 9.33	—	—
October	5.53	1.45–15.83	3.28	2.94– 3.72
November	3.40	1.39– 6.32	—	—
December	3.32	1.02– 7.00	—	—

* Represents only one specimen.

TABLE II

Comparative Diameters of Oöcytes

TIME OF FIXATION	DIAM. OF LARGEST OÖCYTE	DIAM. OF AVERAGE OÖCYTE
January	0.408 mm.	0.324 mm.
February	0.552 mm.	0.420 mm.
March	0.660 mm.	0.540 mm.
April	0.600 mm.	0.564 mm.
May	0.864 mm.	0.672 mm.
June	0.852 mm.	0.720 mm.
July	0.876 mm.	0.804 mm.
August	0.840 mm.	0.840 mm.
September	0.320 mm.	0.160 mm.
October	0.300 mm.	0.240 mm.
November	0.360 mm.	0.264 mm.
December	0.252 mm.	0.192 mm.

Explanation of Figures

The photomicrographs included here are those made of sections of the ovaries taken from specimens of *Acris crepitans*, collected and fixed during the months indicated below. The magnification of Figures 2–8 is $\times 96$; that of Figure 1 is $\times 736$.

Figure 1. Section through portions of several oöcytes from an ovary fixed in January, showing the membranes of the oöcytes.

Figure 2. Section through ovary of a frog fixed in September.

Figure 3. Section through ovary of a frog fixed in October.

Figure 4. Section through ovary of a frog fixed in November.

Figure 5. Section through ovary of a frog fixed in February.

Figure 6. Section through ovary of a frog fixed in March.

Figure 7. Section through ovary of a frog fixed in July.

Figure 8. Section through ovary of a frog fixed in August.

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A Comparison of the Ovaries of Two Species of *Bufo* with Different Ecological Requirements

CAROL BERGTHOLD CLARK AND ARTHUR N. BRAGG

STUDIES on the breeding behavior of Salientia suggest at least three major factors, the interrelated influences of which initiate breeding. There are (1) environmental stimuli such as sufficient rainfall at the proper temperature, (2) hormonal regulations, and (3) physiological cycles in the gonads during the seasons in which sex products are produced. In Oklahoma, rainfall (in both amount and rate of fall) is of greater significance as a stimulus for some species than for others (Bragg, 1946). Salientian species in this state show three distinctly different breeding patterns (the xeric, mesic, and intermediate) which occur respectively (1) in species generally limited to prairie habitat, (2) in others in woodland and savannahs or limited to these, and (3) in those which range through several ecological communities. With few easily explainable exceptions these relations hold widely among the twenty-seven salientians known here. Rugh (1935) demonstrated ovarian stimulation by the hormones of the anterior pituitary gland as well as the initiation of typical breeding reactions, as the clasp reflex of the male. Many laboratories now make use of his techniques to secure eggs of various forms for experimental purposes out of the normal breeding season for the species in question. The seasonal events in the gonads, however, are not well known and almost no study has compared these events in species with different breeding patterns or different ecological requirements. Most laboratory workers have studied species having the mesic pattern of breeding; so far as we are aware, species with the xeric breeding pattern have been overlooked regarding these matters. Fisher and Richards (this volume) traced the seasonal changes in the ovaries of *Acris crepitans* Baird, a species having the intermediate breeding pattern. This is the only paper known to us which deals with the problem of the seasonal change in the gonads of any North American salientian.

This paper compares two species of *Bufo* which occur in large numbers in Oklahoma but have different ecological requirements and correspondingly different breeding patterns. Specifically we set ourselves to answer the following questions: (1) Is there any significant difference in the volumes of the ovaries of the two, each taken as percentage of total volumes of adults? (2) Within each species, what fluctuations in ovarian volume can be determined during different months of the breeding period of each? (3) What

are the cytological conditions, month by month, in the ovaries of representative specimens of each and how do they compare? (4) How can these findings be correlated with other factors already known to be important in the initiation of breeding at different points in the breeding periods?

