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Some aspects of the distribution natural history and zoogeography of the toad genus Bufo in Montana

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SOME ASPECTS OF THE DISTRIBUTION, NATURAL HISTORY AND ZOOGEOGRAPHY OF THE TOAD GENUS BUFO IN MONTANA

By

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TABLE OF CONTENTS

LIST OF FIGURES

LIST OF FIGURES

INTRODUCTION

The intermediate standing of amphibians between the terrestrial and aquatic modes of existence among vertebrates makes them a useful and fascinating group for studies on the evolution of land life. Montana has often been considered a void as far as information on distribution and occurrence of amphibians and reptiles is concerned. Among the major groups of vertebrates, amphibians constitute a rather small and inconspicuous class, although some species are abundant as individuals. Their secretive habits, small size and in some areas their short periods of activity, often cause many amphibians to be difficult to observe or collect.

This present study in Montana was conducted on one family in the Amphibia, the Bufonidae. It was thought that the distribution of bufonids in Montana might be wrong because of incorrect identification and lack of collection records. According to Stebbins (1966) and Conant (1958), there are four toads in Montana; Bufo hemiophrys in northeastern Montana, Bufo boreas boreas in western Montana, Bufo cognatus in eastern Montana and Bufo woodhousei woodhousei in the southern half of Montana. Records indicate that B. boreas boreas, B. woodhousei woodhousei and B. cognatus have definitely been collected in Montana. B. hemiophrys was not definitely collected in Montana until 1966 (Black, 1967, 1968).

Conant (1958) sums up the problems associated with the taxonomy and distribution of toads when he states; "The homely "hoptoad" is readily recognized as such, but telling the different kinds apart is quite

another matter. Recourse must be made to checking the shapes and sizes of the parotoid glands and cranial ridges. This unfortunate state of affairs undoubtedly has been aggravated by mankind's propensity of altering habitats and thus bringing together animals that had remained isolated for one reason or another during prehistoric times".

The primary objectives of this investigation were two-fold: (1) to determine what species of Bufo occur in Montana and their probable distribution, and (2) to study some aspects of their natural history.

REVIEW OF LITERATURE

The history of herpetological work in Montana is very limited. Little herpetological work has been done in Montana as a whole, with most of the work being concentrated in the mountainous western part of the state. No previous work has been done on the toads of Montana, even though nearly all of the papers written have some information on *Bufo sp.*

Early herpetological history in Montana started with J. D. Cooper (1869) who observed *B. boreas* along the Hell Gate and Bitterroot Valley in Montana and F. V. Hayden (1874) who described *B. boreas* from the Pleasant Valley and Yellowstone Basin. J. A. Allen (1874) reported that *B. boreas* was common in the Montana Territory and *B. boreas* was also reported from the Kootanie River, Chief Mountain Lake and the Yellowstone by Coues and Yarrow (1878). *B. cognatus* was first reported in Montana by Cope (1879) as occurring north of the Missouri River with another *Bufo* on the southside of the Missouri River. Cope (1886) also read before the American Philosophical Society a list of North American species of *Bufo* and *Rana* in which he gave a detailed description of six specimens of *B. hemiophrys* from the northern boundary of Montana.

In more recent years, Rodgers and Jellison (1942) listed *B. boreas* in the Bitterroot Valley of western Montana. The herpetology of the Tiber Reservoir area was described by Mosimann and Rabb (1951) who collected eight specimens of *B. cognatus* in an artificial cattle pond on the prairie of Toole County. The herpetology of the Mission Mountains, Montana, was described by Brunson and Demaree (1952) who

found B. boreas with an extensive range both geographically and vertically. Brunson (1952) reported on a collection of B. boreas from western Montana and in 1955 published a checklist of the amphibians and reptiles of Montana which listed B. boreas boreas, B. cognatus and B. woodhousei as occurring in Montana. Manville (1952) listed the amphibians and reptiles of Glacier National Park and reported B. boreas widely distributed throughout the park.

The second complete list of amphibians and reptiles of Montana was published in 1965 by C. V. Davis for McGill Museum, Montana State University. This checklist included four species of toads occurring in Montana; B. b. boreas, B. cognatus, B. w. woodhousei and B. hemiophrys. Black (1967, 1968) discussed some aspects of the natural history and distribution of members of these four species in Montana.

Blair (1957) presented evidence that the Dakota toad, B. hemiophrys, is not conspecific with B. woodhousei as was suggested by Schmidt (1953). Therefore, B. hemiophrys instead of B. woodhousei hemiophrys will be used in this paper.

Even though Cook (1964) pointed out that the common name "Canadian toad" is often used in preference to "Dakota toad" when referring to B. hemiophrys, the common name "Dakota toad" will be used for the sake of uniformity. Other common names follow the recommendations of the Committee on Herpetological Common Names which appeared in Copeia (1956).

METHODS AND PROCEDURES

The main objectives of this research were to determine what species of bufonids occur and what their ranges are within Montana. This was accomplished by use of preserved specimens and collection records from Montana which were located at various museums throughout the United States, and the collecting of live specimens within Montana. Detailed information about a species distribution is basic for determination of the factors which restrict it, and preserved specimens whose identity may be verified are the only sound basis for such information.

During the spring and summer of 1966 and the spring of 1967, preplanned routes were followed throughout Montana and each part of the state was subjected to collecting at least once. Total mileage covered during this study exceeded 30,000 miles within the boundaries of Montana.

Besides personal collecting, high school and grade school biology teachers were sent a letter, collecting and preservation information, and a key to the toads of Montana. This material was intended to enlist teachers and their students in specific areas of the state to collect and preserve amphibians. The response was very poor in 1966. Only ten schools out of 150 contacted furnished specimens. Many of these high school teachers were contacted personally during the spring and summer of 1966 which resulted in a better collecting response in the spring of 1967. National wildlife refuges proved to furnish accurate information on the amphibians within the immediate boundaries of the refuge.

Methods of collecting in the field were uniformly followed throughout the collecting periods. Collecting areas were any types of habitat

which might serve bufonids or other amphibians. When a specimen was collected, a complete set of field notes was taken and included the species name, collection date, locality, time of day, weather, habitat, and external characteristics of coloration. Color slides were taken of live specimens and habitat for future reference. Specimens were usually placed in plastic jars, cloth bags or heavy plastic bags until preserved.

Several weeks at a time were spent in the field and most specimens were not kept alive. It was preferable to kill most specimens by immersing them under warm water. This enabled the specimens to be placed in uniform positions after death before fixation in formalin. This procedure was followed for specimens collected near university facilities. In the field, all live specimens were killed and fixed at the same time by dropping them live into a gallon jar of 10% formalin. This method resulted in a fairly uniform position in preserved specimens. A piece of absorbent cotton, large enough to hold the jaws open, was inserted into the mouth so that the mouth could be readily examined without damage to the specimens hardened in formalin. Specimens were labelled on a hind leg with a tag showing a specific collection number.

Specimens were removed from 10% formalin after 24 hours and placed under running water for at least one hour. They were then permanently stored in 70% ethyl alcohol.

Other specimens used in this study were obtained from: Rocky Mountain Laboratory, Hamilton, Montana; National Museum of Canada, Ottawa, Ontario; University of California, Berkeley, California; Bowdoin National Wildlife Refuge, Malta, Montana; Montana State University, Bozeman, Montana; Medicine Lake National Wildlife Refuge, Medicine Lake,

Montana; Western Montana College of Education, Dillon, Montana; The Charleston Museum, Charleston, South Carolina; Fort Benton High School, Fort Benton, Montana; University of South Dakota, Vermillion, South Dakota; Whitefish Junior High, Whitefish, Montana; Smithsonian Institute, Washington, D. C.; University of Michigan, Ann Arbor, Michigan; Glacier National Park Headquarters, West Glacier, Montana, and University of Montana, Missoula, Montana.

All body measurements of toads were made using a vernier caliper which was read to the nearest 0.1 mm.

Measurements, field notes, photographs and preserved and living specimens were utilized to compile a description of the adults of each species, its range, sizes, sexual characteristics and natural history.

Distributional maps were prepared for each species. Arbitrary range limits were hypothesized from the collection records, observation of habitat, glacial history, and the present physiographic and vegetational patterns.

Bufo boreas boreas (Baird and Girard)

Boreal Toad

Range:

The boreal toad is the most frequently observed toad in western Montana. This toad is found throughout the mountainous and forested areas which make up the western third of Montana, and on some of the isolated low mountain groups in central Montana (Fig. 1). This is the common toad below 6,000 feet elevation in Glacier National Park.

The range of the boreal toad extends eastward in Montana, except for isolated populations on low mountain groups, to the following counties: Glacier, Pondera, Teton, Chouteau, Judith Basin, Wheatland, Golden Valley, Stillwater, and Carbon Counties. Members of this subspecies have been collected in all counties west of this arbitrary limit except for Pondera, Teton and Cascade Counties. The boreal toad should occur in these counties on the basis of habitat observations.

Dr. C. V. Davis of Montana State University has collected and/or observed the boreal toad on the isolated low mountain groups of the Highwood Mountains in Chouteau County and the Little Rocky Mountains in Phillips County. Other isolated populations could occur on the Judith Mountains, Big Snowy Mountains, and the Pryor Mountains of central Montana.

Sexes:

Males and females of the boreal toad are often difficult to tell apart. The darkened throat or vocal sac which is characteristic of males in the other species of Bufo is not present in the boreal toad.

Breeding pads are obvious on males during the breeding season on the thumb and inner two fingers. This thickened pad may be continuous from the thumb to the thenar tubercle. The breeding pads are black or brown and always rough.

Sexual dimorphism is present among many members of this subspecies in Montana. Males frequently have a solid dorsal color, while females do not. Eighty-eight percent of the breeding males collected had a solid dorsal color of brown, light black, green or dark olive-green. The warts and skin were much smoother on males than on the females.

Males of this subspecies chirp readily when handled or grasped behind the forelegs during the breeding season. Females very seldom chirped when handled or when in amplexus with a male.

Females are usually larger in body proportion than males, but size alone will not distinguish the sexes.

Sizes:

Data on size range in adults of B. b. boreas is based on examination of 150 specimens. All measurements refer to snout-vent length unless otherwise specified. The mean was 74.4 mm for males and 83.1 mm for females. The majority of males and females fell into the 85-97 mm size range, with more females attaining lengths greater than 97.0 mm. The largest female was 117.6 mm from Gallatin County. The largest male was 112.0 mm from Flathead County. The minimum size for a breeding male was 67.0 mm from Flathead County. The minimum size for a breeding female was 80.0 mm from Jefferson County.

Wright and Wright (1949) report sizes of 56-108 mm for males and 60-125 mm for females of the boreal toad. From these measurements and

those of the specimens in Montana, it appears that representatives of this subspecies in Montana are average in size to representatives of this subspecies in other parts of its range.

Description:

Most adult boreal toads can be distinguished by the following characteristics:

The average snout-vent length is 2-5 inches and there is complete lack of supraorbital and postorbital crests (Fig. 5). The general dorsal color is light gray or greenish to a dull black. Numerous black-pitted warts cover the dorsal surface. These warts are usually light brown with small black pits and may be set in a black spot. The warts are larger than those found on other toad species in Montana. The vertebral stripe is white and usually continuous from behind the nares to the anus, but may be broken or absent. Parotoid glands are oval, distinct and smooth. The interparotoid distance is greater than the width of the gland. Each eyelid usually contains one large wart. Sole tubercles are light brown and have no cutting edge. A well-developed fold of skin is on the tarsus from the inner sole tubercle to the heel. There is usually a large wart on the tibia. The venter is usually whitish with varying amounts of dark spotting or speckling.

