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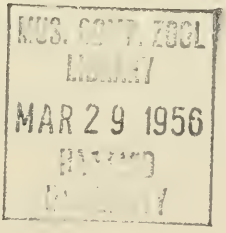

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A FIELD STUDY OF THE KANSAS ANT-EATING FROG, GASTROPHRYNE OLIVACEA

By

Henry S. Fitch

INTRODUCTION

The ant-eating frog is one of the smallest species of vertebrates on the University of Kansas Natural History Reservation, but individually it is one of the most numerous. The species is important in the over-all ecology; its biomass often exceeds that of larger species of vertebrates. Because of secretive and subterranean habits, however, its abundance and effects on community associates are largely obscured.

The Reservation, where my field study was made, is the most northeastern section in Douglas County, Kansas, and is approximately 5½ miles north and 2½ miles east of the University campus at Lawrence. The locality represents one of the northernmost occurrences of the species, genus, and family. The family Microhylidae is a large one, and most of its representatives are specialized for a subterranean existence and a diet of termites or ants. The many subfamilies of microhylids all have distributions centering in the regions bordering the Indian Ocean, from South Africa and Madagascar to the East Indies, New Guinea, and Australia (Parker, 1934). Only one subfamily, the Microhylinae, is represented in the New World, where it has some 17 genera (de Carvalho, 1954) nearly all of which are tropical. *G. olivacea*, extending north into extreme southern Nebraska (Loomis, 1945: 211), ranges farther north than any other American species. In the Old World only *Kaloula borealis* has a comparable northward distribution. Occurring in the vicinity of Peiping (Pope, 1931: 587), it reaches approximately the same latitude as does *Gastrophryne* in Nebraska. The great majority of microhylid genera and species are confined to the tropics.

Nearly all ant-eating frogs seen on the Reservation have been caught and examined and individually marked. By November 1, 1954, 1215 individuals had been recorded with a total of 1472 captures. In the summer of 1950, Richard Freiburg studied this frog on the Reservation and his findings (1951) led to a better under-

standing of its natural history. The numbers of frogs studied by him however, were relatively small and the field work was limited to the one summer. The data now at hand, representing six consecutive years, 1949 through 1954, serve to supplement those obtained by Freiburg, corroborating and extending his conclusions in most instances, and also indicating that certain of his tentative conclusions need to be revised.

While the present report was in preparation, Anderson (1954) published an excellent account of the ecology of the eastern species *G. carolinensis* in southern Louisiana. Anderson's findings concerning this closely related species in a much different environment have been especially valuable as a basis for comparison. The two species are basically similar in their habits and ecology but many minor differences are indicated. Some of these differences result from the differing environments where Anderson's study and my own were made and others certainly result from innate genetic differences between the species.

The frog with which this report is concerned is the *Microhyla carolinensis olivacea* of the check list (Schmidt, 1953: 77) and recent authors. De Carvalho (1954: 12) resurrected the generic name, *Gastrophryne,* for the American species formerly included in *Microhyla,* and presented seemingly valid morphological evidence for this plausible generic separation.

G. olivacea is obviously closely related to *G. carolinensis;* the differences are not greater than those to be expected between well marked subspecies. Nevertheless, in eastern Oklahoma and eastern Texas, where the ranges meet, the two kinds have been found to maintain their distinctness, differing in coloration, behavior, calls, and time of breeding. Hecht and Matalas (1946: 2) found seeming intergrades from the area of overlapping in eastern Texas, but some specimens from this same area were typical of each form. Their study was limited to preserved material, in which some characters probably were obscured. More field work throughout the zone of contact is needed. The evidence of intergradation obtained so far seems to be somewhat equivocal.

Besides *G. olivacea* and typical *G. carolinensis* there are several named forms in the genus, including some of doubtful status. The name *mazatlanensis* has been applied to a southwestern population, which seems to be a well marked subspecies of *olivacea,* but as yet *mazatlanensis* has been collected at few localities and the evidence of intergradation is meager. The names *areolata* and *texensis* have been applied to populations in Texas. Hecht and Matalas (1946:

3) consider *areolata* to be a synonym of *olivacea*, applied to a population showing intergradation with *carolinensis*, but Wright and Wright (1949: 568) consider *areolata* to be a distinct subspecies. *G. texensis* generally has been considered to be a synonym of *olivacea*. Other species of the genus include the tropical *G. usta*, *G. elegans* and *G. pictiventris*.

Of the vernacular names hitherto applied to *G. olivacea* none seems appropriate; I propose to call the species the Kansas ant-eating frog because of its range extending over most of the state, and because of its specialized food habits. The type locality, originally stated to be "Kansas and Nebraska" (Hallowell, 1856: 252) has been restricted to Fort Riley, Kansas (Smith and Taylor, 1950: 358). Members of the genus have most often been referred to as toads rather than frogs because of their more toadlike appearance and habits. However, this family belongs to the firmisternial or froglike division of the Salientia and the terms "frog" and "toad," originally applied to *Rana* and *Bufo* respectively, have been extended to include assemblages of related genera or families. Members of the genus and family usually have been called "narrow-mouthed" toads from the old generic name *Engystoma*, a synonym of *Gastrophryne*. *G. olivacea* usually has been referred to as the Texas narrow-mouthed toad, or western narrow-mouthed toad. The latter name is inappropriate because the geographic range is between that of a more western representative (*mazatlanensis*) and a more eastern one (*carolinensis*). The names *texensis*, *areolata* and *carolinensis* have all been applied to populations in Texas, and it is questionable whether typical *olivacea* even extends into Texas.

HABITAT

In the northeastern part of Kansas at least, rocky slopes in open woods seem to provide optimum habitat conditions. This type of habitat has been described by several earlier workers in this same area, Dice (1923: 46), Smith (1934: 503) and Freiburg (1951: 375). Smith (1950: 113) stated that in Kansas this frog is found in wooded areas, and that rocks are the usual cover, but he mentioned that outside of Kansas it is often found in mesquite flats that are devoid of rocks. Freiburg's field work was done almost entirely on the Reservation and was concentrated in "Skink Woods" and vicinity, where much of my own field work, both before and afterward, was concentrated. On the Reservation and in near-by counties of Kansas, the habitat preferences of the ant-eating frog and the five-lined skink largely coincide. In an account of the five-lined skink on the Reser-

vation, I have described several study areas in some detail (Fitch, 1954: 37-41). It was on these same study areas (Quarry, Skink Woods, Rat Woods) that most of the frogs were obtained.

Although *G. olivacea* thrives in an open-woodland habitat in this part of its range, it seems to be essentially a grassland species, and it occurs throughout approximately the southern half of the Great Plains region. Bragg (1943: 76) emphasized that in Oklahoma it is widely distributed over the state, occupying a variety of habitats, with little ecological restriction. Bragg noted, however, that the species is rarely, if ever, found on extensive river flood plains. On various occasions I have heard *Gastrophryne* choruses in a slough two miles south of the Reservation. This slough is in the Kaw River flood plain and is two miles from the bluffs where the habitat of rocky wooded slopes begins that has been considered typical of the species in northeastern Kansas. It seems that the frogs using this slough are not drawn from the populations living on the bluffs as Mud Creek, a Kaw River tributary, intervenes. The creek channel at times of heavy rainfall, carries a torrent of swirling water which might present a barrier to migrating frogs as they are not strong swimmers. The frogs could easily find suitable breeding places much nearer to the bluffs. Those using the slough are almost certainly permanent inhabitants of the river flood plain. The area in the neighborhood of the slough, where the frogs probably live, include fields of alfalfa and other cultivated crops, weedy fallow fields, and the marshy margins of the slough. In these situations burrows of rodents, notably those of the pocket gopher (*Geomys bursarius*), would provide subterranean shelter for the frogs, which are not efficient diggers.

The frogs may live in many situations such as this where they have been overlooked. In the absence of flat rocks providing hiding places at the soil surface, the frogs would rarely be found by a collector. The volume and carrying quality of the voice are much less than in other common anurans. Large breeding choruses might be overlooked unless the observer happened to come within a few yards of them. Most of the recorded habitats and localities of occurrence may be those where the frog happens to be most in evidence to human observers, rather than those that are limiting to it or even typical of it.