Two species, *Bufo cognatus* Say, which has a xeric breeding pattern, and *Bufo woodhousii woodhousii* Girard, which has a mixed pattern, were the species chosen for study. Ninety-two females of the former from twenty-three counties of Oklahoma and ninety-nine females of the latter from thirty-three counties were used. The specimens of *B. cognatus* were collected between March and September; those of *B. w. woodhousii*, between March and October. The specimens were among those in the collections of the University of Oklahoma Museum of Zoology, covering a period of ten years, altogether representing forty-four counties; but most of these were collected by Arthur N. Bragg and Charles C. Smith during 1939 and 1940. Full data on all of the latter and most of the former specimens as to exact location, ecological community, behavior as caught, and other matters, were at hand.

The methods used were essentially similar to those of Fisher and Richards hence need not be repeated in detail. Briefly, volumetric methods were utilized to determine the volumes of excised ovaries (or, in a few cases, ovulated eggs taken from the coelom), and sections of selected ovaries were prepared and stained by the usual methods. By comparing the size of the individual (total length or body-volume, both of which were determined for each specimen) with the volume of the ovary (or ovary plus eggs if ovulation had occurred) the percentage of total volume represented by the ovary was calculated for the month in which the specimen was collected. The month by month data for the two species make specific difference evident; for each species, the data may be related to the histological and cytological conditions of the gonads. Ecological and other notes taken by the collectors give additional bases for valid interpretations.

We acknowledge with gratitude the aid of (1) Dr. A. I. Ortenberger who permitted use of the specimens in the University Museum, (2) the librarians of the University of North Carolina and of (3) North Carolina State College for loans of literature, and (4) Dr. A. Richards who has read the manuscript critically.

Observations

Fluctuations in ovarian volumes in the two species are presented in Tables I and II. A comparison of the ovarian conditions as seen microscopically follows:

COMPARISON OF OVARIES

TABLE I

Bufo cognatus Say

MONTH	NUMBER OF SPECI- MENS	MEAN OF BODY VOLUMES IN CC. WITH STANDARD ERROR	MEAN OF OVARY VOLUMES IN CC. WITH STANDARD ERROR	MEAN OVARY VOLUME PER- CENTAGE OF MEAN BODY VOLUME	RANGE OF OVARIAN PERCENTAGES
March	8	88.60±0.91	23.30±0.86	26.29	9.48-49.39
April	11	91.00±1.30	29.45±2.07	32.36	10.51-53.73
May	19	84.10±0.96	20.87±0.75	24.81	13.01-34.29
June	16	81.05±3.07	18.59±1.29	22.93	3.44-62.46
July	9	70.26±2.04	10.72±1.37	15.25	4.81-26.92
August	13	63.31±0.83	21.16±0.99	25.39	7.98-29.37
September	15	83.26±0.94	19.07±0.82	22.94	13.64-39.67

TABLE II

Bufo woodhousii woodhousii (Girard)

MONTH	NUMBER OF SPECI- MENS	MEAN OF BODY VOLUMES IN CC. WITH STANDARD ERROR	MEAN OF OVARY VOLUMES IN CC. WITH STANDARD ERROR	MEAN OVARY VOLUME PER- CENTAGE OF MEAN BODY VOLUME	RANGE OF OVARIAN PERCENTAGES
March	5	85.18±3.11	12.72±2.47	14.81	4.63-20.94
April	20	107.67±0.52	32.91±0.73	30.56	15.80-73.74
May	16	87.74±0.88	18.33±0.96	20.89	10.03-64.20
June	12	20.07±2.03	20.07±2.03	22.48	10.91-63.78
July	13	94.44±0.93	15.80±0.96	16.72	4.10-35.22
August	23	81.40±0.81	16.56±0.66	20.34	7.88-49.73
September	1	117.50	10.30	8.76	
October	9	78.13±3.41	2.31±2.92	2.95	1.25- 5.40

Microscopic Structures of the Ovaries

Viewed microscopically, the ovary of a young toad is a double-walled sac in which darkly stained nuclei of the wall itself and many primordial germ cells are visible. Cross-sections through capillaries and a few larger blood vessels are also to be seen, but the peritoneum which normally covers the entire gonad cannot be demonstrated and is therefore presumed to be lost during the preparation of the sections.