Juveniles of the boreal toad are practically identical to the adults. They frequently have a venter which is completely black or spotted with black. The dorsal surface is much like that of the adults. The sole tubercles are often orange or brown.

During June and July of 1966, I collected four specimens of Bufo at 6,700 feet of elevation on Logan Pass, Glacier National Park; all differed

in external characteristics from the typical boreal toad which is common at lower elevations. The Glacier National Park collection also contains two of these unusual toads from other localities within the Park. The specimens are most similar to Bufo canorus Camp which has been reported only above 6,000 to over 11,000 feet of elevation in the central Sierra Nevada of California. Individuals closely resembling B. canorus have been collected at 6,700 feet elevation on Logan Pass, one mile below Swiftcurrent Pass toward Granite Park at 6,800 feet elevation and three miles below Granite Park at 5,700 feet elevation. The specimens collected on Logan Pass were active during the day in the wet alpine meadows.

The question arises, is this population in Glacier National Park an example of B. b. boreas at high elevations approaching the coloration of B. canorus as suggested by Stebbins (1951) and described by Karlstrom (1962) in California, or is it truly B. canorus? Dr. Robert C. Stebbins, University of California, Berkeley, after examination of a specimen from Logan Pass, reported that it corresponded closely in external characteristics to B. canorus from the Sierra Nevada in number of dark blotches, width of the vertebral stripe, wider interorbital distance and a less truncated snout.

Karlstrom (1962) formulated several theories to explain the origin and present distribution of B. canorus. One of these was that the Yosemite toad is a montane relic of a once far-ranging species which in earlier times occupied the Cascade and Sierra Mountain systems, and its origin may have been far north of its present range. The absence of B. canorus in the north or south tends to negate this hypothesis. Instances of apparent convergence of B. boreas with B. canorus may be found in many parts of the range of the boreas group. Myers (1942)

mentions certain specimens of B. boreas from Diaz Lake, Inyo County, California, which approach the coloration but not the structure of B. canorus, and Karlstrom (1962) reported an adult female B. boreas from Lake Louise, Alberta, Canada, which resembled a female B. canorus and suggested that selective factors which have acted to produce a specialized montane form as B. canorus probably have exerted similar influence on related forms which have been exposed to the same or similar environmental agents elsewhere. Stebbins (1954) suggests that B. canorus is a close relative of B. boreas and that B. canorus may be a high mountain differentiate of B. boreas. Camp (1916) recognized the tendencies within certain individuals of the B. boreas group toward the degree of sexual dimorphism exhibited so strongly by B. canorus.

B. b. boreas from other high elevations in Montana show no tendencies towards approaching the structure or coloration of B. canorus. The population in Glacier National Park appears to be an example as suggested by Karlstrom (1962) of environmental factors at high elevations producing a specialized montane form similar to B. canorus in the Sierra Nevada. Glacial history of Glacier National Park adds further support to this hypothesis and will be discussed in the Zoogeography section.

Natural History:

The western mountainous region is where most B. b. boreas are found. In the northern portion, mountain ranges and narrow river valleys parallel each other in a northwestward southeastward direction. The southern portion is a jumble of mountain ranges and wider valleys. The mountains are higher in the southern third of the state. Isolated low mountain groups such as the Highwoods and Little Rockies stand in sharp contrast

to the flat and rolling plains which surround them in central Montana. These mountains, valleys and isolated mountain groups describe the physiographic habitat of the boreal toad.

Vegetational types of habitat include forest and alpine grassland, sagebrush, undifferentiated stream bottoms, intermountain valleys and foothill grassland. Its habitat lies within the forested and non-forested regions of Montana where it is found in the alpine, lodgepole pine, white pine, larch, Douglas fir, spruce and ponderosa pine.

The boreal toad was collected in the following habitats during 1966 and 1967: floodplains of the Clark Fork, Bitterroot and Blackfoot Rivers, spruce-fir forest around Whitefish Lake, a small spring in the open ponderosa pine near Canyon Ferry Reservoir, a moist tall grassy meadow on Grass Mountain, under a log in the Douglas fir around Echo Lake, a lawn in Missoula, the Whitefish skating pond, a grassy spring in the short-grass prairie west of Harlowton and under an old car door in the tall grass of a meadow at 7,000 feet elevation on Kings Hill.

Nine breeding ponds and their breeding populations of the boreal toad were observed in Montana during the springs of 1966 and 1967. Three temporary ponds filled by underground seepage from the Clark Fork River, 7.7 miles northwest of Missoula, and two spring overflow ponds in the Clark Fork River floodplain 6.7 miles northwest of Missoula were observed in both years. Two large ponds one mile north of Victor, Ravalli Co., and two water-filled gravel pits 8 miles southeast of Hamilton, Ravalli Co., along Skalaho Highway 38 were observed during the spring of 1967. Practically all breeding sites

were dry until the spring runoff. Each location will be discussed separately.

The three temporary ponds 7.7 miles northwest of Missoula are located on a large gravel bar which has parts of the Clark Fork River flowing on all sides. The first B. b. boreas each spring were collected at these ponds on 4 April 1966, and 14 April 1967. These were always yearling juveniles of various sizes. They were numerous along quiet water around and in old muskrat holes in the banks. Tall, dry grass along the banks contained numerous spiders and the juvenile toads were often encountered in the grass but would quickly hop to the water or into the nearest muskrat hole. Many of these young were of such a small size that it might indicate some late breeding in this locality. Breeding adults were encountered in these ponds during 1966, but the influx of people ruined these breeding sites in 1967.

The first adult was taken at these ponds on 14 April 1966. This was a sluggish male with its nares above the water surface. The substrate temperature was 9.2°C and the water temperature was 10.5°C at 10:00 A.M.

Seven males and one pair in amplexus were observed in these same breeding ponds on 5 May 1966. The seven males were in a larger pond and discovered when their calling was heard about $\frac{1}{4}$ mile away. This chorus of male calls sounded identical to the "protest" chirps uttered by males when clasped by another male. The seven males were separated from each other by at least one foot of distance and were along the edge of the pond in clumps of grass, beside logs, or with their front feet on the bank. All seven males were facing in the same direction and along the same side of the gently sloping shore. The males when

approached ceased calling and would swim to the bottom of the pond and lie motionless. They would soon rise from the bottom and return to their calling and watching stations. No females were observed in this pool. The water temperature was 22.0°C. and the substrate temperature was 18.0°C. The single pair in amplexus was in a shallow, weed-filled, small pool away from the other males. The water temperature was 21.0°C. The pair was observed at 11:30 A.M. with their heads above water and the female resting her feet on a small mound of grass growing in the water. Amplexus was in the axillary position. The pair would keep going to the bottom of the pool and coming up on the opposite side when disturbed or remain on the bottom for some time. No eggs could be found and the pair was taken to the laboratory where eggs were laid during the night. Flood water during the week destroyed further breeding at these sites in 1966. The water was clear in all breeding sites.

The ponds 6.7 miles northwest of Missoula are depressions in the open ponderosa pine filled by snow melt from a small creek. The water was always turbid. Two gravid females were observed basking on the bank in the direct rays of the sun at 11:20 A.M. on 24 April 1966. The substrate temperature was 17.0°C. and the water temperature was 7.0°C. The first male was collected on 5 May 1966, in the shade along the edge of the water. No other adults were collected at this site in 1966. In 1967, the first male was collected on 5 May. This male was in breeding condition. A gravid female was collected on 19 May 1967, and was the last toad collected at this site in 1967. Even though toads came to these ponds to breed, actual breeding probably did not occur because of the cold water temperatures.

The two large ponds one mile north of Victor, Ravalli Co., are

primarily dry during the winter but fill during the spring runoff. Vegetation is primarily cattails on the north and south ends of both ponds. The southern and larger pond is used by B. b. boreas for breeding while the northern pond is not used. On 16 May 1967, these ponds were visited and numerous males were present in the dry cattails and on the bank at one side of the southern pond. No eggs or females were found. The males were very bold and would come towards any movement in the water whether it was a hand or an aquatic net. When one male saw another male move, it would quickly swim or crawl through the cattails and try to clasp the moving male. The clasped male would immediately utter "protesting" chirps and wrestle with the clasping male. This movement attracted other males and more wrestling resulted. One male was observed in the cattails giving the "protesting" chirp and the fluttering of the throat was obvious. This observation may indicate that the "protesting" chirp is also the breeding call used by the males to attract females. All males were spaced apart from each other and facing a single shore. Two days later on 18 May, all toads were gone except for 5 or 6 males and one pair in amplexus. The males were now secretive and would not come to movements in the water or to recorded "protest" calls. No eggs were observed in the deeper and northern end, but eggs were numerous in the shallow and southern end. Most eggs were twined around the grass on the bottom and a few were in clumps. The pair in amplexus was found in deep water hidden in a floating clump of grass away from the males. Eggs were laid by this pair at night in the laboratory.

Eight miles southeast of Hamilton, Ravalli Co., along the Skalaho Pass Highway 38 are located two gravel pits about 100 feet apart filled with water (Fig. 9). Each pond is about $\frac{1}{2}$ acre in size. Vegetation is

limited to groups of dry cattails. The water is clear and 5 foot deep in the middle. These ponds were used extensively by the boreal toad for breeding. The first male was found on 11 May 1967, and the breeding population was observed until 18 May 1967. On 11 May, only a few males were present on the shores or hiding in the dry cattails. By 14 May, each pond contained at least 30 waiting males. Most males were in the cattails with just their eyes and front legs above the water surface, while others were in the shallow water near shore with their anterior half resting on rocks (Fig. 10). All males were spaced at intervals along a single shore and not around the whole pond. There was at least one foot of distance between each male and all were facing the shore.

Males from one pond were collected and released on the shore of the adjacent pond. As soon as the movement of the new arrivals was noted, the waiting males swam to them and clasping attempts were made. Immediately upon being clasped by another male, the clasped male would start chirping, rolling over in the water and wrestling to free itself. Two males never stayed clasped for any length of time. The wrestling of one pair of males would attract all the others until the water was boiling with wrestling males. If any male was clasped behind the forelegs "protest" chirping was immediate. This "protest" chirping attracted other males towards the sound even if the chirping male was on shore and no movements were made. After a few minutes, the males would start moving apart and space themselves from each other along the shore. They did not appear to always return to the same station along the shore. On 16 May, at least 40 males were present in each pond and the first pair in amplexus was found in a quiet and hidden area. No eggs had yet been laid. The anal temperatures of the waiting males ranged from 17.6°C. to

18.1°C. in water which was 17.6°C. Recorded "protest" calls from the Victor ponds were brought to these ponds on 18 May. From the nearby highway, the water appeared to be boiling and the "protest-like" chirping chorus was very loud. This chorus of slow chirping sounds from many of the males came in part from males uttering their "protesting" calls as other males were attempting to clasp them and also from individuals giving the slow chirps which sounded identical to the "protest" chirping. This slow chirping chorus could be heard for some distance. Two sets of eggs had been laid and one pair in amplexus was hidden in the dense grass. The taped calls were played on the shore which attracted some males and clasping attempts were made. Movements of a net or hand in the water with or without the recorded calls resulted in numerous males being attracted and at one time 31 males were around the moving aquatic net in the water. The pair in amplexus was taken from their hiding place in the grass and placed in the open water. These toads were immediately attacked by 6 males which the male in amplexus kicked away with his hind legs and the mated pair returned to their hiding place where they were not bothered by the other males.