On September 20, 1954, after heavy rains, juveniles dispersing from breeding ponds were in a wide variety of situations, including most of the habitat types represented on the Reservation. Along a small dry gully in an eroded field formerly cultivated, and re-

verted to tall grass prairie (big bluestem, little bluestem, switch grass, Indian grass), the frogs were numerous. Many of them were flushed by my footsteps from cracks in the soil along the gully banks. In reaching this area the frogs had moved up a wooded slope from the pond, crossed the limestone outcrop area at the hilltop edge, and wandered away from the woods and rocks, out into the prairie habitat. In this prairie habitat there were no rocks providing hiding places at the soil surface, but burrows of the vole (*Microtus ochrogaster*) and other small rodents provided an abundance of subterranean shelter. In the summer of 1955 the frogs were seen frequently in this same area, especially when the soil was wet from recent rain. When the surface of the soil was dry, none could be found and presumably all stayed in deep cracks and burrows.

Anderson (1954: 17) indicated that *G. carolinensis* in Louisiana likewise occurs in diverse habitats, being sufficiently adaptable to satisfy its basic requirements in various ways.

BEHAVIOR

Ordinarily the ant-eating frog stays beneath the soil surface, in cracks or holes or beneath rocks. Probably it obtains its food in such situations, and rarely wanders on the surface. The occasional individuals found moving about above ground are in most instances flushed from their shelters by the vibrations of the observer's footsteps. On numerous occasions I have noticed individuals, startled by nearby footfalls, dart from cracks or under rocks and scuttle away in search of other shelter. Such behavior suggests that digging predators may be important natural enemies. The gait is a combination of running and short hops that are usually only an inch or two in length. The flat pointed head seems to be in contact with the ground or very near to it as the animal moves about rapidly and erratically. The frog has a proclivity for squeezing into holes and cracks, or beneath objects on the ground. The burst of activity by one that is startled lasts for only a few seconds. Then the frog stops abruptly, usually concealed wholly or in part by some object. Having stopped it tends to rely on concealment for protection and may allow close approach before it flushes again.

Less frequently, undisturbed individuals have been seen wandering on the soil surface. Such wandering occurs chiefly at night. Diurnal wandering may occur in relatively cool weather when night temperatures are too low for the frogs to be active. Wandering above ground is limited to times when the soil and vegetation are wet, mainly during heavy rains and immediately afterward.

Pitfalls made from gallon cans buried in the ground with tops open and flush with the soil surface were installed in 1949 in several places along hilltop rock outcrops where the frogs were abundant. The number of frogs caught from day to day under varying weather-conditions provided evidence as to the factors controlling surface activity. After nights of unusually heavy rainfall, a dozen frogs, or even several dozen, might be found in each of the more productive pitfalls. A few more might be caught on the following night, and occasional stragglers as long as the soil remained damp with heavy dew. Activity is greatest on hot summer nights. Below 20° C. there is little surface activity but individuals that had body temperatures as low as 16° C. have been found moving about.

Frogs uncovered in their hiding places beneath flat rocks often remained motionless depending on concealment for protection, but if further disturbed, they made off with the running and hopping gait already described. Although they were not swift, they were elusive because of their sudden changes of direction and the ease with which they found shelter. When actually grasped, a frog would struggle only momentarily, then would become limp with its legs extended. The viscous dermal secretions copiously produced by a frog being handled made the animal so slippery that after a few seconds it might slide from the captor's grasp, and always was quick to escape when such an opportunity was presented.

TEMPERATURE RELATIONSHIPS

Ant-eating frogs are active over a temperature range of at least 16° C. to 37.6° C. They tolerate high temperatures that would be lethal to many other kinds of amphibians, but are more sensitive to low temperatures than any of the other local species, and as a result their seasonal schedule resembles that of the larger lizards and snakes more than those of other local amphibians. The latter become active earlier in the spring.

Earliest recorded dates when the frogs were found active in the course of the present study from 1950 to 1955 were in April every year; the 20th, 25th, 24th, 2nd, 25th, and 21st. Latest dates when the frogs were found in the six years of the study were: October 22, 1949; October 13, 1950; October 7, 1951; August 24, 1952; August 18, 1953; and October 27, 1954 (excluding two late stragglers caught in a pitfall on December 5). Severe drought caused unseasonably early retirement in 1952 and 1953.

Body temperatures of the frogs were taken with a small mercury thermometer of the type described by Bogert (1949: 197); the bulb

was used to force open the mouth and was thrust down the gullet into the stomach. To prevent conduction of heat from the hand, the frog was held down through several layers of cloth, at the spot where it was discovered, until the temperature reading could be made. This required approximately five seconds.

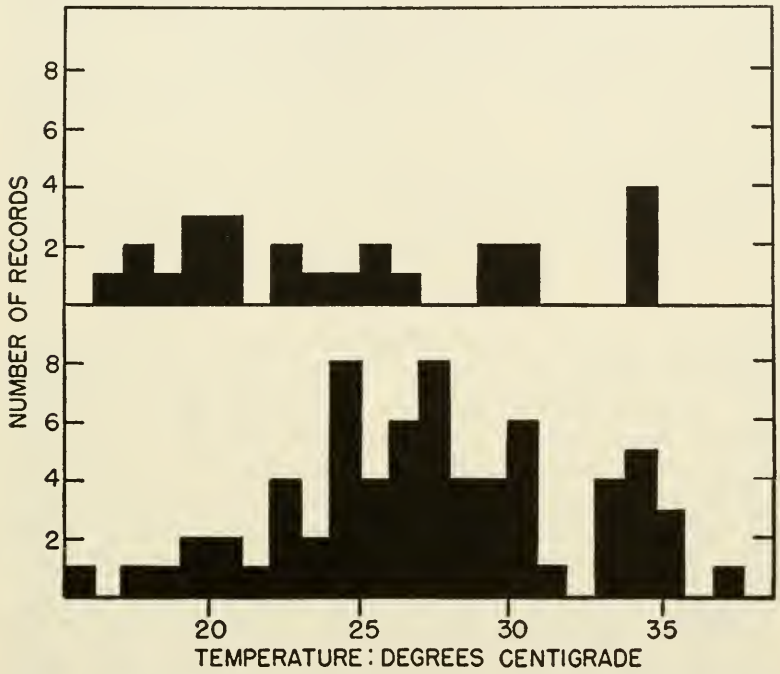

FIG. 1. Temperatures of ant-eating frogs grouped in one-degree intervals; upper figure is of frogs found active in the open, and lower is of those found under shelter. The frogs are active over a temperature range of more than 20 degrees, and show no clear cut preference within this range.

Most of the 79 frogs of which temperatures were measured, were found under shelter, chiefly beneath flat rocks. The rocks most utilized were in open situations, exposed to sunshine. Most of the frogs were in contact with the warmed undersurfaces of such rocks. Forty-three of the frogs, approximately 54.5 percent, were in the eight-degree range between 24° and 31° C. Probably the preferred temperatures lie within this range. The highest body temperature recorded, 37.6° C., was in a frog which "froze" and remained motionless in the sunshine for half a minute after the rock sheltering it was overturned. Probably its temperature was several degrees lower while it was sheltered by the rock. Other unusually high tem-

peratures were recorded in newly metamorphosed frogs found hiding in piles of decaying vegetation near the edge of the pond, on hot afternoons of late August. Temperatures ranged from 17.0° to 30.7° in frogs that were found actually moving about. Several with relatively low temperatures, 22° to 17°, were juveniles travelling in rain or mist on cool days. These frogs, having relatively low temperature, were sluggish in their movements, as compared with individuals at the upper end of the temperature range.

