

ECOLOGY

VOL. 24

JULY, 1943

No. 3

OBSERVATIONS ON THE ECOLOGY AND NATURAL HISTORY OF ANURA IV. THE ECOLOGICAL DISTRIBUTION OF TOADS IN OKLAHOMA¹

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INTRODUCTION

It is rare to find ecological factors stressed in papers dealing with the lives of frogs and toads. On the one hand, herpetologists (with some exceptions) have emphasized taxonomy, geographical distribution, and habits of various groups; on the other, ecologists have commonly regarded these animals as of only minor significance in the communities of which they are a part and, therefore, have mentioned them only incidentally, if at all.

In the earlier papers of this series (Bragg, '40, '40a, '40c) it has been shown that in Oklahoma various species of Anura are segregated in ecological areas and that their habits are such as to fit them nicely into various ecological niches. Even closely related species differ thus in habits; and some of them have habit patterns so firmly fixed in their hereditary constitutions that this alone serves as a very effective barrier to their dispersal. Also, some species, more flexible than others, are able to change their habit pattern to meet different environmental conditions and, therefore, to have a wider dispersal, both geographically and ecologically, than other closely related species. Further evidence of these relations to environment has recently been found in New Mexico (Bragg, '41) and some of the breeding patterns in Oklahoma

have been related to cytological, physiological, and other, environmental, factors (Bragg, '41a, '42a).

During the earlier phases of this study, it became evident that terrestrial and fossorial species especially may play an important part in the communities known as grasslands. Toads of the genus *Bufo*, for example, feed almost exclusively upon arthropods, and, of these, the ground-dwelling nocturnal insects form a large percentage (Smith and Bragg, '42). Toads are not only largely nocturnal but also they often occur in enormous populations in the grassland biome (as defined by Carpenter, '40). No accurate census of toads has been made but we have conservatively estimated populations exceeding one thousand per acre in several portions of the mixed grass prairie of Oklahoma; numbers, moreover, which cannot fail to have profound effects in the whole series of complex successions involved.

Because of these considerations resulting largely from the work of the senior author, it seemed wise to study the whole assemblage of Anura in Oklahoma from an ecological viewpoint and, to this end, the junior author joined the work. Together or individually with coworkers we have collected and studied in all parts of Oklahoma, including from one to several visits to each of the seventy-seven counties. Central and southwestern regions have been most adequately covered in the collection of Amphibia.

The present paper presents our data

¹ Contribution from the Zoölogical Laboratory of the University of Oklahoma, No. 213. Aided by a grant to the senior author from the Faculty Research Fund of the University.

and conclusions concerning the genus *Bufo*. Other genera will be reported upon later. We have collected well over three thousand specimens of *Bufo* in Oklahoma, in every case accompanied by careful observations upon the ecological conditions present. Extensive notes on breeding habits, breeding sites, etc. together with broader ecological observations have guided us in our interpretations of ecological distribution.

In addition, we have had access to all specimens in the Museum of Zoology of the University of Oklahoma and to the field notes of the University of Oklahoma Biological Survey. Altogether, we have examined well over five thousand specimens and have observed uncountable numbers in breeding congresses in all parts of the state. Our field observations were made in the spring, summer, and autumn of 1939 and 1940 and in the spring and summer of 1941.

We have found it necessary to study our subject from the following points of view: (1) to map carefully the ecological associations of Oklahoma, (2) to correlate the distributional records of toads with these, (3) to correlate the habits of the various species with their ecological distribution, and (4) to correlate our findings with those of other workers in adjacent regions, principally Texas, Kansas and Arkansas. We have confined most of our personal observations to Oklahoma, although we have made a few trips to adjacent regions of Arkansas and Texas and the junior author made some observations in Louisiana.

Identification of specimens of toads in Oklahoma is, for the most part, easy. However, the specimens from the eastern part of the state offer certain difficulties, as is explained in the discussion. In order that others may check our identifications, all of our specimens have been deposited in the Museum of Zoology, University of Oklahoma, with the exception of a few which have been retained for our own collection.

ACKNOWLEDGMENTS

We are indebted to Dr. A. I. Ortenburger for use of specimens and records under his care as well as for suggestions and criticisms concerning the strictly herpetological phases of the work, to Dr. A. O. Weese for suggestions regarding the ecological phases of the study, and to the graduate students who accompanied the authors on the numerous field expeditions. We also wish to thank Professor George A. Moore of the Oklahoma A. & M. College and Professor H. D. Chase of the University of Tulsa for permitting us to examine specimens in their collections and to report several new county records from these specimens.

ECOLOGICAL ASSOCIATIONS OF OKLAHOMA AND ADJACENT STATES

The ecological communities in Oklahoma have never been studied adequately although the vegetation of the area was mapped by Bruner ('31) as correctly as the data then available permitted. We have found it necessary to study this matter in some detail in order to determine how the various species of toads are distributed within each association represented in the state. Certain of the boundaries between regions as indicated by Bruner have been changed by us due to additional knowledge. Since most of the major communities overlap into adjacent states and the toads apparently follow them, we have included in our map (figure 1) the vegetation of some of these adjacent areas. For this purpose, we have relied mostly upon the works of Bray ('01) and of Tharp ('26) in Texas and of Gates ('36) and of Albertson ('37) in Kansas, supplemented by more limited observations of our own, particularly in northern and western Texas.

To us, ecological associations are not synonymous with "plant associations;" but we do agree with those who believe that the prominent or dominant vegetation gives a good basis for naming the larger communities, as well as the seral

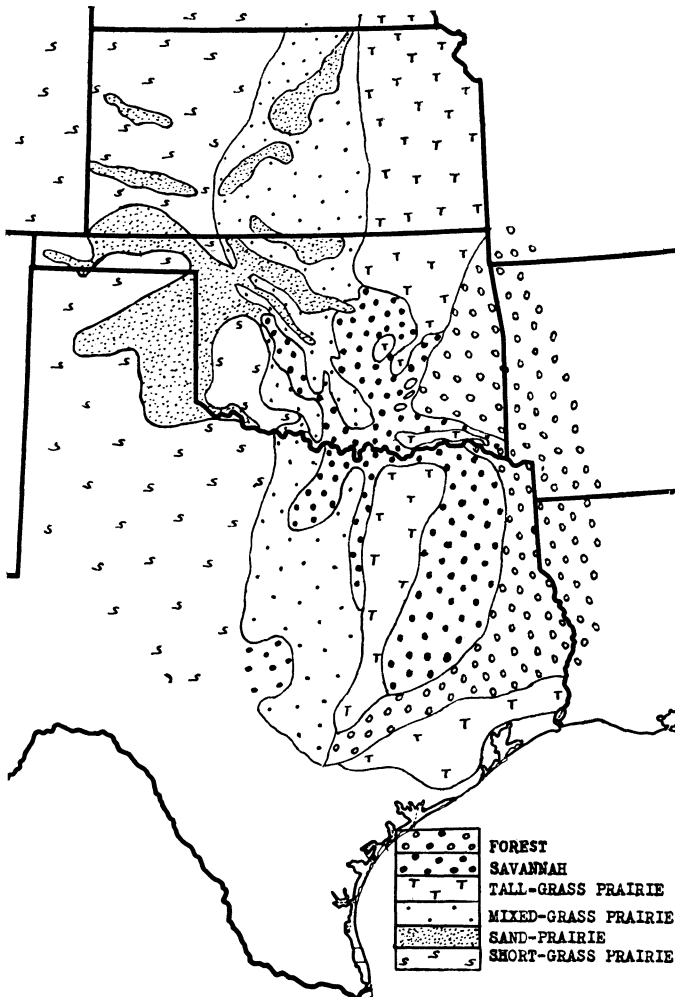


FIG. 1. Plant associations in Oklahoma and adjacent states.

stages in succession. This should be clearly understood in considering all ecological phases of this paper. Toads are distributed with certain plants, not because they depend upon the plants, but because both depend upon climate, amount of available moisture, interrelations of these with other factors and with each other in exceedingly complex ways. In other words, both the toads and the plants are parts of a *biotic* community from which they receive sustenance and to which they, in turn, contribute. Since various types of prairie, woodland, or savannah differing floristically also show

corresponding differences, faunistically, it is possible also to use the plants in naming ecological subdivisions. In order to correlate the distribution of toads with the biotic communities of which they are a part, therefore, it is necessary to give the flora of these subdivisions in some detail.

In Oklahoma we find these associations represented; Oak-Hickory forest in the eastern one-sixth of the state; Oak-Hickory-Andropogon savannah in the east-central part; Mixed-Grass prairie in the west-central portion; Short-Grass prairie in portions of the extreme west

and southwest and Tall-Grass prairie in the northeast central portion of the state. Along the major streams in the western half of Oklahoma and also in regions occupying considerable area away from the streams in the extreme west is a bunch-grass sand-prairie association. This has not been accurately mapped and we have not found it possible to map it with the limited data at hand.