These ponds were visited at night on 18 May, with the recorded "protest" calls. The males at night were extremely hard to find and were floating out in the middle in the deeper water and only a very few were close to shore. The recorded "protest" calls attracted several males and very few attempts at clasping were noted. It appeared that practically all breeding activities had ceased at night. Even though water temperatures were not taken at night, they were not much lower than the daytime temperatures.

Breeding was observed less extensively in the skating pond at

Whitefish, a mud puddle southwest of Whitefish, a high mountain pond in the Highwood Mountains, and a spring two miles northwest of Canyon Ferry Reservoir.

According to Mullally (1956) adults of B. boreas usually frequent the water only once during the breeding season. Schonberger (1945) reported males congregating in the pools before the females and sometimes even before the ice had melted at the higher elevations. Bragg (1940) observing the breeding behavior of B. w. woodhousei noticed that males outnumbered females at the breeding sites. Blair (1943) made similar observations on B. a. americanus. Karlstrom (1962) relates that there are more males than females of B. b. haliophilis and B. canorus at the breeding sites in California, and Logier (1932) found that males of B. b. boreas greatly outnumbered the females during breeding in British Columbia.

Observations on B. b. boreas in Montana show that the breeding behavior of the boreal toad in Montana is similar in many respects to that reported for other Bufo and B. b. boreas in other localities. The boreal toad in Montana is found near water during the breeding season and also at other times of the year. It does not restrict its occurrence to ponds only during the breeding season as was suggested by Mullally (1956). Males greatly outnumbered the females at all breeding sites in Montana. There were usually ten males for every female.

Karlstrom (1962) reported that male B. canorus are in a highly excited state during the height of their chorus at midday and early in the afternoon. Competition for the few females was intense. B. b. boreas males in Montana were also in a highly excited state during the day and breeding activity all but ceased at night. There was also intense compe-

tition among males for females and this was probably the cause of pairs in amplexus being hidden and secretive during the day when the height of the male breeding activity existed.

Males of the B. boreas group lack an enlarged resonating vocal pouch. Therefore the voice is weakly developed. The call of B. boreas is a soft chuckle or a bird-like chirp according to Rickwell (1947), Wright and Wright (1949) and Stebbins (1951). Baxter (1952) described the call of B. boreas in southeastern Wyoming as a short chirp, repeated at regular intervals. These notes from individual toads were similar to the warning chirps uttered by the male when clasped or jostled by other toads or when handled. Karlstrom (1962) described the weakly developed call of B. boreas as consisting of short chirps, five to ten rapidly developed notes in a series. Mullally (1956) reported that male B. boreas vocalized only when other male toads grasp them as if to assume the position of amplexus. Most authors imply that separate and untouched males do not call or form breeding choruses.

Calls of male B. b. boreas at the Hamilton and Victor breeding ponds were recorded during 1967. Audiospectograms were made of these calls in 1969 by Dr. Kenneth R. Porter, University of Denver. He reported that the calls recorded were "protest" or "release" calls which had been described by Karlstrom (1962). Porter suggested that these calls should not be confused with true mating calls and their function in attracting other males and/or females is doubtful, but should be tested.

In Montana these calls were most frequently being emitted by males when they were clasped by another male, and hence were true "release" or "protest" calls. But at the breeding ponds along the Clark Fork River and at the Victor and Hamilton breeding ponds, these calls were observed

being given by single males in an excited state. These males were not being amplexed by other males. These calls could be heard $\frac{1}{4}$ mile away. Recorded "protest" calls also attracted other males. My observations in Montana indicate that these slow chirps uttered by males when clasped or by individual males, do serve as an attractant for other males and probably also for attracting females to the breeding sites and the waiting males.

Breeding of the boreal toad in Montana can be summarized as follows: Breeding occurs from April to July, with the height of activity in May and June. Breeding appears to be dependent primarily on rising temperatures which also assures breeding sites being filled with water from the spring runoff of melting snow from the high mountains. Rainfall appears to have little significance on breeding. These toads exercise little discrimination in selection of breeding sites as long as a strong current is not present. Breeding sites can be gravel pits, ponds, springs, marshy areas and temporary pools. Water in breeding sites is primarily clear, but muddy water is occasionally used.

Males arrive at the breeding sites in large numbers before the females. The males space themselves at intervals along the pond's edge (Fig. 10 & 11). All males face in the same direction, usually towards a gently sloping shore. The lack of a vocal sac in males implies that vocalization is not used to attract the females to the breeding sites. Observations indicate that the slow chirps uttered by males either in a chorus of males spaced at intervals along the shore, or as single individuals giving the slow chirps, or as numerous males attempting to clasp each other which results in a chorus of "protest" chirps, may serve as a vocal attractant for females. Any movement on the shore or at the edge

of the water stimulates all males to move towards the movement. If the initial movement is followed by "protest" chirping, (perhaps indicating competition between males for the rather uncommon female) numerous males respond by swimming towards the sound and movements, attempting to clasp other males or dislodge a male in amplexus with a female. This response to sound and movement is greater than to sound or movement alone, even though movement seems to be the strongest stimulus in producing activity from the numerous males. The competition for females seems very high as the ratio of males to females is about 10:1 at most breeding sites. Females probably enter the ponds and are met by the numerous males. Competition among the males for the female results. Amplexus is in the axillary position. A pair in amplexus is secretive during the day because of the numerous males waiting to attack any movement and compete for the female. Egg laying probably occurs at night when the pond is quiet and breeding activity has practically ceased. Eggs are laid in long strings wound through the vegetation or rocks in the shallow part of the breeding site (Fig. 11). Eggs hatch in about 7 days at lower elevations and metamorphosis takes place about two or three months after hatching, dependent upon temperatures and altitude.

Tadpoles of the boreal toad were frequently observed in nature. In most cases, the dark-colored tadpoles were on the bottom of the breeding site in about 3-6 inches of water or resting on aquatic vegetation. In some places they could easily be scooped up in a net, but often they would swim or crowd the bottom.

Two small ponds with muddy bottoms on the side of Mt. Jumbo, Missoula Co., were observed during the spring of 1967 (Fig. 12). These small ponds contained developing tadpoles of Rana pretiosa and B. b. boreas, and

larvae of Ambystoma macrodactylum. The B. b. boreas tadpoles were observed to show the phenomenon known as scooping aggregations, which has been reported for spadefoot toads (Scaphiopus) by Bragg (1959, 1965). Small groups of 5 or 6 tadpoles were observed to burrow into and stir up the muddy bottom and presumably feed upon the materials so stirred. Further study is needed to verify this social aggregation in tadpoles of the boreal toad.

Newly hatched tadpole of the boreal toad were observed in a small spring near Canyon Ferry Reservoir, Broadwater Co., on 4 June 1966. On 9 August 1966, this same spring was again visited and the young toads were just leaving the water. Most still had remanents of a tail and were on the mud around the edges in the thick sedge (Carex sp.). It appears that metamorphosis occurs about two or three months after hatching in most parts of Montana.

The boreal toad was found to be active during the day as well as at night. Adults were collected diurnally along the Bitterroot and Clark Fork Rivers, a spring west of Harlowton, a meadow on Grass Mountain, along an irrigation ditch north of Divide, the tall grass along Red Rock Lake, and around Rainy Lake.

Adults were collected nocturnally around Whitefish Lake, crossing a dirt road near Libby, on the grassy banks along Echo Lake, a spring near Red Rock Lake, and on a lawn in Missoula.

Juvenile toads were found to be more active during the day than the larger and older toads. Adult toads were found to seek shelter during the day under logs, bark and in mossy crevices. Several adults were found under abandoned car doors and five gallon buckets.

Burger and Bragg (1947) reported on B. b. boreas from the Gothic

region of Colorado. They found that adults jumped into any nearby water, but very seldom dove beneath the surface or ventered far beyond the shallow water. They also found individuals of this toad easy to capture. Carpenter (1953) relates that B. b. boreas will readily hop into the water and dive to the bottom for security.

Observations of the boreal toad in Montana differed in several respects to reports of the species in Colorado. Adults and juveniles were found to jump readily into the water of lakes, streams and ponds whenever disturbed. In ponds, adults would dive immediately to the bottom and lie motionless for several minutes before coming to the surface. Toads would often swim some distance underwater before remaining on the bottom or coming to the surface on the opposite shore. A juvenile toad was collected swimming 200 yards from shore in Whitefish Lake. In a small stream west of Harlowton, about twenty toads were observed to jump from the grass into a fast moving stream and swim underwater for several feet and come up under an opposite bank or stay on the bottom where they attempted to hide.

Adults were often difficult to capture, especially at night. Around Whitefish Lake, adults were collected by walking in the dense forest until a toad was heard moving. They could move very fast through the trees and brush. Adults were found to hop or walk slowly when not disturbed, but could quicken the awkward hop or practically run when frightened.

Bufo cognatus Say

Great Plains Toad

Range:

The range of B. cognatus in Montana covers the eastern half of the state in the plains region (Fig. 2). The western Montana range limits are in Glacier, Pondera, Teton, Chouteau, Judith Basin, Wheatland, Big Timber, Stillwater, and Carbon Counties. Representatives of this species are probably found in all counties east of this western limit. This species has been seldom collected in northeastern Montana (Fig. 2) and this area in Montana is bounded by a lack of collection records to the north in southcentral Saskatchewan (F. R. Cook, pers. comm.) and extreme northwestern North Dakota (Wheeler, 1966). These areas where B. cognatus appears to be absent are difficult to explain but probably show where collectors have not been at the right time.

The Great Plains toad inhabits the short grass prairie of counties within its range in Montana.

Sexes:

The vocal sac, which is often hidden by a flap of light skin, is a definite characteristic of the male. Wright and Wright (1949) describe the vocal sac of the male as large and sausage-shaped when inflated. Deflated, the thin black colored skin is folded under an apron-like extension of the light colored skin of the throat.

The thumb and inner finger of males in the breeding season usually have brown nuptial pads. The sole tubercles on the front feet may also have brown nuptial pads.

Males of this species too, utter a series of soft chirping sounds when handled. The females do not chirp.

Females of the Great Plains toad slightly exceed the males in size.

Sizes:

Discussion of size in the Great Plains toad in Montana is based on 45 specimens. All measurements refer to snout-vent length. B. cognatus is a medium to large toad. The mean was 65.4 mm for males and 67.2 mm for females. The largest female was 85.0 mm from Toole Co. The largest male was 82.0 mm from Rosebud Co. The minimum size for a breeding male was 61.5 mm and the smallest breeding female was 64.7 mm.

Description:

A typical B. cognatus from Montana has the following characteristics which separates it from other bufonids in Montana:

The dorsal color is gray, light brown or olive green. Well defined dark blotches, usually in symmetrical pairs, are sharply outlined on the back (Fig. 6). These blotches are usually on either side of a faint vertebral stripe. The dark blotches contain many small warts and may be outlined with a narrow white line. All warts are small. The supraorbital and postorbital crests are well-developed. The supraorbital crests are divergent and separated at their posterior margins and extend diagonally forward to form a V with a bony elevation between and behind the nostrils (Fig. 13). Postorbital crests are complete and touch the parotoid glands. The interparotoid distance is greater than the interorbital distance. The parotoid glands are elevated, oval and set wide apart. The parotoid gland length is less than twice the parotoid gland width. Each metatarsal tubercle has a cutting edge. Toes are dark tipped. The

ventral surface is light and unspotted. Females are usually larger than males. Males have a vocal sac which forms a black apron on the throat. The sac is partly concealed by a flap of light skin.

Natural History:

Bragg's studies (1936, 1937, 1940a, 1940c, 1941) of B. cognatus in Oklahoma are the most significant in regards to the natural history of this species. His work will be discussed and applied to what little is known of the Great Plains toad in Montana.