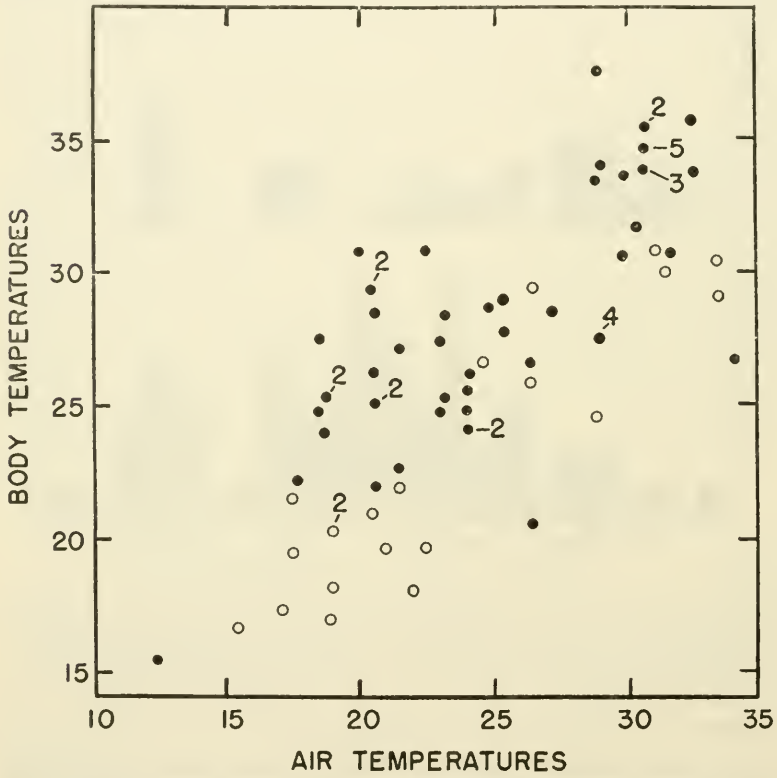

Fig. 2. Body temperatures and nearby air temperatures for frogs found under natural conditions. Dots represent frogs found under shelter; circles represent those found in the open.

After the first frost each year the frogs usually could not be found, either in the open or in their usual hiding places beneath rocks. They probably had retired to deep subterranean hibernation sites. The only exception was in 1954, when two immature frogs were found together in a pitfall on the morning of December 5 after a

rain of .55 inches ending many weeks of drought. Air temperature had been little above 10° C. that night, but had often been below freezing in the preceding five weeks.

Reactions of these same two individuals to low temperatures were tested in the laboratory. At a body temperature of 11° C. they were extremely sluggish. They were capable of slow, waddling movements, but were reluctant to move and tended to crouch motionless. Even when they were prodded, they usually did not move away, but merely flinched slightly. At 6° C. they were even more sluggish, and seemed incapable of locomotion, as they could not be induced to hop or walk by prodding with a fine wire. When placed upside down on a flat surface, they could turn over, but did so slowly, sometimes only after a minute or more had elapsed. Respiratory throat movements numbered 46 and 60 per minute.

BREEDING

Many observers have noted that breeding activity is initiated by heavy rains in summer. In my experience precipitation of at least two inches within a few days is necessary to bring forth large breeding choruses. With smaller amounts of precipitation only stragglers or small aggregations are present at the breeding ponds. Tanner (1950: 48) stated that in three years of observation, near Lawrence, Kansas, the first storms to bring large numbers of males to the breeding ponds occurred on June 20, 1947, June 18, 1948, and May 1, 1949.

In 1954 the frogs were recorded first on April 25, but these were under massive boulders, and were still semi-torpid. Frogs were found fully active, in numbers, under small flat rocks on May 7. They were found frequently thereafter. On the afternoon of May 13, the third consecutive day with temperature slightly above 21° C., low croaking of a frog was heard among rocks at an old abandoned quarry. Throughout the remainder of May, calling was heard frequently at the quarry on warm, sunny afternoons. Often several were calling within an area of a few square yards, answering each other and maintaining a regular sequence. In the last week of May rains were frequent, and the precipitation totalled 2.09 inches. On June 1 and 2 also, there were heavy rains totalling 2.26 inches. On the evening of June 2 many frogs were calling at a pond ½ mile south of the Reservation, and one was heard at the pond on the Reservation. By the evening of June 4, dozens were calling in shallow water along the edge of this pond in dense *Polygonum* and other weeds. There was sporadic calling even in daylight and there was a great

chorus each evening for the next few days, but its volume rapidly diminished.

In mid-June a system of drift fences and funnel traps was installed 200 yards west of the pond in the dry bottom of an old diversion ditch leading from the pond. The ditch constituted the boundary between bottomland pasture and a wooded slope, and therefore was a natural travelway. The object of the installation was to intercept and catch small animals travelling along the ditch bottom. The drift fence was W-shaped, with a funnel trap at the apex of each cone so that the animals travelling in either direction would be caught. The numbers of frogs caught from time to time during the summer provided information as to their responses to weather in migrating to the pond.

Table 1. Numbers of Frogs Caught Within Two Days After Rain in Funnel Traps in 1954, from Mid-June, to the Time of First Frost.

Date	Precipitation in inches	No. of caught frogs
July 1	2.02	8
July 10	.11	none
July 16	1.26	none
July 20-21	.94	3
July 24	.38	2
July 28	.29	none
August 1-2	3.22	31
August 6-7-8	2.43	none
August 12	.28	none
August 16	.29	none
August 19-22	.70	none
August 27-28	1.05	none
September 9	.50	none
September 29-30	.38	none
October 4	.74	none
October 12-14	3.51	none

From the positions of the traps and drift fences, it was obvious that all of the frogs that were caught were travelling toward the pond. Capture of an equal number moving away from the pond a few days afterward might have been expected but none at all was caught while making a return trip. Therefore it seems that the frogs returned by a different route to their home ranges after breeding. Of necessity they make the return trip under conditions drier than those that prevail on the pondward trip, which is usually made in a downpour. Probably the return travel is slower, more leisurely, and with more tendency to keep to sheltered situations.

The call is a bleat, resembling that of a sheep, but higher, of lesser volume, and is not unlike the loud rattling buzz of an angry bee. The call is usually of three to four seconds duration, with an interval

several times as long. Calling males were floating, almost upright, in the water within a few yards of shore, where there was dense vegetation. The throat pouch when fully expanded is several times as large as the entire head. When a person approached to within a few yards of frogs they usually stopped calling, submerged, and swam to a place of concealment.

Having heard the call of typical *G. carolinensis* in Louisiana, I have the impression that it is a little shorter, more sheeplike, and less insectlike than that of *G. olivacea*. The call of *Gastrophryne* is of such peculiar quality that it is difficult to describe. Different observers have described it in different terms. Stebbins (1951: 391) has described the call in greatest detail, and also has quoted from the descriptions of it previously published. These descriptions include the following: "high, shrill buzz"; "buzz, harsh and metallic"; "like an electric buzzer"; "like bees at close range but more like sheep at a distance"; "bleating baa"; "shrill, long-drawn quaw quaw"; "whistled whēē followed by a bleat."

Stebbins observed breeding choruses (*mazatlanensis*) at Peña Blanca Springs, Arizona, and stated that sometimes three or four called more or less together, but that they seldom started simultaneously. Occasionally many voices would be heard in unison followed by an interval of silence, but this performance was erratic. At the pond on the Reservation I noted this same tendency many times. After a lull the chorus would begin with a few sporadic croaks, then four or five or even more frogs would be calling simultaneously from an area of a few square yards. Anderson (*op. cit.*: 34) found that in small groups of calling *G. carolinensis* there was a distinct tendency to maintain a definite pattern in the sequence of the calls. One "dominant" individual would initiate a series of calls, and others each in turn would take up the chorus.

Pairing takes place soon after the breeding aggregations are formed. On the night of June 4, 1954, a clasping pair was captured and kept in the laboratory in a large jar of water. This pair did not separate, and spawning occurred between noon and 1:30 P. M. on June 5. When the newly laid eggs were discovered at 1:30 P. M. most of them were in a surface film. Some were attached to submerged leaves and a few rested on the bottom. The pair was still joined, but the male was actually clasping only part of the time, and as the frogs moved about in the water, it became evident that they were adhering to each other by the areas of skin contact, which were glued together by their dermal secretion. They were unable to separate immediately, even when they struggled to do so. They

were observed for approximately 15 minutes before separation occurred, and during this time they were moving about actively. As they separated, the area of adhesion was discernible on the back of the female. It was U-shaped, following the ridges of the ilia and the sacrum.