A follicular envelope covers each developing oöcyte and is its means of attachment to the ovarian wall. The membrane, consisting of oögonial cells whose oögenesis into mature germ cells has been sacrificed for the good of the one cell which does undergo development in each cyst, is typically inconspicuous in yolky eggs; and in the gonads of *B. cognatus* and *B. w. woodhousii*, it consists of only one to three layers of flattened cells. The zona pellucida is a clear membrane immediately within the follicular envelope. It can be seen in cells of *B. w. woodhousii* as small as 0.18 mm. in diameter

and in slightly smaller oöcytes of *B. cognatus*. No zona radiata, frequently found within the zona pellucida of vertebrate eggs, could be demonstrated as present in these species. After ovulation, the zona pellucida becomes the vitelline membrane.

In any mature ovary, practically every stage of primary oöcyte growth can be found from that of the young oöcytes which are attached to the sac to that of the older and larger cells which are packed together in the ovarian cavity. The development of individual cells in the ovaries of *B. cognatus* and *B. w. woodhousii* is very similar for the two species; therefore, a general blanket description of these events is sufficient.

In the oöcytes of *B. cognatus* ranging up to 0.34 mm., the cytoplasm appears entirely homogeneous and without inclusions. The nucleus is round or ovoid in shape, bears inclusions, and is surrounded by a definite nuclear membrane. With the beginning of yolk synthesis, however, the oöcytes show decided changes in both cytosome and nucleus and steadily increase in size until a maximum diameter, approximately 1.1 mm., is reached.

The first alteration in the cytoplasm occurs when small and irregularly shaped vacuoles appear in the form of a ring near the periphery of the cell. This condition is apparently of brief duration in both species. As growth continues, fine yolk granules appear near the zona pellucida, increasing in number and size nearer the nuclear membrane. Eventually the cytoplasm becomes obscured from view by the heavy yolk globules. Just within the oöcyte membranes, however, a very narrow layer of cytoplasm remains which is never invaded by the accumulating food material. This pattern of yolk formation is consistent in all large cells and in general excites less attention than do the events which occur concomitantly in the nucleus.

The original smooth-surfaced nucleus becomes highly irregular in shape as development continues, and the reticulate and lightly staining chromosomes soon can be located in the central part of the nuclear body. Occasionally one may see as few as three or four nucleoli in the small oöcytes; more frequently the number is very great. In one oöcyte of *Bufo cognatus* measuring 0.085 mm. in diameter whose nuclear diameter was only 0.031 mm., thirty-four nucleolar bodies of various sizes were counted; and this condition seemed not exceptional in either *B. cognatus* or *B. w. woodhousii*. With the beginning of oöcyte growth, these nucleoli, which originally assumed no particular arrangement, form a ring near the nuclear membrane and then gradually proceed inward toward the centrally located chromosomes, maintaining the ring position during this movement. Midway into the center of the nucleus, the number of nucleoli becomes greatly increased and their size range is vastly extended. Further, their staining reaction begins to vary. Many of the larger nucleoli stain very lightly at this time, meanwhile becoming vacuolated; therefore, many large, darkly-staining nucleoli appear to discharge minute dots of nucleolar material both toward and away from the nuclear center. This process continues up to the ovulation period. Then quite suddenly, the entire mass of nucleolar structures seems to disappear. The nuclei of the oöcytes retained in the ovarian cavity after ovulation entirely lack

inclusions as the cells begin the degeneration process which is first characterized by a breaking down of the yolk.

Monthly Changes in the Ovaries

The foregoing account has dealt with the structure of the mature ovary as it may be seen in both *B. cognatus* and *B. w. woodhousii*. The ovarian changes which occur month by month during the breeding periods of the two species were studied in order to see whether there is any correlation between them and to see if this evidence corroborates our ideas concerning the breeding habits of these species. The observations to follow present a condensed review of the average microscopic and macroscopic conditions found in ovaries representative of each month. It is not the purpose of this study to account for all the numerous variations from this general monthly plan; however, striking deviations will be noted.