The Great Plains toad is a species which characteristically breeds only in temporary rain-filled and rain-formed pools, fairly high in the prairies. Toads inhabiting cultivated areas often use flooded fields for breeding. They rarely breed in muddy ditches or any type of muddy water, but usually breed only in clear water. Bragg never found them breeding in relatively permanent pools, nor in artifically formed water-holes. This species breeds only after rain if the temperature is not too low. Breeding occurs from March to September in Oklahoma.

After rain, huge congresses of males develop at the most favorable places for securing females. Males usually call from edges of the pools and females sometimes congregate in other nearby pools before joining the males. Amplexus is pectoral and, as the female moves along the bottom, eggs are laid several hours later.

Breeding of this species in Montana has not been observed. Mosimann and Rabb (1952) collected 15 individuals at night on 18 and 20 July. Two of the three females contained well-developed eggs. All were collected in an artificial cattle pond on the prairie in Toole Co. This artificial cattle pond is an unusual breeding site for the Great Plains toad.

The Great Plains toad in Montana probably breeds from May to July after rain in clear, shallow pools. Breeding sites include temporary rain-filled or rain-formed pools and flooded fields. Other breeding behavior is probably similar to that described for the species in Oklahoma.

Bragg (op. cit.) and Bragg and Smith (1942, 1943) found that B. cognatus inhabits only grasslands in Oklahoma. It was found in higher portions of the prairies, and also in limited numbers along irrigation ditches and other similar low lying areas where sufficient moisture is available. Members of this species in Oklahoma migrate into cultivated fields and gardens, but they are uncommon species under streetlights.

Wheeler (1966) found that members of this species inhabit grasslands, usually living near streams or irrigation ditches in North Dakota. Wright and Wright (1949) list the habitat as grazing or agricultural lands of the Great Plains along ditches, floodplains of streams, and overflow bottom lands.

Collection records of the Great Plains toad in Montana indicate that members of this species are found primarily in the short grass prairie or undifferentiated grassland. This is the most widespread vegetational type in eastern Montana. Most of Montana's cultivated land is taken from the short grass prairie. The Great Plains toad has been collected in the short grass prairie of Toole, Chouteau, Yellowstone, Big Horn, Powder River and Custer Counties at elevations up to 4,000 feet.

The Great Plains toad has also been collected in Rosebud, Powder River and Carter Counties in the eastern ponderosa pine forest and savannah. This is a scattered forest type with open stands of ponderosa pine and many grass meadows. This is the transition type which is

neither pure forest nor pure grassland.

Many of the collections of the Great Plains toad come from the vicinities of streams and rivers in eastern Montana. Agricultural land is prominent in these areas and this should be included as a habitat of B. cognatus.

The Great Plains toad in Montana inhabits primarily the short grass prairie, but it is also found in the eastern ponderosa pine forests and savannah, and near streams and irrigated agricultural lands. This toad is uncommon near human habitations.

Bufo hemiophrys Cope

Dakota Toad

Range:

The Dakota toad is one of the few North American amphibians which has a range that extends into central Canada and is unique in having its range restricted to north-central North America. The range of B. hemiophrys in Canada, according to Cook (1964), includes eastern Alberta, north to the District of Mackenzie, southern Saskatchewan, and the southern half of Manitoba. It enters the United States in the vicinity of Glacier County, Montana, and extends east to northwestern Minnesota. Distribution in the United States includes northern Montana, North Dakota, south to Brooking County, South Dakota, and as far east as northwestern Minnesota. An isolated population is found in southeastern Wyoming along the Big and Little Laramie Rivers to about 15 miles north and 15 miles west of Laramie, Albany County, Wyoming (Stebbins, 1966).

Many problems are associated with the range of the Dakota toad within Montana and in southern Alberta and southwestern Saskatchewan. The Dakota toad has been collected near Brooks in Alberta, Gouverneur and Mankota in Saskatchewan, but none south and west to the Montana border. One old specimen from "Milk River" probably represents the nearest collection record to Montana (F. R. Cook, pers. comm.). Cope (1886) also reported on six specimens of B. hemiophrys from the northern boundary of Montana. Occurrence of members of this species within Montana was verified when two adults were collected one mile west of

Flaxville, Daniels Co., Montana, on 28 and 30 July 1966 (Black, 1967, 1968). This collection record and other habitat observations indicate that B. hemiophrys probably occurs in the northern part of Glacier, Toole, Liberty, Hill, Blaine, Phillips and Valley Counties; throughout Daniels and Sheridan Counties with a southern Montana limit in Roosevelt County (Fig. 3). The range of the Dakota toad in Montana lies within the area formerly covered with the Laurentide Ice Sheet.

Sexes:

Males can usually be distinguished from females by their dark colored throat and nuptial pads on the first two fingers during the breeding season. Females are larger than males and have more and rougher warts.

Sizes:

Maximum size for males is about 85.0 mm and for females 91.0 mm. Most adults are smaller and the usual range is 52-75 mm for females and slightly smaller for males. Females from Montana averaged 68.5 mm.

Description:

A typical B. hemiophrys from Montana has the following characteristics which separates it from other bufonids in Montana:

The average snout-vent length is 2-3 inches for adults. The dorsal color is brown to white with many brown warts. Most of the warts are set in black spots (Fig. 7). A cream or white vertebral stripe is prominent from the interorbital crests to the anus. The parotoid glands are long and not greatly elevated above the dorsal surface. Each eyelid contains a black bar or spot which may have one or more brown warts. The inter-

orbital crests may form a solid "boss" on the head, but there is usually a well developed groove between the parallel interorbital crests. The interorbital crests are nearly always joined across their posterior edges (Fig. 14). Postorbital crests are weakly developed or absent. The legs and feet contain black spots or bars over their total length. The tibia is covered with spiny warts. Both sole tubercles have a free cutting edge; the inner large, the outer small. The ventral surface is light brown to white with numerous black spots of various sizes. Males can usually be distinguished from females by their dark colored throat and nuptial pads on the thumb and inner fingers during the breeding season.

Natural History:

The natural history of the Dakota toad in Montana is totally unknown. Assumptions concerning the Montana populations will be drawn from work in Canada, Minnesota and South Dakota.

Breeding probably occurs anywhere from late April to early June in Montana, with the peak time starting with the first good rain. They are not dependent on rains for breeding but it has a definite effect on them (F. R. Cook, pers. comm.). Tester and Breckenridge (1964) found the peak of emergence took place about the middle of May in Minnesota. Both the time of the first emergence and the peak of emergence were dependent on rising temperature and/or precipitation.

After the breeding period in Minnesota, adults will be encountered most frequently along pond margins throughout their season of activity. Cook (pers. comm.) is of the opinion that members of this species wander from pond to pond the same as any other toad and are found some distance

from pond margins. Underhill (1962) reported that toads were always taken close to water in South Dakota.

Tester and Breckenridge (1964b) found that toads began to hibernate in late August or early September by moving to slight rises in ground level where they burrow to spend the winter. Toads were found to move vertically during the winter, apparently in response to decreasing soil temperature. It was also suggested that some burrow just enough to keep ahead of the frost line in the soil and follow the frost line back up for spring emergence.

The Dakota toad has been definitely collected only once in Montana. Two large females were collected around a five acre pond one mile west of Flaxville, Daniels Co., Montana, on 28 and 30 July 1966. This pond with relatively stable water level, was in a draw surrounded by the rolling prairie. The pond had gradually emerging shores with some mud flats, green grassy banks, and was surrounded by a broad belt of sedges, Carex sp. (Fig. 15). Other plants (Triglochin sp., Juncus sp., Scirpus sp. and Sagittaria sp.) were around the muddy edge, while Hippurus vulgaris formed floating mats over most of the pond. The Dakota toads were collected in the muddy sedge and bullrush belt and tried to escape by running through the bullrushes. Local people reported that this pond supported numerous toads in the spring. Ambystoma tigrinum and Rana pipiens were also collected in the same pond.

This general area of Montana is dominated by a fairly uniform group of grasses including western wheat grass, needle-and-thread, sandburg blue grass and blue stem. This type of area is often called short grass prairie or undifferentiated grassland.

The short grass prairie is common throughout eastern Montana. A belt of short grass prairie is continuous from the Flaxville area directly south to the southern border of Montana. Observations showed scattered ponds throughout this area which were much like the pond habitat described for B. hemiophrys. This short grass prairie region in Montana lies directly north of the isolated population of B. hemiophrys in Wyoming. This raises and interesting problem. Is the population in Wyoming a relict or are there scattered or continuous populations in the valleys through Montana to Wyoming? Habitat observations in Montana lend support to the idea that B. hemiophrys may be collected farther south.

Bufo woodhousei woodhousei Girard

Rocky Mountain Toad

Range:

The range of the Rocky Mountain toad in Montana lies east and south of the Continental Divide (Fig. 4). Its northern range boundary appears to be slightly north of the Missouri River where it may enter Roosevelt, Valley, Phillips, Blaine and Chouteau Counties. Its range then goes south through Judith Basin and Wheatland Counties and west to Gallatin County where it may continue to the Idaho border. This toad is found south of the Missouri River in Richland, McCone, Dawson, Wibaux, Fallon, Carter, Powder River, Custer, Prairie, Garfield, Rosebud, Big Horn, Treasure, Fergus, Musselshell, Yellowstone, Petroleum, Golden Valley, Wheatland, Stillwater, Carbon, Sweet Grass, Park and Gallatin Counties. Members of this subspecies have not been collected west of Gallatin Co. in Montana, but the habitat is such that they should occur in Madison and Beaverhead Counties. The Rocky Mountain toad is probably the most versatile and wide ranging of Montana toads in its distribution.

Sexes:

The throat of males is black from the angle of the mouth forward. The black throat color may be speckled with small dots of white or light brown. The black throat and brown nuptial pads on the thumb and inner fingers are more pronounced during the breeding season.

Males when grasped behind the forelegs or simply handled will usually utter a "protesting" chirp. Females do not usually protest when handled.

Underhill (1961) found that females had a significantly greater number of dorsal spots than did males in South Dakota. This was found to be true in most of the specimens from Montana.

Sizes:

Data on size range in adults of B. w. woodhousei from Montana is based on examination of 150 specimens. All measurements refer to snout-vent length. The mean was 67.5 mm for males and 71.2 mm for females. The mode was 74.0 mm for females and 67.0 mm for males. The majority of the female specimens was in the 70-80 mm size range, while most males were in the 60-70 mm size range. The largest female was 97.8 mm. She was from Sweet Grass County. The largest male was 82.9 mm. He was from Gallatin County. The minimum size for a breeding male was 54.0 mm and the smallest breeding female was 66.8 mm.

Bragg (1950) found that the average male in Oklahoma was 78.2 mm and the average female was 88.8 mm. The largest specimen was 126.0 mm from Kay County, Oklahoma. Underhill (1960) found the minimum size for breeding males was 55.8mm, while the smallest breeding female was 67.3 mm in South Dakota.

From available specimens it appears that the Rocky Mountain toads in Montana are smaller on the average than those of its species further eastward and southward.