Quercus-Hicoria Association, Quercus-Hicoria-Andropogon (Savannah) Association

The woodland area of Oklahoma is extensive and composed of several different types. The south-central part of the state is covered with an open woodland in which *Quercus marilandica* and *Q. stellata* are dominant and in which *Hicoria* spp. were formerly abundant. This woodland is for the most part quite open and much of the ground is covered with grasses, chiefly *Andropogon scoparius*, with *A. ternarius* common. Various legumes are also present. The western boundary of this association in Oklahoma extends from western Payne to central Logan county then south through Cleveland and McClain, eastward into Pontotoc county, then southwestward across northern Love county, and southward to the Red River (figure 1). In Texas the same association extends from the Brazos river in Waller, Brazos and Robertson counties north and east to the Red River (Eastern Cross Timbers) and along the Red River west to Wichita county with an extension southward along the 97th meridian to central McLennan county (Central Cross Timbers) and another in Montague county southwest to Jacks county (Western Cross Timbers). The Western Cross Timbers are represented in Oklahoma by an area in Love, Carter, Stephens, Grady and Caddo counties. The main savannah area in Oklahoma lies between the mixed-grass association along its western edge and the oak-hickory forest on the east. The

northern end of the area joins the true prairie in northern Oklahoma.

The southeast corner of Oklahoma (LeFlore, Latimer, Pittsburg, McCurtain and Pushmataha counties) includes part of the Ouachita uplift and is covered with a mesophytic eastern-deciduous-forest type of vegetation on northern slopes and in moist valleys, oak-hickory-grass on the dry ridges, and woodland on the south slopes. Immature soils formerly supported stands of pine (*Pinus echinata*). Pine also occurs scattered throughout the oak woodland. The Ozark uplift extends into northeastern Oklahoma and is covered with oak-hickory forest in which also scattered pines are found.

The oak-hickory savannah is of particular interest because it lies in a region which, climatically, would be expected to have a prairie climax. Because of the sandy character of the soil, water is readily absorbed during periods of precipitation and readily given up to plants over a long period of time. These conditions favor woody species, such as oaks and hickories, which can utilize the water from the deeper soil horizons that is not available to more shallow-rooted plants. The presence of the woody species provides habitat-conditions somewhat like those in the oak-hickory forest proper. That conditions are more xeric is shown by the wider spacing of trees, their shorter stature, and the presence of western species on some hilltops and in prairie islands. *Opuntia* may be found scattered throughout most of the savannah area and *Buchloe* may become the dominant grass following chronic overgrazing. Along streams in the savannah the woodland is more forest-like. These flood-plain forests extend far westward into the grassland.

Mean annual rainfall in the savannah area varies between 30 and 40 inches and, in the forest, between 40 and 50 inches. Wind velocity in the herb-stratum is considerably less than in the grassland and consequently evaporation of moisture from the soil surface more gradual. This

condition is quite probably an important factor limiting distribution of certain species of toads such as *Bufo a. americanus*, *Bufo woodhousii fowleri*, and *Bufo cognatus*.

Forested areas in Kansas are almost non-existent. Only small local areas have enough trees to be called a forest. Most of the woodland is confined to stream margins throughout the state. Eastern Kansas has the most extensive floodplain forests as well as almost all the remaining woodland. It is along the streams that the American toad has been able to penetrate westward to the greatest distance. The tall grass prairies of eastern Kansas may be occupied to a limited extent by this toad since it is the common toad of the same prairies further north.

Andropogon furcatus Association
(Little, '38)

The southern end of the tall-grass prairie extends across east central Kansas and includes the north-eastern sixth of Oklahoma (see figure 1). In Oklahoma it merges eastward with the oak-hickory forest and to the south and southwestward is replaced by the savannah which has just been described. Along the western limits of the tall-grass prairie, mid and short grasses replace the tall species in dominance. Isolated areas of tall-grass prairie occur throughout the eastern part of the savannah area as well as in forested regions. The Grand prairie and the eastern portion of the coastal prairie of Texas resemble the northern tall grass prairie in physiognomy but differ somewhat floristically.

Little ('38) described the portion of prairie occurring in Muskogee County, Oklahoma as an *Andropogon furcatus*² climax. He found big bluestem to be the dominant species of grass with *Andropogon scoparius*, *Koeleria cristata*, *Manisuris cylindrica*, *Panicum virgatum*, *Paspalum floridanum* and *Sorghastrum nu-*

tans as characteristic, associated species. Short-grass species were not found by Little to extend eastward as far as Muskogee county. Most species characteristic of mixed-grass prairie were not found in the tall-grass prairie of Muskogee county. These include *Bouteloua curtipendula*, *B. gracilis*, *B. hirsuta* and *Buchloe dactyloides*. On the other hand, the dominance of *Andropogon furcatus* and the presence of *Koeleria cristata* are not associated with mixed-grass prairie in Oklahoma.

The association described by Little extends north-eastward across Craig county and north-westward across Kay county into Kansas (see figure 1). In Kay and western Osage counties *Andropogon scoparius* is the common dominant or is at least co-dominant with big bluestem. Mid-grasses are common in this region and short-grasses are widely enough distributed to become dominant very quickly when overgrazing occurs.

Annual precipitation in the tall grass region is rather high, ranging from 35 inches along the western margin to 40 inches per year on the eastern. This rainfall is adequate at all seasons, although summer drought is the rule rather than the exception.

Andropogon scoparius—*Bouteloua curtipendula*—*B. hirsuta*—*Buchloe dactyloides* Association

The mixed-grass prairie occupies a broad zone between the 97th and 99th meridians and extends from the Colorado river in Texas northward across Oklahoma and Kansas into Nebraska. The area is about 100 miles wide on the average but is very poorly defined on its eastern and western borders where these shift with climatic cycles. Disturbances following the white man's occupation of the region have served to expand the area eastward.

The mixed-grass prairie is so named because of the constant association of short, mid, and tall grasses throughout

²*A. provincialis* of some authorities and as used in this paper.

most of its extent. Dominance is shared by the first two types and the tall species are limited to lowlands or other favorable situations. The mid-grasses, *Andropogon scoparius*, *Bouteloua curtipendula*, *Sporobolus asper*, *S. heterolepis* and other grasses midway in stature between the tall species such as *Andropogon provincialis* and *Sorghastrum nutans* and short species like *Bouteloua hirsuta*, *B. gracilis*, and *Buchloe dactyloides* are usually dominant in the eastern portion of the mixed-grass prairie while the short grasses are dominant in the western part. The short grasses may occur as small patches among the taller species or the latter may be reduced to scattered clumps or bunches in an almost solid sod of short grasses. The short species are almost always dominant on hilltops with their extent and dominance on hillsides governed by physiographic and edaphic factors operating in conjunction with precipitation. When the mixed-grass prairie is overgrazed, the taller grasses are reduced in abundance or entirely eliminated from the association and the short grasses become the sole dominants. (Bruner, '26, C. C. Smith, '40).

One fact to be kept in mind when considering the prairie-regions of Oklahoma and adjacent states is that they are dissected by innumerable small streams and ravines along which more mesic floras extend out into the grassland. It is in such situations that eastern species extend westward into arid regions. A wealth of rough, hilly, and sandy land which serves to introduce edaphic factors into the picture are also present in prairie regions. These facts render any indication of boundaries at best only arbitrary.

The mixed-grass prairie is rendered very distinct in central Oklahoma where, due to edaphic factors, a region which one would expect to have a tall grass climatic climax is covered with an oak-hickory savannah. The savannah area joins a region on the west which is covered with a much "tighter" soil and which has a vege-

tation on level uplands and hillsides consisting of varying proportions of short and mid-grasses. Prairie islands, found throughout the savannah, may be of mixed-grass or mid- and tall-grass vegetation, depending upon the soil.

Precipitation throughout the mixed-grass region varies between 25 and 32 inches and evaporation 45 to 55 inches per year. Rainfall occurs mostly in fall and spring and the summers are hot and dry.

The dominant plants of the mixed-grass region vary in importance from east to west and in different edaphic situations. In the eastern half of the area the hilltops and upper slopes are dominated by short grasses and the hillsides and upland valleys by mid grasses but with short grasses quite abundant and becoming dominant following protracted drought or continued overgrazing. Bottomland prairies are dominated by a mixture of tall and mid grasses. In the western half of the mixed-grass area the short grasses dominate on hilltops, hillsides, and level upland, and are codominant in upland valleys. Western bottomlands are dominated by mid grasses but both tall grasses and short grasses are present. Sandy soils along the major streams may be covered with cottonwood parkland (Hefley, '37), ash-elm-cottonwood floodplain forest, bunch-grass sand prairie (C. C. Smith, '40), switch-grass prairie, sagebrush or oak shinnery. These types of vegetation are discussed by Bruner ('31) to whom the reader is referred for further analyses.

The fauna of this prairie has received very little systematic study. Dice ('23) studied the vertebrates near Manhattan, Kansas. The works of Phillips ('36), of C. C. Smith ('40, '40a, '40b), of Blair and Hubbel ('38) and of Blair ('39), are the most extensive. So far as the writers are able to ascertain, no work prior to Bragg ('40) has been done which would indicate which Anura, if any, are restricted to the mixed-grass prairie.