Bufo cognatus Say

March—Macroscopically, the ovary is highly pigmented, several with some lobes collapsed; eggs often present in coelom or oviduct (especially if captured during breeding activities). Microscopically seen, large yolky oöcytes press against the ovarian wall with many others approaching the end of the primary growth period. Disregarding the numerous primordial germ cells, the predominating oöcyte diameters are 0.7 and 0.9 mm. (range to 1.06).

April—Macroscopic signs of ovulation less general; ovaries darkly pigmented and heavily lobed; predominating oöcyte sizes as in March (but range only to 0.94 mm.). Collection data show that fewer of the animals were actually breeding as captured which probably accounts for some of the difference.

May—Much like April, with two notable exceptions: (1) oöcyte diameter generally 0.7-0.8 mm. with no significant range above this, and (2) ten ovaries appearing mature macroscopically with a preponderance of oöcytes of about 0.4 mm., and ovary wall not collapsed. Since there could be no doubt that these were mature toads, it probably indicates that individuals differ in the seasonal relations of the ovarian cycle.

June—Little change from preceding month. Oöcyte diameter generally between 0.3 and 0.5 mm. in collapsed lobes (ranging to 0.62 mm. in nine studied microscopically). In full lobes, 0.9 to 1.0 mm., the rule, the largest being 1.02.

July—In all specimens, an unusual number of collapsed lobes with eggs in coelom and oviducts; full lobes dark and fully prepared to release oöcytes. Predominating diameters 0.8 to 0.95 ranging to 1.12 mm. Most of these specimens were secured from a single breeding congress which accounts for the small range given in Table I. If even half of the animals had ovulated, this would explain the sudden drop in percentages shown.

August—General preparedness for ovulation evident in six available

specimens. Oöcytes 0.6 to 0.8 mm. ranging up to 1.04. In marked contrast to preceding months, only a few young oöcytes seen.

September—No general condition evident. Often macroscopic indication of preparedness for ovulation is belied by many collapsed follicles, yolk degeneration and little indication of growth of young oöcytes. The volumetric data seem to indicate ovaries prepared for ovulation but cytological evidence tends to refute this. Range of ovarian percentages not as great as might be expected.

Bufo w. woodhousii Girard

March—Ovary microscopically similar to condition in *B. cognatus* at same period but volumes different (Tables I and II). No evidence of prior ovulation, oöcytes generally undeveloped (diameters mostly about 0.6 mm., largest 0.72). The five animals available are not sufficient to evaluate the statement of Bragg (1940b) that breeding activity begins in March, though such as it is, the evidence is against this expectation.

April—Ovarian volume suggests (as in *B. cognatus*) a seasonal peak here of general preparedness for ovulation. Pigmentation intense, oöcytes mostly crowded into ovarian cavity (a few in coelom in some individuals). In the eight ovaries observed, oöcyte diameter was about 0.9 mm., the largest measured being 1.01. Again too few individuals were available to prove conclusively an essential similarity in the ovarian oöcytes of the two species.

May—Great variation in ovarian conditions the rule, though most ovaries show tendencies toward maturity. Collapsed lobes with eggs in coelom frequent in those captured in breeding congresses; no evidence of ovulation, past or pending, in others. Many oöcytes present in ovarian wall as well as in cavity in eight examined microscopically. No predominating oöcyte diameter (larger cells usually 0.8 or 0.9 mm., the largest, 1.10; in collapsed ovaries, 0.4 mm. appears to be near the median condition). The range of ovarian percentages (Table II) for May is in keeping with these findings.

June—Essentially similar to May; an oöcyte diameter of 0.5 mm. was characteristic for some animals whereas 0.8 or 0.9 mm. is a better figure for others. The largest oöcyte found in this species was present in this series (1.18 mm.).

July—Conditions essentially unchanged from May and June; oöcyte diameter usually 0.5 to 0.9 mm., largest 1.06 mm.; ovarian percentages (22.40 for June as contrasted with 16.72 for July) might indicate that most specimens had ovulated already. The microscopic evidence does not support this, on the whole. The five animals studied microscopically all had ovaries near the peak of oöcyte production.