Description:

Most adult Rocky Mountain toads can be distinguished by the following characteristics:

The average snout-vent length for adults is 2-3½ inches. The dorsal color is brown or olive green and some are light gray (Fig. 8). Small

light brown warts cover the dorsal surface. Warts are often set in small black spots which may be ringed with a narrow white line. These black spots usually contain only one or two warts, but they may be larger and contain many warts. The vertebral stripe is white and continuous from between the interorbital crests to the anus. The parotoid glands are long, narrow and elevated. There is a black or white spot on each eyelid with one to two warts. The interorbital crests are prominent and parallel or nearly so. Cranial crest variation is only in the supraorbital crests, while the postorbital crests seem uniform. The supraorbital crests may be parallel, slightly divergent, or have a shiny, thin bony area between the parallel or divergent supraorbital crests (Fig. 17, 18, 19). The postorbital crests are well developed and in contact with the parotoid glands. Sole tubercles are brown and the inner has a sharpened edge. Toes are dark brown tipped. The ventral surface is unspotted except for a single black chest spot, but this is often broken up into two, three or a cluster of smaller spots. The chest spot is not always present. Young toads are spotted dorsally in two colors on a grayish background. The larger spots are dark colored, while the smaller are tiny and red. Males can be distinguished from females by their dark throat and nuptial pads on the thumb and inner fingers during the breeding season.

Natural History:

The natural history of the Rocky Mountain toad has been studied extensively in several parts of the United States, but nothing is known about it in Montana.

Bragg (1940b) has found that males of the Rocky Mountain toad become sexually active in quite dry weather and will seek females wherever they

can find water from which to call. Most breeding occurred after spring and summer rains, provided the temperature was not too low. Males called vigorously after rains of one inch or more at any time from March to August in Oklahoma. Fishbeck and Underhill (1960) found that B. w. woodhousei in South Dakota breeds in late April and early May. Thus, the Rocky Mountain toad has a definite breeding season, but breeding activities can be staggered throughout the warm months.

These toads breed in a great number of places such as ditches, flooded fields, backwashes of streams, cattle tanks, or wherever there is shallow, standing, or slightly moving water. Bragg and Smith (1942) found that this toad seems to prefer muddy water in breeding sites.

In Montana, breeding groups have been collected on 4 May near Glendive; near Medicine Rocks on 25 May; at Ekalaka on 29 May and on 16 June near Powderville. In all breeding groups the males largely outnumbered the females. Bragg (1940b) and Underhill (1960) have both reported that males usually appear at breeding sites several days before females begin entering the ponds, and also stay longer at the breeding sites. This could account for the large proportion of males collected at breeding sites in eastern Montana.

A rather unusual breeding situation was observed on Bug Creek near Ft. Peck Reservoir on 1 July 1966. Two adults were found in amplexus in a tumbleweed below a rock ledge. Other toads were active on this day after a warm night rain. The above pair rolled down a steep bank about 50 yards above Bug Creek, which was running slow, muddy water, before coming apart.

Most Rocky Mountain toad breeding occurs in Montana from May to April, with scattered activity to August. Adults prefer waters of streams and

rivers, irrigation ditches or other places where shallow or slightly moving water is present for breeding sites.

Many of the streams in the eastern Montana range of B. w. woodhousei dry up during the hot summers except for isolated pools in the dry creek beds. Around these pools congregate large numbers of amphibians and their reptile predators. The Rocky Mountain toad appears to use these pools for breeding as numerous young toads were collected around them during the summer.

Bragg (1940a, 1940b) in Oklahoma found that as young toads come from pools after metamorphosis, they take advantage of the moist area surrounding the pool. Even in very hot weather many of them remain active throughout the day. This seems to be the case in parts of eastern Montana.

Numerous young toads from 15.5 mm to 22.8 mm were collected during the day around small pools 4 miles northwest of Terry on 7 August 1966. The day was cloudy and rainy with a temperature of 19.0°C. More young toads were collected around scattered pools in dry Moon Creek, 14 miles west of Miles City on 8 August 1966 (Fig. 16).

These juvenile Rocky Mountain toads were numerous and active around small to large isolated water holes in the dry creek beds. Most were in Juncus sp. along the edges and would hop from the Juncus through the mud to water where they would swim. Numerous deep cattle tracks in the mud seemed to prove an obstacle when toads would fall into them. Often they were unable to escape from the deeper tracks. Toads not around the water holes were found under rocks in the dry creek bed. The ground was always wet under the rocks where young toads were found. Five or six juvenile toads would often be found under one flat rock. The larger toads of 27.8

mm or larger were found some distance from water in the dry creek bed under flat rocks or moving up the creek banks.

This type of habitat in eastern Montana is confined to long narrow ribbons along streams. Deciduous trees such as cottonwoods and willows occur along the creeks. As the ground rises away from the streams, the short grass prairie quickly takes over. The juvenile toads were collected in drainages running into the Yellowstone River. Some of the dry creek bottoms were surrounded by rimrocks, sagebrush and juniper. The soil tends to be sandy.

Adults of the Rocky Mountain toad are not restricted so closely to water and are less diurnal than the juveniles. Bragg and Smith (1943) and Bragg (1940b) found that B. w. woodhousei is diurnal more often than the other toads in Oklahoma and emerge to feed later at night as they increase in size. They also reported them common about street lights and human habitations.

Adults were collected diurnally as well as nocturnally in Montana. A female toad of 50.4 mm was collected in an irrigated garden inside the city limits of Custer during the day on 30 June 1966. Two small females were collected at night in the public campground of Glendive on 28 June 1966. The first was collected at 9:00 P.M. under a streetlight at the edge of the campground. It quickly tried to escape under a pile of rocks near the streetlight. The second specimen was found moving towards the streetlight in the gravel road which wound among tents and campers. The day had been extremely hot. The Glendive campground lies parallel to the Yellowstone River. Thus the Rocky Mountain toad is also common around human habitations in Montana.

Habitat preferences of the Rocky Mountain toad are very diverse throughout its range. Bragg (1940b) found that B. w. woodhousei is partial to wooded bottomlands and is the only toad occupying the sandy expanses of the flood plains of the larger streams in the central part of Oklahoma. Fishbeck and Underhill (1960) give the habitat of B. w. woodhousei in South Dakota as common in the floodplains of the Missouri River and its tributaries. Wright and Wright (1949) list the habitat as being very diverse.

Comparison of a distribution map of B. w. woodhousei from Montana with maps of vegetation and forest types from Helburn, Edie and Lightfoot (1962) shows this diversity of members of the subspecies in choice of habitat. Most collection records are from non-forested areas in eastern Montana. A few records appear in the eastern ponderosa pine forest and savannah. These are areas of scattered stands of ponderosa pine with grass meadows among the trees. The eastern ponderosa pine forest and savannah is generally in patches of rough country from the breaks along the Missouri River in central Montana southeast to the Wyoming border.

Vegetation habitat of the Rocky Mountain toad is primarily confined to the floodplains of the larger rivers such as the Missouri and Yellowstone Rivers. It is probably replaced by B. cognatus in the uplands. The short grass prairie, Prairie County grassland, foothill grassland and sagebrush, undifferentiated stream bottoms, intermountain valleys, and grassland and meadows all constitute the vegetation habitat of the Rocky Mountain toad in Montana.

The habitat of the Rocky Mountain toad in Gallatin County is unusual for members of this subspecies. According to Dr. C. V. Davis, Montana

State University, this toad has been collected on the south slope of Blackmore Peak in August at an elevation of approximately 7,000 feet. There was a slight trace of snow in sheltered areas. Dr. Davis also collected the Rocky Mountain toad near Rat Lake and Squaw Creek in the Gallatin Range. This was in June and specimens of B. w. woodhousei were common along the trail between 5,000 and 6,000 feet of elevation. Snow was still present. B. b. boreas is also found at this elevation and is common in the Gallatin Valley where B. w. woodhousei should occur, but has not been collected. Further study is needed on this unusual habitat of B. w. woodhousei.

DISCUSSION

The Pacific Northwest of the United States, with its varied physiography, climatic, glacial and vegetational history, presents a large number of zoogeographical problems in the family Bufonidae.

In the simplest classification, Montana is divided into two vegetation and physiographic regions. The first, intermontane Montana, includes the western third of Montana which is characterized by the Rocky Mountain front, many mountain ranges and by intermontane valleys or basins, parts of which are 10-15 miles in width. The second, the plains region, is found in the eastern two-thirds of Montana and is characterized by rolling short grass prairie which is dissected by several large rivers and small streams of the intermittent type. Intermontane Montana is separated from parts of the plains region by the Rocky Mountain front which in general rises abruptly from the short grass prairie in the east. West of this front are peaks rising to elevations of 9,000 to 10,000 feet in Glacier National Park and 11,000 to 13,000 feet or more in the rugged region north and east of Yellowstone National Park. The lowest passes between the two regions occur above 5,000 feet. In intermontane Montana, very few streams are of the intermittent type. In this area, 24,700 square miles are drained by the Missouri River, 500 square miles drain to the Hudson Bay, and about 25,000 square miles are drained to the Columbia River. Coniferous forests cover large areas on the mountain slopes. In the valleys pines and firs share the wet valley floors with meadows and the deciduous trees of the riparian forests.

The plains region is usually classified as short grass prairie and is largely non-forested except for riparian forests which occur on the floodplains and slopes of the major drainages. North of the Missouri River, glaciation has smoothed the surface leaving glacial potholes and swales which may have water. There are isolated low mountain groups in the plains region, most of which were glaciated, which now stand in sharp contrast to the flat and rolling plains which surround them.

According to Alden (1932, 1953), Flint (1957) and Antevs (1948) the latest glaciation in North America is represented by the classical Wisconsin drift in the central region and by a correlative drift in the Cordilleran region which was laid down in the Pleistocene. The Cordilleran Glacier Complex was a network of glaciers which occupied the mountains of western North America. The drift formed by the Laurentide Ice Sheet is spread over North America from Newfoundland to the Rocky Mountains. The drift formed by the Cordilleran Glacier Complex occurs on the eastern slope of the Rocky Mountains where the glaciers coalesced at some points with the Laurentide Ice Sheet.

During the Wisconsin and earlier stages of the Pleistocene in Montana there was probably an extensive ice cap covering most of the Yellowstone Park plateau and the Absaroka Range and the Beartooth Mountains to the north and northeast. Farther north, northwest and west in the region between Yellowstone Park, the Idaho-Montana border and the Canadian border there were many local glaciers. Some of these glaciers were very large and were headed on the upper slopes of the highest mountain ranges both east and west of the Rocky Mountain front. None, however advanced far from their source.

In the interior of Glacier National Park several features of possible biogeographic importance are found. A high level sloping bench occurs above the Glacier Wall between Heavens Peak to the west and the big bend on McDonald Creek. Another known as Granite Park is located between the McDonald Creek Valley and the rugged mountain crest north and south of Swiftcurrent Pass. The elevation of these smooth, high-level benchlands is between 6,500 and 7,000 feet. Another, an inter-stream and interlake ridge, is in the western part of the broad trough drained by the Flathead River. The fact that these three ridges are well preserved today is probably due to their having been somewhat protected from stream and glacial erosion by their positions between the valley of the North Fork of the Flathead River and that of McDonald Creek where the main glaciation occurred, or between the latter and the Continental Divide of the Rocky Mountain front and where the greatest water erosion occurs today.

These three ridges could have remained unglaciated during the Wisconsin time and therfore could have acted as refugia for animals and plants and the surrounding glaciers acted as barriers to gene flow.

In eastern Montana during the Pleistocene the Laurentide Ice Sheet of the Wisconsin stage of glaciation advanced into Montana from the northeast and diverted the Missouri River from the north to the south side of the Bearpaw and Little Rocky Mountains. This ice sheet reached the mountains just north of the eastern edge of Glacier National Park and extended southwestward nearly to Great Falls and also diverted the Missouri River there.