Bouteloua—Buchloe Association

West of the mixed-grass prairie lie the short-grass plains. At present in southern Oklahoma the eastern boundary of this area extends from central Stephens and Jefferson counties northwestward around the western edge of the Wichita Mountains in Kiowa County then northward to Blaine County then northwestward through Harper County into Clark County, Kansas, extending across this state through Jewell County on the north. Westward the short-grass prairie extends into the foothills of the Rockies and southward in Texas nearly to the Pecos River, being gradually replaced by desert short-grass. In addition to extensive sandy areas along major streams in the region, in the western tier of counties in Oklahoma and in the Texas Panhandle, large areas of very sandy soil occur which are covered with shin oak, sagebrush, bunch-grass or mixtures of these types. Extensive dune areas also exist. The Salt Plains and Glass Mountains also serve to break the continuity of the short-grass plains. The sandy regions as a rule have few breeding sites for Amphibia except on the floodplains and, as a consequence, the population of these animals is low in such areas.

The short-grass prairies in Oklahoma are characterized by the dominance of blue grama (*Bouteloua gracilis*) and buffalo grass (*Buchloe dactyloides*), with sand drop-seed (*Sporobolus cryptandrus*) and *Aristida purpurea* or *A. longiseta* abundant following periods of drought or overgrazing. Cacti are common in the plains regions. Taller species of grass are present but are limited to areas receiving runoff water from higher areas. Big and little bluestem (*Andropogon provincialis* and *scoparius*) and Indian grass (*Sorghastrum nutans*) are found in the moister situations. Little bluestem often occupies drier areas if the competition from the short grasses is lacking. Thus it is found as almost the only peren-

nial grass in old fields and on roadside banks.

Sandy soils are usually occupied by sandhill grass (*Andropogon hallii*), sand dropseed, sand lovegrass (*Eragrostis trichodes*), little bluestem, sand reed-grass (*Calamovilfa gigantea*), blowout grass (*Redfieldia flexuosa*), sideoats grama (*Bouteloua curtipendula*), blue grama, sand sage (*Artemisia filifolia*), skunkbush (*Rhus trilobata*), shin oak (*Quercus* spp.), or *Prunus* spp. in various combinations, depending on soil texture, depth, slope, and position of community on the slope.

Floodplains in the short-grass region are occupied by vegetation composed of switch grass (*Panicum virgatum*), sandhill bluestem, little bluestem, alkali dropseed (*Sporobolus airoides*), muhly grass (*Muhlenbergia arenicola*), feather bluestem (*Andropogon saccharoides*), salt-grass (*Distichlis stricta*), with savannah areas of cottonwood common.

Extensive areas in western Oklahoma and Texas have stands of mesquite (*Prosopis chiliensis*). Such areas are often referred to as mesquite flats. These diminish in abundance as one proceeds northward across the short-grass prairies and are unknown in western Kansas. Cattle grazing has favored the spread of mesquite.

Rainfall in the short-grass plains country is comparatively low (15–25 inches per year) and evaporation high (50–80 inches per year). Thornthwaite ('31) classifies the region as belonging to the semiarid, mesothermal, rainfall-deficient-at-all-seasons, climatic province.

GEOGRAPHIC AND ECOLOGICAL DISTRIBUTION OF SPECIES OF BUFO IN OKLAHOMA

Seven species or subspecies of toads of the genus *Bufo* are certainly known from Oklahoma. These are (1) *Bufo americanus americanus* Holbrook, (2) *Bufo cognatus* Say, (3) *Bufo compactilis* Wiegmann, (4) *Bufo insidiosus* Girard,

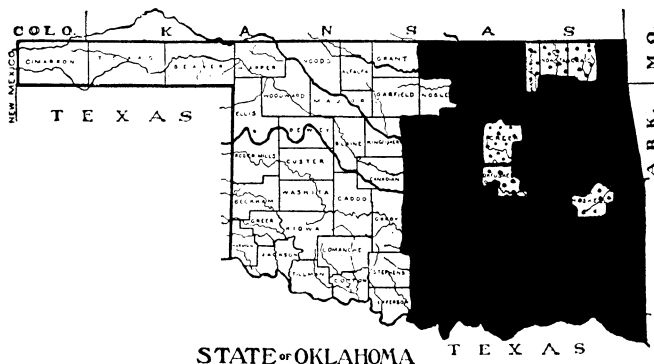


FIG. 2. Known distribution of *Bufo americanus americanus* Holbrook by counties in Oklahoma. The records from Adair and Cherokee counties are from the collection of tadpoles only, that from Ottawa county, by hearing the characteristic call. All others represent specimens examined by us or reported in the literature. Black = known records or specimens; stipple = expected additional range.

(5) *Bufo punctatus* Baird and Girard, (6) *Bufo woodhousii fowleri* (Hinckley), (7) *Bufo woodhousii woodhousii* Girard. *Bufo valliceps* Wiegmann is reported in eastern Texas not far south of the Oklahoma line (most recently by Blair, '41) but so far has not been taken in Oklahoma. Burt and Burt ('29) interpreted with some uncertainty toads taken in southwestern Arkansas near Oklahoma as *Bufo terrestris* Bonnaterre while Black and Dillinger ('38) also indicate that this toad is in Arkansas. Blair ('41), however, restricts the range of this species to the southern coastal plain. If this toad actually occurs in Arkansas, it may enter the southeastern part of Oklahoma, although as yet it has not been discovered in this state.

Definite records of these species in Oklahoma follow in which we give the number of specimens examined by us from each county. It should be remembered, however, that we have actually seen most of these species by the thousands in their breeding congresses and that such specimens are not reported by specific numbers. Records from the literature are given only in cases where we have not seen specimens from the county in question and where we have no reason

to doubt the record. The common name used for each species is selected more or less arbitrarily from several which have been used. For others, see Wright and Wright ('33). The scientific nomenclature which we have adopted follows fairly closely that given by Stejneger and Barbour ('39).³ As Blair ('41) and others have pointed out, the exact taxonomic status of the toads of the *americanus*-group is in confusion but it is hoped that ecological studies will provide a valid basis for taxonomic separation of the species.

Bufo americanus americanus Holbrook
(1836) (American Toad)

The American toad is an eastern species ranging from southern Canada west and south to central Oklahoma and east central Texas.⁴ It is said to be com-

³ However, we are retaining H. M. Smith's ('34) relegation of *Bufo fowleri* Hinckley to a subspecies of *B. woodhousii* Girard for reasons pointed out on page 305.

⁴ Blair's recent paper does not include any part of Texas within the range of this toad. We have found it on the Red River in western Love County, Oklahoma, which gives presumptive evidence of its presence across the river. We have actually seen no specimen from Texas; however, we have heard its call in the northern end of the western cross timbers in Texas.

mon throughout its range (Wright and Wright, '33).

Its general distribution in Oklahoma is east of a line drawn southward from west central Kay county on the north to western Love county on the Red River (figure 2). The western limit of its range is coincident with that of the oak-hickory savannah in central and southern Oklahoma but it occurs in the true prairie in the northern part of the state and in the broad ecotone between this and the mixed grass prairie in east central Kay county. In the edge of the Oak-hickory savannah from Payne county to the Arbuckle Mountains of Murray and Carter counties, these toads are much dwarfed in size (Bragg, '40b) but from Pottawatomie county southeastward they tend on the average to be larger, although some small ones occur. Where their range coincides with that of *B. w. fowleri* the two are often confused but we have independently observed that the characters given by Blair ('41) will always serve to differentiate them. (See also Myers, '27.) In breeding congresses the two can easily be separated by the great differences in their breeding calls. Since almost all of our specimens have been taken from such congresses, we are confident of our identifications.

Numbers Examined by Counties

Adair, tadpoles; Atoka, 13; Bryan, 1; Carter, 5; Cherokee, tadpoles; Cleveland,

158; Coal, 4; Delaware, 20; Garvin, 4; Hughes, 11; Johnston, 7; Kay, 1; Latimer, 15; LeFlore, 58; Lincoln (Burt, 1935); Logan, 8; Love, 3; Mayes, 1; Marshall, 8; McClain, 1; McCurtain, 35; Murray, 9; Muskogee, 9; Oklahoma, 13; Okmulgee, 3; Osage, 3; Ottawa, call heard; Payne, 7; Pawnee, 2; Pittsburg, 7; Pontotoc, 14; Pottawatomie, 2; Rogers, call heard; Sequoyah, 2; Tulsa, 12. Total examined, 436 adults and many tadpoles.

Bufo cognatus Say (In Long, 1823) (Great Plains Toad)

The Great Plains toad is present in suitable habitats from southwestern Minnesota (Breckenridge, '38) and Manitoba (Logier, '31) to the eastern foothills of the coast range in southeastern California (Myers, '30). It is also known in northern Mexico. For a map showing general distribution, see Bragg ('40).