On August 2, 1954, after a rain of 3.22 inches, the previously mentioned funnel trap in the ditch had caught 31 ant-eating frogs. Water had collected to a depth of several inches in the depression where the trap was situated. A dozen of the trapped frogs were clasping pairs. These frogs struggled vigorously as they were removed from the traps, handled and marked. As a result most of the clasping males were separated from the females. In handling those of each pair I noticed that they were glued together by dermal secretions, as were those of the pair observed on June 5. The areas of adhesion were of similar shape and location in the different pairs, and included the U-shaped ridge of the female's back and the male's belly, and the inner surfaces of the male's forelegs with the corresponding surfaces of the female's sides where the male clasped.

This adhesion of the members of a pair during mating may be a normal occurrence. The copious secretion of the dermal glands is of especially glutinous quality in *Gastrophryne*. The adhesion of members of a pair may have survival value. These small frogs are especially shy, and in the breeding ponds they respond to any disturbance with vigorous attempts to escape and hide. Under such circumstances the adhesion may prevent separation. Also, it may serve to prevent displacement of a clasping male by a rival. Anderson (*op. cit.*) who observed many details of the mating behavior of *G. carolinensis*, both in the laboratory and under natural conditions, mentioned no such adhesion between members of a pair.

Anderson (*op. cit.*: 31) discussed the possibility that reproductive isolation might arise in sympatric populations, such as those of *G. carolinensis* in southern Louisiana, through inherent differences in time of spawning. However, in *G. olivacea* at least, such isolation would be prevented by individual males returning to breed at different times in the same season. Furthermore, individual differences in choice of breeding time probably result from environmental factors rather than genetic factors in most instances. In *G. olivacea* in Kansas, time of breeding is controlled by the distribution of heavy rainfall creating favorable conditions. Onset of the breeding season may be hastened or delayed, or an entire year may be missed because of summer drought. If favorable heavy rains are well distributed throughout the summer, frogs of age classes that are not yet

sexually mature in the early part of the breeding season, may comprise the bulk of the breeding population in late summer.

DEVELOPMENT OF EGGS AND LARVAE

Eggs laid on June 5 by the pair kept in the laboratory were hatching on June 7, on the average approximately 48 hours from the time of laying. By June 8 all the eggs had hatched and the tadpoles were active. On August 28 and 29 thousands of newly metamorphosed young were in evidence on wet soil at the pond margin; in some the head still was tadpolelike and they had a vestige of the tail stump. These young were remarkably uniform in size, 15 to 16 mm. (the smallest one found was 14½ mm.) and almost all of them had originated from eggs laid after heavy precipitation, totalling 3.22 inches, in the first 36 hours of August. Allowing one day for adults to reach the pond and spawn, and two days more for eggs to hatch, the tadpole stage must have lasted approximately 24 days in this crop of young.

Wright and Wright (1949: 582) stated that the tadpoles metamorphosed after 30 to 50 days, and that the newly metamorphosed frogs are 10 to 12 mm. in length. Length of time required for larval development probably varies a great deal depending on the interaction of several factors such as temperature and food supply.

GROWTH

Little has been recorded concerning the growth rate of *Gastrophryne* or the time required for it to attain sexual maturity. Wright (1932) found that *G. carolinensis* in the Okefinokee Swamp region has a mean metamorphosing-size of 10.8 mm. Young thought to be those recently emerged from their first hibernation were those in the size group 15.0 to 20.0 mm., while the frogs in the 20 to 27 mm. size class and those in the 27 to 36 mm. class were interpreted as representing two successivly older annual age classes. Anderson (1954: 41) thought he could recognize four successive annual age classes in the same species in southern Louisiana. He found that sexual maturity is attained at a length of 21 to 24 mm. in frogs which he believed to be late in the second year of life.

Allowing for size differences between the two species, Wright's and Anderson's conclusions regarding growth in *G. carolinensis*, on the basis of size groups, are largely substantiated by my own data on the growth of marked individuals of *G. olivacea* living under natural conditions in Kansas.

In 1954, an opportunity to investigate the early growth was af-

forded by unusually favorable circumstances. The population of frogs that emerged from hibernation in the late spring of 1954 included few, if any, that were below adult size; drought had prevented successful breeding in 1952 and 1953. Heavy rains in the first week of June, 1954, and again in the first week of August, resulted in the production of two successive crops of young so widely spaced that they were easily distinguishable. Some young may have been hatched after other minor rains, but certainly these were relatively few. Young from the eggs laid in the first week of August were metamorphosing during the last week of August. Growth in the frogs of this group can be shown by the average size and the size range of the successive samples collected.

Table 2. Growth in Frogs Metamorphosed in the Last Week of August, 1954.

Time of sample	Number in sample	Mean size in mm.	Size range in mm.
August 27 to 31	27	15.55 ± .079	15 to 17
September 11	114	17.2 ± .033	14 to 20
September 15 to 22	12	18.7 ± .090	16 to 20
September 27 to 30	37	19.3 ± .055	17 to 21.5
October 1 to 7	62	20.8 ± .072	17 to 24
October 12 to 17	49	22.3 ± .092	18 to 24

By mid-October, six weeks after metamorphosis, these frogs had increased in over-all length by approximately 50 percent. Having grown a little more than 1 mm. per week on the average, they were approximately intermediate in size between small adults and newly metamorphosed young.

The frogs hatched in June were present in relatively small numbers compared with those hatched in August, and were not observed metamorphosing. In late August a sample of 33 judged to belong to the June brood averaged 26.2 (22-28) mm. long. A sample of 39 from the first week of October averaged 28.1 (24.5-32) mm. Frogs of this group thus were approaching small adult size late in their first growing season. Such individuals possibly breed in the summer following their first hibernation, when they are a year old or a little more. Because recaptured frogs were not sacrificed to determine the state of their gonads, the minimum time required to attain sexual maturity was not definitely determined. The available evidence indicates that sexual maturity is most often attained late

in the second year of life, at an age of approximately two years. The darkened and distensible throat pouch of the adult male probably is the best available indicator of sexual maturity.

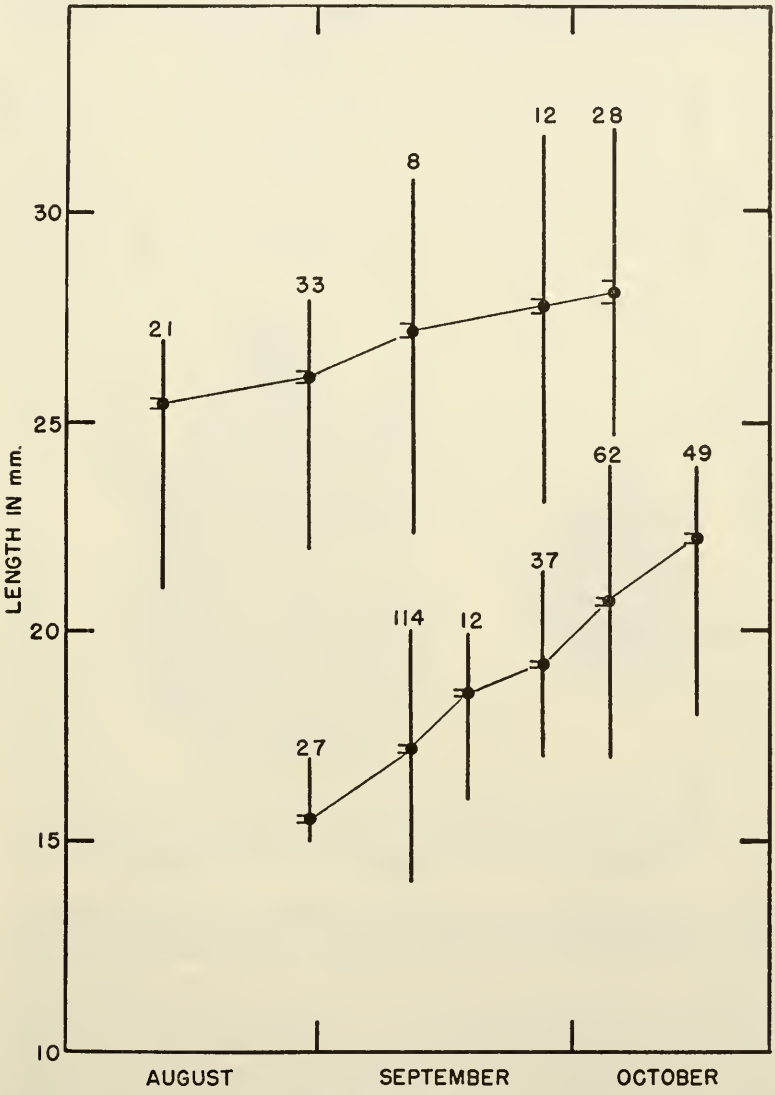

FIG. 3. Growth shown by successive samples of young ant-eating frogs of two size groups in late summer and early fall of 1954. For each sample the mean, standard deviation, and range are shown. Lower series are those metamorphosed in late August, and upper series are those metamorphosed in late June.