On the eastern edge of Glacier National Park there was a glacier in the St. Mary's valley. Here there is a ridge on the west side of Lower

St. Mary Lake which is broad and smooth. There is no indication of the upper limit reached by the St. Mary Glacier on this ridge. A bench on it, nearly 1,500 feet above Swiftcurrent Creek on the south and 800 feet above the South Fork of Kennedy Creek on the north, appears to be non-glaciated and could have also acted as a refugia. At the Wisconsin glacial maximum the Laurentide and the Piedmont glaciers and permanent snow probably covered most of western Montana and the area north of the Missouri River in eastern Montana.

The distribution of the bufonids in Montana can be related to the glacial history and the present topography of the state.

During the Pleistocene the boreal toad, B. b. boreas, must have been associated with the short thermal summer conditions found along the piedmont and continental glacial margins in western Montana and perhaps those east of the Rocky Mountain front. This toad could have survived the Pleistocene glaciation around the margins of glacial Lake Missoula west of the Rocky Mountains. Dr. Philip C. Dumas, Central Washington State College, Ellensburg, Washington, has suggested a general hypothesis which he found probably holds true for Rana pipiens and B. woodhousei in Washington, Oregon and Idaho. This hypothesis suggests that the longer a frog or toad has been in a particular area, the farther it has invaded the surrounding mountain ranges. He suggested that this hypothesis should be limited to problems of direction of migration or migration routes and that one needs to know that the species is capable of existing at higher altitudes than are now obtained in the general region and to know that lack of time for spread is the cause of non-occupancy and not some other limiting factor.

The boreal toad has been collected at recorded elevations of over 9,500 feet northwest of Dillon in Beaverhead County which is east and south of the Rocky Mountains. West of the Rocky Mountains in western Montana, this species has only been collected up to elevations of 7,200 feet in Sanders County with most collection records from elevations of 3,000 to 5,000 feet. Overgeneralizing with Dumas's thesis, this might indicate that the boreal toad has occupied the area east and south of the Rocky Mountains for a longer period of time and reinvaded western Montana through east-central Idaho.

The Rocky Mountain toad, B. w. woodhousei, and the Great Plains toad, B. cognatus, must have occurred during the Pleistocene east of the Rocky Mountains and south of the Laurentide Ice Sheet. These species were probably not periglacial toads but occurred farther south.

The Dakota toad, B. hemiophrys, was probably a periglacial form which occupied a range along the southern border of glaciation from Montana to Wyoming where a relict population is now found on the Laramie Plateau. This species has probably been in Montana since glaciation, but could have moved north in the xeric period between glaciation and the present, and then again moved south into Montana. The Rocky Mountain toad, B. w. woodhousei, could also have moved north and was then pushed south again by changing conditions and the re-invading B. hemiophrys.

On the slopes of the Rocky Mountains perhaps on the bench above Glacier Wall, the bench at Granite Park or the interlake ridge northwest of Lake McDonald, the canorus-like form of B. b. boreas was able to survive the Pleistocene glaciation. Calder and Savile (1959) have shown an analogous situation for a plant of the variety septentrionalis

of the Heuchera cylindrica complex which seems to have been isolated on the eastern slopes of Glacier National Park during the last stages of Pleistocene glaciation and to have spread northward from there as the ice retreated. Karlstrom (1962) suggested that B. canorus in California is a montane differentiate of an ancestral boreas-like form which became isolated in or near its present range in the Sierra Nevada. This same possibility exists for the canorus-like toad at high elevations in Glacier National Park. Unglaciated refugees, several probably suitable for habitation by toads, existed at intermediate elevations in Glacier National Park. In this geographic isolation, the canorus-like toad could have evolved and later extended its range to where it is now found in Glacier National Park.

After the ice withdrawal about 10,000 years ago climatic conditions rapidly changed. Temperatures rose, or rainfall decreased markedly or both. Average yearly temperatures were probably 1-2°C. higher than at present. This period has been termed the altithermal period and the hypothermal period by Antevs (1948). With retreat of adverse conditions in western Montana and north of the Missouri River in eastern Montana, the bufonid members were able to reinvade the glaciated areas of Montana.

The boreal toad reinvaded western Montana from the non-glaciated areas around the margins of glacial Lake Missoula or from east of the Continental Divide through Beaverhead County from east-central Idaho.

The Rocky Mountain toad and the Great Plains toad probably reinvaded Montana from the south. Both species have moved northward within Montana. The Great Plains toad was probably able to survive and reinvade its present range at an earlier stage by following the edge of the mountains in the montane zone which accounts for its occurrence now in Canada.

B. cognatus has no northern competitors (unless B. hemiophrys which seems doubtful now) but B. w. woodhousei presumably competes with B. hemiophrys which would slow its spread even if it and B. cognatus survived as contemporaries.

The Dakota toad probably moved northward from the southern border of glaciation during this xeric period and was eliminated from periglacial areas on the east flanks of the Rocky Mountains except for the relict population in Wyoming. Its present range in Montana is within those areas which were formerly covered by glaciation. This suggests that the habitat of glacial potholes and ponds created by the glaciation are very favorable for the Dakota toad and they are able to withstand competition there from other bufonid species.

The altithermal period was followed by a cooler more moist period termed the hypothermal by Antevs (1948). Yearly temperature averages were then about 1-2°C. lower than now. This caused an increase of moisture in the low passes across the Rocky Mountains which probably permitted increase in range or crossing of the Rocky Mountains by bufonids.

The lower tolerance of adults of B. b. boreas to high temperatures would probably prevent this species from occurring in the warmer plains region of Montana but allow it to occur throughout intermontane Montana. Competition with B. w. woodhousei, B. cognatus and B. hemiophrys which have a higher tolerance to high temperatures might also limit its range in the plains region.

Adults of B. w. woodhousei in the floodplains and of B. cognatus in the uplands of the plains region have less tolerance to low temperatures which would prevent them from inhabiting intermontane Montana. Compe-

tition with B. hemiophrys in the north and B. b. boreas in the west perhaps also has some affect on their present ranges.

Adults of B. hemiophrys were found by Schmid (1965) to have a lower tolerance to high temperatures than adults of B. cognatus. The temperature factor, plus competition with B. w. woodhousei near the Missouri River, probably accounts for the Dakota toad's occupying its present range north of the Missouri River in the areas formerly covered by the Laurentide Ice Sheet.

The situation of B. b. boreas and the canorus-like form of B. b. boreas in Glacier National Park can only be postulated at present. It appears that B. b. boreas is reinvading elevationally the mountains to approach the habitat at 6,000 feet elevation of the canorus-like form. The canorus-like form probably has not migrated to any extent during the post-Pleistocene because of barriers formed by lower elevations, temperature, moisture and habitat cover of the available migration routes. The occurrence of this toad at such high elevations where adverse weather conditions exist, indicate that it is a species which is tolerant to this habitat and that it therefore has been present in this region for some time.

The simplest explanation of bufonid distribution in Montana would be as follows: B. hemiophrys and B. b. boreas were periglacial toads. The former in the plains region and the latter in intermontane Montana. With warming and drying in post-glacial times and especially with the approach of the altithermal, these periglacial toads withdrew northward to higher latitudes. This vacant region east of the Rocky Mountains was invaded from the south and east by B. w. woodhousei and B. cognatus. Some interspecific competition may have been involved but this can only

be postulated. The canorus-like form of B. b. boreas may be a Wisconsin isolate of an ancestral boreas-like toad which became isolated in or near its present range in Glacier National Park and is an example of altitude convergency in very small populations.

SUMMARY

1. The boreal toad, Bufo boreas boreas, is found throughout intermontane Montana. It may also occur on the isolated low mountain groups in the plains region. This toad breeds from March to June in Montana and uses any body of water without a strong current. Preferred habitat is moist areas near water.

2. A variation in the typical boreal toad is found at several high elevations in Glacier National Park. This toad resembles Bufo canorus of the Sierra Nevada in California. This canorus-like toad is found in the high meadows.

3. The Great Plains toad, Bufo cognatus, has an extensive distribution in the short grass prairie of eastern Montana. Breeding occurs only after rain and in clear shallow pools. The Great Plains toad prefers the higher portions of the short grass prairie.

4. The Dakota toad, Bufo hemiophrys, has a range within the area formerly covered with the Laurentide Ice Sheet in northern Montana east of the Rocky Mountains. These toads will be encountered most frequently along pond margins throughout their season of activity.

5. The Rocky Mountain toad, Bufo woodhousei woodhousei, is the most versatile and wide ranging of Montana toads in its distribution. Its range lies east and south of the Continental Divide. Breeding occurs from late April to August depending upon spring and summer rains. This is primarily a toad of the floodplains of eastern Montana.

6. A simple explanation of bufonid distribution in Montana is as follows: B. hemiophrys and B. b. boreas were periglacial toads. The

former in the plains region and the latter in intermontane Montana. With warming and drying in post-glacial times and especially with the approach of the altithermal, these periglacial toads withdrew northward to higher latitudes. This vacant region east of the Rocky Mountains was invaded from the south and east by B. w. woodhousei and B. cognatus. Some interspecific competition may have been involved but this can be only postulated. The canorus-like form of B. b. boreas may be a Wisconsin isolate of an ancestral boreas-like toad which became isolated in or near its present range in Glacier National Park and is an example of altitude convergency in very small populations.

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FIGURES

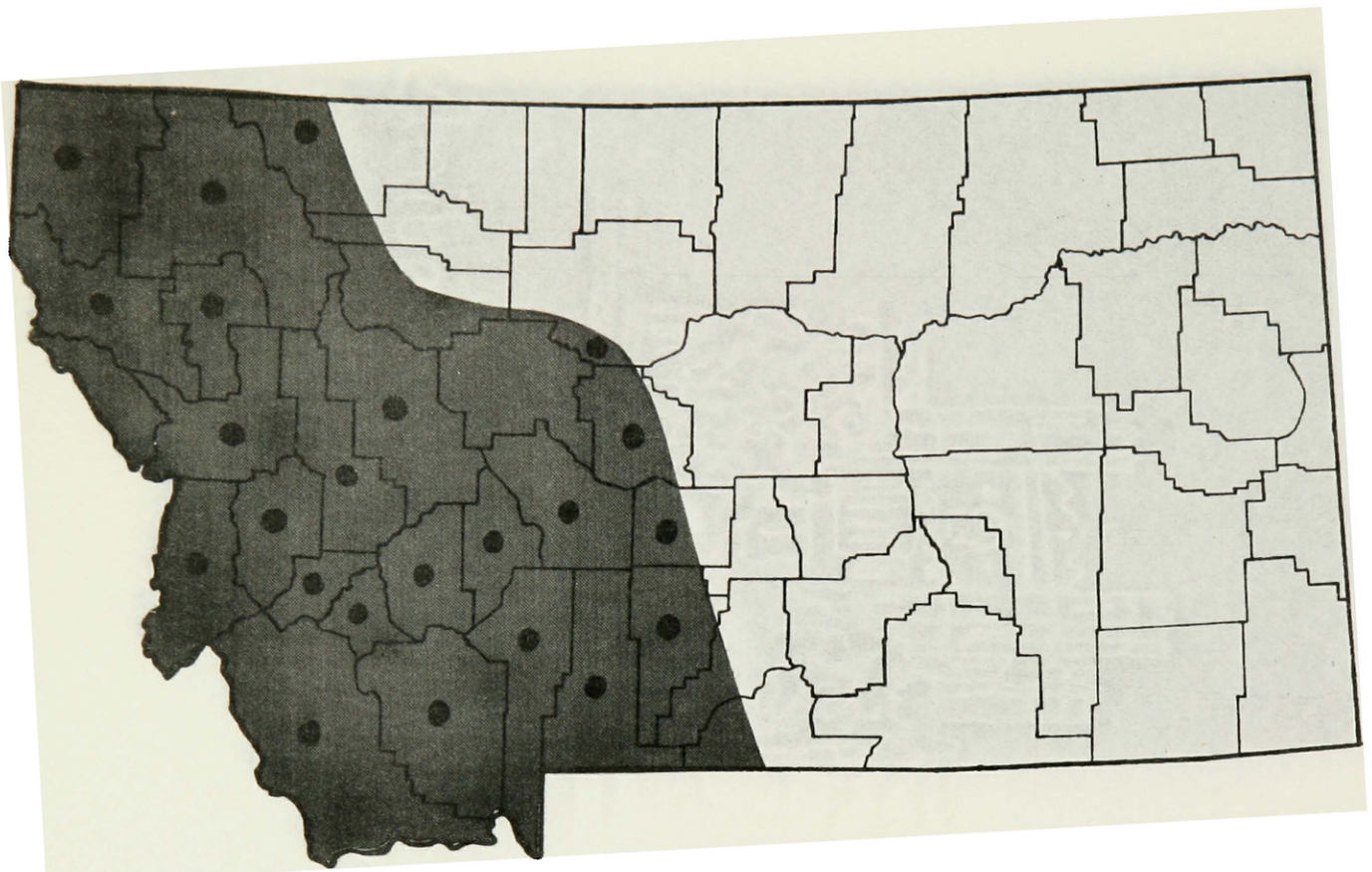

Figure 1. Shaded portion of map shows general distribution of the boreal toad, B. b. boreas, in Montana. A black dot indicates a county where this subspecies has been collected.