In Oklahoma (figure 3) it is generally present west of a north-south line passing through west-central Osage county and slightly west of south through Pottawatomie and Murray counties. In southern Carter county its distribution swings sharply to the westward at the northern edge of the oak-hickory savannah to central Jefferson county then southward to the Red River. It is not known in Love county the southern part of which is largely wooded because of the influence

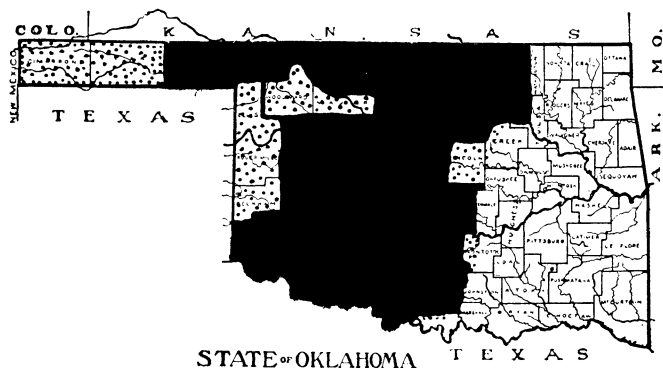


FIG. 3. Known distribution of *Bufo cognatus* Say by counties in Oklahoma. All are from adult specimens examined by us.

of the Red River valley. It will probably eventually be found in the northern part of this county which is largely prairie-land.

Bufo cognatus is the characteristic toad of the mixed-grass prairie and of the larger prairie islands in the western portion of the savannah and it also occurs in the tall-grass prairie in western Osage county, its range extending at least forty miles east of Ponca City. It is also present in the short-grass plains but its numbers thin out rapidly as one passes southwestward through the short-grass area and it becomes restricted to stream banks, irrigation ditches and similar situations. Along the ecotone between mixed-grass and short-grass prairies, *Bufo cognatus* is gradually replaced by *Bufo compactilis* as the characteristic toad. The Great Plains toad has never been taken in the woodland in Oklahoma and it ordinarily does not enter the floodplains of the large rivers (Bragg, '40), although it may do so in very limited areas under special conditions (Bragg, '42b).

Numbers Examined by Counties

Alfalfa, 51; Beaver, 2; Blaine, 22; Caddo, 1; Canadian, 34; Carter, 1; Cleveland, 2398; Comanche, 11; Cotton, 14; Custer, 12; Dewey, 9; Garfield, 27; Garvin, 12; Grady, 6; Grant, 1; Greer, 15; Harmon, 1; Harper, 6; Jackson, 2; Jefferson, 1; Kay, 9; Kingfisher, 19; Kiowa, 2; Logan, 2; McClain, 1; Murray, 11; Noble, 7; Oklahoma, 32; Osage, 32; Payne, 9; Pottawatomie, 2; Stevens, 1; Tillman, 70; Washita, 1. Total examined, 2824.

Bufo compactilis Wiegmann (1833) (Desert Toad)

The desert toad is generally distributed from south central Texas through southern Utah and Nevada, southward into Mexico. The northern limits of its range are at present uncertain. It is common in some parts of Texas (Strecker, '15; Wright and Wright, '38) but we have

failed to find specific records from the Texas Panhandle. We have one specimen taken in Childress County, Texas, near the Oklahoma line and many specimens from Lubbock county, just south of the panhandle. At Lubbock, Texas, this toad is very common according to information received from Dr. H. M. Hefley to whom we are indebted for the specimens. The junior author spent several nights collecting amphibia in the vicinity of San Angelo, Texas after heavy rains and *Bufo compactilis* was the only representative of the larger Bufos found in that region.

Bufo compactilis was first reported from Oklahoma in 1940 by Bragg and Kuntz and we have since determined it to be very abundant all over southwestern Oklahoma (Bragg, '41b). We have recently found young individuals at the edge of a cattle tank near Buffalo, Oklahoma in Harper county, which extends the known range some 100 miles to the northward and to within about fifteen miles of the Kansas line. This is of especial interest since as late as 1934, no one knew certainly of this toad north of Texas. Our evidence indicates the strong probability that Cope's record for western Kansas, doubted by H. M. Smith ('34), is really valid.

We find *Bufo compactilis* to be strictly limited to the short-grass plains in Oklahoma (figure 4). Its numbers give way very rapidly in the ecotone between the short and mixed-grass prairies as one passes eastward from Washita or Kiowa county and its place is taken by *Bufo cognatus* as explained earlier. On favorable nights, when both species are in large breeding congregations over wide areas, this condition is very apparent. We have transected the ecotone several times and at several places on such nights, always with consistent results.

Numbers Examined by Counties

Comanche, 36; Cotton, 44; Custer, 3; Greer, 48; Harmon, 5; Harper, 2; Jack-

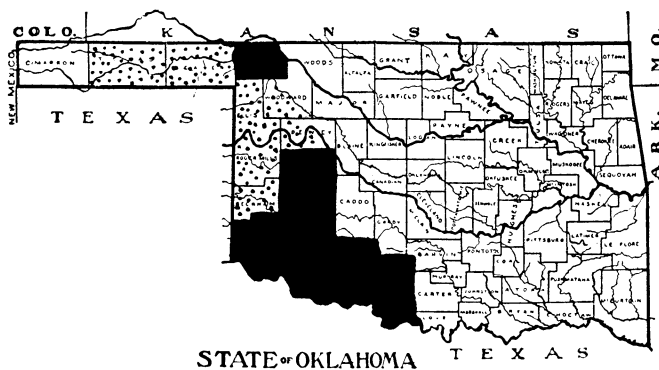


FIG. 4. Known distribution of *Bufo compactilis* Wiegmann by counties in Oklahoma. All are from adult specimens collected and examined by us.

son, 36; Jefferson, 3; Kiowa, 49; Stephens, 12; Tillman, 29; Washita, 3. Total examined, 270.

Bufo insidiosus Girard (1856) (Northern Little Green Toad)⁵

The northern little green toad is known to range from somewhere in south central Texas north through western Kansas. The exact limits of its range are unknown at present, due in part to its rarity, in part to confusion with *B. debilis*, and in part to its secretive, nocturnal habits. Both H. M. Smith ('34) and Stejneger and Barbour ('39) mention it from New Mexico on the west and the northern part of Mexico on the south. Taylor ('36), who understands the toads of this group probably better than anyone else, knew it from Kansas, Texas, New Mexico, and Mexico (Chihuahua, Durango, and Zacatecas). We have one specimen from Armstrong county in the Texas panhandle for which we are in-

debted to Mr. Elmo Bonifield who procured it for us.

It has only recently been reported from Oklahoma (Bragg, '41b). We found it breeding in most of the southwestern counties on the night of August 8, 1939 but none were taken on roads. It was congregated at cattle tanks and on the edges of deeper pools in company with *B. compactilis*, *B. w. woodhousii*, *Microhyla olivacea* (Hallowell), *Pseudacris clarkii* Baird, *Scaphiopus couchii* Baird, *Rana sphenoccephala* Cope, and sometimes, when the water was clear, with small numbers of *B. cognatus*. The most northern record in Oklahoma is northern Garvin county, but its presence in Kansas makes it very probably present all over western Oklahoma. We are indebted to Mr. Robert Kuntz for a single specimen taken on the streets of Lawton, Comanche county during a summer evening's rain and to Mr. Wayne Randel for another taken at a pool on or near the Murray-Carter county line in the Arbuckle mountains (see figure 5).

Judging from the relatively small numbers found breeding when compared to those of *B. compactilis* on several favorable nights, *B. insidiosus* is very rare in Oklahoma. For example, on a spring night after a very heavy rain in Greer county, only six specimens of this toad were seen and no others heard even

⁵ *Bufo debilis* Girard has long been known as the little green toad. Till recently shown by Taylor ('36) to be an error, *B. insidiosus* Girard was thrown into synonymy with *B. debilis* Girard. Of the three toads in this group now recognized, *B. insidiosus* is the northern form. Therefore, we propose the common name given above for *B. insidiosus*, leaving the name, little green toad, for *B. debilis* of southern Texas and Northern Mexico as now understood.

though the whole countryside was one continuous roar with the calls of other species.

Bufo insidiosus is primarily a toad of the short grass plains but it enters the mixed-grass prairie for a short distance along its western edge. It therefore shares the range of *B. compactilis* in Oklahoma for the most part but ranges slightly farther to the east and, perhaps, to the west. Neither of them has yet been found in the Oklahoma panhandle, but both are to be expected

Number Collected by Counties

Comanche, 1; Cotton, 2; Garvin, 1; Greer, 6; Jackson, 8; Kiowa, 3; Tillman, 3; Murray-Carter line, 1. Total examined, 25.

Bufo punctatus Baird and Girard (1852) (*Canyon Toad*)

The general distribution of *Bufo punctatus* was stated by Wright and Wright ('33) to be "south central Texas west to southern California and Lower California." It has since been reported from Kansas (H. M. Smith, '34) and from Arkansas (Black and Dillinger, '38).