August—Variability in ovarian conditions still the rule; two groups indicated, (1) those which apparently had ovulated, and (2) those which had not. In the first, a few young oöcytes appeared to be growing in and larger oöcytes were beginning degeneration, the latter with 0.9 to 1.0 mm. diameters. In the second group, diameters were generally 0.8 mm., the largest 0.97 mm. Nine ovaries were studied microscopically.

September—The single large specimen available had few growing young oöcytes and many large degenerating ones (0.9 diameter, the rule). The ovary was very small in relation to the size of the toad, suggesting the end of the summer breeding period.

October—All specimens indicated that the summer reproductive period was past. Young developing oöcytes abundant, all larger ones degenerating. The drop in ovarian percentages from 20.34 in August to 2.95 in October substantiates the microscopic findings.

Discussion

In *Bufo cognatus* in Oklahoma, breeding behavior is initiated by rainfall at any time between March and September (Bragg, 1940). In *B. w. woodhousii*, rainfall stimulates this behavior during this same period, but some females produce eggs each spring (usually during March or April) whether rain falls or not; whereas others do not respond to the spring rains but await the summer months (Bragg, 1940a). The difference in the time of actual production of eggs would seem to lie principally in a difference in the females, since some males of each species usually call after rains; and we might expect these differences also to occur in ovarian volumes and in cytological details.

Within any month there seem to be variations in the ovarian volume percentage of *B. cognatus* and *B. w. woodhousii* (last columns of Tables I and II). These variations are distinctly greater in *B. w. woodhousii* than in *B. cognatus*; and seem to indicate differences in the breeding habits of the two.

On the basis of the volumetric analysis made here, therefore, Bragg's separation of *B. cognatus* and *B. w. woodhousii* into different behavior groups is substantiated.

The fluctuation in the mean ovarian volume percentage of the mean for body volumes in *B. cognatus* is not very great from month to month. (Column 5 of Table I, except for April and July.) Since the usual breeding period of *B. cognatus* (Bragg, 1941a), is from March to September, the volumetric analysis could indicate that, in general, the ovaries would be equally ready for ovulation during these periods. This seems to be the case with the maximum of preparedness for ovulation in April. Though the sudden drop in July of 10.25 per cent is out of line, the discrepancy can be explained. If the collections of July had included animals taken from other sites, the percentage would very likely have been higher and the range greater. Though reproduction continues into September, it is to be expected that the tapering off of egg production will be followed by reduced volume. The mean ovarian volume percentage of 22.94 does not bear this out, however; only the microscopic evidence is useful in determining that the end of the cycle was approaching.

The figures in Table II for the mean percentage of ovarian volume to body volumes show noticeable fluctuations from month to month for *B. w. woodhousii*. These evidences are interpreted as indicating that, while there is a general gonadal preparedness for ovulation, individual variation in the

actual time of ovulation is great, particularly during the summer. The breeding period seems definitely to have passed in October.

The cytological changes in the gonads which accompany the beginning of breeding behavior in *Bufo* has been previously noted.

Fisher and Richards noted peculiar nucleolar changes in the oöcytes of *Acris crepitans*. These changes are similar in gross features to those in *B. cognatus* and *B. w. woodhousii*. Though no definite cyclic changes in the ratio of small to large nucleoli were observed, there was a migration of nucleoli from the outer edge of the nucleus toward the chromosomes and a gradual increase in their abundance from the fall months to the next ovulation period in July. They believed that these nuclear inclusions are probably "chromatin nucleoli," clumps of chromatin migrating along linin threads to several common points.

Rogers (1942), in her study of the nucleolar changes accompanying oöcyte growth in the zebra fish, *Brachydanio rerio*, first described the young nucleus as bearing one to five basophilic nucleoli which, though they remain near the nuclear membrane almost constantly, undergo processes similar in many respects to those which have been described for *Bufo cognatus* and *Bufo w. woodhousii*. Numbers of nucleoli increase by fragmentation, lose their intense staining reaction, and become vacuolated. In *B. rerio* the nucleolar events seem to indicate a utilization of this material during yolk formation.

While the nucleolar variations described in detail by Rogers are not entirely the same as those indicated for *B. cognatus* and *B. w. woodhousii* in our section on the microscopic structure of the ovaries, they are paralleled in an increase in the numbers of nucleoli, in small basophilic discharges (in *B. cognatus* and *B. w. woodhousii* these are produced away from, as well as toward, the center of the nucleus) and the disappearance of the nuclear inclusions.