Frogs that metamorphose in late summer have little time to grow before hibernating, and still are small when they emerge in spring. The smallest one found was 19 mm. long (May 19, 1951), and in each year except 1954 many such young were found that were less than 25 mm. in length in May or early June. None of the frogs

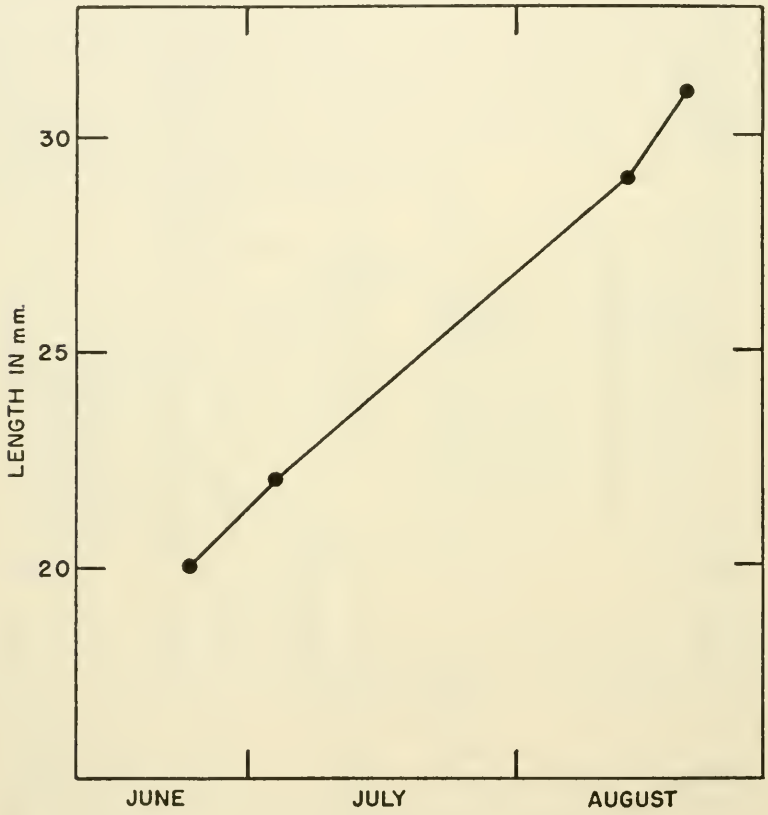

Fig. 4. Rapid growth of a young female caught in June, July, and August, 1949. Presumably this individual metamorphosed late in the summer of 1948, and at the age of approximately one year it was near small adult size.

marked at or near metamorphosing size has been recaptured, but the trend of early growth is well shown by Table 2 and Fig. 3. However, many juveniles that were captured and marked within a few weeks of metamorphosis were recaptured as adults. The selected individuals in Table 3 are considered typical of growth from "half-grown" to small adult size. Growth in many other individuals is shown in Figs. 6 and 7.

TABLE 3. GROWTH IN FROGS MARKED AS YOUNG AND RECAPTURED AS SMALL ADULTS.

Individual and sex	Dates of capture	Length in mm.	Probable time of metamorphosis
No. 1 ♀	August 28, 1951	21.5	Mid-July, 1951
	May 5, 1952	23	
	July 3, 1952	32	
	August 31, 1952	33	
No. 2 ♀	June 8, 1950	25	Late July, 1949
	May 24, 1951	31	
	July 30, 1951	34	
	June 24, 1952	35	
No. 3 ♂	August 31, 1951	24	Late June, 1951
	May 23, 1953	32	

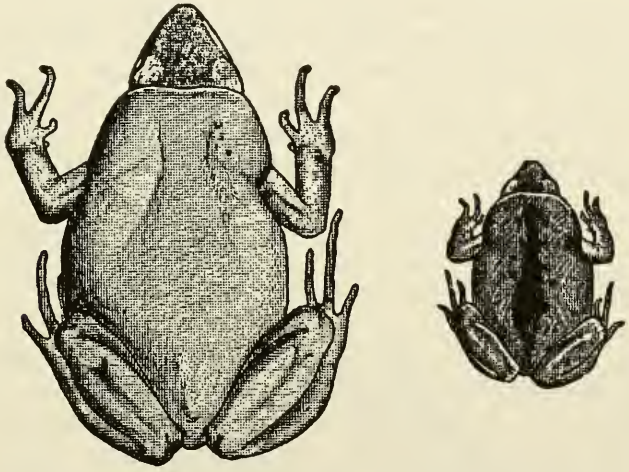

FIG. 5. Ant-eating frogs, a little less than twice natural size, adult and newly metamorphosed young, showing differences in size and coloration. The young is darker and has a leaflike middorsal mark which fades as growth proceeds.

The trend of growth after attainment of minimum adult size is also well shown by the records of marked individuals recaptured. Many of these were marked while they were still small so that their approximate ages are known. For those recaptured in their second year, after one hibernation, length averaged 30.92 mm. Some of this group were young metamorphosed late the preceding summer and still far short of adult size (as small as 23 mm.) when recaptured. Others were relatively large, up to 33 mm. A group of 22 recaptured frogs known to be in their third year averaged 33.3 mm. (males 31.9, females 35.3, excluding four individuals of undeter-

mined sex). Fifteen other recaptured frogs were known to be in their fourth year at least, and some probably were older, as they were already large adults when first examined. These 15 averaged 36.6 mm. (males 34.7, females 37.9 mm.). Size was similar in a sample of 58 individuals intercepted en route to the breeding pond in heavy rains of June and August, 1954. The 38 males in this sample ranged in size from 30 mm. to 38 mm., averaging 34.5. The 20 females ranged from 34 mm. to 40 mm., averaging 37.65. The large average and maximum size in this sample of a breeding population may be typical after periods of drought years have prevented successful reproduction. Summer drought in 1952 and 1953 prevented breeding in those years, or, at least, it drastically reduced the numbers of young produced. One-year-old and two-year-old frogs may not have been represented at all in the sample of 58. Three-year-old frogs presumably made up a substantial part of the sample, since 1951 was a year of successful breeding.