In Oklahoma this toad has been formerly reported from three widely separated sections of the state (figure 6). Here, as elsewhere, its distribution seems to be associated with the presence of rocky areas. Jones and Derrick ('39)

took juvenile specimens of this toad near a small pool close to White Mound in the Arbuckle Mountains; we collected two specimens in the Wichita Mountains and found hatching eggs in small pools in the rocky ravine below Soldier Lake in the same mountains. There had been several clutches of eggs (probably six or more) produced and all of them were in about the same stage of development. The eggs had been laid in very small pools formed in the solid rock, some of which were no more than one foot square and two inches deep. The eggs were in short files similar to those observed by Strecker ('26), not as described by Wright ('29) as "single or firm or scattered mass on the bottom." Dr. A. B. Leonard of the University of Kansas reports to us by letter that he has collected specimens in Woods County, Oklahoma near the Kansas line. New records are included in the county list below. This list actually includes all specimens from Oklahoma of which we are aware. We have never seen the species in breeding congresses, as we have all other species being considered. This is the rarest toad in the state and we know very little about its habits here.

Records by Counties

Blaine, 1; Comanche, 6; Major (Burt, '35); McCurtain (Trowbridge, '37);

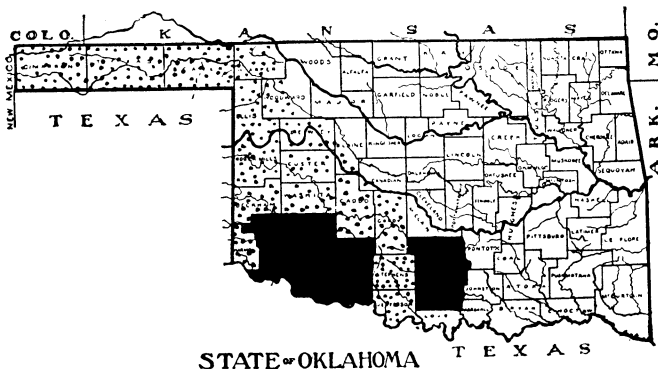


FIG. 5. Known distribution of *Bufo insidiosus* Girard by counties in Oklahoma. All are from adult specimens collected and examined by us.

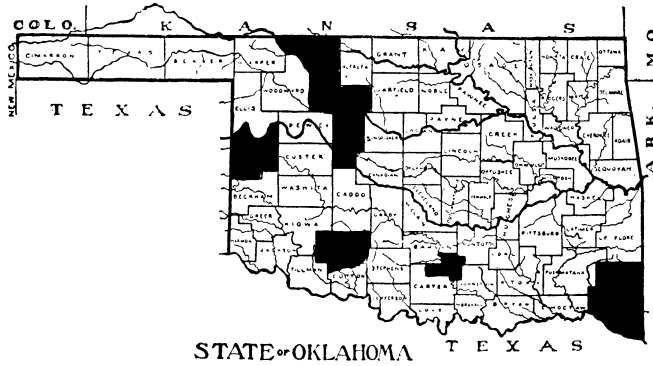


FIG. 6. Known distribution of *Bufo punctatus* Baird and Girard by counties in Oklahoma. Made up from the few specimens seen by us and from the literature cited.

Murray (Jones and Derrick, '39); Roger Mills, 1; Woods (letter from A. B. Leonard). Total examined, 8.

Bufo woodhousii fowleri (Hinckley)
(1882) (*Fowler's Toad*)

Bufo woodhousii fowleri occupies certain ecological situations in eastern and southeastern United States, its exact range being still somewhat uncertain because of confusion with several other species (principally *B. a. americanus*, *B. w. woodhousii*, and *B. terrestris* Bonnetierre) (figure 7). Over the greater part of the East, its geographic range coincides with that of *B. a. americanus* but the range of the latter extends farther north and farther west than that of the former. In

Texas the toads of this group are in great confusion, some maintaining that *americanus americanus* does not occur (Blair, '41), others reporting it from several places in eastern Texas. In southern Texas, one group of workers (e.g., Gunter, '41) trace *B. w. fowleri* westward along the gulf to Corpus Christi; others identify the same form as *a. americanus*; but Wright and Wright ('38) call it *B. woodhousii*.

Prior to the initiation of our study, *B. w. fowleri* was known certainly in Oklahoma only in Adair County in the Northeast (Ortenburger, '29a). We have since found it to be the common toad over much of the southeastern part of the state where it is ecologically segre-



FIG. 7. Known distribution of *Bufo woodhousii fowleri* (Hinckley) by counties in Oklahoma. Record from Adair county, from Ortenburger ('29a) and from Cherokee county by Blair ('41); the remainder from specimens examined by us.



FIG. 8. The approximate limits of the possible intergrading zone of toads of the *americanus*-group in Oklahoma. West of the area designated one may expect to find typical *Bufo woodhousii woodhousii* Girard intermingled with dwarf *Bufo americanus americanus* Holbrook like those described by Bragg ('40b), both widely dispersed in the savannah and the former (but not the latter) extending with *Bufo cognatus* into the grassland. East of the zone, one may expect to find typical members of *Bufo woodhousii fowleri* (Hinckley) intermingling with typical members of *B. americanus americanus* (not dwarfed) and no typical *B. woodhousii woodhousii*. Within the area designated, intergradations of characters occur, especially between *B. w. woodhousii* and *B. a. americanus* in the northeast; less among all three in the southeast.

gated, particularly in breeding, from *B. a. americanus* of the same region. Our observations on this point need no great elaboration for they confirm those of Blair ('41) in almost all particulars.

We have further observed that *B. w. fowleri* is greatly influenced in its breeding activities by temperature, for it breeds only at a higher air temperature than any other toad known to us. On evenings when the temperature is rising, calling begins at about 70° F. and may continue till well after midnight. On the other hand, if the temperature is falling, all calling stops when this temperature is neared or reached. Most calling (as well as actual breeding), therefore, occurs before midnight. These observations, made in southeastern Oklahoma, were clearly confirmed by the junior author at Monroe, La. in the warm spring of 1941 in which region this was the only *Bufo* which could be found. They also agree in general with some of the first observations ever recorded on the breeding of this toad in Massachusetts (see Cope, '89).

Numbers Examined by Counties

Adair (Ortenburger, '29a); Atoka, 3; Latimer, 6; McCurtain, 20; Pittsburg, 4; Cherokee (Blair, '41); Choctaw, 5; LeFlore, 15. Total examined, 53.

Bufo woodhousii woodhousii Girard (1856) (Rocky Mountain Toad)

The Rocky Mountain toad inhabits the central and southwestern plains and mountains from eastern Kansas, eastern Oklahoma, and east central Texas, westward approximately to the continental divide, although it crosses this in the southwest (figure 8).

If we confine ourselves to typical members of this subspecies in Oklahoma we may say that it is known from nearly every county except in the southeast and the extreme northeast (figure 9). It probably occurs in Haskell county and it may be in western Atoka county, although we have no definite records from these regions. We believe it not to occur from central Pittsburg county south-

eastward through Pushmataha, southern LeFlore, Latimer, and McCurtain counties; that is, from the northwestern edge of the Ouashita mountains southeastward. *B. w. woodhousii* is the most versatile and the most widely distributed toad in the state. No authentic record from Arkansas was known to Black and Dillinger ('38). We have found it in only one county in Oklahoma on the state boundary, that is, in Sequoyah county. Its eastward extension at this point is probably due to the influence of the Arkansas river, since this toad is partial to sandy floodplains in Oklahoma (Bragg, '40a). From this, one might expect to secure this animal in the region of Fort Smith, Arkansas, as well as in the Oak-hickory savannah in northern LeFlore county, Oklahoma where the oak-hickory pine woodland is interrupted. Although we have no records from this specific area, our expectation, based upon our ecological findings, agrees with the approximate limits of distribution as mapped by Blair ('41).

Numbers Examined by Counties

Alfalfa, 10; Beckham, 2; Beaver, 2; Blaine, 14; Bryan, 4; Caddo, 12; Canadian, 1; Carter, 50; Cherokee, 1; Cleveland, 1077; Cimarron, 14; Coal, 4; Comanche, 106; Cotton, 13; Craig, 1; Creek, 11; Custer, 72; Dewey, 9; Garvin, 37;

TABLE I

This table shows the various plant associations through which the various species of *Bufo* discussed in this paper range. See also figure 11.

	Forest	Savannah	Tall-grass	Mixed-grass	Short-grass	Desert-grass
<i>Bufo woodhousii fowleri</i>						
<i>Bufo a. americanus</i>						
<i>Bufo w. woodhousii</i>						
<i>Bufo cognatus</i>				*	†	‡
<i>Bufo insidiosus</i>					†	
<i>Bufo compactilis</i>						
<i>Bufo punctatus</i>						

restricted to rocky areas in all associations.

* In prairie islands.

† Enters west edge.

‡ Along irrigation ditches, streams.

Grady, 17; Greer, 24; Harmon, 16; Harper, 1; Hughes, 21; Jackson, 3; Jefferson, 7; Johnston, 8; Kay, 20; Kingfisher, 4; Kiowa, 295; Lincoln, 13; Logan, 22; Love, 18; Major, 11; Mayes, 21; Marshall, 8; McClain, 12; McIntosh, 2; Murray, 18; Muskogee, 5; Noble, 1; Okfuskee, 10; Oklahoma, 87; Okmulgee, 13; Osage, 14; Payne, 3; Pawnee, 11; Pittsburgh, 1; Pontotoc, 4; Pottawatomie, 21; Roger Mills (Ortenburger, '26); Rogers, 11; Seminole, 10; Sequoyah, 4; Stevens, 7; Tillman, 24; Texas, 17; Tulsa (Force, '28); Wagoner, 6; Washita, 1; Woods, 47; Woodward, 4. Total examined, 2280.