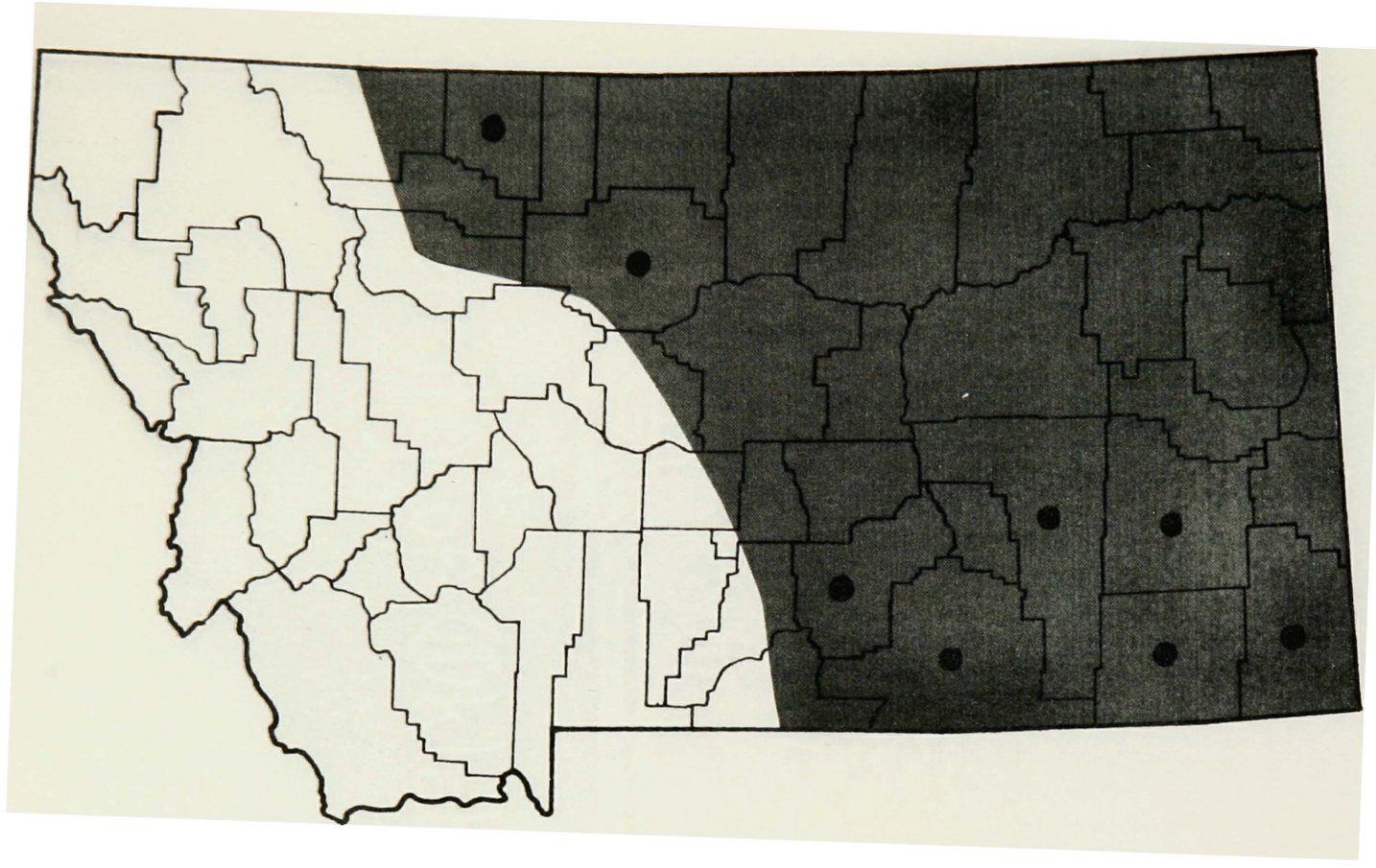

Figure 2. Shaded portion of map shows general distribution of the Great Plains toad, B. cognatus, in Montana. A black dot indicates a county where this species has been collected.

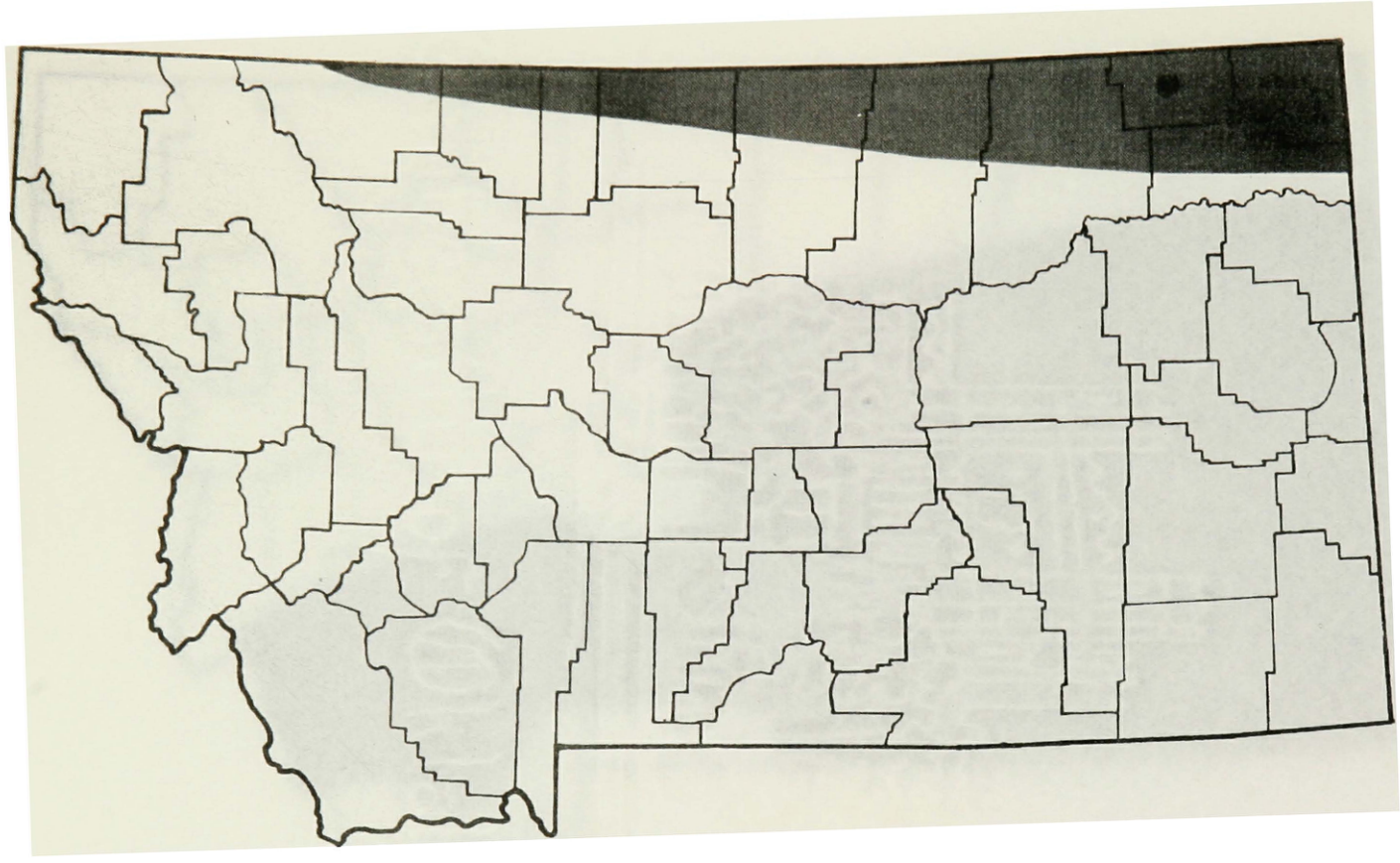

Figure 3. Shaded portion of map shows general distribution of the Dakota toad, B. hemiophrys, in Montana. A black dot indicates a county where this species has been collected.