Differences in size between species and geographic variation in size in *Gastrophryne* have been given little attention by herpetologists, but if understood, would help to clarify relationships. Hecht

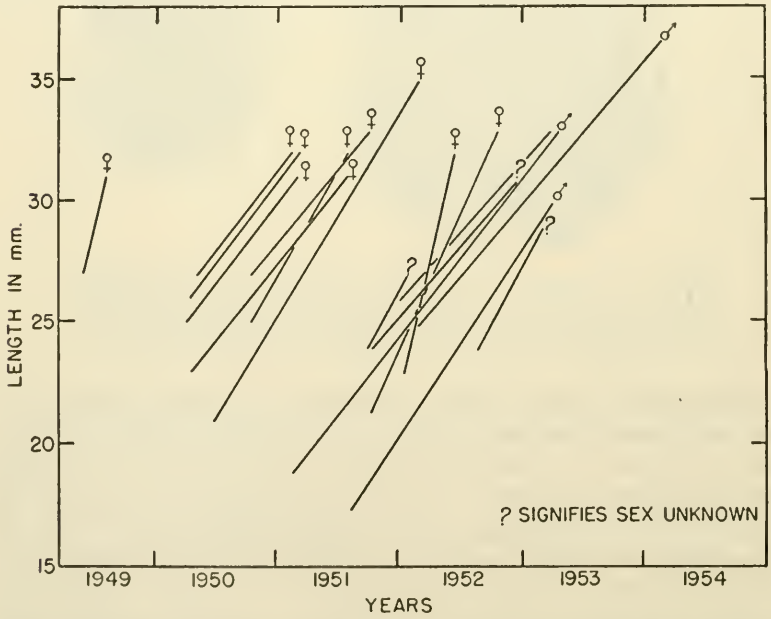

Fig. 6. Growth in a group of frogs, each marked while still short of adult size and mostly recaptured after lapse of one or more hibernation periods. Each line connects records of an individual frog.

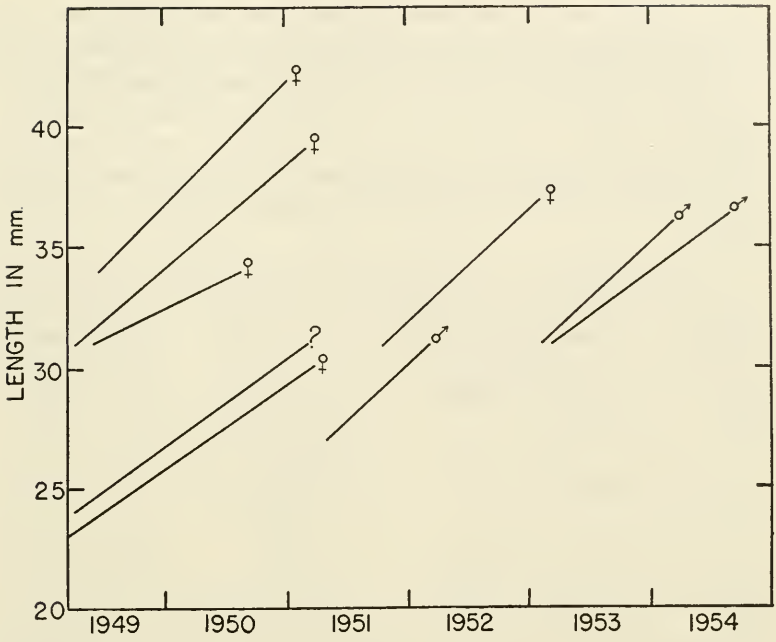

FIG. 7. Growth in another group of frogs that were marked as young or small adults and recaptured after intervals of more than a year. Frogs of this group were, on the average, larger than the individuals shown in Fig. 6, and they made less rapid growth.

and Matalas stated in their revision (1946: 5) that size is of no importance as a taxonomic character, as typical *carolinensis, olivacea,* and *mazatlanensis* all averaged approximately the same—26 to 28 mm.—females slightly larger than males. However, they arbitrarily classed as adults all individuals 22.5 mm. in length or larger, having found individuals this small that showed the darkened and distensible throat pouches characteristic of adult males. From the trend of my own measurements of *G. olivacea* in northeastern Kansas, I conclude that either many immature individuals were included in their samples, or that the populations sampled included some with individuals that were remarkably small as adults.

The population which I studied may be considered typical of *G. olivacea.* They averaged large, including individuals up to 42 mm. in length, well above the maximum sizes for any reported in the literature. At metamorphosis these *olivacea* are of approximately 50 percent greater length than *G. carolinensis* as reported by Wright and Wright (1949: 573) and Anderson (1954: 41). Yet Blair (1950: 152) observed that in eastern Oklahoma, where the

ranges of *olivacea* and *carolinensis* overlap, the latter is larger. On the basis of field and laboratory observations he tentatively concluded that one of the main barriers to interbreeding was the reluctance of the males of *carolinensis* to clasp the smaller females of *olivacea*.

That size differs in different populations, and is still poorly understood, is illustrated by the following discrepant figures from various authors.

Table 4. Size Range of Adults in Various Populations of Gastrophryne.

Species or subspecies	Geographic population sampled	Authority	Size range of adults in mm.
olivacea	Douglas Co., Kansas	present study	31 to 42
olivacea	entire range	Wright and Wright (1949)	19 to 38
carolinensis	entire range	Wright and Wright (1949)	20 to 36
carolinensis	southern Louisiana	Anderson (1954)	22 to 35
areolata	southeastern Texas	Wright and Wright (1949)	23 to 29
mazatlanensis	Arizona and New Mexico	Wright and Wright (1949)	22 to 30
mazatlanensis	Santa Cruz Co., Arizona	Stebbins (1951)	25.2 to 31.5

COLOR AND PATTERN

The color pattern changes in the course of development, and the shade of color changes in response to environmental conditions. At the time of metamorphosis, young are dark brown with specks of black and with a dark, cuneate, leaflike middorsal mark. The narrow end of this mark arises just behind the head, and the mark extends posteriorly as far as the hind leg insertions. At its widest, the mark covers about half the width of the dorsal surface. The lateral edges of the mark are sharply defined, but at its anterior and posterior ends it blends into the ground color. In most individuals smaller than 20 mm., this dorsal mark is well defined and conspicuous. As growth proceeds, however, it becomes faint. In frogs 19 to 25 mm. long the marks have disappeared. In individuals of this size the brown ground color is markedly paler than in those newly metamorphosed, but is darker than in adults.

In large adults the dorsal coloration is a uniform pale tan, paler on the average in females than in males. Temperature and mois-

ture both affect the shade of coloration. In frogs that were partly desiccated, the color was unusually pale, with a distinctly greenish tint, and at high temperatures coloration tended to be relatively pale.

Hecht and Matalas (1946) have described and figured color patterns in various populations of *Gastrophryne*, demonstrating geographic trends and helping to clarify relationships. Their account indicates that the dark dorsal mark present in young of *olivacea* but not present in adults, is better developed and longer persisting in other forms. Specimens of *carolinensis*, presumably adult, are figured which have the dark middorsal area contrasting with paler color of the sides. The dark area is seen to consist of dots or blotches of black pigment which may be in contact producing more or less continuous black areas, or may be separate and distinct producing a spotted pattern. Pigmentation is usually most intense along the lateral edges of the dorsal leaflike mark; the central portion may be so much paler that the effect is that of a pair of dorsolateral stripes. This latter type of pattern is best developed in the population of Key West, Florida. Hecht and Matalas did not consider these insular frogs to be taxonomically distinct, because only 48 per cent of specimens from the Florida keys had the "Key West" pattern, while 29 per cent resembled *olivacea* and 23 per cent resembled *carolinensis*. In the southwestern subspecies (or species) *mazatlanensis*, recorded from several localities in Sonora and from extreme southern Arizona, the dorsal pigmentation similarly tends to be concentrated in dorsolateral bands, but is much reduced or almost absent, and there is corresponding pigmentation dorsally across the middle of the thigh, across the middle of the shank, and on the foot. When the leg is folded, these three dark areas are brought in contact with each other and with the dorsolateral body mark, if it is present, to form a continuous dark area, in a characteristic "ruptive" pattern. Hecht and Matalas found similar leg bars, less well developed, in certain specimens of *olivacea* including one from Gage County, Nebraska, at the northern end of the known geographic range.

MOVEMENTS

Freiburg (*op. cit.*: 384) concluded that ant-eating frogs seem to have no individual home ranges, but wander in any direction where suitable habitat is present. However, from records covering a much longer span of time, it became increasingly evident that a frog ordinarily tends to stay within a small area, familiar to it and providing its habitat requirements.