Table I presents graphically the distribution of *Bufo* in Oklahoma as correlated with the major ecological com-

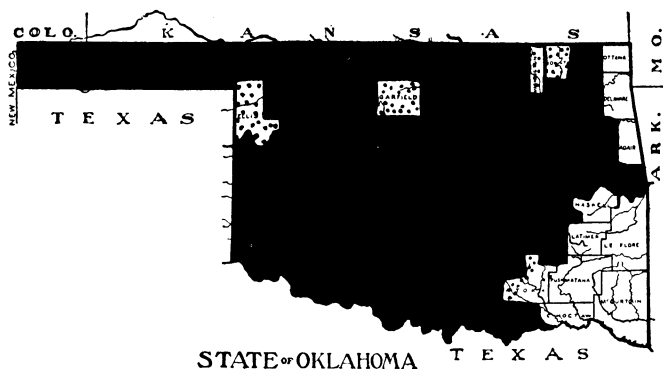


FIG. 9. Known county distribution of *Bufo woodhousii woodhousii* in Oklahoma. Earlier records in the southeast are deleted because based upon specimens of *B. a. americanus* or *B. w. fowleri*.

TABLE II. *Summary of habits of several species of toads*

Species	Feeding Habits	Breeding Habits	Authorities
<i>Bufo a. americanus</i> (American Toad)	Feeds at night during spring and summer when ground is moist. Usually nocturnal and uncommon about streetlights in Oklahoma.	In shallow pools, stream borders, cattle tanks, ditches. During April-June, perhaps earlier; males call from bank, females come into pools during night. Breeding not dependent on rain.	<i>General:</i> Miller, '09; Wright, '14; Wright and Wright, '33. <i>Oklahoma:</i> Bragg, '40b; Smith and Bragg, '42.
<i>Bufo w. woodhousii</i> (Rocky Mountain Toad)	Nocturnal throughout warm months, often diurnal, especially when young. Common under streetlights even in hot dry weather. Chief habitat, floodplains and bottomlands (sandy soil).	Usually in small groups in either temporary or permanent water. Uses all types of sites except buffalo wallows. Seems to prefer muddy water. Not all mature individuals breed each year. Breeding not dependent upon rain though most frequent after it.	Ruthven, '07; Burt, '32; Pack, '22; Storer, '25; Bragg, '40a, '41; Smith and Bragg, '42.
<i>Bufo cognatus</i> (Great Plains Toad)	Feeds during spring and summer during moist periods, nocturnal but may be active during daytime following rain. Often almost social in feeding activities. Feeds heavily during favorable periods then aestivates in hot dry weather. Uncommon under streetlights.	Huge congresses form after heavy rain in spring or summer (Mar.-Sept.) Uses only temporary, clear water. Flooded fields and buffalo wallows favorite sites. Seldom in tanks, ditches or permanent ponds. Tadpole period between 28 and 45 days (observed), depending on temperature.	Strecker, '10; Bragg, '36; '37, '37a, '40, '40b; Smith and Bragg, '42.
<i>Bufo insidiar</i> (Northern Little Green Toad)	Not much known, usually has been taken during or just after rain.	In congresses after big rains. Breeds in temporary pools and streams (latter not observed in Oklahoma). Cattle tanks also used.	Strecker, '15; '26.
<i>Bufo compactilis</i> (Desert Toad)	Much like <i>B. cognatus</i> except that it is common under streetlights. "Social feeding" has not been observed.	Will breed in tanks, ponds or any body of temporary water whether clear or muddy. Other habits like <i>B. cognatus</i> .	Wright and Wright, '33; Bragg, '40c.
<i>Bufo punctatus</i> (Canyon Toad)	Usually nocturnal, among rocks under which it hides during day.	Probably in small groups, usually in pools in rocks, or in canyons, sometimes in edges of streams.	Storer, '25; Strecker, '26.
<i>Bufo w. fowleri</i> (Fowler's Toad)	Similar to <i>B. a. americanus</i> .	Small congresses in early evening when temp. exceeds 70° F., in late May to early July; large streams and pond margins, preferred breeding sites.	Wright and Wright, '33.

munities (see also figure 11). Table II summarizes the habits of these same forms so far as now known.

DISCUSSION

The authors are students of that school of biologists who conceive of all organisms as being grouped into fundamental units on the basis of similar toleration and responses to factors of the habitat.

This is a part of the concept of the biotic community. A community can extend no further than the critical range of the factors controlling its development. When these factors exceed a certain limit, some species drop out and others enter or replace them and a new community is then recognizable. The size of the community to be delimited depends somewhat upon the worker and the organisms with which

he is dealing. A convenient grouping is to include all portions of the habitat dominated by the same organism. Thus, in a given climatic province, we could have one or several communities, depending upon factors other than climate. Related communities, that is, those having some common components but differing in others, are commonly grouped into associations; and associations with a common physiognomy, into formations.

By recognizing diffuse communities (e.g., aquatic habitats and wooded ravines through a prairie; prairie islands in woodland; woodland islands in prairie; rock outcrops; seeps; etc.) we find that two or more communities may be coextensive geographically and that care must be taken to indicate to which community an organism belongs. For example, *Bufo alvarius* is found only in desert regions yet is not a member of the desert community proper since it lives along streams and irrigation ditches and is somewhat frog-like in its habits (Wright and Wright, '33). Similarly, *Bufo punctatus*, is found in many different associations but is always associated with rocky areas where it spends much of its life in the cool, damp environment provided beneath rocks; and it breeds in small pools in the rocks. It does not associate with the characteristic toads of any association.

Ecological Segregation

It has long been our observation that habits of animals in general and of toads in particular tend to differ in different habitats and that sometimes these differences cut across taxonomic lines. Certain types of habits, especially those of feeding, tend to remain fairly stable whereas those dealing with reproduction may change more markedly as barriers are met in the dispersal of species. Those individuals of any species which change to meet the new situation at a barrier continue to spread their range; those which do not change are stopped.

These changes in an organism may be of three kinds: (1) in structure, without essential changes in habits; (2) in habits without essential change in structure; or (3) in both habits and structure in various degrees of each. If the structure changes sufficiently (whether with corresponding changes in habits or not) we designate a new species; if habits change without essential change in structure, we say that we have a wide-ranging, versatile, species. The greatest difficulty, of course, is centered in those species, subspecies or varieties which change slightly in structure without marked changes in habits.

Since variations in ecological conditions (physical or biotic) markedly effect the lives of individual organisms, and through this, of species, it follows that there is a broader line between the usual ecological emphasis upon succession of communities to the climatic or edaphic climax of a given region, on the one hand, and the taxonomic and geographic distributional emphasis of taxonomists and biogeographers on the other. The study of habits of animals, interpreted in the light of both ecology and taxonomy is, thus, an aid—indeed an absolute essential—to a complete understanding by either group of workers of the peculiar problems of either. This becomes especially true (and there more easily seen) in regions where ecological conditions change radically within a short distance and where, at the same time, two essentially different faunas meet. Similarly, while these principles almost certainly have a wide application, semiaquatic forms in a region of diverse environments can be expected to demonstrate them most clearly. This is one reason why the study of the habits of toads and frogs in Oklahoma was undertaken from the ecological viewpoint.

If we now look again at the distribution of *Bufo* in Oklahoma we see two toads (*B. a. americanus* and *B. w. fowleri*) in the more heavily forested areas; two (*B. a. americanus* and *B. w. woodhousii*) in the savannah; three (*B. cognatus*, *B.*

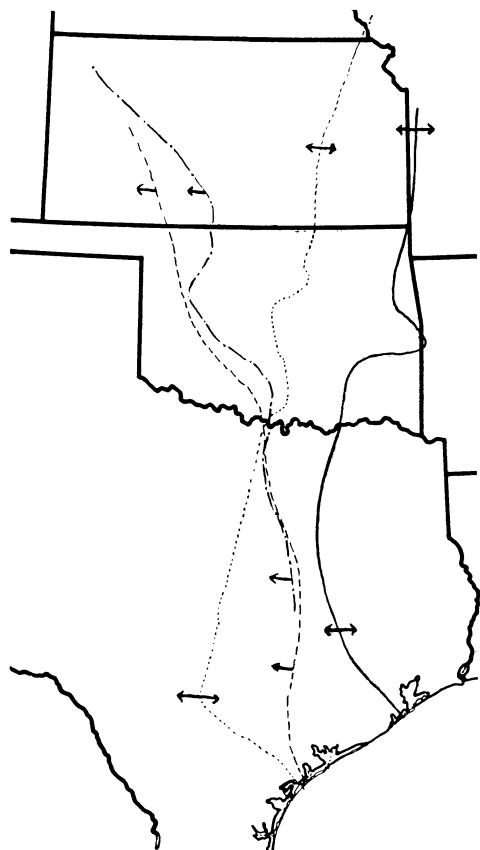


FIG. 10. The approximate east-west limits of the species of *Bufo* (except *punctatus*) in Oklahoma and adjacent states. Arrows show in what direction each species extends. Solid line, *B. w. woodhousii* to the west, *B. w. fowleri* to the east. Dotted line, *B. cognatus* to the west, *B. a. americanus* to the east. Dashed line, *B. compactilis*. Irregular dashed line, *B. insidior*. Compare with figure 1 to see correlation of distribution with the major ecological associations.