Painter and Taylor (1940) described oöcytes of a toad in which small nucleolar-like bodies develop as pseudopods from the germinal vesicle during yolk synthesis and are cut off into the cytoplasm. In a few oöcytes of *B. cognatus*, though not in *B. w. woodhousii*, a similar process was seen. The infrequency of this occurrence indicates, however, that it is not a typical feature in development, even in *B. cognatus*.

The pattern by which yolk is deposited near the periphery of the cell in fine granules and then in heavy spherules as accumulation continues toward the nucleus is in keeping with that described for *Acris crepitans*. The presence of "yolk nuclei" was originally described by King (1908) in *Bufo lentiginosus*¹ as "irregular, granular masses" appearing in the otherwise homogeneous cytoplasm of young oöcytes. These structures, which seemed to arise from a previously formed generation of cytoplasmic bodies called "vitelline bodies" by King, were believed by her to be responsible for the initiation of yolk formation in *Bufo*. Fisher and Richards failed to find "vitelline bodies," but laid considerable stress on the function of the "yolk

¹ Probably the toad now known as *B. terrestris americanus* Holbrook.

nuclei." In *B. cognatus* and *B. w. woodhousii* neither the "vitelline bodies" nor the "yolk nuclei" appeared in the long-stored material, and the only traces of the beginning of yolk synthesis was seen in the form of slight cytoplasmic vacuolization, a condition more obvious in *B. w. woodhousii* than in *B. cognatus*.

King suggested that the process of yolk formation is possibly quite different in various genera and species, and a comparison of the evidences available in *Bufo lentiginosus*, *B. cognatus*, *B. w. woodhousii*, and *Brachydanio rerio* would certainly indicate this to be true at least so far as the finer features of the yolk development are concerned.

From this study of *B. cognatus* and *B. w. woodhousii* it may be said that yolk formation is associated with nucleolar function.

In the observations of the ovaries of *B. cognatus* and *B. w. woodhousii*, the state of the fat bodies was noted in each case. In both species their size during the breeding period was found to be extremely variable. The condition of these structures, therefore, gave no additional clue as to the duration of the breeding period. Apparently, if the size of the fat body is to be used as an indicator in this relationship, other factors such as a variable food supply will have to be carefully controlled. Attempts to locate Bidder's organ in both *B. cognatus* and *B. w. woodhousii* were unsuccessful.

Summary

The ovaries of ninety-one mature females of *Bufo cognatus* Say and ninety-nine mature females of *Bufo woodhousii woodhousii* Girard collected during the known breeding periods were studied volumetrically, macroscopically, and microscopically in an effort to determine the nature of the changes which occur in the ovaries during primary oöcyte growth, and to see if there is any correlation between the conditions found and the known breeding habits of each.

The studies reveal that:

1. The general structural features of the mature ovaries of *B. cognatus* and *B. w. woodhousii* are those typical for many related species and genera.
2. Nucleolar behavior in these species very probably is related to yolk synthesis; though the first formed deutoplasmic material may be organized *in situ* or originate from sources not demonstratable here.
3. Volumetrically, macroscopically, and microscopically, the ovaries of *B. cognatus* appear about equally prepared for ovulation in the months of March through August; while in September there is a gradual waning in this preparation.
4. The ovaries of *B. w. woodhousii* are not equally ready for ovulation during the known breeding period, but instead they exhibit a variation of preparedness from animal to animal in the months of March through August with a general decrease in ovulation potential definitely seen in October.