Nevertheless, in all but a few instances the marked frogs recaptured were in new locations a greater or lesser distance from the site of original capture. The movements made by these frogs were of several distinct types:

1. Routine day to day movements from shelter to shelter within the area familiar to the animal, the "home range."
2. Shifts from one home range to another; such shifts may have been either long or short, and may have occurred abruptly or by gradual stages.
3. Travel by adults to or from a breeding pond. In most or all instances these adults were regularly established in permanent home ranges, and they often moved through areas unsuitable as habitat to reach the ponds.
4. Movements of dispersal in the young, recently metamorphosed and not yet settled in a regular home range.

Usually there was uncertainty as to which types of movements had been made by the recaptured individuals. Some may have made two or three different types of movements in the interval between captures.

On many occasions individuals were found beneath the same rock on two consecutive days, or occasionally on several successive days. Rarely, such continued occupancy of a niche lasted several weeks. In 1949, a frog was found under the same rock on June 4, 6, 26, 27, and July 1, 3 and 11. This was an immature female, presumably metamorphosed late in the summer of 1948. During the five weeks period covered by the records, it grew from 27 mm. to 34 mm. In 1952, another individual was found under its home rock on June 23 and 30, July 2 and 3, and August 14 and 20. In 1952 a juvenile was found under a rock on May 30, June 4, and June 17. These three individuals were exceptional in their continued occupancy of the same niches. Among the hundreds of others recorded, none was found more than twice in any one place.

Despite the fact that field work was concentrated on small areas which were worked intensively, only eight per cent of the frogs recorded were ever recaptured, and most of those were recaptured only once. Only 13 individuals yielded series of records, well spaced, in two or more different years. These few individuals recaptured frequently may not be typical of the entire population. The low incidence of recaptures indicates that relatively few of the frogs present on an area at any one time have been taken. Because of their secretive and subterranean habits most of the frogs are missed by a collector who searches by turning rocks, or trapping

with pitfalls. Therefore, even though a marked frog may survive and remain within a radius of a few hundred feet of one point for months or even years, the chances of recapture are poor.

One female was caught first as a juvenile on June 8, 1950. On April 24, 1951, when first recaptured, she had grown to small adult size, and was only 18 feet from the original location. On July 30, 1951, however, she was recaptured 750 feet away. At a fourth capture on May 21, 1952, she had shifted 70 feet farther in the same direction. At the final capture on June 24, 1952, she was approxi-

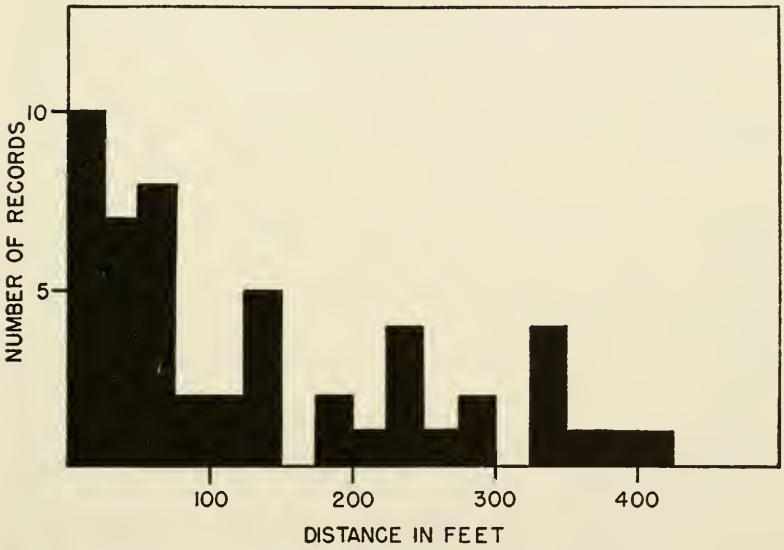

FIG. 8. Distances between captures in frogs marked, and recaptured after substantial intervals including one or more hibernations. Distances are grouped in 25-foot intervals. For longer distances the trend is toward progressively fewer records, indicating that typical home ranges are small.

mately 140 feet from both the third and fourth locations. The sequence of these records suggests that the frog had already settled in a home range at the time of her first capture in 1950, and that approximately a year later she shifted to a second home range, which was occupied for the following year, at least.

In several instances, after recaptures as far as 400 feet from the original location, frogs were again captured near an original location, suggesting that for some individuals, at least, home ranges may be as much as 400 feet in diameter.

Figure 8 shows that for movements of up to 400 feet, numbers of individuals gradually decrease with greater distance. For distances

of more than 400 feet there are comparatively few records. Of the 59 individuals recaptured after one or more hibernations, only nine had moved more than 400 feet from the original location. Twenty-five were recaptured at distances of 75 feet or less. The mean distance for movement for all individuals recaptured was 72 feet. A typical home range, therefore, seems to average no more than 75 feet in radius. Of the 59 individuals recaptured after one or more hibernations, 47 were adults and probably many of these had made round-trip migrations to the breeding pond. This was not actually demonstrated for any one individual, but several were captured in each of three or four different years near the same location.

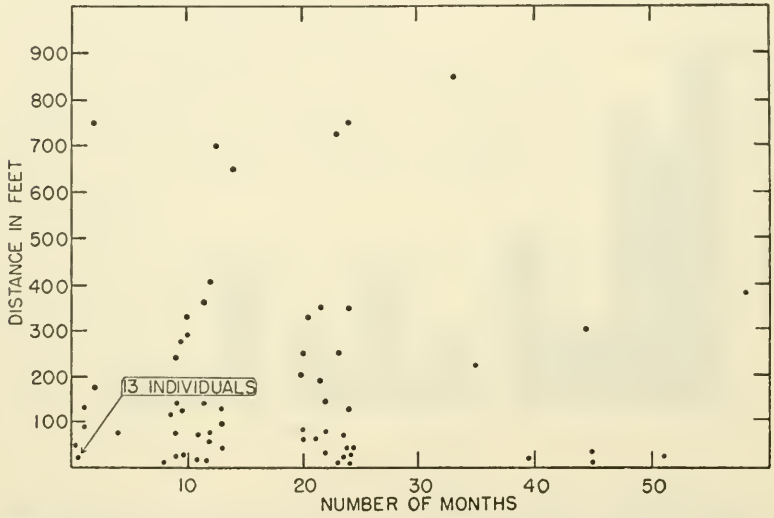

Fig. 9. Distances between captures and elapsed time in months in marked frogs recaptured. Few records are for distances more than 400 feet. There is but little tendency to longer movements in those caught after relatively long intervals.

The trend of movements differed in the sexes. Males are more vagile. Of 21 adult males recaptured, none was less than 40 feet from its original location, whereas six of the 26 adult females were less than 40 feet away from the original point of capture. Of seven frogs that had wandered 700 feet or more, five were males.

FOOD HABITS

According to Smith (1934: 503) stomachs of many specimens, from widely scattered localities in Kansas, contained only large numbers of small ants. Tanner (1950: 47) described the situation of

a frog found on the Reservation buried in loose soil beneath a flat rock, beside an ant burrow, where, presumably, the frog could snap up the passing ants without shifting its position. Anderson (*op. cit.*: 21) examined alimentary tracts of 203 specimens of *carolinensis* from Louisiana, representing a year round sample for several different habitats. He found a variety of small animals including ants, termites, beetles, springtails, bugs, ear-wigs, lepidopterans, spiders, mites, centipedes, and snails. Most of these prey animals were represented by few individuals, and ants were much more numerous than any of the other groups. Anderson concluded that ants, termites, and small beetles were the principal foods. He noted that some of the beetles were of groups commonly found in ant colonies. Tanner reported that in a large number of the frogs which he collected in Douglas, Riley, Pottawatomie, and Geary counties, Kansas, the digestive tracts and feces contained only ants. Wood (1948: 226) reported an individual of *G. carolinensis* in Tennessee found under a flat rock in the center of an ant nest.

Freiburg (*op. cit.*: 383) reported on the stomach contents of 52 ant-eating frogs collected near the Reservation. Ants constituted nearly all these stomach contents, though remains of a few small beetles were found. The ants eaten were of two kinds, *Lasius interjectus* and *Crematogaster* sp. The latter was by far the more numerous.