insidior and *B. w. woodhousii*) in the mixed grass prairie; three (*B. a. americanus*, *B. w. woodhousii*, and *B. cognatus*) in the tall-grass prairie; four (*B. cognatus*, *B. compactilis*, *B. insidior*, *B. w. woodhousii*) in the short-grass plains; and one (*B. punctatus*) which has been taken once in the forest, three times in the savannah, twice in the short-grass plains, and once in the ecotone between the short- and mixed-grass prairies. It

is to be noted that some overlapping, both geographic and ecological (figures 10 and 11) occurs among some species but not among others. No species is statewide in its distribution. It is of further interest to observe that each of the species discussed except *B. punctatus* has a part of either the eastern or the western border of its range in Oklahoma. This means that the western group of species (*cognatus*, *compactilis*, *w. woodhousii*, and *insidior*) tends to meet the eastern group (*a. americanus* and *w. fowleri*) somewhere within the state and that one could expect the highways for the one group to be the barriers of the other.

The toads of the Oak-hickory forest belong to the eastern group of species, as might be expected from the geographic location of the forested areas. But even there, their ecological distribution differs. *B. a. americanus* is the toad of the mountains whereas *B. w. fowleri* is the toad of the valleys, so that these forms, even though being co-inhabitants of a large geographic area, actually meet ecologically only in local habitat situations somewhat suitable for both. In the extreme southeastern part of the state, *B. w. fowleri* is by far the more abundant, in some localities replacing *B. a. americanus* practically entirely. Farther north, as the land rises rapidly into the pine-covered foothills of the Ouashitas, *B. w. fowleri* and *B. a. americanus* both occur but the former tends more and more to give way to the latter until, as we pass from the Oak-hickory-pine woodland to the Oak-hickory savannah, *B. w. fowleri* disappears completely.

B. a. americanus, however, continues in the savannah, almost immediately becoming associated with *B. w. woodhousii* to the north and particularly to the west. The savannah is progressively drier (in terms of average annual rainfall) as one passes westward but the two toads maintain their numbers well clean to the western edge where this community meets the grassland. But here again, one notes an ecological restriction, though not so

marked as between *B. a. americanus* and *B. w. fowleri* in the Oak-hickory-pine woodland. The toads of the sandy flood plains are mostly *B. w. woodhousii*, those of the less heavily wooded hills, *B. a. americanus*, although some of each are to be expected in either situation. In the northern sections of the state, where the Oak-hickory-savannah meets the tall-grass prairie, both of these toads continue into the grassland over the ecotone—although the American toad becomes progressively rarer to the west. Blair ('41) noted that *B. w. woodhousii* was abundant in the Osage prairie and he calls this the prairie toad of the region to distinguish it from the American toad which tends to be confined to islands of the Oak-hickory community here. We have noticed similar tendencies, although we know the American toad to be in the true prairie in the eastern portion.

As pointed out earlier, the ecotone between the Oak-hickory-savannah and the grasslands is very abrupt, due to a sudden change in the fundamental soil type. In the south, this abrupt transition is to short grass plains; in the northeast, to tall grass prairie; and in the larger central portion of the state, to mixed grass prairie. The characteristic toads of the mixed grass prairie (*B. cognatus*, *B. w. woodhousii*) differ in their behavior at the ecotone. Passing over the ecotone to the west on a night of breeding, one immediately hears numerous calls of *B. cognatus* in the prairie. We have often stood at such times at the edge of the savannah and grassland and noted large choruses of this species on the grassland side, similar but smaller choruses of *B. a. americanus* in the savannah, with calls of *B. w. woodhousii* intermingled with both of the others. *B. cognatus* does not enter the savannah nor *B. a. americanus* the grassland along this transition but the Rocky Mountain toad is here unrestricted.

In the typical mixed grass prairie, however, *B. cognatus* and *B. w. woodhousii* tend to be partially segregated ecologically. The former is more abundant in

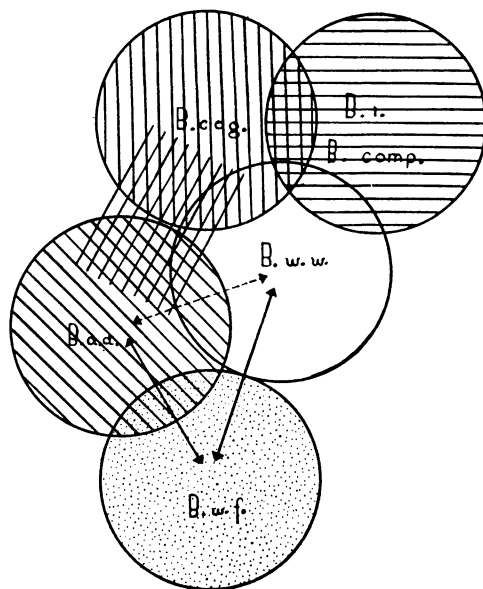


FIG. 11. Diagram showing ecological distribution of *Bufo* in Oklahoma, *B. punctatus* excepted. Circles represent species (names abbreviated); crosshatching and stippling, ecological association. |||| mixed grass prairie; //// tall grass prairie; \\\ oak hickory savannah; |||| short grass prairie; stipple, oak hickory woodland. Arrows indicate probable ability to interbreed in nature (dashed) or known ability (solid). Not shown is the possible hybridization of *B. cognatus* and *B. w. woodhousii* where not sexually isolated (Bragg, 1939).

the higher areas, the latter in the lowlands along the ravines and floodplains. In fact, only exceptionally and quite rarely does the Great Plains toad enter the sandy flood plains or the large rivers at all (Bragg, '40, '42b). There is, however, just enough mixing of the two species at medium elevations so that their partial segregation is not easily apparent. At the extremes, of course, this is more easily seen and we know several areas where it is rare to find a Rocky Mountain toad, the local population being almost entirely of *B. cognatus*, even though in some cases calls of the former may be heard while standing in the midst of a large population of the latter. Repeated detailed collection of toads feeding along roads traversing both types of areas has

confirmed our observations based upon calls in breeding congresses.

In the broad ecotone between the mixed and short grass prairie, *B. compactilis* and *B. insidior* join *B. cognatus* as prairie forms, *B. w. woodhousii* continuing here to occupy the same ecological region as before. *B. insidior* is only a minor component of the fauna anywhere in Oklahoma but southwestward, within the short grass plains, *B. compactilis* replaces *B. cognatus* as the conspicuous and abundant form. Both *B. cognatus* and *B. insidior* occur, however, in all parts of the short grass plains in Oklahoma (as well as in the Texas panhandle). In the northwestern part of the state, *B. compactilis* is rarer than farther south and we have not found it in the Oklahoma Panhandle although we predict its presence there. If this toad is extending its range northward (a distinct possibility, though not proved) then it probably is replacing *B. cognatus* as the characteristic form in the short-grass in the Northwest. It is perhaps worth noting in passing that the distribution (both ecological and geographic) of *B. compactilis* in Oklahoma is strikingly like that of the southern spadefoot toad, *Scaphiopus couchii* Baird.

What factors control these distributions? In the first place, it should be recognized that some of these phenomena are probably merely expressions of geographic extensions in time. That is, some species will eventually occupy a larger area whenever they have had time to extend into suitable adjacent areas, as suggested above for *B. compactilis*. However, most of the phenomena are the results of ecological barriers of one sort or another, samples of which are presented below.

B. a. americanus is usually considered to be a medium sized toad of partly diurnal habits. In central Maine, in the White Mountains of New Hampshire, in southeastern Wisconsin and the East generally it is not at all uncommon to find these animals, especially the females, hopping about gardens and lawns in the day-

time (observations of the senior author). At and near the western limits of its range in Oklahoma these animals are never diurnally active, are dwarfed in size, and are difficult to find even at night (except when breeding), even though breeding congresses show that a fair-sized population occurs (Bragg, '40b). But in the eastern part of the Oak-hickory savannah and in the forested areas of the southeastern part of the state, they average larger (some small ones also occur) and a few may be diurnally active just as is *B. w. fowleri* in the same region.

This suggests that humidity is one of the chief factors limiting distribution of this species and that temperature is another. It seems probable that a climate and soil which favor development of a mixed-grass prairie serve as an absolute barrier to the dispersal of this species. Indeed, it is probable that the American toad is enabled to live at the western limits of the savannah in Oklahoma only through a change to completely nocturnal habits and through becoming dwarfed. In this connection it should be noted that *B. a. americanus* can and does live in tall grass prairie. Presumably the taller grasses serve the same function as trees in the life of this toad in providing shade, moist and cool crevices in which to rest, etc.