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Index

- Acris crepitans*: 20, 61; keys, 10, 11, 14, 15, 16, 19; breeding habits, 34, 35, 68–72, 123; range extension, 39; adaptations and distribution, 64, 65, 72, 73, 88–90; breeding sites, 93, 96, 98; ovarian cycle, 129–152; ovarian volume, 131, 141; external changes in ovaries, 132; changes in microscopic structure, 133–135, 141
- Adaptations and distribution: 59–100
- Ambystoma maculatum*: key, 32
- A. opacum*: key, 32
- A. talpoideum*: key, 32
- A. texanum*: key, 32
- A. tigrinum mavortium*: 100; key, 30, 32
- A. t. tigrinum*: key, 32
- Amphiuma means tridactylum*: key, 30
- Breeding: dates, 34–38; habits and behavior, 66–100; initiation of, 67–73; sites, 73, 93–100; sex recognition and mating, 81–83; production and fertilization of eggs, 83, 84; see also under each species.
- Bufo cognatus*: 20, 67; keys, 11, 16, 17; breeding habits, 34, 35, 47–58, 67–72, 79–83, 117, 124, 125; range extension, 39; growth rate, 47–58; adaptations and distribution, 65, 72, 74, 89, 90; breeding sites, 96, 98; ovarian cycle, 143–152; changes in volume and microscopic structure, 144–147
- B. compactilis*: 21, 61; keys, 11, 14, 16, 17; breeding habits, 34, 35, 67, 70, 72, 82, 117; range extension, 40; adaptations and distribution, 65, 72, 74, 90; breeding sites, 98, 100
- B. insidiator*: 21, 61; keys, 10, 16, 17; range extension, 40; breeding habits, 67, 70, 72, 83; adaptations and distribution, 65, 72, 74, 86, 90; breeding sites, 95, 98
- B. punctatus*: 21, 61; keys, 11, 17; range extension, 40; adaptations and distribution, 65, 72, 74; breeding habits, 72; breeding sites, 96
- B. terrestris americanus*: 20, 61; keys, 11, 15, 16, 18; breeding habits, 34, 67, 71, 72, 80–83, 124, 125; adaptations and distribution, 65, 72, 74, 86, 89; larvae, 84, 85; breeding sites, 93, 96, 98
- B. woodhousii fouleri*: 22, 61; keys, 11, 14, 16, 18; breeding habits, 34, 35, 67, 71, 72, 81, 83, 124, 125; range extension, 40; adaptations and distribution, 65, 72, 75, 89
- B. w. woodhousii*: 22, 61; keys, 12, 16, 18; breeding habits, 34, 35, 68–72, 80–83, 117, 123, 124; adaptations and distribution, 65, 72, 75, 89, 90; breeding sites, 96, 98, 99, 100; ovarian cycle, 143–152; volume, 144; microscopic structure, 145–147; monthly changes, 148
- Calls, frequency of sex: 117–125
- Cryptobranchus alleganiensis*: key, 30
- Desmognathus fuscus brimleyorum*: key, 31
- Development, tadpole: 84–86
- Distribution and adaptation: 59–100
- Eggs, production of: 83–84
- Eurycea griseogaster*: key, 33
- E. longicauda melanopleura*: key, 33
- E. lucifuga*: key, 32
- E. multiplicata*: key, 33
- E. tynerensis*: key, 33
- Extension of range: 39–44
- Gastrophryne*: see *Microhyla*
- Glossary: 27–28
- Growth rates: 47–58
- Habitat patterns of Amphibia: 64–66
- Hyla cinerea cinerea*: 22, 61; keys, 12, 13, 15, 19; breeding habits, 72; adaptations and distribution, 72, 75
- H. crucifer crucifer*: 22, 61; keys, 15, 18; adaptations and distribution, 72, 75
- H. versicolor versicolor*: 23, 61; keys, 12, 13, 15, 19; breeding habits, 34, 35, 72, 80, 81, 83, 84, 117–121, 124, 125; range extension, 41; adaptations and distribution, 72, 75, 89; larvae, 84–86; breeding sites, 96, 98

H. v. chrysoscelis: 22, 61; keys, 10, 12, 13, 19; state record, 41; breeding, 72; habitat, 75; breeding site, 94

Identification: Salientia, 9-22; Caudata, 30-33

Keys: frogs and toads, 11-29; eggs, 11-13; tadpoles, 13-17; adults, 17-20; salamanders, 30-33

List: annotated, 20-27; 39-44; 73-79; check, 61

Manculus quadridigitatus: key, 31

Metamorphosis and dispersal: 86-87

Microhyla carolinensis carolinensis: 23, 61; keys, 12, 15, 18; breeding habits, 34, 35, 67, 72, 124, 125; range extension, 42; adaptations and distribution, 64, 72, 76; breeding site, 94