Although I made no further study of stomach contents, the myrmecophagous habits of *Gastrophryne* have come to my attention frequently in the course of routine field work. Individuals kept in confinement for a day or more almost invariably voided feces which consisted mainly or entirely of ant remains, chiefly the heads, as these are most resistant to digestion.

Often upon examining frogs I have found ants (*Crematogaster* sp.) or their severed heads, attached with mandibles embedded in the skin. To have been attacked by ants, the frogs must have been in or beside the ants' burrow systems. Frequently the frogs that were uncovered beneath rocks were adjacent to clusters of ants or to their nests or travelways, in a position strategically located to feed upon them, as described by Tanner. Often the feces of the frogs were found in pitfalls or under flat rocks. Although these feces were not analyzed, they seemed to consist mainly or entirely of ant remains.

The species of *Crematogaster*, which is the chief food of *Gastrophryne* in this region, is largely subterranean in habits, and is extremely abundant. Any flat rock in damp soil is likely to harbor

a colony beneath it. Colonies are situated also in damp soil away from rocks, beneath almost any kind of debris, and in hollow weed stalks and decaying wood. Live-traps for small mammals, having nest boxes attached, almost always were occupied by colonies of *Crematogaster*, if they were left in the field in warm, humid weather. Occasionally the ants attacked and killed small mammals caught in such traps. Among the thousands of kinds of insects occurring on the Reservation, this ant is one of the most numerous in individuals, one of the most important on the basis of biomass and provides an abundant food source for those predators that are ant eaters. Food supply probably is not a limiting factor to populations of *Gastrophryne* on the area.

PREDATION

Young copperheads are known to feed upon ant-eating frogs occasionally (Anderson, 1942: 216; Freiburg, 1951: 378). Other kinds of snakes supposedly eat them also. The common water snake (*Natrix sipedon*) and garter snake (*Thamnophis sirtalis*) probably take heavy toll of the adults at the time they are concentrated at the breeding pools. Larger salientians may be among the more important enemies of the breeding adults, the tadpoles, and the newly metamorphosed young. Bullfrogs (*Rana catesbeiana*) and leopard frogs (*Rana pipiens*) are normally abundant at the pond on the Reservation. These large voracious frogs lining the banks are quick to lunge at any moving object, and must take heavy toll of the much smaller ant-eating frogs that have to pass through their ranks to reach the water. The newly metamorphosed young often are forced to remain at a pond's edge for many days, or even for weeks, by drought and they must be subject to especially heavy predation by ranid frogs. Even the smallest newly metamorphosed bullfrogs and leopard frogs would be large enough to catch and eat them.

As a result of persistent drought conditions in 1952 and 1953, bullfrogs were completely eliminated from the pond by early 1954. Re-invasion by a few individuals occurred in the course of the summer; these probably made long overland trips from ponds or streams that had persisted through the drought. Leopard frogs reached the pond in somewhat larger numbers, but their population in 1954 was only a small percentage of that present in most other years. Notable success in the ant-eating frog's reproduction in 1954 may have been due largely to the scarcity of these large ranids at the breeding ponds.

Freiburg (*loc. cit.*) noted that many of the ant-eating frogs he

examined were scarred, and some had digits or limbs amputated. He did not speculate concerning the origin of these injuries. However, it seems likely that many or all of them were inflicted by the short-tailed shrew (*Blarina brevicauda*). Five-lined skinks living on the same area were likewise found to be scarred by bites which I identified (Fitch, 1954: 133) as bites of the short-tailed shrew. This shrew is common on the Reservation, especially in woodland. Many have been trapped in the pitfalls. On several occasions when a short-tailed shrew was caught in the same pitfall with ant-eating frogs, it was found to have killed and eaten them. Like the frogs, the shrews were most often caught in pitfalls just after heavy rains. Once in 1954 a shrew was found at the quarry in a pitfall that had been one of those most productive of frogs. The bottom of the pitfall was strewn with the discarded remains (mostly feet and skins) of perhaps a dozen ant-eating frogs. All had been eaten during one night and the following morning, as the trap had been checked on the preceding day. On other occasions shrews caught in pitfalls with several frogs had killed and eaten some and left others unharmed.

SUMMARY

In northeastern Kansas the ant-eating frog, *Gastrophryne olivacea*, is one of the more common species of amphibians. This area is near the northern limits of the species, genus, and famliy. The species prefers a dry, rocky upland habitat often in open woods or at woodland edge where other kinds of salientians do not ordinarily occur. It is, however, tolerant of a wide variety of habitat conditions, and may occur in river flood plains or cultivated land. In these situations where surface rocks are absent, cracks and rodent burrows presumably furnish the subterranean shelter that it requires.

This frog is secretive and spends most of the time in subterranean shelter, obtaining its food there rather than in the open. Only on warm rainy nights is it inclined to venture into the open. Then, it moves about rapidly and with a scuttling gait, a combination of running and short hops. However, it may be flushed in daylight from a hiding place by the vibrations from footsteps of a person or an animal, or it may move about in the daytime when temperatures at night are too low for activity. Though not swift of foot, the frogs are elusive because of their tendency to keep under cover, their slippery dermal secretion, and the ease with which they find and enter holes, or crevices to escape.

Breeding occurs at any time from late May through August and

is controlled by the distribution of rainfall. Heavy precipitation, especially rains of two inches or more, stimulates the frogs to migrate in large numbers to breeding ponds. Even though there are several well spaced periods of unusually heavy rainfall in the course of a summer, each one initiates a new cycle of migration, mating and spawning. Heavy rainfall is a necessity, not only to ensure a water supply in temporary pools where the frogs breed, but to create the moist conditions they require for an overland migration. An individual male may migrate to a pond and breed at least twice in the same season. Whether or not the females do likewise is unknown. Amplexus and spawning occur mainly within a day or two after the frogs reach the ponds. The males call chiefly at night, but there may be daytime choruses when breeding activity is at its peak. Many males concentrate within a few square yards in the choruses and float upright usually beside or beneath a stem or leaf, or other shelter, rendering them extremely inconspicuous. The call is a bleat of three seconds duration, or a little more. In amplexus the members of a pair sometimes become glued together by their viscous dermal secretions. The eggs hatch in approximately 48 hours. The tadpoles metamorphose in as few as 24 days. Newly metamorphosed frogs are 15 to 16 mm. in length, or, rarely as small as 14.5 mm. They are thus much larger than newly metamorphosed *G. carolinensis,* which have been described as 10-12 mm. or even as small as 8.5 mm. The newly metamorphosed frogs disperse from the breeding ponds as soon as there is a heavy rain. The young grow a little more than one mm. in length per week. Those metamorphosed in early summer may attain minimum adult size before hibernation which begins in October. It seems that sexual maturity is most often attained in the second season, at an age of one to two years.

Gastrophryne belongs to a family that is primarily tropical in distribution, and frogs of this genus have much higher temperature thresholds than most other amphibians of northeastern Kansas, with a correspondingly short season of activity. For more than half the year, mid-October to early May the frogs are normally in hibernation. Body temperatures of active frogs ranged from 17.0° C. to 37.6° C., but more than two-thirds were within the relatively narrow range, 24.0° to 31°. Near the date of the first autumn frost the frogs disappear from the soil surface and from their usual shelters near the surface, presumably having retired into hibernation in deep holes and crevices.

The natural enemies include young of the copperhead. The bullfrog and leopard frog probably take heavy toll of both the adults and the newly metamorphosed young at the breeding ponds. Reproductive success of the ant-eating frogs was much greater in 1954 when these ranids were unusually scarce. The short-tailed shrew is an important enemy. On occasion it took heavy toll of frogs trapped in pitfalls, and many of the larger adults were scarred or mutilated from bites, probably of the shrew.

Each of several frogs was found consistently under the same rock for periods of weeks. The hundreds of other frogs that were marked were rarely found twice in any one spot. Usually an individual recaptured after weeks or months was still near the original site. In many instances the distance involved was only a few yards, but there is some evidence that home ranges may be as long as 400 feet in greatest diameter. Of those caught in two or more different years only 15 per cent were shown to have moved more than 400 feet. These few exceptionally long movements, up to 2000 feet, involve shifts in home range or migrations motivated by reproductive urge.

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