It is more difficult to understand the apparent aversion to trees exhibited by *B. cognatus*, nor is it clear why *B. compactilis* has not crossed the ecotone to the mixed-grass prairie. In general it is easy to believe that a progressively dried environment will somewhere stop the spread of a species of frog or toad (as *B. a. americanus* passing westward) but why a progressively moister one should serve as a barrier within the limits of the prairie climates is not at all clear.

One of the most critical areas in Oklahoma occurs along the zone shown in figure 8. This is the area where the ranges of *B. w. woodhousii* and *B. w. fowleri* meet and where *B. a. americanus* is somewhat intermixed with both. Ecological

segregation tends to inhibit extensive interbreeding between the American and Fowler's toads (Blair, '41) but this is not so clearly evident between *B. w. woodhousii* and *B. w. fowleri*. In the southern portion of this zone, a small population of *B. w. woodhousii* meets a large population of *B. w. fowleri* and intermingling of individuals is inevitable. This is because both toads are animals primarily of the lower areas such as stream valleys. Furthermore they are not well isolated sexually. The spring breeding of *B. w. woodhousii* begins before that of *B. w. fowleri* but the proclivity of the former to "stagger" its breeding (Bragg, '40a) makes it usual for some individuals to breed later with *B. w. fowleri*. Blair ('41) and others have noted that some individuals from this region give evidence of hybridization and integration and this is confirmed by our own observations. That more intermediates are not found is easily explained on the reasonable assumption that the smaller population of the Rocky Mountain toad is genetically swamped by the much larger numbers of Fowler's toads along the zone of union of their respective ranges. In other words, the morphological characters which distinguish the less numerous western form are blanked out by those which distinguish the more numerous eastern form, so that, whereas integradation in reality occurs, it is less evident than in many other well known cases. In this connection, it is well to remember that *B. w. woodhousii* and *B. w. fowleri* are practically identical anyhow, except as to size (Smith, '34).

In the northern portion of the zone shown in figure 8, a peculiar variant of *B. w. woodhousii* occurs, which, except for size, strongly suggests *B. a. americanus* (Bragg, '40a).

We found specimens of *Bufo* in the Arkansas River Valley of northern Oklahoma which appeared to offer evidence of hybridization between the American toad and the Rocky Mountain toad. At Ponca City, we collected a good number of speci-

mens in August of 1939, all of which varied from our concept of typical *Bufo w. woodhousii* and which appear to represent either a cross of *B. w. woodhousii* and *B. a. americanus* or an ecad of the former. In size they are intermediate between the two species. In spinosity and markings they resemble the American toad. Some individuals have spotted venters like the latter species while others have the spots reduced to a single breast spot, a condition usual in *Bufo w. woodhousii* although somewhat variable in specimens from Oklahoma (Bragg, '40a). These forms have been taken together under street lights in northern Oklahoma. We have noticed similarities and differences in the behavior of typical *Bufo w. woodhousii* and the variant. When approached, typical *B. w. woodhousii* commonly becomes alert, sits up straight, and, if blinded by light, sits quietly. The variant remains in a crouched position until approached closely, when it suddenly starts rapidly hopping away and keeps going until out of danger. They usually refuse to sit quietly even when light is shone into their eyes.

We have not collected the variants while they were breeding so have no record of their calls. We have found typical *Bufo w. woodhousii* calling on the banks of the Arkansas River near Ponca City and at that point collected one of the largest female specimens we have seen, the only larger being one taken in Carter county, Oklahoma, the same summer.

Whether these variants are really hybrids or only ecads can be determined only with further field and laboratory work. We do not consider the specimens to be *Bufo woodhousii fowleri* because of their considerably larger size and because they are quite far out of the known range of *B. w. fowleri*.

It is of some interest to note that the breeding habits of the grassland-limited toads (as well as of members of other genera) differ in characteristic ways from those not so limited. This has been mentioned for several species in earlier papers

(Bragg, '40, '40a, '40c, '41a, '42, '42a; Bragg and Smith, '42) but needs re-emphasis. The grassland-limited species have the following tendencies in common: (1) breeding only after rain in temporary water, (2) breeding call very attractive to both sexes, (3) tendency to gather quickly into large congregations at breeding, and (4) lack of a definite breeding season (correlated clearly with the stimulus of rain). It is to be specially noted that these tendencies form a breeding pattern especially adaptive to xeric conditions such as found in the drier types of grassland and deserts.

SUMMARY

Since little had been done in delimiting ecological communities in Oklahoma and almost nothing on ecological distribution of toads of the state, it was found necessary to present the ecological communities in some detail, using the dominant plants in the naming of communities, in order to trace the ecological distribution of the toads.

Two biomes are represented (deciduous forest and grassland) with an extensive savannah, mostly between them, related to each. Edaphic factors give savannah in many places where a climatic climax of grassland is to be expected. The forest is limited to the eastern portion of the state, but has long tongues following the major rivers westward into the grassland. The trees of the savannah are largely oaks and hickories, the grasses varying with conditions of climate, soil, and exposure. Pines are locally abundant in the forests of the southeast and four mountain-masses break up the continuity of communities in places. The grasslands are short-mixed-and tall-grass prairies (the first often called plains). In general the tall-grass prairie is in the northeast, the mixed-grass in the central, and the short-grass in the west. "Islands" of one community are common in another, usually due to local peculiarities of soil. Sand prairies of tall grasses and an extensive

oak-shinnery community also occur in the west.

We find seven species or subspecies of *Bufo* to occur in Oklahoma, none of them statewide. *B. a. americanus* is mostly abundant in the savannah but occurs in the woodland and tall-grass prairie. *B. cognatus* is most abundant in mixed-grass prairie, fairly abundant in the plains, and enters the tall-grass for some distance along the ecotone between the tall- and mixed-grass areas. It is never in woodland nor savannah except in extensive islands of prairie and is very rare on floodplains. *B. compactilis* is limited to the plains, in the southern portions of which it is very abundant. *B. insidiosus* is not numerous in Oklahoma. It occupies the plains, principally, but is present in the western edge of the mixed-grass prairie as well. *B. punctatus* is not an integral part of any of these ecological communities but has been found in several of them in rocky areas only. *B. w. fowleri* is the toad of the lower areas in the woodland only. *B. w. woodhousii* occupies this same niche in all other parts of the state. In addition, it spreads onto the prairies in smaller numbers.

A zone of varying width occurs along the west edge of the oak-hickory forest in which the population of *Bufo w. woodhousii* from the savannah to the west meets the population of *B. w. fowleri* from the forest to the east. Because of their close relationship and great similarity, hybrids between the two subspecies are difficult to assign to either group. The final assignment usually depends upon which of the group is more familiar to the individual worker. Although the breeding season of *B. w. woodhousii* starts much earlier than that of *B. w. fowleri*, it extends through that of the latter; thus, hybridization is enhanced. The chief differences in these subspecies are a difference in body size and a difference in their calls. Intermediate forms are intermediate in both call and size.

The habits of each of the various species are adjusted to the type of habitats

afforded by the biotic community in which it occurs. The American toad has a different habitat here than it does in the eastern part of the United States and is much dwarfed in size at the western limit of its range. Here it is largely nocturnal and more secretive in its habits.

Bufo woodhousii fowleri breeds only when the temperature is about 70° F. and in permanent or semipermanent water. These factors tend to restrict the subspecies to the southeastern United States where the spring is warmer and the rainfall heavier than northwestward, such as in central or western Oklahoma and Texas.

All species of *Bufo* of the grassland take advantage of bodies of water produced by the first rains of the spring or early summer (where temperatures are not too low) to breed and, in one of them at least (*B. cognatus*), this habit has become so fixed that the species will not breed until or unless the rains come even when there is sufficient water in suitable pools. The "breeding season" which is so commonly mentioned as a part of the life cycle of the species of the East and North tends therefore to be superseded in these drier regions by an absolute dependence upon rainfall and its seasonal distribution. Similarly, these same species tend to have more nocturnal habits than their relatives to the east. All retreat to burrows in the earth or other retreats with the coming of excessively hot, dry weather and remain there till conditions become favorable for their activities. In this way they escape desiccation.

Bufo w. woodhousii usually is found in moist, sandy areas, which in Oklahoma commonly occur along river floodplains. It, too, is largely nocturnal, but it does not aestivate like the typical prairie species nor is it dependent upon the stimulus of rainfall to begin its breeding activities; and it does not often form huge breeding congregations characteristic of the species of the prairie. These habits fit the Rocky Mountain toad to more moist situations such as open woodland, floodplains, and

bottomlands where it is the most important and usually the only toad. The habits of *Bufo w. fowleri* differ from those of *B. w. woodhousii* in that the former will not breed when the air temperature is much below 70° F. and the water is not quite warm while the latter will breed when the air and water temperature is below 60° F. and will breed in all types of temporary pools as well as in permanent bodies of water.

These distributions and ecological restrictions apparently apply not only to the biotic associations of Oklahoma but also to those of adjacent states.

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