M. c. olivacea: 23, 61; keys, 12, 15, 18; breeding habits, 34, 35, 67, 70, 72, 80-84, 118-125; range extension, 42; adaptations and distribution, 64, 72, 76, 86, 89; larvae, 84, 86; breeding sites, 96, 98

Necturus m. maculosus: key, 30

Oklahoma, conditions of existence in : 62-64

Ovarian cycle: *Acris crepitans*, 129-142; volume, 131; external changes, 132; microscopical structure, 133-135; *Bufo cognatus* and *B. w. woodhousii*, 143-152; microscopic structure, 145

Plethodon cinereus angusticlavus: key, 32

P. g. glutinosus: key, 32

P. ouachitae: key, 32

Pseudacris clarkii: 23, 61; keys, 13, 15, 19; breeding habits, 34, 35, 67, 72, 80-84, 117-122; range extension, 43; adaptations and distribution, 59, 65, 72, 76, 86, 90; larvae, 86; breeding sites, 94, 98

P. streckeri: 24, 61; keys, 13, 15, 19; breeding habits, 34, 35, 67, 72, 81, 84, 117-122; range extension, 43; adaptations and distribution, 65, 72, 76, 86; larvae, 84-86; breeding sites, 93, 96, 98

P. triseriata: 24, 61; keys, 13, 15, 19; breeding habits, 34, 35, 68, 71, 72, 84 118-125; range extension, 43; adaptations and dis-

tribution, 72, 77, 89; breeding sites, 93, 94, 96, 97, 98, 99

Rana areolata areolata: 25, 61; keys, 10, 20; breeding habits, 67, 72; adaptations and distribution, 64, 72, 77

R. a. circulosa: 25, 61; keys, 12, 20; breeding habits, 72; habitat, 72, 77

R. berlandieri: 26, 61; keys, 12, 17, 20; breeding habits, 34, 35, 68-72, 83, 124; range extension, 43; adaptations and distribution, 64, 72, 78, 88, 89; larvae, 84-86; breeding sites, 84, 85, 86

R. brachycephala: 20, 26, 68, 99

R. catesbiana: 25, 61; keys, 12, 14, 17, 19; breeding habits, 34, 35, 67, 71, 72, 80; range extension, 43; adaptations and distribution, 64, 72, 77, 88-90

R. clamitans: 25, 61; keys, 12, 17, 19; breeding habits, 67, 72; adaptations and distribution, 64, 72, 77, 89, 90

R. palustris: 26, 61; keys, 13, 17, 19; breeding habits, 67, 72; habitat, 64, 72, 77

R. pipiens: 68, 69, 80, 83, 88

Scaphiopus bombifrons: 26, 61; keys, 13, 14, 17, 18; breeding habits, 34, 35, 66, 71, 72, 83, 84; range extension, 43; adaptations and distribution, 66, 72, 78, 86, 101, 106; breeding sites, 93, 96, 97, 98, 99, 100

S. couchii: 26 61; keys, 12, 14, 17, 18; breeding habits, 34, 35, 71, 72, 79, 81, 83, 84; habitat, 72, 78; breeding site, 98

S. hammondi: 27, 61; keys, 13, 17, 18; range extension, 43; breeding habits, 71, 72, 79, 83, 84; adaptations and distribution, 72, 78, 101; breeding sites, 98, 99, 100

S. holbrookii: 90, 101

S. hurterii: 27, 61; keys, 13, 14, 17, 18; breeding habits, 34, 35, 71, 72, 79, 81-84, 123-125; adaptations and distribution, 72, 78, 86, 89, 90, 101, 116; larvae, 84, 85; breeding sites, 96, 98

Sex calls, frequency of: 117-125

Siren intermedia nettingi: key, 30

Spea: see *Scaphiopus*

Taxonomy, habits and: 87-88

Toads, spadefoot, adaptations of survival value in: 101-116

Triturus viridescens louisianensis: key, 31

Typlotriton nereus: key, 33

T. spelaeus: key, 33