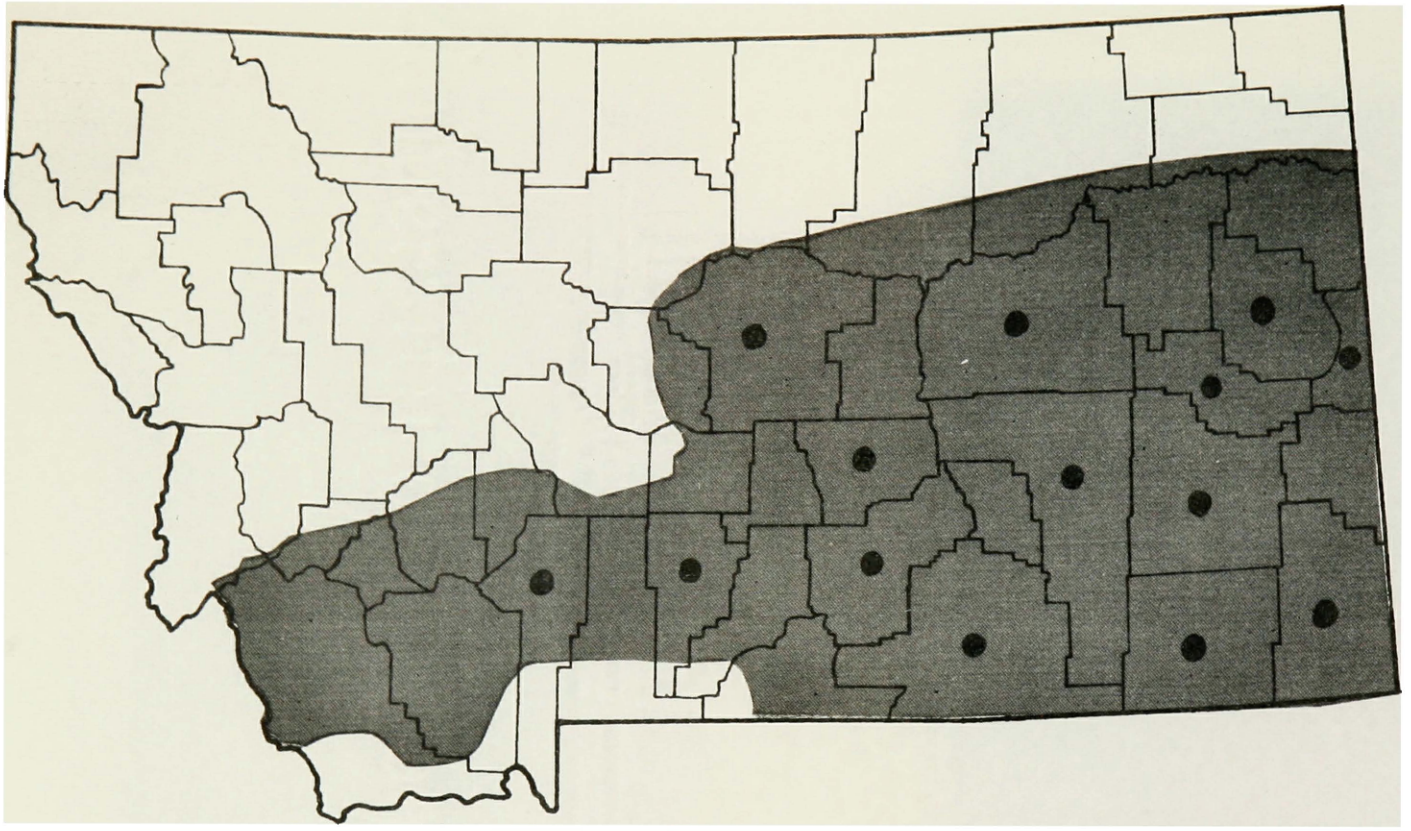

Figure 4. Shaded portion of map shows general distribution of the Rocky Mountain toad, B. w. woodhousei, in Montana. A black dot indicates a county where this subspecies has been collected.

Figure 5. Boreal toad, Bufo boreas boreas. Note the large warts on the dorsal surface and the large wart on the tibia. Interorbital and postorbital crests are not present in this species.

Figure 6. Female Great Plains toad, Bufo cognatus. Note the well defined dark blotches in symmetrical pairs on the dorsal surface.

Figure 5

Figure 6

Figure 7. Dakota toad, Bufo hemiophrys. Adult female collected one mile west of Flaxville, Daniels County, Montana. Light color phase showing most of the external characteristics of the species.

Figure 8. Rocky Mountain toad, Bufo woodhousei woodhousei. Adult female collected on Bug Creek near Ft. Peck Reservoir, Garfield County, Montana. This female shows the normal coloration and other characteristics which are typical of this subspecies in Montana.

Figure 7

Figure 8

Figure 9. Pond used for breeding by the boreal toad, B. b. boreas. This pond is located 8 miles southeast of Hamilton, Ravalli County, Montana. Breeding behavior was observed in this pond during the spring of 1967.

Figure 10. A male boreal toad at the breeding pond 8 miles southeast of Hamilton, Ravalli Co., Montana. This is the typical waiting position of a male along the shallow shore.

Figure 9

Figure 10

Figure 11. Male boreal toad and eggs of the boreal toad at the breeding pond 8 miles southeast of Hamilton, Ravalli Co., Montana. The eggs have been laid in the shallow water near shore.

Figure 12. Breeding site of the boreal toad on the side of Mt. Jumbo, Missoula County, Montana.

Figure 11

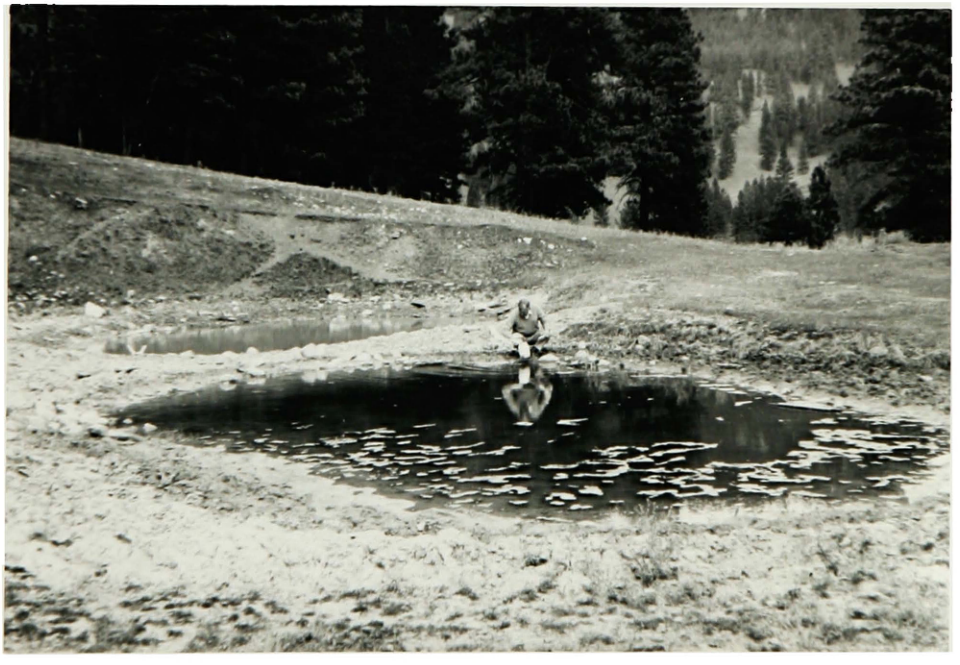

Figure 12

Figure 13. Adult female B. cognatus from Powder River County, Montana. Note the supraorbital and postorbital crests which are well developed. The supraorbital crests are divergent and separated at their posterior margins and extend diagonally forward to form a V with the bony elevation between and behind the nostrils. Postorbital crests are complete and touch the parotoid glands.

Figure 14. Cranial crest and parotoid gland development in an adult female B. hemiophrys from Montana. The supraorbital crests are joined at their posterior margins. Note the groove between the elevated and parallel supraorbital crests. Postorbital crests are absent.

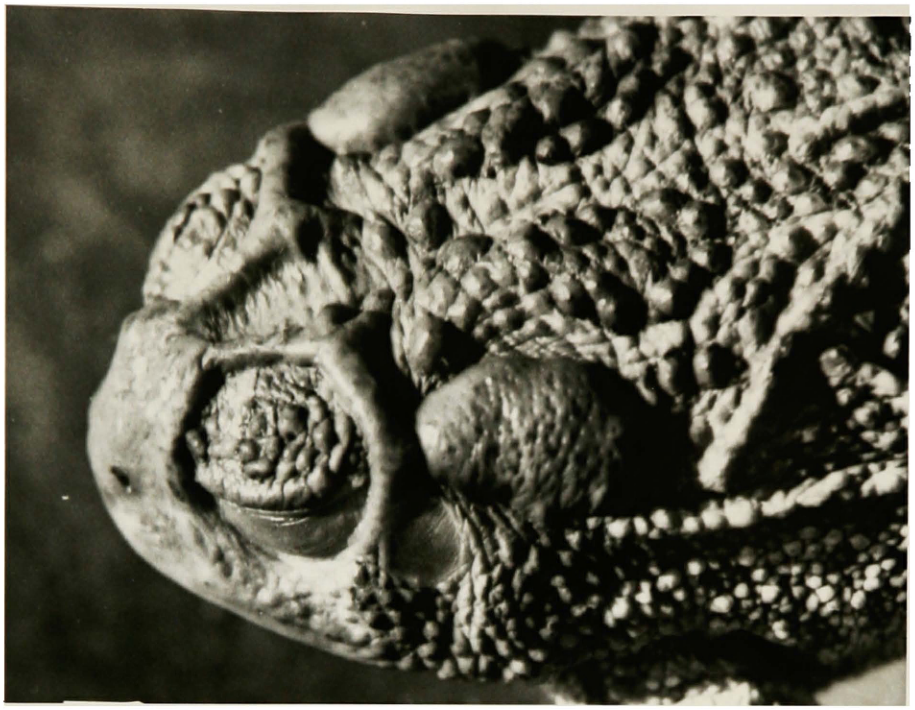

Figure 13

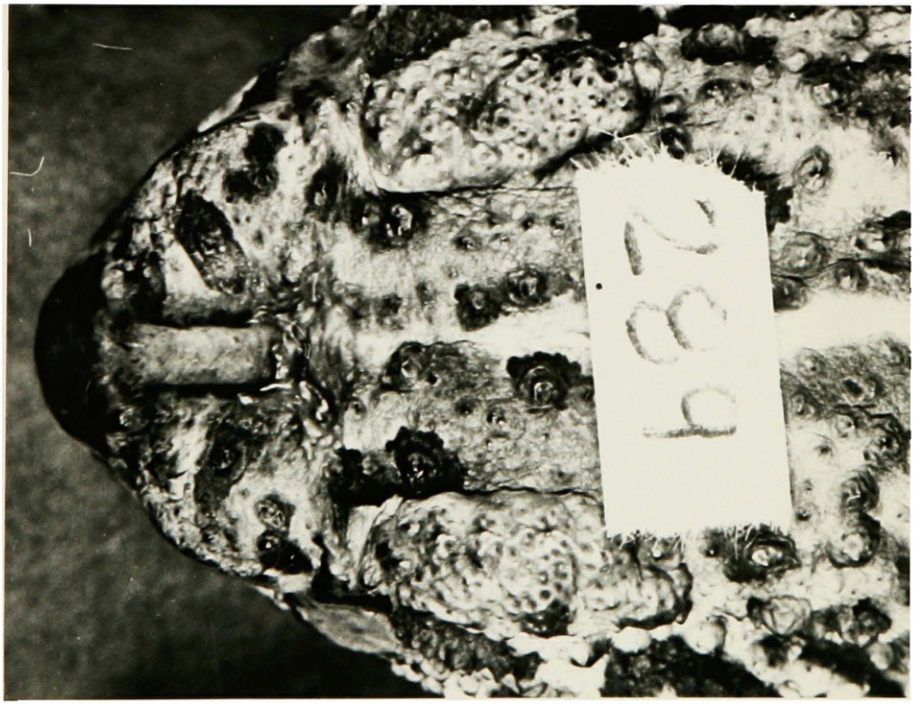

Figure 14

Figure 15. Habitat of B. hemiophrys, one mile west of Flaxville, Daniels Co., Montana. Two adult females were collected in the Carex and Scirpus along the edge of the pond. The rolling short grass prairie is shown in the background.

Figure 16. Habitat of juvenile Rocky Mountain toads, B. w. woodhousei, on Moon Creek which is 14 miles west of Miles City, Montana. On 8 August 1966, numerous juvenile toads from 15.5 mm to 27.8 mm were collected in small isolated pools of water in the dry creek bed.

Figure 15

Figure 16

Figure 17. Cranial crest development in a Rocky Mountain toad from Garfield County, Montana. Note the parallel supraorbital crests and well developed postorbital crests which touch the parotoid glands. The white vertebral stripe is evident between the supraorbital crests.

Figure 18. Cranial crest development in a Rocky Mountain toad from Montana. Note the slightly divergent supraorbital crests with a shiny bony area between them. There is also the absence of the vertebral stripe between the supraorbital crests.

Figure 17

Figure 18

Figure 19. Cranial crest development in a Rocky Mountain toad from Montana. Note the slightly divergent supraorbital crests without the bony area between them. The vertebral stripe extends between the supraorbital crests.

Figure 19

Figure 19. Cranial crest development in a Rocky Mountain toad from Montana. Note the slightly divergent supraorbital crests without the bony area between them. The vertebral stripe extends between the supraorbital crests.

Figure 19